Nesting and nighttime behaviours of captive chimpanzees (*Pan troglodytes*)

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Declaration

I declare that the research undertaken and reported in this thesis is my own, and has not been submitted in consideration of any other award or degree.

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Abstract

Studies of nesting behaviours of free-ranging apes typically focus on ecological variables such as preferred tree species and areas within the home range, heights of nests, and nest group sizes. However, nesting in captive apes is rarely studied, despite the ubiquity of this sleep-related behaviour. The paucity of field data is often attributed to the inherent difficulty in observing what is essentially a nighttime behaviour. Captive settings can provide researchers with an ideal opportunity to record nesting and sleep-related behaviours, yet such research on captive apes is also scant. Topics addressed include current practices in zoos regarding conditions for sleep in great apes, the potential effects of social and environmental factors on sleep site selection, the motor patterns involved in nest construction, preferred nesting structures and substrates, and nocturnal behaviours. This thesis documented and empirically tested hypotheses concerning nest-related activities in captive chimpanzees, with an aim to generate practical recommendations for enclosure design, sleeping areas, sleeping structures, and nesting substrates that have implications for the welfare of captive apes.

As with the few reports that already exist, most chimpanzees in this research frequently constructed night nests. When building a nest, some techniques appeared to be universal across individuals and groups, where others were group-specific or occasionally characteristic of only certain individuals. An experiment showed that specific materials are preferred over others for nest building. Many chimpanzees appeared to express persistent preferences for particular sleeping sites, and for some this was to maintain proximity to kin or other closely bonded individuals. In one group, individual sleeping site preferences changed across seasons, although again this was subject to individual differences.

Video analyses of nighttime behaviours demonstrated that, although nests/sleep sites are primarily used for rest subsequent to retirement, a number of social and non-social activities were performed throughout the night. In conjunction with analysis of postural and orientation shifts, these data are unique in describing the nocturnal behaviours of chimpanzees out with a laboratory setting.

Several aspects of nest-related behaviours showed a high degree of inter-and intra-group variation. Although this cautions against generalising findings across captive populations, research of this type has applied implications for the management of captive ape species, and can add to our as-yet meagre understanding of their nest and sleep-related behaviours.

Publications

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Presentations

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Chapter 1

Sleep-related activities of monkeys and the great apes

"There is a time for many words, and there is also a time for sleep" ~ Homer

1.1 The biological functions and determinants of sleep – a brief overview

Sleep is a ubiquitous, time-consuming, and vulnerable behavioural state in the animal kingdom (Campbell & Tobler 1984; Hornyak et al. 1991; Lima et al. 2005), although its exact function has yet to be resolved (Lima & Rattenborg 2007; Rial et al. 2007). Increasingly evidence is indicating that sleep serves a restorative function – resting and repairing the brain and body, and reorganising the neural processes associated with memory and learning (Savage & West 2007; Siegel 2005, 2008). Sleep-related decreases in body temperature and metabolic rate, and indeed sleep itself, help conserve energy, and so promote individual fitness (Webb 1975). The 'behavioural shutdown' (Lima & Rattenborg 2007) state of sleep may also be related to environmental factors – if an animal is inactive and immobile, the risk of detection by predators will be minimised (Meddis 1975).

Across all mammals, the sleep-wake cycle is regulated by homeostatic processes determined by prior amounts of sleep/wakefulness, seasonal and daily circadian rhythms ('biological clocks') that influence the timing of sleep onset, and within-sleep ultradian processes (the alternation of the two basic sleep states – non-rapid [NREM] and rapid [REM] eye movement sleep) (Kunz & Herrmann 2000). The circadian activity-rest cycle that restricts human sleep to periods of darkness (Stanely 2005) is also typical of anthropoid non-human primates (Campbell & Tobler 1984; Kappeler 1998).

Irrespective of its function, the fact that multiple non-human primate species (hereafter referred to as ‘primates’) sleep during periods of darkness has resulted in a general lack of data on nighttime activities (Fruth & Hohmann 1996), despite the fact that primates spend significant proportion of their daily activity budgets – and up to half of their life spans - resting and sleeping (Anderson 1998; Zhang 1995). The majority of easily measurable primate behaviours, such as foraging activities or social interactions, occur in the daytime, probably accounting in the bias toward behavioural observations in this time period (Fruth & McGrew 1998). Moreover, locating and monitoring nocturnal sleeping sites in the dark may be difficult, if not impossible (Anderson 1984).

Despite these inherent complications, an increasing number of studies are focusing on nighttime activities across a broad range of primate species, including selection of sleep sites, the ecological variables that influence sleep site selection, and also the social nature of grouping around a sleep site. Not only do resting sites highlight species-specific adaptations to ecological pressures, they can also provide insights into primate social relationships and social structures. In conjunction with adding to our knowledge of daily activity and rest patterns, the socioecological context of primate sleeping habits may have implications for the evolution of human sleep patterns (Anderson 2000).

1.2 Sleep-related behaviour of monkeys – selecting the sleep site

Sleep site selection as an anti-predation strategy

Observational studies of free-ranging monkeys suggest that the presence of predators (e.g., birds of prey, snakes and felids) is one of the main determinants of sleep site selection (Caine et al. 1992; Peetz et al. 1992; Tenaza & Tilson 1985). During sleep, responsiveness to external stimuli is greatly reduced (Issa & Wang 2008), and so choosing a sleep site that affords protection from predators may be crucial for individual survival. In choosing concealed or inaccessible sleeping areas, sites that facilitate observation of the surrounding environment, or by remaining inconspicuous around a sleep site, risk of predation can be reduced.

The steep cliff faces, emerging tall trees and closed canopy forest chosen by several species of free-ranging baboon (*Papio* spp.) were not only largely inaccessible to predators, but also provided easy escape routes in the event of attack (Hamilton 1982). Wild bonnet macaques (*Macaca radiata*) most frequently chose the tallest trees for sleeping - approximately 24 meters above ground - rendering them inaccessible to terrestrial predators such as large felids and domestic dogs (Ramakrishan & Coss 2001). Tufted capuchin monkeys (*Cebus apella nigritus)* repeatedly returned to the same sleeping trees, suggesting familiarity with these trees would allow them to easily flee from a potential predator. As with bonnet macaques, large trees within tall forest were most often utilised, again minimising the likelihood of contact with a predator. Those most vulnerable to predation (females and juveniles), slept in close proximity to each other, while the larger males most frequently slept alone (Di Bitetti et al. 2000). This sex-related difference has also been observed in free-ranging Costa Rican spider monkeys (*Ateles geoffroyi*, n = 42), with females and their offspring forming subgroups in frequently used sleeping trees, while adult males more frequently retired to peripheral sites (Chapman 1989).

Behaviours around the selected sleeping site, as well as the selection itself, may be an adaptation to minimise predation risk. Free-ranging black and white snub-nosed monkeys (*Rhinopithecus bieti*) chose the tallest trees available for sleep, and were much quieter around the sleep site compared to other periods during the day (Cui et al. 2006), a behavioural change also documented in white-handed gibbons (*Hylobates lar)* (Reichard 1998). Failure to change behaviour appropriately around the sleeping site can increase the risk of predator attack. Scent marking around the sleeping site, for example, increased rates of scent tracking and subsequent attacks on golden lion tamarins (*Leontopithecus rosalia*), resulting in a sharp decrease in population numbers (Franklin et al. 2007).

Even in captive settings, primates may display anti-predator behaviours comparable to those of wild populations. Typically, free-ranging tamarins (*Saguinus* spp.) sleep in tree holes and densely tangled vines (Sussman & Kinzey 1984 in Caine et al. 1992). In captivity, red-bellied tamarins (*Saguinus labiatus*) consistently chose a sleeping (‘nest’) box that offered maximum concealment over boxes that offered moderate or minimum concealment. All three groups of tamarins (total n = 10) selected the sleeping box that was the maximum distance from the ground. When presented with only the nest box that offered minimum concealment, all tamarins significantly increased their levels of vigilance (visual scanning behaviours) prior to entering the nest box (Caine et al. 1992). In another study, two groups of captive-born and -reared Geoffroy’s marmosets (*Callithrix geoffroyi*) (total n = 15) were presented with two stimuli, a mock predator (freeze-dried rattle snake), or a similarsized piece of cloth prior to retirement. When presented with the snake only, the marmosets alarm-called and mobbed the perceived threat, and retired significantly later in the evening. On the mornings after the snake presentation, the marmosets continued to alarm call and inspect the area where the predator had been, accompanied by a significant delay in descending to the ground to forage (Hankerson & Caine 2004).

Sleep site selection for comfort

In conjunction with predation pressure, free-ranging monkeys are often subject to severe environmental conditions. To reduce nocturnal energy expenditure (Webb 1975; Di Bitetti et al. 2000) and minimise heat loss (Anderson 1984), sleeping sites that afford protection from inclement weather can facilitate more comfortable rest. In their natural habitat, several species vary their choice of sleep site in accordance with seasonal fluctuations in weather conditions and temperature. Observations of snub-nosed and golden monkeys, for instance, showed a clear disparity in sleep site selection during autumn-winter months versus spring-summer months. As temperatures fell to below zero degrees Celsius, sleeping trees at lower altitudes - with warmer temperatures, weaker winds and higher levels of morning sunlight - were increasingly selected (Cui et al. 2006; Li et al. 2000, 2006). The direction of slopes may also provide comfort at certain sleeping sites. In colder environments, primates have been observed to sleep on slopes that have morning sun exposure, as documented in Himalayan langurs (*Semnopithecus entellus*) (Bishop 1979), Japanese macaques (Furuichi et al. 1982) and snub-nosed golden monkeys (*R. roxellana*) (Liu & Zhao 2004). Chacma baboons (*Papio ursinus*) (Barrett et al. 2004) used caves more frequently in low nighttime temperatures, as did white-headed langurs (*Trachypithecus leucocephalus*) (Huang et al. 2003).

Free-ranging rhesus monkeys (*M. mulatta*) were found to increase the size of their sleep groups during periods of low temperatures (Southwick et al. 1965). Similarly, red howler monkeys (*Alouatta seniculus*) increased sleeping cluster size when nighttime temperatures dropped (Gaulin & Gaulin 1995). Chivers (1974) observed a juvenile and adult male siamang gibbon (*Hylobates syndactylus*) ‘huddling’ at the coldest period of the day, although they had previously been at least one meter apart at dusk (all cited in Reichard 1998). Japanese macaques formed significantly larger sleeping clusters at lower temperatures (Wada et al. 2007). Similarly, Takahishi (1997) documented that the largest sleeping clusters occurred in winter: up to twenty-seven individuals formed an en-masse huddle during winter, whereas in autumn the largest number of individuals in a cluster was six.

Varying the use of different sleeping sites can also reduce the risk of parasitic infestation, and thus improve the animals’ overall health. It has been suggested that short stays at a variety of sleeping sites within the home range may reduce infestation or re-infestation by ecto-parasites (such as ticks), as hypothesised for wild baboons (Hausfater & Meade 1982), and golden-handed tamarins (*Saguinus midas*) (Day & Elwood 1999).

Sleep site selection to maximise food intake

In times of food scarcity, bonnet macaques, chacma baboons and howler monkeys (*Alouatta palliata*) all changed their habitual sleep sites to remain closer to readily available food sources (Rahaman & Parthasarathy 1969; Hamilton 1982; Milton 1980 in Ramakrishnan & Coss 2001). In areas of lower predation pressure, ecological variables such as food resources have been proposed to be an important determinant of sleep site selection. Pontes and Soares (2005) observed that common marmosets (*Callithrix jacchus*) in urban forests most frequently retired to trees in close proximity to their last-visited feeding place. Howler monkeys used sleeping sites in close proximity to food trees along well-used pathways (Garcia 1988 cited in Garcia & Braza 1993). Wild golden-handed tamarins also frequently chose sleep sites in close proximity to food sources (Day & Elwood 1999).

Social factors affecting sleep site selection

Nighttime sleeping clusters or huddles may be a strategy to minimise heat loss, but may also be a reflection of monogamous pairings, daytime social affiliations, or close family bonds. Anderson and McGrew (1984) observed that Guinea baboons (*P. papio*) formed sleeping huddles composed of adult males and females, juveniles, and mother-dependent infants, in which individuals clung to each other while perched on branches of the sleeping tree. Generally, huddling did not appear to be affected by weather conditions. In free-ranging rhesus macaques, sleeping clusters were mainly composed of kin (Vessey 1973). Subgroups of sleeping bonnet macaques also showed distinct preferences for specific partners – individuals mainly formed sleeping groups with members of the same age and sex (Koyama 1973), and sub-adult females maintained nighttime contact with their mothers (Ramakrishnan & Coss 2001). Cui et al. (2006) reported that snub-nosed monkeys of the same matriline slept in the branches of the same sleeping tree, and that nighttime grouping patterns were generally similar to those observed during daytime.

1.3 Nocturnal behaviours of monkeys

It would be reasonable to assume that, for diurnal primates, after selecting a sleep site nighttime is a period of behavioural quiescence. However, there is evidence, albeit somewhat fragmentary, to suggest the contrary. One of the few studies that have been able to document nighttime behaviours of free-ranging primates was by Vessey (1973), who studied rhesus macaques. Using infrared scopes and flashlights, this report describes the active nature of these diurnal primates around sleep sites. After sunset, vocalisations and movements continued for several hours. During full moons, activity levels increased. Data from captive primate populations have yielded similar findings. Although primate sleep patterns have traditionally been researched in terms of electrophysiological architecture (e.g., rhesus macaques: Weitzman et al. 1965; pig-tailed macaques: Reite et al. 1965; baboons: Bert et al. 1975), non-invasive methods, such as infrared video recording (e.g., Noser et al. 2003) and ultra sensitive video cameras (e.g., Munoz-Delgado et al. 1995) are increasingly being employed to investigate behavioural, rather than structural, characteristics of sleep. Evidence from laboratory-housed adult stump-tailed macaques (*M. arctoides*, Munoz-Delgado et al. 1995, 2004a) and infant pig-tailed macaques (Kaemingk & Reite 1987) indicates that social and non-social activities can continue throughout the night. Studies on sleep-related behaviours under captive conditions, then, may be a valid means of adding to our as-yet scant knowledge of nocturnal behaviours and sleep patterns in primates.

1.4 Sleep-related behaviours of the great apes – the construction of night nests

Like humans and the previously cited monkey examples (*Aotus* excepted), the great apes are diurnal, and subject to the same array of ecological and social constraints that are mirrored in their nocturnal sleeping habits. However, the nightly sleeping platform constructed by bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*) lowland (*Gorilla gorilla gorilla*) and mountain gorillas (*G. g. beringei*), and orangutans (*Pongo pygmaeus*) sets them apart from all the other anthropoid primates, possibly as an adaptation to avoid falling from heights, as the larger-bodied apes would have been unable to perch safely on branches as monkey do (Baldwin et al. 1981).

The construction of this sleeping structure, traditionally referred to as a 'nest' (e.g., Bolwig 1959; Goodall 1962, 1968; Nissen 1931)[1], but also described as a 'bed' (Hiraiwa-Hasegawa 1986) or 'shelter' (McGrew 2004) is one of the most prevalent and normative behaviours in the daily behavioural repertoire of apes (Fruth & Hohmann 1994, 1996; McGrew 2004). Despite fundamental differences in habitat, ecology and social structure, the ontogeny and sequence of nest building across great ape taxa is remarkably similar.

Beginning in infancy (Fruth & Hohmann 1994), nest building is practised by constructing 'day nests', usually as a form of play activity (Goodall 1962). Day nests tend to be simple cushion-like structures (Hiraiwa-Hasegawa 1989) that are used mainly as a type of 'rest stop' (Brownlow et al. 2001) between feeding and travelling periods. Functionally and structurally distinct from the more elaborate night nests, the construction of day nests is usually less time-consuming (Ghiglieri 1984), requires less effort (Fruth & Hohmann 1993), and the resulting structures are generally less well constructed than their nighttime counterparts (Ancrenaz et al. 2004). Although all great apes are known to construct day nests for resting periods

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[1] The term 'nest' will be retained throughout this document

(Fruth & Hohmann 1994), the frequency of doing so may depend on age and sex – chimpanzee infants and juveniles reportedly made day nests more frequently than adults (Goodall 1968), with females doing so more regularly than males (Hiraiwa-Hasegawa 1989).

Once proficient in nest building – usually around the period of weaning (Goodall 1962) – 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 a approximately circular shape around the circumference), and finally lining the nest by picking and adding softer twigs and leaves (Fruth & Hohmann 1996). As with day nests, night nest construction can vary according to sex, which is most likely attributable to sexual dimorphism in body size and weight. In gorillas (Groves & Sabater Pi 1985) and orangutans (Rayadin & Saitoh 2009), males construct larger nests in comparison to the smaller females or immatures. Larger orangutans tended to construct nests at lower levels within the sleeping tree, where the tree's physical structure was probably more stable (Rayadin & Saitoh 2009).

Nest site selection as an anti-predation strategy

The only broad difference across the great apes is in the vertical distribution of nests. Bonobos, chimpanzees and orangutans most frequently construct arboreal nests (Fruth & Hohmann 1996). Nocturnal predation, by leopards for example, can be a significant risk to gorillas (Yamagiwa 2001), orangutans (Rayadin & Saitoh 2009) and chimpanzees (Boesch 1991a), and so it is unsurprising that arboreal sleep sites are favoured. Gorillas, however, differ from the other apes in that they typically construct nests closer to, or on, the ground. This is broadly true across both eastern (Casimir 1979; Reynolds 1965) and western (Mehlman & Doran 2002; Tutin et al. 1995) populations. Observations have also indicated that gorillas will sometimes even sleep on bare ground – making no attempts to construct even a rudimentary nest (Mehlman & Doran 2002; Remis 1993). The propensity for ground-sleeping in free-ranging gorillas is generally attributed to their large body size, especially in reference to large, silverback males, which may inhibit arboreal nest construction and act as an anti-predator strategy in itself (Yamagiwa 2001).

Although gorillas frequently sleep, especially in the case of mountain gorillas, on the ground, some evidence suggests that this reflects the degree of security afforded by the dominant, silverback males. At one site, following the death of the silverback, adult females and immature individuals more frequently constructed arboreal nests; the arrival of a new silverback resulted in the adult females, and to a lesser extent immatures, resuming previous levels of ground nest construction (Yamagiwa 2001). It appears, then, that more vulnerable group members were especially cautious in their sleeping arrangements in the absence of a silverback. A similar finding has been reported among Asian apes: adult male and adult female (without infants) Sumatran orangutans typically nested in close proximity to the last-visited food source (Sugardjito 1983). The most vulnerable classes – females with infants and immature individuals - moved further away from food trees prior to nest construction, possibly to avoid nocturnal disturbance and predation. These vulnerable individuals also consistently constructed nests at higher levels. Similarly, vulnerable juveniles at three sites across Borneo typically constructed nests toward the end of sleeping branches, possibly facilitating a better view of the surroundings, and so favouring early detection of predators (Rayadin & Saitoh 2009).

In areas with high risks of predation, for instance at the Tai forest (Cote d'Ivoire), chimpanzees can construct nests at heights of up to twenty-three meters, whereas average nest height at most chimpanzee study sites is between ten and twenty meters (Fruth & Hohmann 1994). Kortland (1992) reported that chimpanzee groups in Zaire frequently retired to the tallest trees that afforded the best view of nearby human dwellings and forest pathways, thus allowing early detection of potential danger. Field research comparing the nesting habits of chimpanzees in areas of high versus low predation pressure adds weight to the predation-avoidance hypothesis. The median height of chimpanzee nests at Mt. Assirik (Senegal) was higher than in rainforests in Equatorial Guinea; leopards are more common at the former site (Baldwin et al. 1981). Pruetz et al. (2008) compared nest site data from two chimpanzee communities (*P.t verus*) in southeastern Senegal. The Assirik community faced predation risk from several carnivores, including leopards (*Panthera pardus*) and lions (*P. leo*). The Fongoli community were not exposed to the same levels of predation – indirect evidence indicated the presence of only a single predator over 286 days. Assirik chimpanzees consistently built nests closer together and at higher levels, and they generally avoided 'open' nest sites (such as grassland and woodland) of the type that were frequently utilised by Fongoli chimpanzees.

Chimpanzee nesting patterns at Issa (W. Tanzania) suggested a preference for nesting on slopes versus flat areas, possibly as terrestrial vegetation is lower on slopes, and so impedes predator hunting (Hernandez-Aguilar 2009). If arboreal nesting is indeed a behavioural adaptation related to predation pressure, then we would expect that terrestrial nest building would be more frequent in areas of low predator presence. This is indeed the case. In Bwindi National Park and Kalinzu forest (both in Uganda), there are few known large carnivores. In these areas chimpanzees frequently construct terrestrial night nests (Maughan & Stanford 2001), and relatively low arboreal nests (approximately nine meters above ground) in small trees (Furuichi & Hashimoto 2000). The risk of predation, however, may not be the only determining factor in nest site selection, as addressed below.

Nest site selection for comfort

Pruetz et al. (2008) noted that the Fongoli chimpanzees constructed ground nests infrequently, despite the low density of predators. It is conceivable that comfort is also an important determinant of sleep site selection – an arboreal nest may simply be more comfortable than a nest on the ground. Nissen (1931) proposed that, given the large body size of chimpanzees, the construction of an arboreal nest provides not only support during sleep, but also warmth and a soft base, and therefore offers a more comfortable sleep.

Bonobos (Fruth & Hohmann 1993) showed preferences for nesting at canopy heights, where there was an abundance of more flexible and softer twigs and leaves, which presumably facilitates the construction of a more comfortable nest. Stewart et al. (2007) reported similar findings at Fongoli: chimpanzee nests that contained additional material (leaves, twigs and branches) were more comfortable (at least for the human who tried them out) in the central area, where most of the body weight is distributed. Ghiglieri (1984) reported that Mahale chimpanzees often pulled ‘padding material’ from up to four surrounding trees and added them to the nest.

In keeping with the previously cited examples from free-ranging monkeys, protection from the elements also appears to influence nesting behaviour of the great apes. Nests of orangutan females with infants across three populations in Borneo (Rayadin & Saitoh 2009) tended to be closed (covered by layers of tree crown) rather than in more open locations, thus sheltering the infants from exposure to wind and rain. Adult orangutan males were reported to leave their rain-soaked nests in the early morning, construct new nests and stay in these for one hour until the sun came out (MacKinnon 1974). Conversely, chimpanzee nests might be more open, even during rains; however, this may be a strategy to facilitate faster drying the following morning, and so also appears linked to comfort (Baldwin et al. 1981). Rainfall and temperature appeared to exert a strong influence on nest construction by western gorillas at Mondika (Mehlman & Doran 2002). Increases in rainfall were highly correlated with increased frequency of building complex versus bare earth or minimal nests at both terrestrial and arboreal levels. Similarly, full nest construction, again at both ground and arboreal levels, was associated with lower daily temperature. The more elaborate nests might provide more comfort and thermoregulatory benefits against inclement weather conditions.

Nest site selection to increase proximity to resources

Bonobos (Fruth & Hohmann 1994), chimpanzees (Furuichi et al. 2004; Goodall 1962), and orangutans (Rjiksen 1978 cited in Babose & Yamagiwa 2002) rarely construct nests in fruiting trees, but do stay in relatively close proximity, enabling them to quickly return to the food source the following day. There are exceptions to this general rule - chimpanzees at Kahuzi National Park (Democratic Republic of Congo), for example, regularly nested in fruit trees (Basabose & Yamagiwa 2002), but avoided trees whose fruit may also be consumed by sympatric gorillas. In contrast, western lowland gorillas often choose nest sites in close proximity to preferred fruit sources (Tutin et al. 1995). Further, sleep sites are most often reused during the fruiting season (Iwata & Ando 2007), suggesting that areas with high food availability facilitate repeat visits. In seasons of fruit scarcity, Wamba bonobos reduced nest party size; the opposite was true in seasons of fruit abundance (Mulavwa et al. 2010).

In the Petit Loango forest (Gabon) low density of herbaceous vegetation (nesting substrate), precluded the construction of terrestrial nests by gorillas – only seven percent of nests were built on the ground (Furuichi et al. 1997). By contrast, in areas abundant in shrubs and herbaceous materials, such as Virunga, almost all gorilla nests were constructed terrestrially (Schaller 1963, cited in Yamagiwa 2001). At Mondika (Central African Republic, DRC), the frequency of gorilla bare-earth sleeping may also be linked to low availability of vegetation substrate (Mehlman & Doran 2002).

Several studies have shown that the reuse of old nests is relatively common among orangutans (Ancrenaz et al. 2004; Rayadin & Saitoh 2009), but less so in bonobos (Fruth & Hohmann 1996), chimpanzees (Plumptre & Reynolds 1997) and gorillas (Iwata & Ando 2007). As orangutans typically construct larger nests than chimpanzees (Groves & Sabater Pi 1985), and at greater heights than gorillas (Fruth & Hohamnn 1996), their higher proportion of nest reuse may reflect limited resource availability, that is, insufficient raw material for constructing a new nest on a daily basis.

Social factors affecting nest site selection

At a basic level, nest groups (clusters of nests built in close proximity at the same time) mirror the social organisation of apes. The group-living chimpanzees, bonobos and gorillas all form social nesting groups (Fruth & Hohmann 1996). Chimpanzees tend to split into smaller nest groups (Goodall 1962); a gorilla nest group is generally composed of the same individuals that form daytime groups, and bonobos often merge with smaller sub-groups to form a large, overnight nesting party (Fruth & Hohmann 1994, 1996). In comparison, although sociable as immatures and sub-adults, orangutans are mainly solitary as adults (Russon et al. 2007), and so rarely form nesting groups. Although there is a marked lack of data for chimpanzees, gorillas and orangutans, bonobos (Fruth & Hohmann 1993) will indulge in social grooming and social play after constructing day nests – indicating that nests are not restricted to their main function of rest or sleep.

Analysis of nearest neighbour proximity of free-ranging gorillas indicated that daytime associations continue into nighttime, with affiliative individuals sleeping in close proximity. However, with the exception of this gorilla example (cited in Fruth & Hohmann 1996), there appears to be no available data on day and nighttime associations in the remaining three ape species. There are also recorded instances of apes abandoning completed nests, seemingly to be closer to specific group members or attachment figures. Goodall (1968) reported that a sub-adult female abandoned a completed nest in order to build another closer to the rest of her group. Similarly, a weaned juvenile was observed on three separate occasions to abandon her completed nests and construct new night nests that were in closer proximity to her mother. Izawa and Itani (1966, cited in Ghiglieri 1984) reported finding several larger than average chimpanzee nests, which they presumed to have been built to accommodate more than one individual. However, there were no direct observations to confirm this.

Similar to Pruetz et al.'s (2008) observations that Fongoli chimpanzees rarely constructed ground nests, even in the absence of predation risk, Koops et al. (2007) reported that ecological factors did not appear to influence chimpanzee ground nesting in the Nimba Mountains (Guinea). Although predation pressure was known to be low, the authors examined several other ecological reasons for the high prevalence of ground nesting in this region. Frequency of ground nesting was not affected by altitude, wind-speed, or shortage of appropriate nesting trees. Rather, this behaviour appeared to be sex-linked, with more males constructing terrestrial nests – possibly as a strategy for guarding oestrus females. Male bonobos (Fruth & Hohmann 1993) and chimpanzees (Brownlow et al. 2001) are known to nest lower than females. As males are heavier than females, this sex-linked behaviour may also be a strategy to reduce the risk of injury from a fall, or alternately to protect the more vulnerable group members from terrestrial predator attack (Brownlow et al. 2001). Given the lack of compelling ecological explanations, the authors conclude that social or cultural dynamics may be stronger determinants of ground nesting in this area.

Other examples of population-specific nesting behaviours have been documented in the other ape species. Western lowland gorillas build more arboreal nests than mountain gorillas (Mehlman & Doran 2002); bonobos construct ground nests at

Yalosidi and Lake Tumba, but not at Lomako (all in Zaire); chimpanzees construct nests in oil palms at Gombe and Guinea, but not at other research sites (Fruth & Hohmann 1996); in orangutans, leaf-carrying for nest building is common on Kaja Island, but rare or absent in surrounding regions (Russon et al. 2007). Although some of these differences undoubtedly arise from ecological pressures, socially learned traditions – or cultural variations - may also result in behavioural variation across populations (Russon et al. 2007). Although the issue of primate culture can be controversial (Laland & Janik 2006), the evidence does tentatively suggest that inter-population variation in nesting patterns reflects culture. However, nest-related behaviours are generally not included in primate cultural research (McGrew 2004), with the exception of orangutans (e.g., van Schaik et al. 2003), and so warrant further investigation across ape taxa.

1.5 Nesting and sleep in the great apes – neglected behaviours?

Nesting behaviour in the great apes is often investigated in terms of sleeping tree choice (e.g., Brownlow et al. 2001; Ghiglieri 1989; Stanford & O'Malley 2008), or the influence of ecological variables on nest site selection (e.g., predator avoidance: Pruetz et al. 2008; fruit availability: Iwata & Ando 2007; season and habitat: Ancrenaz et al. 2004, Baldwin et al. 1981; climatic variables: Mehlman & Doran 2002). Nests have also been exploited as a means of censusing free-ranging populations (e.g., chimpanzees: Anderson et al. 1983, Furuichi et al. 2001, Plumptre & Reynolds 1997; orangutans: Ancrenaz et al. 2004; gorillas: Tutin et al. 1995; sympatric chimpanzees and gorillas: Sanz et al. 2007). These studies are not without their merits, and have greatly contributed to our understanding of nest-related activities of the great apes; and census methods are of course critically important for developing conservation strategies for endangered ape species.

Moreover, the documented socioecological factors that underpin nest site selection have implications for reconstructing early hominid behaviour. It has been proposed that ape night nests are more functionally related to human beds (Fruth & Hohmann 1996; Kappeler 1998), and so may represent a primitive form of architecture (e.g., Sept 1992). Given the phylogenetic closeness of African apes (gorillas and both *Pan* species) and the earliest forms of *Homo*, it is not unreasonable to propose that all of these species shared the common trait of nest building (Sabater Pi et al. 1997). Further, the social nature of nesting groups around the same area may have led to early hominid ‘home bases’ (Issac 1971 in Sept 1992) or ‘fix points’ (Groves & Sabater Pi 1985). Increasingly secure sleep, facilitated by arboreal nest construction, may have contributed to the development of these sleep-related patterns, and so may have also facilitated the evolution of cognitive abilities (Fruth & Hohamnn 1996). Thus, nesting patterns and the nest sites of the great apes may have important implications for studying the evolution of human dwelling sites and sleep patterns.

However, some authors have commented that by focusing almost exclusively on these factors, data on nest building techniques, nest uses, and the social context of nest building, are almost nonexistent (see Anderson 1984, 1998, 2000; Fruth & Hohmann 1994, 1996 for comprehensive reviews). The absence of data on these specific nest-related behaviours is most likely due to the inherent difficulty in recording behaviour that occurs during failing light conditions, as succinctly observed by Nissen (1931 p39):

“…nest construction was delayed until it was so dark that one could see practically nothing, even if in a favourable position.”

Given such limitations, it seems reasonable to turn to captive settings for conducting systematic research on nest and sleep-related behaviours, where behaviours can be monitored and documented regularly, and animals are generally more visible (Stevens et al. 2008). However, and perhaps surprisingly, the same lack of direct observations of nesting in free-ranging apes applies to captive apes (Videan 2006b; Weiche & Anderson 2007). To illustrate, the terms “nesting behaviour of great apes”, “bed-building behaviour of captive apes” and “sleep in captive apes” were used in a literature search of four academic journals specializing in primate behaviour (*American Journal of Primatology, Folia Primatologica, International Journal of Primatology,* and *Primates*), two less specific animal behaviour journals (*Animal Behaviour, Applied Animal Behaviour Science*), and two zoo-related publications (*International Zoo Yearbooks, Zoo Biology*). The total number of ‘hits’ thus generated was 325 for nesting behaviour, 70 for bed-building behaviour, and 283 for sleep. Using the same journals, the terms “sexual behaviour of captive apes”, “social behaviour of captive apes” and “feeding behaviour of captive apes” generated totals of 1,088, 1,395, and 1,772 results, respectively[2]. This literature search was restricted to specific journals and so does not reflect the true amount of literature available on these topics. However, the figures do appear to mirror the lack of data on nest and sleep-related behaviours in the great apes compared to activities observed during daytime. .

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[2] These figures correct at end March 2011

Although not subject to much scientific review, several aspects of nesting and sleep-related behaviours have been researched in captive apes. As with monkeys, some studies focusing on sleep patterns and architecture on laboratory housed (and individually housed) chimpanzees have used EEG measurements (e.g., Adey et al. 1963; Bert et al. 1970; Freemon et al. 1970), yet nocturnal behaviours are rarely observed and still poorly understood.

Social factors, such as the presence of kin or unrelated individuals that share an affiliative bond, have been proposed as affecting nest and sleep-related behaviours in captive chimpanzees (Riss & Goodall 1976; Videan 2006b) and gorillas (Lukas et al. 2003; Weiche & Anderson 2007). Social learning, age and experience also influence nest construction ability in chimpanzees, gorillas and orangutans (Bernstein 1969; Morimura & Mori 2010; Videan 2006a). Likewise, environmental factors such as season, humidity, and temperature can influence nesting and sleep behaviour in captive populations – as documented in laboratory housed chimpanzees and zoo-housed gorillas (Lukas et al. 2003; Videan, 2006b; Weiche & Anderson 2007).

It is clear that the amount of literature available focusing on nesting/sleep behaviour of captive apes is negligible. Excluding the aforementioned EEG studies, at the time of writing, there appears to be one article on captive bonobos (Berle et al. 1995) and captive orangutans (Bernstein 1969), three articles on gorillas (Bernstein 1969; Lukas et al. 2003; Weiche & Anderson 2007), and only six articles on chimpanzees (Bernstein 1962, 1967, 1969; Riss & Goodall 1976; Videan 2006a, 2006b). The findings reported in these articles are more thoroughly detailed in the relevant chapters.

1.6 Nesting and sleep in captive apes – welfare issues?

Despite the paucity of data on nest and sleep-related behaviours, it is clear that the construction of nests is generally a daily behaviour performed by free-living and, if provided with appropriate environmental conditions, laboratory and zoo-housed apes. This activity can be regarded as a species-typical behaviour, described by one author as "…the cornerstone of chimpanzee nature" (McGrew 2004 p108). In conjunction with biological and feelings-based approaches (briefly outlined below), the expression (or lack thereof) of such natural, species-typical behaviours is included in definitions of captive animal welfare (Fraser 2009; Fraser et al. 1997).

Although a precise definition of animal welfare is still elusive (Barber 2009; Goulart et al. 2009), it is generally held that animal welfare is fundamentally linked to quality of life (Duncan & Fraser 1997), an animal's attempts to cope with its environment (Broom 1986, 2010), environmental control and levels of stress (e.g., Swaisgood 2007), and relates to both physical (e.g., Broom 1991) and psychological (e.g. Dawkins 1980, 1988, 1990; Duncan 1993) health. There are three broad, although not necessarily mutually exclusive, approaches that define 'good' and 'poor' welfare from various standpoints.

The biological approach to defining and assessing animal welfare

The biological functioning, or biological fitness, approach places particular importance on the physiological health of captive animals. From this perspective, welfare will be good if animals are in physiologically healthy condition, i.e. free from deformity, disease, injury, and incapacity (Dawkins 2003; Webster 2005). Poor welfare, then, arises when physiological systems are impaired in some way, and so fitness is reduced (e.g. Barnett & Hemsworth 1990; McGlone 1993).

Fluctuations in heart rate, respiration rates and core body temperature (Broom & Johnson 2003), impaired growth and reproduction, and reduced life expectancy are all indicators that health, and consequently welfare, are sub-optimal (Broom 1986, 1991; Rushen 2003). Broom (1988, 1991, 1996) states that welfare can be defined in terms of how an animal ‘copes’ with its environment. If an animal is coping successfully, then biological fitness, thus welfare, will be good. When animals fail to cope in inadequate environmental conditions, biological functions such as growth, immunity, and reproduction will suffer, and signal reduced welfare.

There are however, problems in defining welfare on a strictly physiological basis. Heart rate and corticosteroid (stress hormones) levels, for example, fluctuate with exercise and anticipation of feeding (Dawkins 2003), and so may not always be reliable indicators of poor welfare. Moreover, it is increasingly acknowledged that captive animals should be psychologically, as well as physically, healthy to ensure good welfare (Dawkins 2003; Duncan 1993; Mendl 1991), with a heavier emphasis on how animals *feel*.

The feelings-based approach to defining and assessing animal welfare

According to this feelings-based (or ‘affective states’) approach, welfare can be comprised if animals are subject to unpleasant feelings, or negative affective states, such as pain, hunger, fear, stress, frustration (Dawkins 1990; Fraser 2009; Mason & Veasey 2010) and boredom (Wemelsfelder 2003). When these negative feelings become intense and/or prolonged, animals will suffer, and so welfare will be poor (Dawkins 1980). By contrast, positive states, such as pleasure and comfort, will enhance welfare (Dawkins 1990; Fraser 2009). These positive states, or pleasant feelings, need not be restricted to daytime activities such as eating, play or exercise (Yeates & Main 2008). Fraser (1983) describes the state of sleep as a pleasure, where the correlated negative feeling would be fatigue.

This approach has been criticised for being anthropomorphic, fundamentally difficult to measure, and lacking in definitive evidence that demonstrates these subjective feelings (e.g., Barnard & Hurst 1996). However, several methods have been developed that have sought to clarify animals' feelings. 'Preference tests' (also discussed in chapter 5), have traditionally provided animals with a choice about a feature of their environment, under the assumption that choices will be made depending on their feelings (e.g., Dawkins 1977). Thus, animals will show preference for environments that afford pleasant feelings whilst avoiding environments that cause unpleasant, negative feelings, and so base the choice on its own welfare interests (Duncan 1992). In providing environmental and social choices, captive animals can exercise some degree of control over what is fundamentally a restricted setting. Choice and control are widely acknowledged to be beneficial for animal welfare (e.g., Ross 2006; Swaisgood 2007; Watters 2009; Wickins-Drazilova 2006; Young 2003).

Engaging in stereotypic behaviours is often hypothesised to be an external indicator of undesirable internal states, mainly due to their association with environments that are identified as fearful, frustrating or stressful (Mason 1991; Shepherdson et al. 2004). Therefore stereotypies may be a reliable indicator that welfare is poor (Mendl 1991). However, it should be noted that there is no clear-cut relationship between aberrant behaviours and welfare (Mason 1991), and their performance can also vary with age, sex, and temperament (Bourgeois & Brent 2005), rearing history and social experience (Mallapur 2005).

The natural behaviour approach to defining and assessing animal welfare

According to some, the extent to which captive animals can lead a ‘natural life’ by performing behaviours comparable to their wild-living counterparts, will affect their welfare (e.g., Brambell 1965; Hediger 1950; Thorpe 1965). That is, welfare is not only related to the control of pain and negative affective states, but is also associated with the ability to express a repertoire of natural behaviours (Rollin 1993). Hughes and Duncan (1988) stated that all species have ‘ethological needs’ to perform certain behaviours for acquiring specific resources. When the environment does not allow these behaviours, welfare will suffer. Duncan (1970) and Baxter (1982 cited in Jensen & Toates 1993), for example, suggested that laying hens and farrowing sows performed stereotypic behaviours when deprived of appropriate nesting sites and substrates, respectively. The constraints of natural behaviours have also been implicated in the performance of stereotypies in zoo-housed carnivores (e.g., restricted ranging behaviour: Clubb & Mason 2007) and in health problems in zoo-housed elephants (e.g., colic and tooth disorders from unnatural diets: Kawata 2008).

According to Carlstead (1996), the ability to perform species-appropriate behaviours that result in functional outcomes (such as finding food through foraging, hiding from perceived predators, or building a nest) leads to greater control over the environment. As previously discussed, control of certain aspects of the environment promotes good welfare. Novak and colleagues (2007) put forward that having control over social opportunities and objects that can be altered and manipulated could be beneficial to welfare by promoting species-typical behavioural patterns.

Comparison to free-living counterparts is often used to assess whether welfare standards are poor or good according to this approach, where quality of life can be directly measured from the species-typicality of an animal's behaviour (Markowitz 1997). In conjunction with self-injurious and stereotyped behaviours, deviations from wild-type behaviours are regarded by some as a behavioural indicator of compromised welfare (Melfi 2009). In recent years, changes in husbandry practices, particularly in zoos, have sought to encourage appropriate behavioural patterns to promote good welfare standards (Hill & Broom 2009).

As with the previously discussed approaches to welfare, some criticisms have been aimed at the natural behaviour approach. Dawkins (2003, 2004) questions whether welfare would necessarily be adversely affected if an animal does not display *all* of the behaviours seen in natural-living counterparts. For example, fleeing from predators is ubiquitous for many species, but animals under the care of humans may have no need to perform this behaviour. This leads to the question of whether the inability to perform such behaviours necessarily results in reduced welfare.

Toward integrating all three approaches to welfare

As previously stated, these three approaches need not be mutually exclusive. According to Broom (2010), for example, unsatisfied biological needs may be associated with unpleasant feelings, whereas satisfied needs may be coupled with positive feelings. Similarly, unpleasant feelings (e.g. frustration) may arise from the non-performance of species-typical behaviours (Poole 1992; Shyne 2006), where positive affective states can be facilitated by the expression of behavioural needs (Spinka 2006). Moreover, if captive environments allow the performance of species-typical behaviours, animals may be psychologically healthier than those with restricted repertoires (Mason 1991). This can have direct benefits for physical health, with reductions in stress and injury through excessive aggression or self-injurious behaviours (Honess & Marin 2006a,b).

For many years, authors have sought to combine the three broad approaches to welfare. With reference to captive apes, for example, Maple (1979) stated the importance of eliminating suffering and stress-related disease, whilst also encouraging the provision of complex environments and social opportunities that facilitate a …"normal array of activities." (p240). Dawkins (2003, 2004) has made further attempts to incorporate all three approaches by posing the questions: (a) are animals healthy, and (b) have what they 'like' and 'want'. From this perspective, if health is good, if animals are not fearful, frustrated, or bored, and if an animal is allowed to perform a natural behaviour it shows evidence of wanting to perform, then welfare will be good. More recently, Bracke and Hopster (2006 p80) incorporated affective states and biological health into their definition of natural behaviour:

> "Natural behavior is behavior that animals tend to perform under natural conditions, because it is pleasurable and promotes biological functioning."

This need to consider biological functioning, prevent suffering and encourage natural behaviours is also reflected in animal welfare legislation for domestic livestock (e.g., ‘five freedoms’, Farm Animal Welfare Council 1992), laboratory (e.g. Animal [Scientific Procedures] Act 1986), and zoo animals (e.g. Secretary of State’s Standards of Modern Zoo Practice 2004). The use of ‘environmental enrichment’ husbandry practices in zoos and other captive settings is also geared toward integrating these three approaches by promoting species-typical behaviours (Wells 2009; Young 2003) and reducing self injurious behaviours, stereotypies and/or abnormal repetitive behaviours (Gilloux et al. 1992; Mason et al. 2007) that can be detrimental to psychological and physical health.

1.7 Thesis aims

With few exceptions, nest and sleep-related activities of captive chimpanzees have typically focused on sleep architecture and the learning process involved in nest construction. Although zoos and other captive settings strive to provide environments that maintain or improve captive animal welfare, sleeping sites have been overlooked in this regard.

One of the aims of this thesis was therefore to consider nest-and sleep-related activities from the three aforementioned welfare perspectives. Not only can species-appropriate sleeping structures and nesting materials facilitate natural nest construction behaviours (in keeping with the natural behaviour approach to welfare), they may also provide comfort and security (relating to feelings-based approaches to welfare), and also potentially facilitate comfortable sleep (thus contributing to biological health). Increased understanding of how sleeping facilities are utilised can have practical implications for the design/refinement of sleeping areas, sleeping structures, and the types of bedding substrates that are routinely provided to captive apes, with an aim to ensuring good standards of welfare.

The second aim of this thesis was to document aspects of nest-related behaviours that have generally been neglected, including the techniques involved in construction, the potential of inter-group (cultural?) variation in these techniques, and socioecological contexts of nest building. A nationwide survey, direct observations, overnight video recording and experimental procedures[3], have all been employed in order to gain insight into multiple aspects of nesting and nocturnal behaviours of captive chimpanzee populations. Several of the following chapters represent a series of ‘firsts’ in this field of primatology – such as documenting overnight sleeping postures, testing the effects of kin and daytime associations on sleep site selection, and specifically testing for nesting material preferences. Also for the first time, the nighttime behaviours of captive chimpanzees immediately following the death of a long-term group member were recorded, while the body remained *in situ*.

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[3] Data collection procedures, details of chimpanzees and environments, and statistical analyses are described separately in each chapter.

Chapter 2

Provision of nesting structures and substrates for captive apes: A nationwide survey

"...captive apes provided with appropriate materials will engage in nest building activities and will build recognisable nests." ~ Bernstein 1962, p1

2.1 Introduction

Increasingly, the stated role of zoos worldwide is to promote research and conservation efforts, educate visitors and increase standards of welfare of their captive animals (Melfi 2005; Seidensticker & Doherty 1996; Swaisgood & Shepherdson 2005). One of the strategies that have been employed to promote good standards of animal welfare has been to preserve and encourage species-typical behaviour (Dickie 1998; Markowitz 1997; Mellen & MacPhee 2001), in keeping with the natural behaviour approach to defining and assessing captive animal welfare described in the preceding chapter. To briefly reiterate on this approach, it is argued that captive animals can become frustrated if denied the chance to express natural behaviours, which can result in stereotypies (Roder & Timmermans 2002), stress (Morgan & Tromborg 2007), and perhaps prolonged suffering (Dawkins 1990). Moreover, it has been suggested that animals that display a repertoire of natural behaviours are psychologically healthier than animals with restricted behavioural patterns (e.g. Line 1987; Mason 1991).

Although this natural behaviour approach to animal welfare has been criticised (e.g. Dawkins 2003, 2004), current legislation regarding the keeping of animals in laboratories and commercial facilities unequivocally states the importance of facilitating the expression of natural, species-specific behaviours (e.g. United Kingdom: Secretary of State's Standards of Modern Zoo Practice 2004; Europe: Official Journal of the European Communities Council Directive Relating to the Keeping of Wild Animals in Zoos 1999; U.S.A.: U.S.D.A Regulations on Animals in

Laboratories and Commercial Facilities 1998). These legislation clearly state that zoos must accommodate their animals in a manner that satisfies the biological and psychological needs specific to each species. For example, 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).

'Environmental enrichment' techniques have been used for a number of years in order to promote the psychological welfare of captive animals (Maple & Perkins 1996) by providing stimulation and reducing inactivity (arguably especially relevant to laboratory primates: Hosey 2005), providing social and physical complexity that promote behavioural repertoires similar to those expressed by wild populations (Carlstead & Shepherdson 1994), and increasing frequencies of goal-directed behaviours (Shyne 2006). As with the term animal welfare, environmental enrichment suffers from the lack of a universal definition (Newberry 1995). However, one description that is of particular relevance here is:

> "A practice aiming to provide environments of greater physical, temporal and social complexity that affords animals more of the behavioural opportunities found in the wild." (Carlstead & Shepherdson 1994, p448)

This technique of enriching captive animals' environments can take many forms, including introducing foraging devices, manipulating social structures, introducing sensory stimulation, and supplying physical structures and furnishings (see Wells 2009; Young 2003 for reviews), in order to decrease undesirable behaviours, increase desirable (naturalistic) behaviours, and so improve/maintain welfare (Lutz & Novak 2005; Tarou & Bashaw 2007). Environmental enrichment should be developed and implemented in accordance with each species' natural history (Mellen & MacPhee 2001), or 'wild-type' behaviour patterns (Young 2003). By adding biologically relevant features such as platforms, climbing structures, and substrates that reflect aspects of those utilised by primates in their natural habitat, enclosures can be made more complex, with a concurrent increase in species-typical behaviour(s).

Many studies have demonstrated the benefits of this type of enrichment. The inclusion of elevated perches into cages, for example, was reported to facilitate daytime species-typical behaviours in laboratory-housed squirrel monkeys (*Saimiri sciureus*, n = 250) (Wolff 1989) and long tailed macaques (*Macaca fascicularis*, n = 20) (Shimoji et al. 1993). More vertical space was utilised by both monkey species, and more behaviours consistent with those of free-ranging populations were observed, such as using perches for feeding and locomotor behaviours.

Two pairs of laboratory-housed female rhesus macaques showed a preference for higher perches (versus low or median level) and top levels (versus bottom levels) when these were introduced into the cage. As free-ranging macaques use height as a means of predator avoidance and as a safe sleep site, the authors concluded that this simple change in cage structure is an effective means of enrichment for this small captive population (Clarence et al. 2006). Mother-infant pairs of chimpanzees (n = 9) in laboratory cages spent most time on platforms located up to 2.5 meters above the floor, again indicating a preference for elevated structures (Goff et al. 1994). Arboreal primates whose enclosures prohibited them from using vertical spaces demonstrated several abnormal behaviours, including self-mutilatory behaviours and stereotypies (for example lion-tailed macaques, *Macaca silenus*: Mallapur et al. 2005).

The success of structural enrichment is not restricted to laboratory-housed primate populations. A singly housed adult female orangutan in a zoological park showed activity levels similar to free-ranging orangutans on the introduction of a multi-level climbing structure with numerous platforms for feeding and daytime resting. More time was spent at the higher levels than lower or ground levels, more in keeping with the natural arboreal behaviours of this species (Pizzuto et al. 2008). Similarly, in a naturalistic enclosure with high trees and vines, captive orangutan adolescents (n = 3) spent the majority of their observed time budget (62%) in the upper and lower canopy levels rather than the ground (Herbert & Bard 2000), sitting and resting on the elevated tree limbs. Six zoo-housed chimpanzees spent significantly longer periods of time at the top tier of their exhibit, despite the fact that this area made up less than 20% of the total exhibit (Ross & Lukas 2006). Gorillas in the same study (n = 14) utilised the lower tiers of the exhibit more frequently than the chimpanzees. These results are in keeping with the natural behaviours of these species – chimpanzees can spend as much as 68% of their time in trees (Doran & Hunt 1994), while gorillas are the least arboreal species of great ape (Mehlman & Doran 2002), possibly as their large body size precludes predation (e.g., Yamagiwa 2001).

As with physical enrichment such as climbing structures and platforms, the provision of substrate and nesting materials has been shown to alleviate abnormal behaviours and promote species-typical behaviours in a variety of primate species. The introduction of deep litter (straw and wood wool) was associated with an increase in active and affiliative behaviours in a small group of zoo housed Wolf's guenons (*Cercopithecus wolfi*, n = 4) (Fuller et al. 2009). Introducing wood wool and peat as floor coverings also resulted in positive behavioural changes in captive capuchins (n = 10) more in keeping with free-ranging behavioural profiles (Ludes & Anderson 1996). Woodchip "bedding" decreased abnormal behaviours and increased play and manipulatory behaviours in 16 juvenile laboratory chimpanzees (Brent 1992). The provision of straw coupled with forage material was associated with increased exploration, manipulation, play and tool use in adult laboratory chimpanzees (n = 13) (Baker 1997), again changing behaviour toward more species-typical activity budgets.

Based on this evidence, it appears that the provision of substrates and structures can enhance the variety of behavioural opportunities available to laboratory and zoo-housed primates. This may conceivably reduce stress and frustration, increase species-typical behaviours, reduce aberrant behaviours, and so improve welfare. However, it is notable that the previously cited research has emphasised the effects of this type of environmental enrichment on daytime behaviours and activities. It is widely recognised that most wild-living monkey and ape species sleep arboreally (see chapter 1), yet there are few reports on the structures and substrates that support the expression of species-specific nighttime behaviours.

Nighttime research on two groups of common marmosets (total n = 10) involved introducing new sleeping (nest) boxes in elevated locations in the home cage. One group showed a strong preference for a specific box – even after it had been reduced in size, thus indicating that this was a preferred sleeping area. However, on moving the non-preferred box to a more elevated position, the same marmoset group ceased to use their previously preferred box, and switched their preference to the higher nest box. This was also broadly true when the position of the boxes were reversed (Hosey et al. 1999). Thus it appears that, although subject to inter-group variation, more elevated sleeping locations were preferred – in keeping with arboreal sleep site selection in free-ranging populations. The provision of elevated structures, substrates and materials is also important for a behaviour which is not subject to much empirical investigation, namely, the nest building behaviour of great apes (Anderson 1998; Fruth & Hohmann 1996).

Nest building forms an integral part of the behavioural repertoire of all wild populations of great apes (Fruth & Hohmann 1996), and has been described as "…the most solid of norms" (McGrew 2004 p107) in their daily activity budgets. Although variations exist between *and* within ape populations, generally bonobos, chimpanzees and orangutans construct arboreal nests, while gorillas more frequently construct ground nests (Fruth & Hohmann 1994). However, despite their emphasis on replicating biologically relevant behaviours and environments, one of the problems facing zoos is that access to data on the behaviours of free-living species may be restricted (e.g., Hill & Broom 2009). The following example is used to illustrate. As part of a zoo-based enrichment study, a silverback gorilla with no prior experience of nesting material was given wood wool substrate. The material was immediately used to construct a day nest in which the gorilla subsequently rested.

Unaware that resting in a day nest is a behaviour performed in wild-living apes, zoo-staff removed the material, fearing that the increased frequency in daytime resting was a result of illness (Hill 2004 cited in Hill & Broom 2009). The lack of information on wild ape's nighttime behavioural patterns in comparison to daytime activities (see preceding chapter) may be a contributing factor in the limited amount of data available for corresponding behaviours in captive-housed apes.

Of the few published studies, it is clear that the motivation to build night nests persists in captivity. One of the first studies on nest building behaviours in laboratory-housed chimpanzees showed that the majority of individuals (15/25: 60%) attempted to construct night nests, using a variety of materials and techniques (Bernstein 1962). Further, the introduction of the nesting materials elicited manipulatory and play behaviours in these adult chimpanzees. Bernstein's succeeding research (1969) included observations of gorillas and orangutans as well as chimpanzees. Again, apes as young as 2.5 years built nests or resting platforms; adult orangutans regularly produced "good to excellent nests" when provided with adequate nesting materials. Juveniles of all species also used nesting materials in play. Of six adolescent laboratory-housed chimpanzees, only two were observed to construct night nests when given nesting materials, although it was noted that all individuals climbed onto an elevated (3 meters from ground) platform to sleep (Riss & Goodall 1976).

Although there appears to be no literature specifically on the nesting behaviour of zoo-housed chimpanzees or orangutans, such data are available for bonobos and gorillas. Over a total period of five months, 6 juvenile and adult bonobos consistently constructed night nests to rest and sleep, using a variety of materials presented to them under experimental conditions (although unfortunately no specific details are given) (Berle et al. 1995). Lukas et al. (2003) reported that zoo-housed gorillas (n =17) utilised both terrestrial levels and elevated structures for nest building; the latter were used more than would be expected by chance. Observations of this population also indicated that certain nesting materials might be preferred over others. Browse, for example, was never used in nest construction. Weiche and Anderson’s (2007) subsequent research on zoo-housed gorillas also indicated preferences for particular nesting sites.

Study aims

Current zoo legislation and normal practice within zoos dictate that the performance of species-typical behaviours should be promoted as a means of ensuring good standards of welfare for captive animals. Structural enrichment and bedding materials have been used to facilitate species-typical daytime behaviours in a number of laboratory and zoo-housed primates. Details, however, on the structures and materials that facilitate natural nest building behaviours in captive apes are lacking, although there is some evidence that some nesting areas, structures and materials are preferred over others.

As a first step towards documenting sleeping areas, sleeping structures and nesting substrates that are made available to captive ape populations, a nationwide survey was undertaken. These data provide information on the structures and materials that facilitate the species-typical behaviour of nest construction, and can be used to generate recommendations for enclosure design and husbandry practices, and guide directions for further research.

2.2 Methods and analyses

Following ethical approval from the University of Stirling, and endorsement from The British and Irish Association of Zoos and Aquariums (BIAZA), a brief questionnaire (Appendix 1) was developed and modified after recommendations from BIAZA and following comments from the primate care staff at the zoo where the questionnaire was piloted.

The questionnaire, along with a letter of support for the research provided by BIAZA, was electronically distributed to 26 zoos and wild animal parks across the United Kingdom and Ireland that were known to house chimpanzees, gorillas and orangutans[4]. The questionnaire consisted of four broad sections and contained both open and closed questions. The first section sought background information, such as details of environmental enrichment programmes and any research into nesting behaviours of the great apes. Sections 2 and 3 requested information on the sleeping quarters and nesting materials provided, respectively. The final section requested any additional information primate care staff wished to offer. In order to ascertain total number of individual apes, birth status and age/sex classes for each captive population, a taxon report for all apes currently housed at each zoo/park was also requested. Descriptive statistics only are used to display results.

2.3 Results

Background information

Primate care giving staff completed and returned 23 questionnaires and taxon reports (response rate: 88 %) from 16 zoos and wildlife parks in England, Ireland and Wales.

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[4] Bonobos were excluded from the survey, as at time of writing only one zoo in the UK is known to house this species.

These reported information on several chimpanzee, gorilla and orangutan populations. Five of these facilities housed only chimpanzees, with four housing only gorillas. Two zoos/parks held both chimpanzees and gorillas in their collections. No zoos or parks held only orangutans. However, two facilities held both chimpanzees and orangutans, and a further three housed both gorillas and orangutans.

There were 9 captive groups of chimpanzees in the survey, totalling 99 individuals. The majority of chimpanzees were adult females (55/99 – 56%), with adult males (29/99) and juveniles (14/99) accounting for 29% and 14% of the total number of individual chimpanzees, respectively. Only 1 infant (1% of total) was reported (see table 2.1 for details of all apes). Similarly, there were 9 captive groups of gorillas in the survey (total: 105 individuals), mainly juveniles (45/105 – 43%) and adult females (35/105 – 33%). Adult males (17/105) and infants (8/105) accounted for 16% and 8% of total gorillas surveyed, respectively. There were 5 captive groups of orangutans in the survey, totalling 16 individuals. The majority of orangutans were adult females (8/16 – 50%), with 4 adult males and 4 juveniles accounting for 25% of the total number of individual orangutans, respectively.

The majority of all the apes currently held in these collections were born in captivity (table 2.2), as detailed in the taxon reports for each species.

Table 2.1 Total number of apes per facility, plus breakdown of age/sex classes per facility and across all facilities

Species/Facility	**Age/sex class**				**No. apes per facility**
Chimpanzee	**Adult male**	**Adult female**	**Juvenile**	**Infant**	
1	1	1	0	0	**2**
2	2	4	0	0	**6**
3	5	16	7	0	**28**
4	2	3	3	0	**8**
5	0	7	0	0	**7**
6	0	2	0	0	**2**
7	11	16	0	1	**28**
8	5	4	3	0	**12**
9	3	2	1	0	**6**
Age/sex distribution across facilities	**29**	**55**	**14**	**1**	
Orangutan					
1	0	1	3	0	**4**
2	1	0	0	0	**1**
3	0	2	1	0	**3**
4	2	2	0	0	**4**
5	1	3	0	0	**4**
Age/sex distribution across facilities	**4**	**8**	**4**	**0**	
Gorilla					
1	4	3	0	0	**7**
2	0	2	1	0	**3**
3	1	2	2	1	**6**
4	1	1	4	0	**6**
5	2	17	25	5	**49**
6	0	2	1	0	**3**
7	1	0	4	0	**5**
8	8	5	7	2	**22**
9	0	3	1	0	**4**
Age/sex distribution across facilities	**17**	**35**	**45**	**8**	

Table 2.2 Birth status across all individuals in each species (plus percentage of total individuals in each species)

Species	Captive born	Wild born	Unknown
Chimpanzee	86 (87%)	10 (10%)	3 (3%)
Gorilla	93 (89%)	12 (11%)	0
Orangutan	15 (94%)	1 (6%)	0

Section 1 – Occurrence of nesting studies and environmental enrichment programmes

Of the 23 returned questionnaires, only one reported research into the nesting behaviours of captive apes. In this instance, a member of staff had recorded that chimpanzees showed a preference for a specific nesting material (hay) over another (straw), and also appeared to manipulate this material more successfully in nest building. No information was provided on the duration of the study or the methods used. There were no reports of students or researchers undertaking any research into nesting behaviours.

All facilities reported that a daytime environmental enrichment programme was currently being applied. Some failed to provide specific details of the programme (see Table 2.3); however, the most prevalent type of enrichment was feeding enrichment, including daily scatter feeds, puzzle boards and puzzle feeders. Indeed, 88% of all zoos and wildlife parks that responded used this type of enrichment. A similar number of zoos and parks (81% of total) reported the use of physical and structural enrichment techniques, including clothes, ropes, cardboard boxes and balls.

Table 2.3 Number of zoos and wildlife parks using feeding and physical/structural environmental enrichment for apes

Feeding enrichment	No specific description	Physical/ structural enrichment	No specific description
14	2	13	3

Section 2 – Sleeping quarters

Fifty-seven percent of captive ape populations (13/23) in this survey have no access to outdoor areas at night, and so use indoor quarters for sleeping. A total of seven populations (30% of total populations surveyed) have some access to outdoor sleeping areas at night, most frequently during summer months. Two respondents (9% of total) stated that it was unknown if apes slept overnight in their outdoor enclosures, as staff were not present during this time. One facility reported that, at the time of research, apes had only very recently been introduced into a new outdoor enclosure, and so it was unlikely that it had been used for overnight sleeping.

When in indoor sleeping quarters, 16 out of the 23 populations were reported as being housed communally (see figure 2.1 for percentage of total populations). Three institutions stated that males slept separately from the rest of the group, in their own sleeping areas. Two facilities reported that older individuals (aged 30 years and above) slept separately from younger adults and juveniles (age range 6 to 17 years). One zoo reported that all individuals used separate sleeping quarters, with another submitting a non-applicable answer as only one ape was in the collection.

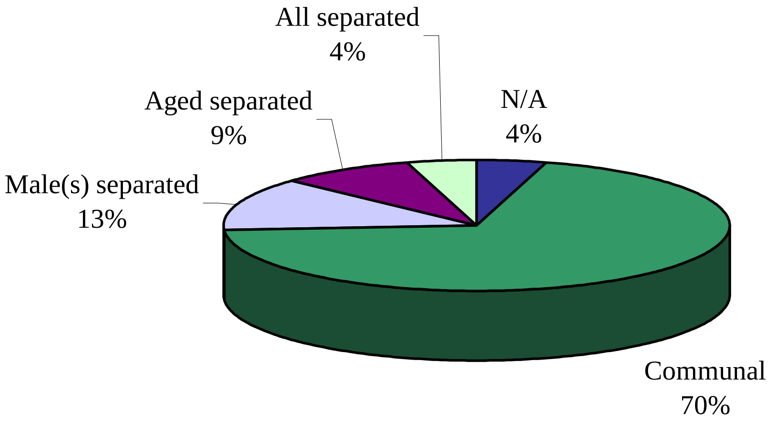


Figure 2.1 Percentage of total populations surveyed housed communally or separated according to age/sex class.

The number of potential sleeping structures (such as sleeping platforms, sleeping pods and combinations of sleep sites) available to the apes ranged from 1 per facility to 19. Several reports gave no exact number of sleeping structures, and so the mean number of sleep sites per zoo/ park (7.8) must be considered approximate.

Zoos and wildlife parks typically offered a combination of structures on which apes might construct their night nests; sixteen of the populations (70%) had a variety of structures on which they could nest build and sleep. For example, sleeping berths/platforms were available with a combination of nets, hammocks, tunnels or nesting baskets. Sleeping pods plus nets were available for one population. Several zoos/parks also provided platforms, sleeping pods and tunnels, nets or logs. Seven (30%) provided sleeping berths/platforms only.

Although several potential sleeping structures were available to them, several populations were reported to sleep on the floor of their indoor night quarters. Table 2.4 shows that for over half of the populations surveyed, at least one individual in the group constructed ground nests for sleeping.

Table 2.4 Number (and percentage) of ape populations reported to have nested at different levels

Species	Built ground nests	Built elevated nests	Reported as unknown
Chimpanzee	6 (67%)	2 (22%)	1 (11%)
Gorilla	7 (78%)	2 (22%)	0
Orangutan	4 (80%)	1 (20%)	0

Several respondents gave no indication of the frequency of ground nesting according to age/sex class. Of the nine chimpanzee populations surveyed, three respondents failed to report any age/sex distinctions (see table 2.5). This was also the case for the nine gorilla populations surveyed. For the five orangutan populations, only one respondent did not indicate age/sex class distinctions.

From the total of six respondents for chimpanzee groups, three facilities reported that most ground nests were constructed by adult females; there were no reports of adult males building ground nests more frequently than any other age/sex class. The six facilities that did report an age/sex distinction for gorillas stated that adult males constructed ground nests more frequently than any other age/sex class. This was also true for the four reported orangutan populations. In conjunction with a between-population disparity in ground nest building (table 2.4), these data may also indicate possible age and sex differences for each species.

Table 2.5 Number of reports of ground nest construction across age/sex classes

Species	Predominantly male	Predominantly female	Predominantly juvenile	No age/sex distinction	No response
Chimpanzee	0	3	2	1	3
Gorilla	4	2	0	0	3
Orangutan	3	1	0	0	1

Section 3 – Provision of nesting materials

All respondents reported that nesting materials were provided for great apes. Some provided only one type of material (figure 2.2); most provided a combination of several types of material, for example straw combined with browse, shredded paper, cardboard boxes or sheets. Wood wool could be combined with browse, bark, shredded paper, hessian sacks or sheets. One population of gorillas also received vegetation (plants, grasses, shrubs, clover) as potential nesting material, used in conjunction with wood wool. Some zoos/parks also regularly provided materials including hay, paper sacks, newspaper and items of clothing.

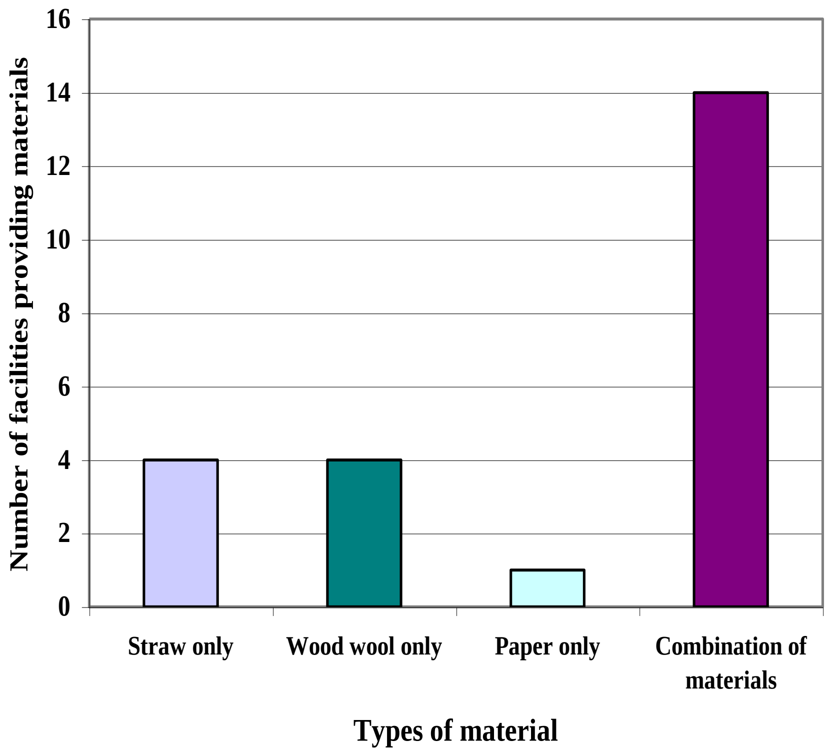


Figure 2.2 Types of nesting material provided, and number of zoos/parks providing these materials

Although all returned questionnaires showed that a wide variety of nesting materials was offered to apes, these materials were not changed/rotated on a regular basis (for example providing straw for one week, wood wool for one week). Table 2.6 shows that most zoos and wildlife parks across the UK and Ireland use only specific types of nesting materials.

Table 2.6 Number (and percentage) of zoos/ wild life parks reporting regular rotation of nesting materials

No. facilities that rotated materials	No. facilities that did not rotate materials	No. facilities used materials as/when available
0	22 (97%)	1 (3%)

Six facilities gave specific reasons for not providing specific materials. Two cited health reasons (dusty materials dried out skin, some apes ate the nesting materials). Three zoos/parks cited hygiene as a concern (materials that generated dust were not used). One zoo regularly provided a specific material (hay) as apes had shown a preference for this material when constructing nests.

Section 4 – Request for additional information

A total of ten questionnaires were returned with additional information. Two gave further information on husbandry practices, such as details on cleaning regimes. Two other responses detailed the social structure of a chimpanzee and orangutan groups – providing information on familial relationships and dominance hierarchies.

Six responses focused specifically on aspects of nesting behaviours across taxa. For one chimpanzee and one gorilla population, the presence of kin was reported to affect sleep site selection. For chimpanzees, mother-infant pairs were observed to share nests, with mother-juvenile pairs building nests in close proximity to one another. Nests of grandmother, mother and offspring were also arranged together in close proximity. Sub-adult gorillas were reported to continue to nest build in close proximity to their mother.

Two zoos/parks reported that individual chimpanzees showed preferences for specific sleeping areas that they would habitually return to each night, despite availability of several other potential nesting sites. Similarly, a preference for a particular sleep site was reported in two gorilla populations. Environmental temperature also affected sleep site selection. Social factors such as dominance rank also appeared to affect choice of sleep site for these gorilla populations, with high-ranking individuals reportedly occupying favoured nesting sites and also usurping nests constructed by lower-ranking group members.

Disruptions to the social structure also changed the nesting and sleeping habits in a small chimpanzee group. Following the death of the adult male, it was reported that the two remaining adult females changed their habitual sleeping sites. Having previously slept on opposing sides of the structure, after the male's death they slept together in close proximity on the same platform, before returning to their respective favoured sleeping sites after approximately one week.

2.4 Discussion

Zoos (e.g. Secretary of State's Standards of Modern Zoo Practice 2004), laboratories (e.g. Animal [Scientific Procedures] Act 1986) and farms (Farm Animal Welfare Council 1992) place a high level of importance on providing captive animals with opportunities to express species-typical behaviours that are common to their free-ranging counterparts. Although this importance is also reflected in legislation governing the housing of captive animals, to date there has been more emphasis on the effects of environmental enrichment on the daytime activities of captive primates.

Recent surveys of laboratory-housed primates in the United States (facilities surveyed = 22; Baker et al. 2007) and a variety of zoo-housed mammals worldwide (facilities surveyed = 60; Hoy et al. 2010) demonstrated that feeding and manipulable/tactile objects (e.g. balls, cardboard, toys) are the most frequently employed enrichment interventions. The laboratory-based data revealed that *all* participating facilities provided primates with these specific enrichments, with 73% providing primates with structural enrichments, and 50% of facilities providing bedding materials (Baker et al. 2007). The zoo-based data (Hoy et al. 2010) showed that approximately 88% and 70% of facilities rated feeding and tactile enrichment, respectively, as ‘very important’. Despite 67% of total zoos describing structural enrichment (natural/artificial structures and ground coverings) as ‘very important’, almost 30% of these same zoos failed to implement enrichment of this type.

The zoos and parks surveyed here also incorporated feeding and manipulable objects for daytime enrichment. However, contrary to the research cited above, the majority of respondents to this questionnaire reported that great apes were provided a wide variety of structures and materials that were incorporated into nest building activities. It therefore appears that, at least in the areas surveyed, efforts were made to promote natural nesting behaviours. However, despite regular provision of structural and substrate enrichment, of the 23 questionnaires returned, only one referred to any research (an observational study on the nesting behaviours of one chimpanzee group), reflecting a general lack of data specifically focusing on nesting behaviours of apes (see Anderson 1998; Fruth & Hohmann 1996). No details were given about the duration of the study or the exact methods used to collect data. Given that apes may spend up to half of their lifetimes in nests (Fruth & Hohmann 1994), it is surprising that so few studies are conducted in this area, especially as the provision of nesting structures, substrates and materials has been shown to encourage species-typical, natural behaviour (e.g., Berle et al. 1995; Bernstein 1962, 1969; Hill 2004; Lukas et al. 2003; Videan 2006a).

It is interesting that the majority (over 80% for each species surveyed) of apes across the United Kingdom and Ireland were captive-born, yet they construct night nests. Laboratory-based research by both Bernstein (1962, 1969) and Videan (2006a) indicated that wild-born chimpanzees more frequently utilised nesting material, and generally built ‘better’ nests, than their captive-born counterparts. Although there is no means of knowing if the captive apes in this survey constructed ‘good’ or ‘crude’ nests (as measured by Bernstein 1962), the fact that even apes born and raised in captivity are motivated to build a nest highlights the importance of providing suitable areas and materials to express this species-typical behaviour.

The majority (70% of total surveyed) of apes in the British Isles sleep communally in night quarters. Only five of the returned questionnaires reported separation of individuals based on age and gender. In the wild, bonobos, chimpanzees and gorillas (Fruth & Hohmann 1996) are known to form sleeping groups, with bonobos congregating to form large *en masse* sleeping parties, gorillas remaining in their daytime groups, and chimpanzees splitting into smaller sleeping parties (Fruth & Hohmann 1996), thus reflecting the social nature of spatial arrangements at sleeping sites. Free-ranging chimpanzees often build night nests in one single tree or closely adjoining trees, and there have been instances of individuals abandoning completed nests to move closer to other group members (Goodall 1968). These species-typical grouping patterns should be taken into consideration in the design of sleeping quarters by providing communal sleeping areas that are large enough to accommodate sleeping parties, as seems to be the case in the majority of the zoos and wildlife parks surveyed here.

Several respondents provided additional information indicating that kin relations choose to nest in close proximity. Gorilla mother-infant and mother-juvenile dyads were reported to nest in close proximity, with one regular chimpanzee nesting party comprising of three generations of females (grand-mother, daughter and offspring). Comparable findings have been documented in wild apes: gorillas nest in closer proximity to those that they are closely affiliated with (Hess 1992 cited in Weiche & Anderson 2007), and two rehabilitant (but free-living) adolescent orangutans were observed sleeping together in one nest (Rayadin & Saitoh 2009). At Gombe, two adult male chimpanzees, believed to be siblings, reportedly built and shared a night nest, sleeping in close physical contact throughout the night (cited in Riss & Goodall 1976). Previous research in captive settings has shown that chimpanzees (e.g., Riss & Goodall 1976; Videan 2006b) and gorillas (e.g. Weiche & Anderson 2007) sleep with kin and other closely affiliated individuals. Again, this demonstrates the importance of providing enough space within sleeping quarters so that individual apes can form sleeping parties with kin or other closely bonded individuals.

Vertical structures, perches and platforms not only promote arboreal behaviours; they can also facilitate conflict-avoidance; allowing subordinates to flee more easily from dominant group members (Honess & Marin 2006b), and add complexity into the captive environment (Lukas et al. 2003). Although measures of structure and space use in the captive environment can be valuable in the study of species-specific arboreal/terrestrial requirements and preferences (Ross et al. 2009), most research has focused on the use of structures for daytime activities (e.g. chimpanzees daytime use of upper levels of their exhibit versus gorillas preference for lower levels: Ross & Lukas 2006).

The results of the survey indicated that captive apes are typically provided with a variety of elevated structures on which to rest and sleep (70% of total zoos surveyed), and so do provide the opportunity to perform species-typical arboreal nesting behaviours. What is of interest is that, despite the availability of elevated nesting platforms, baskets etc.; ground nesting is quite frequent in these chimpanzee and orangutan populations. This may have been expected of gorillas, the least arboreal of the apes (particularly mountain gorillas: Mehlman & Doran 2002), but it is generally accepted that chimpanzees and orangutans are arboreal nest builders (Fruth & Hohmann 1994), with a few exceptions (Koops et al. 2007).

The absence of any predation risk within captive settings may have contributed to this high frequency of ground nesting, as this has been hypothesised to facilitate ground nesting in free-ranging chimpanzees (Maughan & Stanford 2001). Alternatively, ground nesting may be linked to comfort; this factor was recently suggested to be important in the structure and composition of night nests (Stewart et al. 2007). It is conceivable that floor substrates may be softer and more comfortable to sleep on, compared to wooden or metal nesting platforms or baskets.

A common view is that environmental enrichment techniques should be implemented in accordance with each species natural history (Mellen & MacPhee 2001; Young 2003). The current data do not dispute this; several populations of chimpanzees and orangutans did build elevated nests, in keeping with their typically arboreal nesting habits. However, the present data also demonstrate that, at least for the populations surveyed here, there can be deviations from some aspects of species-typical nesting behaviour in otherwise normal individuals. Similarly, Lukas et al. (2003) reported that zoo-housed gorillas (n =17) utilised elevated structures more than would be expected by chance. Accordingly, sleeping quarters should provide, not only elevated sleeping structures, but also suitable floor coverings on which nests can be built.

Although several respondents failed to indicate the prevalence of ground nest construction, there is some indication of a sex differences in this form of nest building; female chimpanzees were reported to construct the majority of ground nests in three captive populations. Again, this finding contradicts observations of free-ranging chimpanzees, where males typically nest at lower levels than females (Brownlow et al. 2001; Koops et al. 2007). In contrast to the chimpanzee data, gorilla and orangutan adult males most frequently constructed ground nests in six and four populations, respectively. This is in keeping with observations of wild gorillas and orangutans; females generally nest at more elevated heights (Fruth & Hohmann 1996). Zoo-housed bonobo females also constructed higher nests compared to males (Berle et al. 1995). Future studies could more thoroughly research these possible age and sex disparities in ground nest construction.

The questionnaires revealed that captive apes were regularly presented with a combination of several potential nesting materials, including browse, hessian sack, wood wool, sheets and straw. A few populations were provided with only one type of nesting material, reportedly for health and hygiene reasons. One zoo provided plant and shrub materials to gorillas, to simulate the herbaceous raw materials used in nest construction by free-ranging gorillas (Sanz et al. 2007). Bedding and substrate materials can successfully serve as ‘functional substitutions’ (Robinson 1998) for natural nesting materials, and are a simple and cost-effective means of facilitating natural behaviours. This form of enrichment has been deemed effective for laboratory-housed monkeys (e.g. capuchins: Ludes & Anderson 1996) and apes (e.g., chimpanzees: Baker 1997; Brent 1992). It should be noted, however, that previous studies, although scant, have indicated that certain materials are preferred over others for nest construction. Bernstein's (1962) chimpanzees more frequently made nests from a combination of burlap and pine needles than combinations of cardboard, newspaper and hose, or palm leaves, rope and chain. In a more recent study, hay elicited higher rates of nest building compared with butcher paper or browse (Videan 2006a). Zoo-housed gorillas used only hay in nest construction (Lukas et al. 2003), even when browse was seasonally available to them. By presenting or rotating different material sets, we can gain further knowledge about what materials are preferred by captive apes at group and individual levels.

When asked for additional information, respondents provided details that are of interest for future study and that, like providing communal areas, elevated structures and floor substrates, should be considered in the design of sleeping areas. Several groups of chimpanzees and gorillas, for example, showed preferences for specific sleeping areas within their enclosures, even if several alternatives were available. Apes typically spend a significant proportion of their lifespan within nests, so it seems reasonable to conclude that sites are decided upon with some degree of deliberation. Wild-living bonobos and chimpanzees have preferred localised nesting areas, even down to specific types and species of trees, and can re-use these sleep sites over several generations (Fruth & Hohmann 1994; van-Lawick Goodall 1986). Similarly, zoo-housed gorillas used specific rooms for sleeping significantly more than others (Weiche & Anderson 2007).

One returned questionnaire stated that a dominant male gorilla usurped nests constructed by other group members; nest usurping has also been documented in free-ranging chimpanzees (van Lawick-Goodall 1971). Social rank is known to influence the sleeping arrangements of wild living monkeys (e.g., macaque spp.: Estrada & Estrada 1976, Vessey 1973), and the choice of sleep site and sleeping arrangements in free-ranging gorillas (Schaller 1963; Yamagiwa 2001). In general, though, little is known about how dominance structure influences captive ape sleeping arrangements; the topic warrants further investigation.

One respondent described how a significant change in a chimpanzee group's social structure affected their nesting behaviours. In this instance, adults who had previously nested separately slept in very close proximity following the death of a companion. This continued for approximately one week, then the chimpanzees eventually resumed nesting in their previously preferred areas. Similarly, an early anecdotal account described how a zoo-housed male chimpanzee (age not given) changed sleeping site after the death of his long-term cage mate (Brown 1897). Observing group responses to the death of another captive ape is, of course, uncommon; however, such reports suggest that, as well as the presence of kin and closely affiliated individuals and the effects of dominance rank, major changes in social structure can influence the nesting and sleeping behaviour of apes.

Conclusions and recommendations

The questionnaire data shows that, as stated by Bernstein (1962), captive apes will construct nests in captivity – if provided the opportunity. The zoos and wildlife parks that responded to the questionnaire regularly provided sleeping structures and nesting materials to their great apes that facilitate the species-typical behaviour of nest construction. Under current legislation, and in keeping with the natural behaviour approach to assessing animal welfare, this expression of natural behaviour should be incorporated into maintaining good standards of ape welfare. Based on the current findings, several preliminary recommendations can be made, in terms of both enclosure design and directions of future research:

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.

Information provided by primate care staff suggested that social factors such as the presence of kin, and significant disruptions to social structure (death of a group member) can affect nesting behaviour. Given the paucity of data on these aspects of nest-related activities, further research is needed before firm conclusions can be drawn. Further analysis of preferred nesting materials, preferred sleeping areas and sleeping partners will not only add to our understanding of captive ape nesting behaviour, but may also have practical implications for enclosure design and husbandry practices, and so merit further investigation.

Chapter 3

Direct observations of nest-related activities

"O bed! O bed! Delicious bed! That heaven upon earth to the weary head".
~Thomas Hood

3.1 Introduction

As previously discussed (chapter 2), one of the aims of the zoological community is to promote appropriate behavioural repertoires in captive animals, by providing social conditions and physical environments that recreate aspects of those of wild conspecifics (Hill & Broom 2009). It is argued by some (e.g. Makowitz 1997) that the performance of these species-typical behaviours is essential in establishing the best quality of life, i.e., welfare, for each animal.

In the wild, all great apes of weaning age and beyond build a fresh nest in which to rest and sleep each night (Fruth & Hohmann 1994; Goodall 1962, 1968). As well as a comfortable sleeping area, the nest may provide some protection against predation and harsh climatic conditions (discussed in chapter 1). These nests, as with the night nests of bonobos and orangutans, (Fruth & Hohmann 1993; MacKinnon 1974) are generally constructed arboreally, at heights ranging from 3-11meters (Equatorial Guinea: Groves & Sabater-Pi 1985), 4-24m (Senegal: Baldwin et al. 1981), and even up to 46m (Uganda: Stanford & O'Malley 2008). Goodall (1968) stated that Gombe chimpanzees rarely nested on the ground. More recently, Hernandez-Aguilar (2009) reported that 5354 chimpanzee nests in Ugalla (W. Tanzania) were exclusively arboreal.

At several sites across western Africa (e.g., Guinea, Cote d'Ivoire), however, there are recorded instances of ground nesting in free-ranging groups of chimpanzees.

Matsuzawa and Yamakoshi (1996) reported that 35% (of a total of 464) night nests were constructed terrestrially. A later study by Koops et al. (2007) in a neighbouring region, in contrast, reported that ground nesting was much less frequent, with only 32 night nests (3.4% of a total nest count of 994) being built on the ground. Similarly, Pruetz et al. (2008) documented that only 3% of 1665 nests at Fongoli (Senegal) were constructed on the ground. Furuichi and Hashimoto’s (2000) examination of abandoned nests within 3 nesting groups also indicated a relatively low frequency of ground nesting in the Kalinzu Forest (Uganda). Of nests groups of 3,7, and 7, only 1,2 and 1 of these, respectively, were ground nests. These instances of terrestrial nesting are mainly attributed to lack of predation pressure (e.g. Furuichi & Hashimoto 2000; Maughan & Stanford 2001).

As a general rule, apes construct nests before the onset of darkness. MacKinnon (1974) noted that orangutan nests were built thirty minutes prior to sundown, and Fruth and Hohmann (1993) describe how bonobos construct nests ‘late in the afternoon’ - presumably before sunset as researchers were still in the vicinity. Gorillas in the Rio Muni region were observed to begin nest construction at dusk, with times of retirement ranging from 17.26-18.34hrs (Groves & Sabater-Pi 1985). For free-ranging chimpanzees, nests are also typically constructed at, or prior to, dusk. Nissen (1931) reported that Western French Guinea chimpanzees generally began nest construction at dusk (evidenced from the sound, rather than direct observations, of tree branches being broken). One individual was observed constructing a nest one hour after sundown during the dry season, at 18.00hr. Goodall’s later observations (1962) on the chimpanzees at Gombe showed that during the dry season, nests generally were built between 18.45 and 19.15hrs. During the rainy season (December – May), nesting usually began before the onset of darkness, approximately one and a half before sundown, indicating a seasonal variation in retirement times, seemingly based on light conditions. Four chimpanzees that formed part of a reintroduction programme into the Conkouati-Douli National Park (Democratic Republic of Congo) constructed nests prior to dusk (mean retirement time 17.47h, with sundown between 18.05-18.36hrs) (Farmer 2002).

As well as seasonal variations in nesting patterns, there is some evidence of differences in nest construction across age/sex classes. Juvenile eastern lowland gorillas, for example, nest at higher levels than other age classes (Yamagiwa 2001), as do immature Bornean orangutans (Rayadin & Saitoh 2009). Fruth and Hohmann's (1993) observations of wild bonobos suggests a sex difference in both height of nests and retirement times, with females typically constructing nests at higher heights, and at earlier times, than males. Adult male Sumatran orangutans also nest at lower heights than females (Sugardjito 1983). Two separate studies on chimpanzee communities at Budongo (Uganda) (Brownlow et al. 2001; Plumptre & Reynolds 1997) also reported that female nests were constructed at higher heights than males. The former authors also found that females constructed day nests significantly more frequently than males, a finding also documented at Mahale (Tanzania) (Hiraiwa-Hasegawa 1989).

Wild Bornean orangutans may take up to approximately 6.5 minutes to construct their night nests (Davenport 1967 cited in Fruth & Hohmann 1996), although there are conflicting reports that Sumatran orangutan nest construction generally takes only between 2 and 3 minutes (MacKinnon 1971, 1974); bonobos can take anywhere between one and seven minutes to construct a nest (Fruth & Hohmann 1993). Early observations of lowland gorillas stated an average nest construction time of 5 minutes (Schaller 1961). Groves and Sabater-Pi's later reports (1985) on gorillas and chimpanzees at Rio Muni stated an average nest construction time of between one and five minutes for these ape species.

Similarly, direct observations of Gombe chimpanzees showed that nest construction generally lasted between one and five minutes (Goodall 1962, 1968), although some individuals in the community could take up to eight minutes to complete a nest (van-Lawick Goodall 1971). Although Nissen's (1931) report of nesting in chimpanzees mainly focused on used nests, direct observations of nest construction showed a duration of three minutes – although one individual was timed as taking over 25 minutes to complete a nest, due to interference by frequent social 'visits' to other group members in the same sleeping tree, and also by feeding.

There are recorded instances of seemingly completed chimpanzee nests being abandoned – either spontaneously (i.e. voluntarily), or through being usurped by another individual, although these are limited to anecdotal accounts of Gombe communities (Goodall 1962, 1968; van Lawick-Goodall 1971). The abandonment of seemingly completed nests was attributed to faulty construction (unable to bear the weight of a female plus her infant), insufficient materials to complete the nest, and unstable nest location. A juvenile female was also observed to abandon a nest to move closer to other group members. Van Lawick-Goodall (1971) later described how a subordinate female abandoned a nest after the group's dominant male displayed 'violently' over her nest, effectively removing her from it and claiming it for himself. Schaller (1963) also noted that mountain gorillas abandoned a communal nesting site when another group approached their site.

Early observations of the Gombe chimpanzees (Goodall 1962) suggested that there is little activity once a nest has been completed, although the author does describe an adult female making amendments (gathering and arranging extra material into the existing nest) before lying down to sleep. Later reports of the same community, however, revealed that males left their sleeping sites to feed (e.g. Goodall 1968). A young female (similar to Nissen's 1931 description) was observed to leave her nest to 'visit' a male in the same sleeping tree, returning to her nest after being groomed by him (van-Lawick Goodall 1971). Similar post-retirement behaviours have been documented in other ape species. Orangutans have been observed to leave their completed nests to feed (MacKinnon 1974), also reported in free-living gorillas (Schaller 1963 cited in Fruth & Hohmann 1996). Groves and Sabater-Pi (1985) also report that gorillas continue to vocalise after nesting; they have also been documented to chest-beat until 20.00hrs.

Study aims

The welfare of captive animals is often linked to the extent to which their behaviours resemble those of wild conspecifics. Data from the preceding chapter have indicated that zoos and wildlife parks are aware of the importance of providing structural and tactile enrichment that promotes natural nesting patterns. However, the same data also emphasised the rarity of direct observations of nesting behaviours, despite their relevance for captive ape welfare. In view of this, the aim of the present study was to report multiple aspects of nest-related behaviours that were directly observed in two groups of captive chimpanzees, and use these for comparison to nest-related activities that have been documented in free-ranging populations. These can be used to influence design of appropriate sleeping areas and husbandry regimes, and so have welfare implications for captive apes.

Ethical approval

Research in this study, and all subsequent studies (chapters 4-9), were carried out in accordance with BIAZA (2000) zoo research guidelines and national laws. Ethical approval for all studies was granted from the University of Stirling, Blair Drummond Safari Park, and Edinburgh zoo, and all research procedures were in compliance with the ethical codes of these institutions.

3.2 Methods and analyses

Chimpanzees and housing

Blair Drummond (BD) Group

The first study group consisted of chimpanzees (*P.t. verus*) (n = 4) housed at Blair Drummond Safari and Adventure Park (Stirling). There were two mother-adult offspring dyads: Pansy (estimated age: late 50’s) and daughter Rosie (19 years), and Blossom (estimated to be in her 50’s) and son Chippy (19 years). Both Chippy and Rosie were born and mother-reared at the park. Records dating back to the introduction of Blossom and Pansy are incomplete (see appendix 2), but it is believed that both were wild-born.

From spring through autumn, the chimpanzees live on a water-surrounded island, only accessible to park staff by boat. During winter months (November through

February), they are housed in an indoor housing facility consisting of separate day (9m x 7.5m x 9m) and night enclosures (6m x 7.5m x 6m). The chimpanzees have no access to the night enclosure during the day, but are confined there at night. Median temperature of the night enclosure during these winter months was 19°C (IQR = 1, range = 16-20°C).

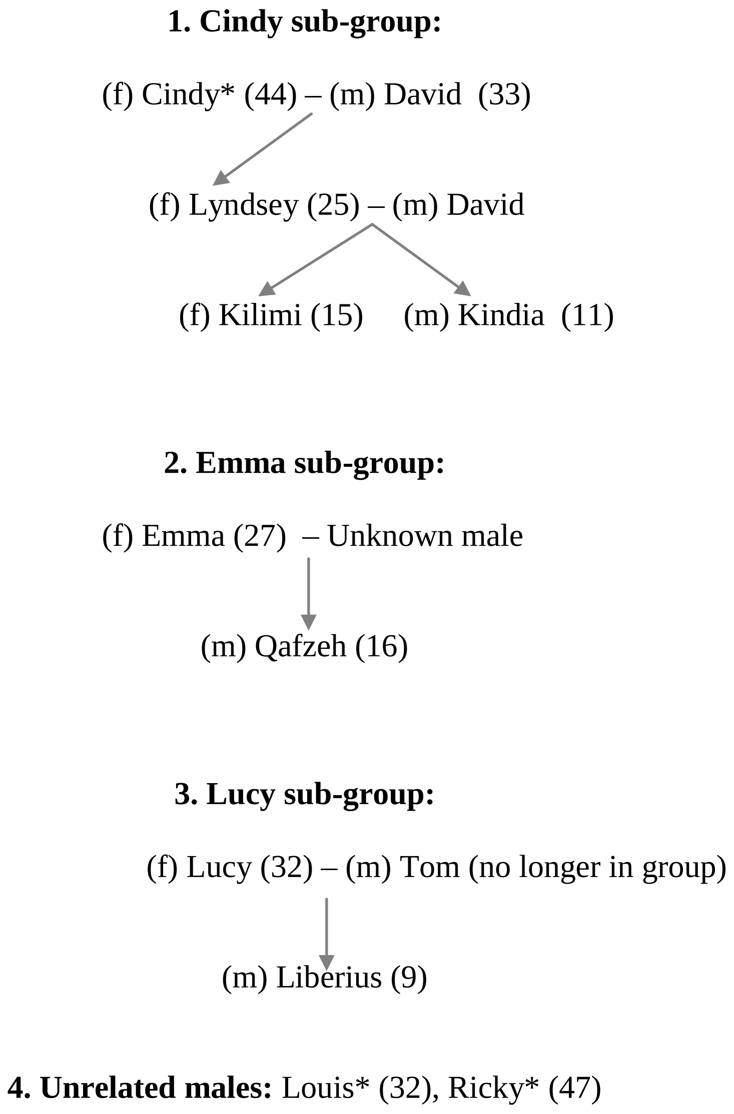
The night enclosure (plate 3.2) contains two elevated wooden platforms in two of the corners (2.16 m x 2.07 m, diagonal 3.02 m), situated approximately 2.8 meters above floor level; these are referred to as sleeping platform A and sleeping platform B. A third wooden platform (L) runs along the remaining wall, adjacent to a vertical wooden ramp (plate 3.3). This platform measures approximately $1.5m^2$, and is 1.5 meters above the floor. A series of four circular sleeping ‘pods’ of varying heights and depths stem from a central vertical pole in the middle of the enclosure (plate 3.2). These pods, consisting of a metal rim with an attached heavy duty canvas lattice “mattress”, were installed in the hope that the chimpanzees would sleep in them, but there is no evidence that they have ever done so (pers. comm. with chimpanzee care staff). The floor is covered with a mixture of wood-bark chips and wood-shavings, and is kept at constant temperature by an under floor heating system. A skylight in the ceiling (situated approximately above and between the sleeping platforms) allows natural light into the night enclosure, which also features artificial (electric) lighting directly above. Lighting is switched off as primate care staff leaves the indoor housing facility, at approximately 17.15hrs for the duration of this particular study.

Plate 3.2 (left to right): Sleeping platform B, central pods (in foreground), sleeping platform A.

Plate 3.3 (left to right): Wooden ramp, lower platform (L) on opposing wall to sleeping platforms A and B.

Edinburgh Zoo (EZ) Group

The second study group (n = 11) resided at RZSS Edinburgh Zoo in the relatively new, large and complex ‘Budongo Trail’ enclosure. Figure 3.1 depicts familial subgroups, gender, and age at time of research. Chimpanzees marked with * are wild-born, the remaining chimpanzees were captive-born.



1. Cindy sub-group:

(f) Cindy* (44) – (m) David (33)

(f) Lyndsey (25) – (m) David

(f) Kilimi (15) (m) Kindia (11)

2. Emma sub-group:

(f) Emma (27) – Unknown male

(m) Qafzeh (16)

3. Lucy sub-group:

(f) Lucy (32) – (m) Tom (no longer in group)

(m) Liberius (9)

4. Unrelated males: Louis* (32), Ricky* (47)

Figure 3.1 Family sub-groups, gender and age at time of research.

In contrast to the BD chimpanzees, the EZ group have access to four potential sleeping areas. The first area (7.5x2x2.5m approx.), is accessible only to staff and chimpanzees, and off-exhibit to the public. Above this area are the main 3 rooms that are always accessible to the chimpanzees and for public view. These rooms ('pods') are distinct but connected to each other and the off-exhibit area via connecting tunnels. During opening hours, the chimpanzees have access to all three pods, the outdoor enclosure and the off-exhibit (OE) area.

After zoo closure, access is restricted to the indoor area (OE area, pods and tunnels). Each pod measures approximately 12x12x14m, and all contain climbing apparatus. Attached to each climbing frame at varying heights are several elevated, rectangular nesting baskets, measuring approximately 123x90x15cm (at lowest depth). Pod 1 contains 5 baskets, plus a compost-covered flat floor. Pod 3, next to pod 1, contains 3 baskets, plus four ascending floor levels with medium/large bark chips as substrate (see plate 3.4). Pod 2, across from pod 3, contains 5 nesting baskets at various levels, plus 4 ascending floor levels covered with coir (crushed coconut husk). Median temperatures of each pod during these winter months was approximately 21°C (pod 1), 25°C (pod 2) and 23°C (pod 3 – see also chapter 6). As with BD, an under floor heating system is in operation throughout the pods, as is an artificial (electric) lighting sysytem. The lighting system at EZ is switched off as cleaning staff leaves the exhibit, at approximately 18.40hrs during winter months.

Plate 3.4 An example of the ascending floor levels, climbing structures and wire nest baskets (top right and middle foreground) in pod 3.

Data collection

Blair Drummond

Between December 2007 and January 2008, the nesting and post-nesting behaviours of these chimpanzees were recorded over 28 days from a vantage point at the top of the enclosure – affording a ‘birds-eye’ view of all areas and activity in the night enclosure. At 15.15hrs each day the chimpanzees were moved into the night enclosure, where caretakers had already distributed nesting substrate (straw) in each of the four vertical sleeping pods. Behavioural recording began 1 minute later, and lasted 105 minutes. Group scans were conducted every minute to record the activities and locations of each chimpanzee onto pre-prepared data sheets. Behaviours occurring while the chimpanzees were in their nests/sleeping sites were also recorded (see table 3.1).

Edinburgh Zoo

The EZ data used for this chapter formed part of separate study on daytime behaviours and sleep site selection (detailed in chapter 4). During these observations (December 2008 - January 2009) the nesting and post-nesting behaviours of all (observable) chimpanzees were also manually recorded onto pre-prepared check sheets for 29 days. For this group, group scan samples were conducted every five minutes, recording time and place (e.g., pod 1/pod 2) of retirement, specific sleeping sites (e.g., specific basket/floor level) for each chimpanzee. Activities performed subsequent to nest construction/retirement were also noted (table 3.1)[5]. As with BD

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[5] Across both groups, the techniques used in nest construction were also recorded, but are described elsewhere (see chapters 5 and 7).

chimpanzees, straw was also provided as a nesting substrate, although additional browse was available to the EZ group.

Table 3.1 Retirement and post-retirement behaviours observed across both groups

Behaviour	Description
Retirement	**For nest builders**: First indication of the onset of nest building (gathering of nesting materials) **For non-nest builders**: The adoption of a rest posture (lying on left/right side, or in a prone/supine position) on enclosure substrate/nest basket/platform
Nest building	Using available materials to arrange a recognisable circular/oval nest around the body that is subsequently used to rest in
Nest amendment	Manipulations to materials that have already formed an apparently completed nest
Nest usurping	The taking of another individuals nest or nest site, either when a nest has been briefly vacated (e.g. to gather extra material) (coded as ‘sneaky technique’), or by standing in close proximity to a nest until the original nest builder leaves the nest site (coded as ‘intimidation technique’)
Nest abandonment	The abandonment of an apparently completed nest that is not returned to.
Feed	Consumption of food items while sitting/in a rest posture whilst in the nest
Self-directed	Manipulation of own body, including autogrooming, picking at hair, foot-clasp, inspection of body parts
Social	Social interaction with another individual including touching, allogrooming
Substrate manipulation	Unrelated to constructing/amending nests. Nesting material (straw) is manually separated, run through the fingers, and/or lifted to the mouth

Data analyses

Kolmogorov-Smirnov tests were used to determine if data were normally distributed (Dytham 2003), and this test was used in all subsequent data analysis (chapters 4-8). Data for retirement times and sex-related differences in the frequency and duration of nest construction were not normally distributed. Therefore, medians and inter-quartile ranges (IQR) have been used in descriptive statistics, and the non-parametric Mann-Whitney U test was used in these analyses. Randomisation tests can be applied for small sample sizes (Plowman 2008), but are more appropriate for sample sizes of less than 5 (Seigel 1956); therefore the Mann-Whitney U test was applied.

Although Bonferroni correction can be applied to reduce type I statistical errors, it is also known to increase type II errors, and some authors argue that its use should be discouraged (e.g. Nakagawa 2004). Therefore this correction was not used in analysis. Rather, a more conservative alpha of 0.025 was set, and was used in all subsequent data analysis (chapters 4-8). All tests were two-tailed, and analysed in SPSS 17.0. With large discrepancies between groups and the low frequency of several activities (e.g. post-retirement social behaviours), group frequencies are used to describe data.

3.3 Results

Time of retirement

For the EZ chimpanzees (males Qafzeh and Louis; females Kilimi and Lucy) that retired to the off-exhibit area, retirement time was estimated as 5 minutes from the last observation of the chimpanzee – allowing time to gather nesting materials and construct a nest[6]. Across both groups, the median time of retirement was approximately between 16.00-16.30hrs (table 3.2), although times as early as 15.10h were recorded. Generally, the EZ chimpanzees retired later than the BD group.

Table 3.2 Median (plus IQR), minimum and maximum retirement times (hours and minutes) per group

Group	Median	IQR	Minimum	Maximum
BD (n = 4)	16.09	0.76	15.14hr	16.44hr
EZ (n = 11)	16.35	0.85	15.10hr	18.25hr

Time of retirement - sex differences

The median retirement time for all males (n = 7) was 16.30hrs (IQR = 0.85), and for all females (n = 8) was 16.28hrs (IQR = 0.38). Although females retired generally earlier than males, this difference just failed to reach significance (U = 17468.50; z = -2.16; p = 0.03).

Time of retirement in relation to sunset

During winter 2007-2008, when the BD chimpanzees were under observation, times of sunset ranged from 15.38-16.43hrs (www.orcadian.co.uk). The maximum time of retirement (table 3.2) of 16.44hrs for this group indicates that chimpanzees generally retired prior to, or at, dusk. Sunset times during winter 2008-2009, when the EZ chimpanzees were being observed, similarly ranged from 15.38-16.44hrs. In contrast to the BD group, there were instances of nest construction almost 2 hours after sunset.

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[6] Although nesting behaviours were not directly observed, staff confirmed the presence of nests in the off-exhibit area the following morning.

Frequency and duration of nest construction

During winter 2007-2008, the four BD chimpanzees constructed a total of 76 nests over a 28-day period (median number of nests per night = 4; IQR = 1; range per night = 0-4). On 5 days of observation at BD there was no evidence of nest construction before recording ceased. In the EZ group, only five individuals were observed to regularly construct nests (4 chimpanzees retired to the OE area, and 2 elderly chimpanzees failed to construct any nests). During this study (Winter 2008-2009), the EZ group constructed a total of 78 nests (median number of nests per night = 3; IQR = 2; range per night = 0-5). For the EZ group, there was one day when no nests had been constructed by the time recording ceased.

Across both groups, a combined total of 154 nest-building episodes were recorded. Nest construction generally took a median time of 1-2 minutes (table 3.3), although some individuals in each group could spend up to 5 minutes constructing a nest.

Table 3.3 Median times (minutes) taken to construct nests across groups

Group	Median	IQR	Minimum	Maximum
BD (n = 4)	2	2	1	5
EZ (n = 5)	1	1	1	5

Frequency and duration of nest construction – sex differences

Of the 154 nests constructed by both groups, the majority were constructed by females (98/154: 64%) (table 3.4). Males generally constructed fewer night nests; 36% (56/154) of total observed nests were constructed by males, although this difference failed to reach significance (U = 3.50; z = -1.61; p = 0.11). Duration of nest construction also varied between the sexes; with females typically taking longer to nest build (table 3.4), a difference that was significant (U = 1826.50; z = -3.66; p = 0.01).

Table 3.4 Total number of nests constructed and median duration of nest construction (in minutes) according to sex

Sex	Total number nests built	Median duration of nest building	IQR
Male (n = 4)	56	1	1
Female (n = 5)	98	2	2

Location of nests

For the BD group, all individuals exclusively (100% of total nests constructed) nested on the elevated wooden platforms within their night enclosure (depicted on colour plates 3.2 and 3.3). In contrast, the majority of nests (57/78: 73% of total nests) at EZ were built on substrate-covered flooring, particularly the highest floor levels in pods 2 and 3 (see for example colour plate 3.4), although it should be noted that there was a higher proportion of substrate nests built by females in the EZ group.

Location of nests - sex differences

Although both sexes at BD invariably constructed arboreal nests, there was a discrepancy in the frequency of building nests arboreally in the EZ group. EZ males (n = 3) most frequently constructed (21/35) nests in elevated locations (nesting baskets and elevated tunnels), although nesting on substrate was also recorded (figure 3.2). The females (n = 2) at EZ that were regularly observed to build nests never did so on an elevated location; they invariably nested on substrate flooring.

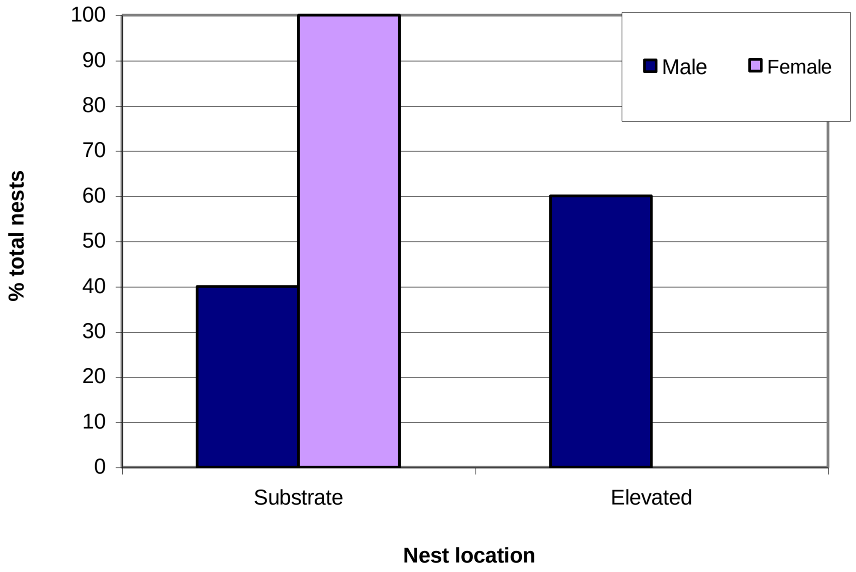


Figure 3.2 Percentage of nests built on substrate versus elevated structures in the EZ group according to sex

Nest amendments

All chimpanzees at BlairDrummond made amendments to their nests after construction, totalling 84 amendments (table 3.5). Indeed, this group spent almost 3 hours (177 minutes) in total amending their nests. In contrast, only one female at Edinburgh Zoo ever performed this behaviour, and this was infrequent throughout the 29-day study.

Table 3.5 Total frequency and duration (in minutes) of nest amendments per group

Group	Total frequency of amendments	Duration of amendments
BD (n =4)	84	177
EZ (n = 1)	7	5.5

Nest usurping and nest abandonment

Nest usurping was relatively infrequent during the course of observations of each group. At BD, only 9 instances of nest usurping were recorded, the usurpers being two females. At EZ, 6 individuals (4 female, 2 male) performed usurping behaviours, totalling 14 occurrences. Similarly, instances of nest abandonment were infrequent across groups, and not observed in all chimpanzees. Three (1 male, 2 females) chimpanzees in the BD group were observed to spontaneously abandon 8 apparently completed nests. Five individuals (1 male, 4 female) in the EZ group abandoned a total of 7 nests.

Post retirement behaviours

For the BD group, the majority of time in nests was spent performing a behaviour coded as 'substrate manipulation' (see table 3.1 for description, and table 3.6 for group frequencies of all recorded post-retirement behaviours). This behaviour was observed in all 4 members of this group. In the EZ group, this behaviour was only observed twice, performed by two females. Feeding was also observed in all 4 BD chimpanzees, and in 7 of the observable EZ group.

Table 3.6 Group and combined frequencies of post retirement activities

Group	Substrate manipulation	Feeding	Self-directed	Social
BD	83 (n = 4)	23 (n = 4)	10 (n = 3)	2 (n = 1)
EZ	2 (n = 2)	29 (n = 7)	15 (n = 8)	0

Self-directed behaviours, such as self-grooming and self-inspection were infrequently observed in either group. At BD, the male chimpanzee and two females performed self-directed behaviors. At EZ, eight individuals performed a total of 15 self-directed behaviours. Similarly, little social behaviour was recorded, with no evidence of any social interactions within the EZ group. At BD, only one chimpanzee was recorded to groom another group member while in a nest. The remaining time in nests was spent in inactive resting postures, lying on the left or right side, or in a prone or supine position – most likely as a precursor to sleep.

3.4 Discussion

One of the problems that zoos face when trying to provide desirable behavioural opportunities for captive animals is a lack of knowledge of a particular species' normal behavioural patterns (Hill & Broom 2009). Although less well documented than daytime behaviours (see chapter 1), the construction of night nests in which to rest and sleep has been reported for decades.

In keeping with the majority of reports on wild-living apes (Fruth & Hohmann 1994), the chimpanzees in this study regularly constructed night nests, although all members of each group did not necessarily build a nest each night. This is in contrast to Goodall's (1968) statement that chimpanzees will unfailingly build a nest each night, barring weakness or illness. For the BD chimpanzees, there were high levels of extraneous noise (due to building works) on several of the days when nesting was postponed, which may account for the lack of nest construction on these specific days. It is also possible that nest building occurred after observations had ceased. CCTV or cameras suitable for low-level light conditions could be an appropriate, non-invasive alternative to record nesting and subsequent sleep-related behaviours that cannot be directly observed.

Generally, the chimpanzees in the BD group retired around dusk, again in keeping with reports from free-ranging chimpanzees (Goodall 1962), orangutans (MacKinnon 1974), bonobos (Fruth & Hohmann 1993), and gorillas (Groves & Sabater-Pi 1985).

Although with individual variance, chimpanzees within the EZ group generally retired later, and in individual cases, delayed retirement until almost two hours after sunset. This may be linked to the timing of the artificial lighting systems across both facilities, with lighting remaining on for longer at EZ. Reports from free-living apes have indicated that nest construction is influenced by lighting conditions, with retirement generally being later in lighter conditions (e.g., chimpanzees: Goodall 1962; orangutans: MacKinnon 1974; see also chapter 6). It is possible that the artificial lighting system at EZ delayed retirement for some group members. However, it is also possible that this may have been due to intra-group conflicts; daytime observations of the EZ group (chapter 4) showed that male-male conflicts were relatively frequent, and could conceivably have delayed retirement times.

These data also suggest that females typically retire slightly earlier, and construct nests more frequently, than males - although not significantly so. Although comparative data for chimpanzee sex differences in retirement times are lacking, Fruth and Hohmann (1993) reported that female bonobos generally retire earlier than males. In terms of sex differences in frequency of nest construction, there are several reports of sex differences in the construction of day nests for chimpanzees, with females typically building with more regularity than males (Brownlow et al. 2001; Hiraiwa-Hasegawa 1989). Similarly, orangutan and gorilla males are known to construct night nests less often than females (Fruth & Hohmann 1996).

Direct observations of free-living chimpanzees suggest a nest construction time of between one and five minutes (e.g. Goodall 1962; Groves & Sabater-Pi 1985), with averages in some communities of three to four minutes (e.g. Guinea: Nissen 1931;

Senegal: Baldwin 1979 cited in Groves & Sabater-Pi 1985). The nine chimpanzees that were observed in the present study showed remarkably similar nest building durations, ranging between one and five minutes. Further, there was a sex difference in the duration of nest building, with females taking significantly longer than males. Again, field data on chimpanzees are lacking, but similar findings have been documented for female bonobos (Fruth & Hohmann 1993).

Across both groups, the chimpanzees in the present study most frequently constructed nests on elevated platforms, tunnels and nesting baskets, recalling the arboreal nesting pattern most typical of their wild counterparts (e.g. Baldwin et al. 1981; Goodall 1968; Stanford & O'Malley 2008). What is notable, however, is the inter-group variation in ground substrate nesting. This was never observed at BD, whereas the majority of observable nests that were constructed at EZ were built directly onto substrate flooring. Ground nesting has been documented in wild chimpanzees (Furuichi & Hahimoto 2000; Koops et al. 2007; Matsuzawa & Yamakoshi 1996), and is usually attributed to release from predation pressure, and/or lack of suitable nesting trees (e.g. Maughan & Stanford 2001). These ecological factors are not applicable here, and so alternative explanations must be considered.

The first of these is comfort. Nissen (1931) suggested that freshly constructed nests provide warmth and a soft, comfortable sleeping area. Numerous authors (e.g. Bolwig 1959; Ghiglieri 1984; Goodall 1962) have described how additional materials, such as leafy twigs, are incorporated into nests, seemingly to increase comfort levels. A recent study (Stewart et al. 2007) has indicated that this is indeed the case. When additional materials contained in chimpanzee nests were removed by researchers, the nests were scored as significantly less comfortable, at least for a human. It thus seems that comfort is an important factor in nest construction. For individuals in the EZ group, it is conceivable that building nests onto softer substrate such as bark and coir was more comfortable than nesting on hard, unyielding wire nesting baskets. Comfort may also underlie the inter-group difference in the number of nest amendments made. Stewart et al. (2007) noted that complex nests (as judged by humans) were significantly more comfortable than those that were less complex (i.e. those that had insubstantial construction with little/no extra material added). Observations of the techniques indicated that the EZ group typically used more complex techniques in nest construction (chapter 7), plus had extra material (browse) to incorporate into the nest. Therefore, the initial effort in nest construction may have precluded any need to further adjust the nests.

However, it must also be considered that both groups did have access to substrate-covered floors, yet the BD group never nested on this substrate. This still may be linked to comfort and thermoregulation. At EZ, the most frequently used floors were not at ground level. Within pods 2 and 3, the substrate flooring ascends from the off-exhibit area in a series of ‘steps’, forming four different floor levels (see plate 3.4). It is notable that only the highest floor levels were used for nesting, potentially shielding chimpanzees from any draughts from the off-exhibit area. It should also be considered that enclosure temperatures were slightly cooler in the BD night enclosure. This, coupled with a potential draught from the doorway to the keeper’s kitchen area, may have precluded incidences of substrate nesting. Nesting at higher heights could therefore have been a strategy to insulate the BD group from colder temperatures. In colder temperatures, western gorillas are known to significantly increase frequency of complete ground and arboreal nests (versus bare ground nests), presumably to insulate themselves against colder climatic conditions (Mehlman & Doran 2002; see also chapter 6).

Alternatively, the inter-group variation in substrate nesting may reflect a cultural difference in nesting patterns. Koops et al.’s (2007) observations on wild chimpanzees in Guinea failed to establish any ecological explanation for the high frequency of ground nests in this area; appropriate potential nesting trees were abundant and altitude and wind-speed appeared to have no effect on the frequency of terrestrial nesting. The authors concluded that ground nest construction may be determined by social or cultural factors. Nesting behaviours are not traditionally allied to the primate culture debate, yet there is fragmentary evidence of between-population differences in several nest-related behaviours (e.g., McGrew 2004). Therefore, comparisons of nesting patterns across captive groups may give us insight into possible nest building cultures.

It is also possible that differences in nesting locations simply reflect group-specific preferences in sleeping sites. In their natural habitat there are several examples of bonobos and chimpanzees habitually returning to preferred areas (Fruth & Hohmann 1994; Sept 1998). This may also account for the finding that the females at EZ habitually nested at lower levels (on substrate flooring) than males – a finding that contradicts numerous reports from all wild ape populations. Male orangutans (Sugardjito 1983), gorillas (Yamagiwa 2001), bonobos (Fruth & Hohmann 1993) and chimpanzees (Brownlow et al. 2001) typically nest lower down than females, most

likely due to sexual dimorphism in body size (Fruth & Hohmann 1996), or as a strategy for ‘guarding’ oestrus females nesting above (Koops et al. 2003).
Instances of both nest abandonment and nest usurping that have been documented in free-ranging chimpanzees (Goodall 1962; van Lawick-Goodall 1971), and were observed in both the captive groups studied here, although both were relatively infrequent. In wild communities, nest abandonment has been attributed to errors in construction resulting in an unstable nest, insufficient nesting substrate, and unsuitable nesting trees (Goodall 1962), or by the presence of neighbouring ape groups (Schaller 1963). In these captive groups there was no clear motivation (for a human observer) for abandoning nests; the factors that lead to nest abandonment in the wild were not applicable. It may be linked to the previously mentioned individual preferences for specific sleeping sites, and nests being abandoned in order to move to a favoured location. Van Lawick-Goodall’s (1971) described a dominant male usurping the nest of a subordinate female, possibly indicating that dominance may be a factor in this behaviour. This did not appear to be the case here; in both groups females were the most frequent nest usurpers. There was never any attempt to claim back a usurped nest, nor any aggressive behaviours associated with claiming another chimpanzee’s nest as described by van Lawick-Goodall (1971). There were however, instances of apparently ‘intimidating’ the nest builder from their nest (particularly in the EZ group) by standing over the nest builder until they abandoned their nest.

Little is known about how nests are actually utilised by chimpanzees, with the obvious exception of rest and sleep, most likely attributable to the fact nesting behaviours are rarely observed. Existing data do indicate, however, that several behaviours take place prior to sleep, with free-living chimpanzees and orangutans leaving the nest to feed (Goodall 1968; MacKinnon 1974), gorillas continuing to chest-beat (Groves & Sabater-Pi 1985), and bonobos frequently utilising day nests to feed and indulge in social play and social grooming (Fruth & Hohmann 1993). Likewise, the chimpanzees in the current study performed a range of behaviours after they had built a nest or seemingly retired for the night, with feeding being the most frequently performed in both groups. Accounts of social activities in nests are rare, although this may be due to the general paucity of direct observations of nesting behaviour in apes. Fruth and Hohmann’s (1993) report of day nests in bonobos suggested that social play and grooming occurred in nests, and both Nissen (1931) and van Lawick-Goodall (1971) describe nighttime ‘visits’ to group members in the same sleeping tree. Social interactions in both the captive groups were rare, indeed never observed in the EZ chimpanzees. This is most likely due to group differences in nearest neighbour proximity. At BD, the chimpanzees most frequently retired to the two elevated platforms, generally sharing the sleep site with another individual, allowing easier contact with another individual. The chimpanzees at EZ were never observed to nest or retire within arm’s length of another individual, more in keeping with wild chimpanzee nesting patterns of sleeping up to four meters apart (Baldwin et al. 1981; Jones & Sabater-Pi 1971 cited in Groves & Sabater-Pi 1985).

Conclusions and recommendations

The nest-related behaviours of two groups of captive chimpanzees closely mirrored those of wild populations in terms of retirement times, frequency and duration of nest construction, nest location, the abandonment and usurping of nests, and post-retirement behaviours. In conjunction with data from the survey detailed in chapter 2, it is clear that zoo-housed apes are motivated to construct night nests, and so enclosure designs and husbandry practices should enable these appropriate behaviours to enhance welfare. The current findings further demonstrate the importance of providing suitable nesting substrates and multiple nesting sites, as discussed in the preceding chapter.

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).

Chapter 4

Kin, daytime associations, or preferred nest sites?: Determinants of sleep site selection

"Think in the morning. Act in the noon. Eat in the evening. Sleep in the night." ~ William Blake

4.1 Introduction

For both monkeys and apes, there is a known social component in both sleep site selection and spatial arrangements around the sleep site (see also chapter 1). Wild-living capuchins (Di Bitetti et al. 2000), golden monkeys (Li et al. 2006), Japanese (Wada et al. 2007) and rhesus macaques (Vessey 1973), for example, are known to typically share sleeping trees with kin.

Degrees of relatedness, however, are not the only factor that can influence nighttime spatial proximity. Several species of primate (e.g. rhesus monkeys: Vessey 1973; Tibetan macaques: Ogawa & Takahashi 2003) have been documented to share sleep sites and form sleeping huddles with those that they frequently socially interact with (e.g. groom) during daytime. Socially dominant individuals can directly influence choice of sleep site by being the first to ascend the sleeping tree, as documented in stump-tailed and bonnet (Estrada & Estrada 1976; Ramakrishnan & Coss 2001) macaques. The dominant male in a group of Japanese macaques most frequently huddled with kin and the highest-ranked female, whereas subordinate males frequently slept alone (Wada et al. 2007). Similarly, the alpha male and female in a free-ranging population of tufted capuchin monkeys (Di Bitetti et al. 2000) slept together in the principal-sleeping tree.

These social factors influencing sleeping arrangements in free-ranging primates also operate in captive populations. Laboratory-housed stump-tailed macaques (n = 10) showed a preference for huddling with kin: mother-daughter pairs, juveniles and even young adult sons frequently shared the same nighttime huddle (Munoz-Delgado et al. 2004a). In contrast, reports on another group of captive longtailed macaques (*M. fascicularis*, n = 24) showed that the composition of sleep clusters was variable, and not necessarily dependent on relatedness (Gygax & Tobler 2001). Although infants invariably slept with their mothers, kin combinations such as mother-daughter and siblings did not necessarily sleep within the same cluster. Dominance rank also seemed to be a secondary factor in the formation of sleep clusters, which could be formed by both high- and low-ranking individuals.

The social factors that affect ape nesting arrangements, however, have been subject to less empirical investigation, even though the formation of nesting groups (clusters of nests built at the same time in the same area) by bonobos, chimpanzees and gorillas indicates that nest building itself is an inherently social activity (Fruth & Hohmann 1996).

With the exception of the more solitary orangutan (Rayadin & Saitoh 2009) - although adult males have been recorded to sleep in the same nesting tree as a female-infant pair and a juvenile (e.g. Schaller 1961 cited in Harrison 1969) – wild apes generally sleep socially. As in differences in daytime social organisation, there is a certain element of species-specificity in nesting groups (Fruth & Hohmann 1996). Gorillas, for example, nest and sleep in the same groups as daytime, whereas bonobo daytime parties (‘unit groups’) frequently congregate to form larger nesting parties (Fruth & Hohmann 1996). Recent data have shown that at Wamba (DRC), daytime unit groups consisted of a maximum mean of 9 bonobos, whereas up to 24 individuals could form an overnight nesting group (Mulavwa et al. 2010). In contrast to bonobos and gorillas, chimpanzee daytime groups will split into smaller factions to sleep, similar to their ‘fission-fusion’ (e.g., Boesch 1996b) social grouping during daytime. At Gombe, nest groups usually consisted of 2 and 6 chimpanzees within a single tree or closely adjoining trees (Goodall 1962). Later reports from Guinea and Senegal indicated a median of 2 and 4 nests per group, respectively (Baldwin et al. 1981).

The spatial distribution of nests within a given nesting group may also reflect social dynamics. Schaller (1965) reported that medium-sized mountain gorillas (e.g. females, black-backed males) and juveniles might nest in closer proximity to each other compared with other age/sex classes in the same group. Medium-sized gorillas, for example, nested at a mean distance of approximately 1.5meters from each other, less than 1m from juveniles, but 4m from silverback males. Closely affiliated gorillas may nest in closer proximity to other group members (Hess 1992 in Weiche & Anderson 2007). Low-ranking bonobos have been observed to sleep at the periphery of the nesting party (Fruth & Hohmann 1996).

As with gorillas (e.g. Schaller 1965), female and juvenile chimpanzees have been documented to nest in close proximity to each other, with mature males nesting further away from the main nesting group (Goodall 1968). Relatives have also been observed to sleep in especially close proximity; two adult male brothers at Gombe were observed to build and share one nest; they slept in close contact throughout the night (cited in Riss & Goodall 1976). However, when Goldberg and Wrangham (1997) used DNA analysis to determine matrilineal kinship in 138 nest groups (total nests surveyed = 232) in the Kibale Forest region of Uganda, they found no evidence that nesting groups were composed on the basis of matrilineal relatedness.

This is in direct contrast to evidence from captive ape populations. Although scant, data from captive apes do appear to indicate a relationship between the presence of kin, other socially affiliated individuals and sleep site choice. Weiche and Anderson (2007) reported a high frequency of associations between kin, including siblings and mother-offspring pairs in zoo-housed gorillas (n = 16-21). Unrelated female dyads that frequently associated during daytime also continued their association during nighttime. Respondents to the survey detailed in chapter also reported that chimpanzee mother-infant dyads shared nests, while mother-juvenile pairs nested in close proximity. Sub-adult gorillas were reported to continue to nest build in close proximity to their mother.

Riss and Goodall’s (1976) observations of unrelated laboratory housed sub-adult chimpanzees (n = 6) demonstrated that sleeping partner preferences reflected long-standing social bonds – chimpanzees that had been reared together in small subgroups continued to sleep together. Moreover, chimpanzees sometimes moved from one night cage to another, seemingly to determine who was inside before choosing a specific site to sleep. Daytime associations, however, did not exert the same influence on sleeping partner choice: no correlations were found between social grooming, play and sleeping partner choices. More recent data on laboratory-housed chimpanzees (n = 20) showed that an adult female pair who were closely affiliated, along with a mother-daughter pair, were consistent sleeping partners over eight months. Individuals that had recently been introduced to the group tended to sleep in isolation from other group members (Videan 2006b).

It is worth reiterating that chimpanzees and other great apes may spend up to one half (or more) of their lifetime in nests. On this basis, it seems fair to expect that nest and sleep sites are carefully considered. Like several monkey species that frequently utilise the same sleeping sites in their home range, wild chimpanzees are known to have preferred, localised nesting areas, and even show preferences for specific types and species of tree (Goodall 1986; Sept 1992). Recent data from Issa, western Tanzania show that chimpanzee night nests followed a non-random pattern of distribution, with specific concentrations of nests found on sloped areas (Hernandez-Aguilar 2009). Of 287 nests counted in southern Guinea-Bissau, 92% were constructed in oil-palm trees, indicating a distinct preference for this tree species (Sousa et al. 2011).

Both bonobos and chimpanzees (Fruth & Hohmann 1994) are known re-use sleep sites over several generations. These are often attributed to environmental features, such as abundance of food resources (e.g., Goodall 1986), vegetation type (e.g., Furuichi & Hashimoto 2004), type of forest (e.g., Baldwin et al. 1981), and predation pressure (e.g., Pruetz et al. 2008). However, data from captive populations, not subject to such pressures, also indicate that some sleeping sites are habitually used, suggesting that they are preferred areas for sleep. Chimpanzees in the BD group (preceding chapter), for instance, consistently used only two elevated platforms for sleep, despite the availability of several other sites. Similarly, zoo-housed gorillas slept in specific areas significantly more frequently than others over a period of several years, again suggesting enduring sleep site preferences (Weiche & Anderson 2007).

Study aims and hypotheses

Both social dynamics and preferred areas appear to influence sleep site selection in free-living and captive chimpanzees, yet there are no studies that have examined the influence of both of these factors concurrently. Therefore, the aim of the present study was to document sleep site selection in a group of chimpanzees with multiple familial relationships and multiple available sleeping areas. Not only can these data further our understanding of the influence of daytime associations and kin on choice of sleeping site, they may also have practical uses in the design of appropriate sleeping and resting areas. Although data from wild chimpanzee populations are contradictory, observations of captive apes indicate a relationship between strength of social bonds and sleep partner preference, and that specific areas within an enclosure are habitually frequented. As this study was conducted in a captive setting, it was predicted that:

a. Chimpanzees that frequently associated during daytime would sleep in the same area.

b. Kin-related individuals would sleep in the same areas.

c. Each individual would express a clear preference for a particular sleep site, measured by the frequency in which they retired to that site.

4.2 Methods and analyses

Chimpanzee social structure, housing, and sleep sites

Budongo Trail at RZSS Edinburgh Zoo is a relatively new, large and complex enclosure that housed 11 chimpanzees at the time of research (see also chapter 3). To briefly reiterate, the group consisted of 3 matrilines: Cindy and her offspring and grand-offspring (Lyndsey, Kilimi and Kindia, respectively), Emma and her offspring Qafzeh, and Lucy and offspring Liberius. Males Louis and Ricky were unrelated to any other group members, but DNA testing showed that adult male David had sired Lyndsey, Kilimi and Kindia.

The dominance hierarchy for males, females and across the group (at time of research) was provided by zoo staff, based on daily observations and recordings of vocalisations and various social and non-social behaviours (e.g. display, aggressive and submissive behaviours, greeting, grooming and feeding behaviours).

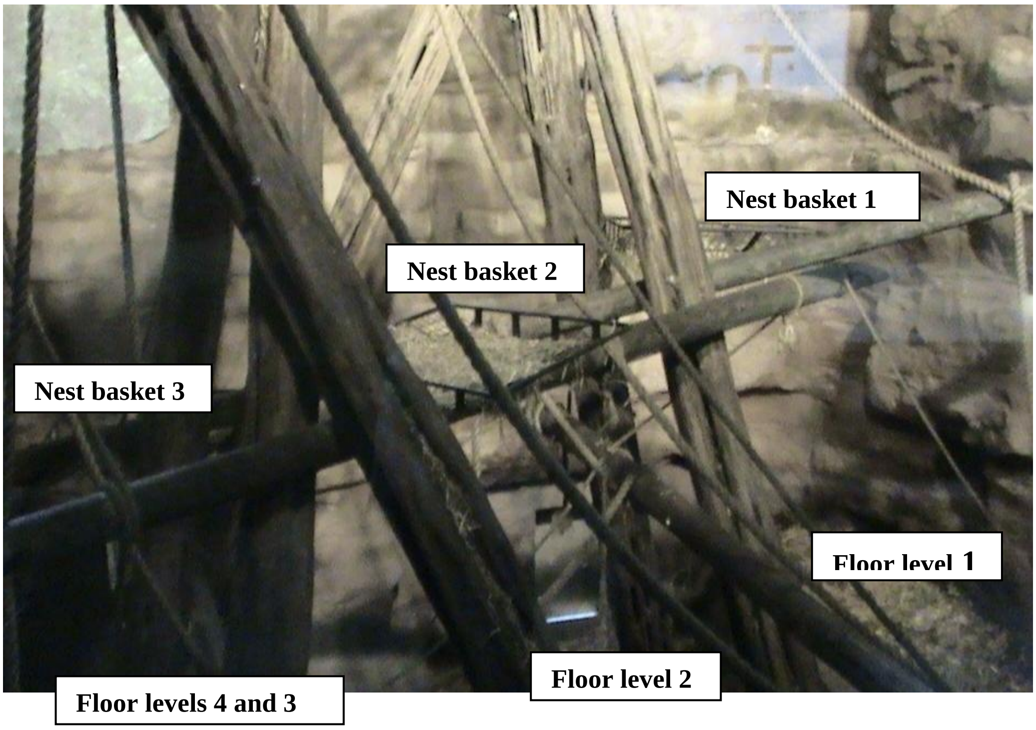
Table 4.1 Dominance hierarchies across males, females, and all group members

Males	Females	All group members
Qafzeh	Emma	Qafzeh
Louis	Lucy	Emma
David	Lyndsey	Louis
Kindia	Kilimi	David
Liberius	Cindy	Kindia
Ricky		Lucy
		Liberius
		Lyndsey
		Kilimi
		Cindy
		Ricky

EZ chimpanzees have daytime access to an outdoor enclosure and four indoor areas (see also chapter 3); 3 rooms (‘pods’) that are always available for public view (plate 4.2), and an off-exhibit area that was not accessible for public viewing. Pods 1, 2 and 3 each had a different flooring substrate and had several rectangular nesting baskets (123 x 90 x 15cm at lowest depth). In the evening, there is access to the off-exhibit area and all three pods, but not the outdoor enclosure. For the purposes of this research, each pod, the connecting tunnels, and the off-exhibit area were defined as: ‘general sleeping sites’ (see plate 4.3).

Plate 4.2 Indoor area of the Budongo Trail exhibit. Pod 2 (far left), the connecting tunnel that joins pods 2 and 3, and pod 3 (far right). Pod 1 is the extremely light area in the background on the right hand side.

Plate 4.3 Example of a 'general sleep site' (pod 3), and the specific sleeping sites (floor levels 1-4, and nest baskets 1-3) within the area.



For the purposes of this research, these specific areas were defined as: ‘specific sleeping locations’. Along with the nesting baskets, each floor level was classed as a potential specific sleep site. Pod 1, with 5 nesting baskets and the substrate floor, had 6 potential specific sleeping locations. Pod 2, with 5 nesting baskets and 4 floor levels had 9 specific locations. Pod 3, with 4 floor levels and 3 baskets, had 7 potential specific sleeping locations.

Data collection

Between December 2008 and January 2009, the daytime behaviour and sleep site selection of the EZ chimpanzees were recorded for a total of 29 days[7]. Group scan sampling began at 13.25h and ended at 18.30h on each day of observations. Between 14.45h and 15.00h each day, the chimpanzees were scatter-fed while staff gave talks to zoo visitors – no data were collected during this interval. Thus, 60 group scans were collected per day, totalling 1800 group scans over the duration of the study.

During daytime observations, the location, social behaviour(s), and proximity to nearest neighbour (see plate 4.4) of each (observable) chimpanzee were manually recorded onto pre-prepared check sheets every 5 minutes (table 4.2). Upon retirement, group scans continued, and were expanded to record nest building techniques[8], (when possible) time and place of retirement (pod 1, pod 2 etc) and the specific sleeping location (such as a particular nest basket or floor level) for each observable chimpanzee.

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[7] On the final day of observations (day 30), there were considerable social tensions within the group. Several males and two females were involved in sustained, aggressive charging displays. At time of leaving the Budongo exhibit (approximately 18.40hrs), the group had failed to retire, and so this final day was excluded from analysis.

[8] Although recorded, nest building techniques are not described here, as they form the basis of another study (detailed in chapter 5).

Table 4.2 Descriptions of day and nighttime behaviours

Behaviour	Description
Daytime behaviours	
Affiliative social	Allogroom: examine/pick through the skin of another individual Social play: chase/wrestle with another individual Food share: proffer food/allow another to take food Close proximity: <1meter from nearest neighbour
Agonistic social	Aggressive (non-contact): Charging at one or more group members without physical contact Aggressive (contact): Charging at one or group members with subsequent physical attack (e.g. hit, bite)
Nighttime behaviours	
Nest building/ retirement (as with chapter 3)	Using available materials to arrange a recognisable circular/oval nest around the body that is subsequently used to rest in. The adoption of a rest posture on substrate/nest basket
Post-retirement behaviours (as with chapter 3)	Nest amending, nest usurping/abandonment, feeding, self-directed behaviours, substrate manipulation

Plate 4.4 An example of a close proximity association. Left to right: Eldest female Cindy, her adult female offspring Lyndsey, and Lyndsey's father, David.

Data analyses

Data did not follow a normal distribution, as determined by Kolmogorov-Smirnov test. Therefore, non-parametric statistics were used throughout. Spearman's correlation coefficient was used to assess frequency of daytime associations and frequency of sharing a sleep site. Kruskall-Wallis and Mann-Whitney U-tests were used for group analysis of preferred sleep sites.

Chi-square tests were used to compare the expected and observed values of sharing sleep sites with kin/non-kin (corrected for number of kin within the group), and for comparing the expected versus observed frequencies of general and specific sleeping locations. All tests were one-tailed, and run using SPSS 17.0. As with the previous chapter, Bonferroni correction was not used, but a conservative alpha was again set at 0.025.

4.3 Results

Daytime associations and frequency of sharing a general sleep site

For females, there was no relationship between frequency of daytime social associations and frequency of sharing a general sleep site (group coefficient: $r_s = -0.09$; $n = 5$; $p = 0.43$). Even individuals who frequently associated during daytime, for example Lucy and Emma, typically did not retire to the same general sleep site (see table 4.3 for individual frequencies).

Table 4.3 Most frequent female-female association partners (plus total number of daytime associations), and frequency of sharing a sleep site

Chimpanzee	Frequent associations (total number of associations)	Sharing sleep site (number nights)
Emma	Lucy (108)	1
Lucy	Emma (108)	1
Lyndsey	Kilimi (55)	3
Kilimi	Lyndsey (55)	3
Cindy	Lyndsey (43)	11

In contrast to females, male chimpanzees showed a stronger, significant relationship between frequency of daytime affiliative associations and frequency of sharing a general sleep site (group coefficient: $r_s = 0.82$; $n = 6$; $p = 0.025$). This was especially marked in the highest-ranking males, Qafzeh and Louis, who continued their day associations into evening (table 4.4).

Table 4.4 Most frequent male-male association partners (plus total number of daytime associations), and frequency of sharing a sleep site

Chimpanzee	Frequent associations (total number of associations)	Sharing sleep site (number nights)
Qafzeh	Louis (94)	22
Louis	Qafzeh (94)	22
David	Louis (44)	9
Kindia	Ricky (42)	11
Liberius	Kindia (24)	7
Ricky	Kindia (42)	11

Generally, there was no significant relationship between frequency of daytime social associations and frequency of sharing a general sleep site between males and females (group coefficient: $r_s = 0.60$; $n = 6$; $p = 0.11$), although Qafzeh and Lucy frequently associated during the day and at nighttime (see table 4.5).

Table 4.5 Most frequent male-female association partners (plus total number of daytime associations), and frequency of sharing sleep site

Chimpanzee	Frequent associations (total number of associations)	Sharing sleep site (number nights)
Qafzeh	Lucy (65)	23
Louis	Emma (39)	4
David	Kilimi (38)	4
Kindia	Lyndsey (39)	11
Liberius	Lucy (41)	2
Ricky	Kilimi (18)	0

Sharing a general sleep site with kin and non-kin

With few individual exceptions (e.g. Lyndsey, Cindy), the majority of the chimpanzees shared general sleeping locations with kin and non-kin in an apparently random fashion (table 4.6).

Table 4.6 Frequencies of sharing a general sleep sites with kin and non-kin, plus chi-square statistic and probability value (p)

Chimpanzee	Nights with kin	Nights with non-kin	χ^2	p
Emma	3	26	16.13	0.48
Lucy	1	28	1.38	0.12
Lyndsey	19	10	7.87	0.01
Kilimi	8	21	1.86	0.09
Cindy	24	5	38.43	0.01
Qafzeh	3	26	16.13	0.48
David	14	15	4.61	0.36
Kindia	18	11	5.89	0.27
Liberius	1	28	1.38	0.12

Preferred general sleep sites – group data

Table 4.7 shows that, generally, nesting groups (individuals retiring to/nesting in the same areas) were larger in pods 2 and 3, and in the OE area. Pod 1 and the connecting tunnels appeared to be the least favoured sleeping sites at group level.

Table 4.7 Median size (plus IQR and range per night) of nesting groups in each general sleeping site

Sleep site	Median	IQR	Range
Pod 1	0	1	0-4
Pod 2	3	2	1-5
Pod 3	3	2	0-6
Tunnels	0	1	0-4
Off-exhibit	4	1	2-6

A Kruskall-Wallis test showed that there was significant variation in the number of individuals retiring to each sleep site (χ^2 =82.47; df = 4; p = 0.01). *Post hoc* Mann-Whitney U-tests showed that pod 1 was used by significantly fewer chimpanzees than pod 2 (U = 76.00; z = -5.49; p = 0.01), pod 3 (U = 67.50; z = -5.62; p = 0.01), and the OE area (U = 29.50; z = -6.23; p = 0.01), but not the connecting tunnels (U =

385.50; z = -0.65 p = 0.55). Pods 2 and 3 were used by significantly more chimpanzees than the tunnels (U = 94.00; z = -5.20; p = 0.01, U = 79.50; z = -5.42; p = 0.01, respectively). There was no significant difference between pods 2 and 3 (U = 335.00; z = -1.38; p = 0.17), nor between pod 3 and the OE area (U = 325.50; z = -1.54; p = 0.12). The OE area, however, was used by more chimpanzees than the tunnels (U = 33.50; z = -6.15; p = 0.01), and pod 2 (U = 224.50; z = -3.17; p = 0.02).

Preferred general sleep sites – individual data

Although some sites were especially preferred, most of the chimpanzees showed an individual preference for a general area in which to retire. Lucy, Kilimi, Qafzeh and Louis, for example, retired to the off-exhibit area on most occasions. Lyndsey most frequently retired to pod 2, and Ricky most frequently retired to pod 3. Chi-square analysis showed that sleeping sites were not chosen randomly. The only chimpanzee who appeared to show randomness in sleep site choice was David; see table 4.8 for results of all individuals

Table 4.8 Individual frequencies of nights spent in each general sleep site, plus chi-square statistic and probability value (p)

Chimpanzee	Pod1	Pod2	Pod3	Tun*	OE**	χ^2	p
Emma	0	9	17	0	3	8.60	0.01
Lucy	1	2	0	1	25	54.80	0.01
Lyndsey	0	25	1	0	3	34.20	0.01
Kilimi	0	5	0	0	24	10.80	0.01
Cindy	1	13	12	0	3	14.00	0.01
Qafzeh	0	0	0	2	27	21.55	0.01
Louis	0	0	0	8	21	5.83	0.02
David	9	5	5	6	4	2.55	0.64
Kindia	0	10	15	3	1	17.21	0.01
Liberius	3	8	18	0	0	11.40	0.01
Ricky	5	0	24	0	0	10.80	0.01

*Tun denotes connecting tunnels (connecting pod 1 to pod 3, pod 2 to pod 3)
** OE denotes off exhibit area, not visually accessible

Preferred specific sleep sites

As previously demonstrated, several chimpanzees most frequently slept in the off-exhibit area, thus we cannot establish a specific sleep site for these individuals. Consequently, Qafzeh, Louis, Kilimi and Lucy are excluded from the following analysis. As with the general sleep sites (pods, connecting tunnels, off-exhibit area), several chimpanzees returned habitually to specific areas within a sleep site, such as a particular nest basket or floor level. Table 4.9 shows that David was again the only chimpanzee whose choice of specific sleep site was random; in pod 1 he retired to three separate nest baskets (nest baskets 1, 2 and 3). The remaining chimpanzees showed a non-random bias for a specific sleep site. Emma and Lyndsey invariably nested on the uppermost floor level in pods 3 and 2, respectively. Cindy was only observed to retire to one specific nest basket (nest basket 2) in pod 2, and Ricky only ever retired to one specific nest basket (nest basket 2) when in pod 3. Both Kindia and Liberius most frequently nested in pod 3, both frequently returning to nest basket 3 (although not on the same nights) and the uppermost floor level.

Table 4.9 Most frequently used general sleep site, number of potential sleeping locations in each site, number of specific sites used, with chi-square and probability value (p)

Chimpanzee	Frequently used site (pod no.)	Potential sleep locations	No. specific locations used	χ^2	p
Emma	3	7	1	102.00	<0.01
Lyndsey	2	9	1	200.00	<0.01
Cindy	2	9	1	104.00	<0.01
David	1	6	3	10.33	>0.05
Kindia	3	7	2	60.00	<0.01
Liberius	3	7	2	77.29	<0.01
Ricky	3	7	1	144.00	<0.01

4.4 Discussion

There are several methodological aspects in this study that could be improved upon in future research. For example, the predilection of several individuals (Qafzeh, Louis, Kilimi and Lucy) for the inaccessible off-exhibit area meant that there are no available data on their specific sleeping locations. The use of low-level lighting and recording equipment could remedy this problem. Further, I was only able to collect data until approximately 18.30hours each night. It is possible that some chimpanzees changed sleeping location after this time. Again, overnight recording would overcome this constraint. Nonetheless, the data obtained not only inform us of the factors that influence sleep site selection in a captive group of chimpanzees, they also have implications for sleeping area design and welfare.

In contrast to previous research on captive apes (e.g. chimpanzees: Videan 2006b; gorillas: Weiche & Anderson 2007), choice of sleep site for the majority of EZ chimpanzees was not necessarily influenced by the presence of kin or daytime associations - with the exception of male-male daytime associations. Contrary to expectation, these findings are more in keeping with data from wild chimpanzee populations. In her description of the nesting groups at Gombe, Goodall (1962) stated that there appeared to be “no rigid social pattern” governing the composition of sleeping groups. Goldberg and Wrangham (1997) more recently reported no association between matrilineal kinship and nesting in the same group for 14 communal sleep sites. A similar relaxation of the influence of daytime associations and kin relationships appears to be broadly true of the EZ group.

Of further interest is that the pattern of nighttime associations for the male chimpanzees in this group concords with the general view that social bonds are stronger between male-male dyads than those of female-female and male-female dyads (e.g. Gilby & Wrangham 2008; Mitani 2009). Daytime observations have shown that chimpanzee males are often highly affiliative toward each other, expressing their social bonds through behaviours such as grooming and close inter-individual proximity (Mitani et al. 2000, 2002). With a relatively small sample size the findings from the current study must be interpreted with caution; however, it appears that male-male associations may also be a defining factor in the EZ males' choice of sleep sites.

The number of individuals occupying the sleeping areas also reflects species-typical nest group patterns, with a maximum of six individuals retiring to the same area on the same night. Daytime wild chimpanzee groups are known to divide into two or three smaller sub-groups groups to nest (Goodall 1962), with nesting groups typically comprising of two-six individuals. Although nest sharing has been documented (cited in Riss & Goodall 1976), individuals within one nesting group can nest at distances of between three and ten meters distant from their nearest neighbours (Jones & Sabater-Pi 1971 cited in Groves & Sabater-Pi 1985).

In the present study, the nearest nests were several meters distant; if a chimpanzee built a nest in one corner of the substrate flooring; for example, the next individual to build a nest would often do so in the opposing corner (pers. observation). Although rehabilitant chimpanzees more frequently nested within a group than alone, Farmer (2002) reported that mean distance to the nearest nesting neighbour was approximately 8 meters. Baldwin et al. (1981) found that the distance of nests in both Senegal and Equatorial Guinea (regardless of whether nests were in the same tree or in adjoining trees) were always at a minimum distance of four meters from nearest neighbours. The authors suggest that this spacing may reflect an ‘optimal distance’ between nests, allowing communication between group members while avoiding intimidating levels of proximity.

These similarities to wild-living chimpanzee populations should be considered when designing appropriate captive sleeping areas. As discussed in preceding chapters, one of the aims of the modern zoo is to provide captive animals behavioural opportunities that resemble those of their free-ranging counterparts (e.g., Markowitz 1997; Mellen & MacPhee 2001), taking the view that the expression of species-typical behaviours maintains/improves welfare (Carlstead 1996). Thus, multiple areas that allow chimpanzees to disperse at nighttime in a manner that is in keeping with their natural nesting patterns, and that afford an ‘optimal distance’ from nearest neighbours (several meters), should be provided. It should also be considered that even kin relatives or other closely bonded individuals may not sleep in the same area if given the choice of multiple sleep sites.

The factor of social dominance should also be considered in the design of sleeping sites. In the present study, the highest-ranking males frequently interacted during daytime observations and subsequently retired to the same area, although I was unable to determine their nighttime proximity, as the OE area was inaccessible. As with gorillas (Schaller 1965), wild-living female and juvenile chimpanzees reportedly nest in closer proximity to each other than they do to mature males, who typically nest further away from the main nesting group (Goodall 1968). It is notable that the less mature males Kindia and Liberius, and the lowest-ranked Ricky rarely retired to the OE area, possibly reflecting a strategy to avoid social conflict with the higher-ranking males; zoo-housed blackback gorillas also showed a tendency to be out of the visual range of dominant silverbacks (Weiche & Anderson 2007).

On the final day of observation, there were multiple and sustained aggressive (contact) displays by high-ranking males Qafzeh and Louis and lower-ranked males David and Kindia, with subsequent physical attacks. Females Emma and Lyndsey were also involved in aggressive behaviours, although to a lesser extent than the males. By the time evening observations ended most individuals had not yet constructed a nest or retired to any specific sleeping location. Indeed, when I left the zoo at approximately 18.50hrs screaming could still be heard from the enclosure, and so it is highly unlikely that the chimpanzees had retired. Reports on nighttime aggressive behaviours are infrequent, although de Waal (1986) describes a fatal attack on a dominant male by two other high-ranking males in the night cages at Arnhem Zoo. In contrast to daytime, the EZ chimpanzees had no access to the outdoor enclosure in the evening, similar to the majority of zoos and safari parks across the UK and Ireland (57% of captive ape populations surveyed, see chapter 2). It is therefore recommended that there are enough sleeping areas to allow subordinate chimpanzees to avoid/flee from dominant group members, and provide some degree of control over social opportunities, which may also be beneficial to welfare (e.g., Novak & Suomi 1998). Vertical structures can reduce stress by providing an escape route from alarming situations (Roder & Timmermans 2002); conceivably, elevated nesting baskets/platforms can also serve this purpose.

Moreover, as well as restricting natural behaviours (Honess & Marin 2006a,b), overcrowding in captive environments can generally be a stressor (Morgan & Tromborg 2007), possibly leading to stereotypic and other aberrant behaviours (Chamove 1989a,b), and so be deleterious to welfare.

It has been suggested that the positioning of captive animals in relation to other group members and their environment can reliably inform of what animals ‘like’ or ‘want’; in effect, making choices based on their own welfare requirements (Dawkins 2004, 2006). Daytime observations of enclosure space use have shown that several ape species have preferred areas (e.g. orangutans: Herbert & Bard 2000; western lowland gorillas: Stoinski et al. 2001). Several authors (e.g., Ross et al. 2009; Traylor-Holzer & Fritz 1985) have argued that how enclosure space is utilised and preferences for environmental features have important consequences for welfare, in terms of matching the biological requirements of captive animals to their free-ranging counterparts, and also providing information on animal’s requirements and preferences.

With individual exceptions, the data also indicate that sleeping area preferences exist at group and individual levels - the tendency to return to preferred sleeping sites is more influential than daytime associations or the presence of kin. Typically, pod 2 was favoured by mother-adult offspring pair Cindy and Lyndsey, pod 3 by unrelated group members Emma, Kindia, Liberius and Ricky. Unrelated males and females Qafzeh, Louis, Lucy and Kilimi most frequently retired to the off-exhibit area.

Again, this pattern is broadly in keeping with reports from wild chimpanzee communities, who frequently return to preferred, localised areas, and even show preference for specific types and species of tree (Goodall 1986; Pruetz et al. 2008; Sept 1992; Stanford & O'Malley 2008). Longitudinal data (over three years of field work) indicated that free-ranging bonobos also regularly used the same sleeping sites, the same nesting trees, and even the same locations within a tree (Fruth & Hohmann 1993). Variations in season and environment also influence sleep site selection and nest-related behaviours across free-living apes (e.g., chimpanzees: Basabose & Yamagiwa 2002; bonobos: Fruth & Hohmann 1993; gorillas: Iwato & Ando 2007). As social factors such as kin and daytime associations do not appear to greatly influence sleep site selection in the EZ group, it would of interest to document changes in sleep site selection in relation to environmental/seasonal variables, particularly as it has been suggested that habitual daytime use of space is likely influenced by a combination of social pressures and desirable environmental features in other captive ape groups (e.g., chimpanzees and gorillas: Ross et al. 2009; chimpanzees: Traylor-Holzer & Fritz 1985).

Within each area, individuals expressed preferences for specific arboreal nesting baskets and substrate covered flooring levels. In conjunction with multiple sleeping rooms, exhibit designs should therefore incorporate multiple levels and multiple niches as potential sleep sites. Complex enclosures providing social and physical stimulation necessary for species-typical behaviours (Hoff et al. 1994) should therefore improve welfare. Further, by 'asking' captive animals what they want, that is, by giving them choices about features of their environment, our understanding of their needs for specific resources can increase (Hill & Broom 2009).

Conclusions and recommendations

As with the nest-related behaviours detailed in chapter 3 (e.g. retirement times, frequency and duration of nest construction, post-retirement behaviours), the nighttime spatial arrangements of captive chimpanzees, at least in this group, broadly mirror those of wild populations. Given that 70% of captive apes in the UK and Ireland (data from survey, chapter 2) have communal sleeping quarters, these data may have practical considerations for the design of sleeping areas and welfare for captive chimpanzees.

Similar to free-living groups, the chimpanzees in the present study showed a nighttime spatial distribution typical of their ‘fission-fusion’ social grouping patterns – forming small overnight nesting groups. These groups were not necessarily composed of kin relatives or obviously closely bonded individuals. Rather, the majority of group members habitually returned to preferred general and specific sleeping sites, with individual preferences for arboreal and terrestrial sleep sites. Lower ranking individuals rarely retired to the same area as the highest-ranked males.

To allow small nesting groups to be formed, individual preferences for specific sleeping areas to be expressed, and to allow subordinate group members to withdraw from dominant individuals/social tensions, multiple sleeping areas are required if zoos are to fulfil their aim of facilitating natural, species-typical sleep-related behaviours. Multiple sleeping quarters should also be considered to reduce social stress resulting from space restriction, and incorporate several elevated levels as possible escape routes for subordinate group members. These will also add elements of choice to the environment, in terms of both where to sleep, and with whom.

Chapter 5

Nest construction techniques and preferred nesting materials

"As you make your bed, so you must lie in it" ~ Daniel J. Boorstin

5.1 Introduction

Chimpanzees of weaning age and beyond construct a new nest each night (Goodall 1962; 1968), and may sleep in it from dusk until dawn - yet little is known about nests and nest building in either free-ranging or captive apes (McGrew 2004).

An early description of chimpanzee nesting behaviour was provided by Nissen (1931), but this was mainly based on notes of abandoned nests, rather than direct observation of nest construction. Despite this, Nissen did describe in great detail the locations and structures of several abandoned night nests in Guinea, documenting the shape (circular/oval), materials used in construction (peripheral branches, smaller twigs and leaves as lining), and the basic techniques likely used in construction (intertwining of branches to form the nest shape). When conditions allowed direct observation, one chimpanzee was seen to stand in the middle of nest being constructed, reach out to pull branches toward it, and use the feet to hold branches in place while inter-weaving the nest rim. Bolwig (1959) added considerably to this detail, describing how branches were first arranged in criss-cross fashion to form the basic platform. This was followed by the formation of the nest 'ring' (or rim) by standing on the platform and bending and breaking smaller branches to form an approximately circular shape around the chimpanzee.

Goodall (1962) also described how Gombe chimpanzees use the horizontal forks or parallel branches to form the nest foundation, onto which several smaller crosspieces are bent over and held down. Using both the hands and the feet, these crosspieces are bent and interwoven to form the basic nest structure. Smaller branches and leafy twigs may then be added, with the entire nest typically taking between one and five minutes to complete (Goodall 1962, 1968).

Observations of gorilla populations in Uganda also showed that pulling vegetation together is the first stage in nest building (Bolwig 1959). The material was then criss-crossed together to form a platform, and then the outside nest rim was fashioned by bending and breaking twigs. Branches on the outside of the nest rim were then twisted inwards and tucked into the structure. MacKinnon (1974) described a broadly similar pattern in free-ranging orangutans. Moving in a circle, branches from the surrounding areas were bent in toward the individual. Using the feet, these branches were held down while being manually twisted, bent and tucked together, eventually forming a concave platform. The back of the hand was also used to push errant branches back into place and pat down the rim of the nest. After construction (generally two to three minutes), further amendments were made, although no specific details of this were given.

It has been suggested that comfort afforded by night nest construction was a driving influence for the persistence of this behaviour across ape species (e.g., Baldwin et al. 1981, see also chapter 1). Nests not only provide thermoregulatory benefit during inclement weather (e.g. gorillas: Mehlman & Doran 2002; orangutans: Rayadin & Saitoh 2009), but also are also simply a soft, warm and comfortable sleeping area (e.g. Nissen 1931). Although direct observations are relatively scarce, descriptions of nest building behaviour of apes often describe how nests are ‘lined’ with extra branches and leaves, widely believed to add to the overall comfort of the nest (e.g. Baldwin et al. 1981; Bolwig 1959; Ghiglieri 1984; Reynolds & Reynolds 1965;

Rothman et al. 2006). In keeping with anecdotal reports that lining nests with additional materials provides a more comfortable resting area, Stewart and colleagues (2007) reported that the removal of additional lining materials significantly increased levels of physical discomfort, at least for a human lying in a nest. Moreover, nests that were constructed using complex construction techniques (e.g., interweaving external materials, incorporating additional substrate into the central nest area) were significantly more comfortable than those that were built using less complex techniques. Thus, it does appear that comfort is an important factor in nest construction.

In describing a previously used night nest, Nissen (1931) used such phrases as “well-padded” and “…very springy…doubtless a comfortable resting place”. Similarly, in her description of orangutan nesting behaviour, Harrison (1962 p71) stated that the male under observation was seeking a “comfortable sleeping-place”. Groves and Sabater-Pi (1985) described gorilla nests in Equatorial Guinea as a “… springy, comfortable platform”, made so by the use of leafy plants in construction.

This use of particular materials to apparently improve nest comfort may also be a determinant of sleep site. Bonobos, for example, appeared to choose sleeping trees based partly on leaf attributes (Fruth & Hohmann 1993). Nests were more frequently constructed in trees with small- to medium-sized leaves, leading the authors to conclude that smaller leaves may improve nest comfort. Similarly, chimpanzees in the Budongo forest were observed to prefer specific types of sleeping tree – all noted by the authors as having high foliage density that provide, a “particularly good substrate” for nests (Brownlow et al. 2001). Eastern lowland gorillas used particular types of nesting plants that are also favoured as a bedding substrate by humans in the same region, due to their comfortable and flexible properties (Rothman et al. 2006).

If provided with appropriate nesting materials, apes kept in captivity will build, or at least attempt to build, nests (questionnaire data: chapter 2; Bernstein 1969; Videan 2006a). Bernstein's (1962) research included provision of several potential nesting materials and recording their influence on nest building 'patterns' (techniques). Although the main focus of his experiment was to compare nest construction by captive- and wild-born laboratory-housed chimpanzees, this research was the first of its kind to describe nest building behaviour. Three sets of nesting materials were presented to the apes. Set 1 consisted of a burlap bag, burlap strips, and pine needles. Set 2 consisted of a cardboard box filled with newspaper, and several lengths of plastic and rubber hose. The final set consisted of palm and palmetto leaves, and several lengths of rope and chain. The construction techniques were broadly similar to those of free-living apes. After transporting material(s) to a selected sleep site, longer, more flexible materials, such as hose, palm leaves and burlap, were 'wound' around the body. Smaller, less flexible materials, including newspaper and pine needles, were folded in toward the centre of the nest. Although no 'weaving' of materials was observed, the folding of materials was believed to strengthen the nest. The ends of nesting materials were often held down with a foot whilst folding the rest of the material into the nest centre.

This research was later extended to include juvenile gorillas and orangutans. By bending and tangling the tops of small trees in their outdoor enclosure, juvenile orangutans (n = 2) were able to form a sturdy sleeping platform. Juvenile gorillas (n

= 8) of the same age (between 2.5 to 3.5 years) failed to utilise broken branches to form any kind of recognisable nest (Bernstein 1969). As well as these reported between-species differences, individual differences within species also emerged. Only one of six juvenile gorillas consistently used hay and lengths of hose to build “the best” nests (large, almost circular, with a relatively defined rim); her counterparts most frequently used the materials for play. For these older juvenile gorillas, nest construction included ‘sweeping out a small circle’ and ‘piling and pounding’ materials around its centre. Despite results being confounded by age, the author concluded that the techniques used in nest construction were generally similar across three of the great ape species. Apes begin by sitting or standing in the nest centre, gathering materials toward them, and turning around in the nest to form a rim around them. Hay was separated, ‘fluffed’ and ‘folded’ into the nest and ‘pounded’ into position, using the hand or wrist.

Videan (2006a) also provided some descriptions of nest construction techniques in captive chimpanzees. Butcher paper, hay and browse were presented to 73 laboratory-housed adult chimpanzees. In contrast to Bernstein’s reports, some chimpanzees in this study were observed to bend and weave materials, although these techniques were restricted to wild-born individuals. Similar to free-ranging apes gathering materials toward the body (e.g. Nissen 1931) and forming the nest ring and folding materials into the nest rim (e.g. Bolwig 1959), Videan’s chimpanzees ‘arranged and tucked’ nesting materials around themselves, and also used material from the outside rim of the nest and arranged into the inside of the nest (‘outside-in’).

Even captive chimpanzees with limited access to nesting materials can demonstrate some nest building ability. Only one description of nest construction by bonobos exists, and it is limited to the behaviour of one (estimated to be) 5-year-old. Yerkes (1943) described the nest building as a ‘simple process’ consisting of selecting the nesting site, pulling down branches, and bending/breaking them underneath the body. Wild-born adult male chimpanzees (n = 5) with restricted access to bedding materials used most of the materials available to them (including bamboo, burlap and straw), and demonstrated some of the techniques previously described – shaping materials around their body, and holding materials down whilst shaping the rest of the nest (Morimura & Mori 2010). Again, wild-born chimpanzees more frequently used nesting materials than captive-born subjects (n = 8), although the latter did sometimes made nests.

Work by both Bernsein (1962) and Videan (2006a) indicated that, as with wild apes, nest building behaviour may be influenced by the levels of comfort provided by certain materials. In the former study, the first set of materials (burlap and pine needles) produced the greatest number of nests, indicating clear preferences: all seven wild-born chimpanzees and eight captive-born chimpanzees built, or attempted to build, nests with these materials. The third set of materials (palm leaves, palmetto leaves, rope and chain – presumed to be metal, but not specified by author) produced the fewest number of nests, with only twelve chimpanzees attempting to build or building a nest (Bernstein 1962). However, it is perhaps not surprising that chain, in particular, failed to facilitate any type of nest construction. Videan’s (2006a) study also demonstrated that certain materials resulted in higher rates of nest building. Again wild- (n = 27) and captive-born (n = 46) laboratory-housed chimpanzees were presented with three sets of potential nesting materials. Set one consisted of sheets of butcher paper, set two contained a section of hay, and set three contained lengths of browse (branches and foliage). Overall, hay produced higher rates of nest building than either paper or browse. In another study zoo-housed gorillas (n = 17) only used hay in nest construction (Lukas et al. 2003); when another material was available (browse), it was never incorporated into nests.

The provision of bedding/nesting materials can be beneficial for welfare in several ways, including facilitating the expression of species-typical behaviours (Honess & Marin 2006), increasing environmental complexity (Baker 1997), decreasing abnormal behaviours (e.g., coprophagy, regurgitation and reingestion behaviour in zoo-housed gorillas: Brown & Gold 1995), allowing animals control over thermoregulation, and increasing levels of physical comfort (Tuyttens 2005).

Given the important role of softness in physical comfort (Boe et al. 2007), the preference of captive apes for soft bedding materials is unsurprising; such preferences have also been documented in a variety of farm and laboratory settings using ‘preference tests’. These methods are employed to indirectly assess the subjective feelings of animals, where an animal is given a free choice of two or more resources in its environment (Jensen & Pedersen 2008). The resources or stimuli that are most frequently chosen or used over time are said to be preferred over alternatives (Kirkden & Pajor 2006). Preference tests are based on the theory that animals will base choices on their feelings (Duncan 1992, 2006), seeking stimuli that will enhance welfare, and avoid stimuli that are detrimental to welfare (Dawkins 1983). That is, if an animal is given a choice about a particular aspect of its environment, it will make a choice according to how it feels, based upon its own "…best interests of welfare." (Duncan 1992 p 658). In conjunction with observations of wild conspecifics, preference tests can provide useful information on what is important to captive animals (Yeates & Main 2008), by ascertaining what resources they 'like' and want' (Dawkins 2004, 2006).

Several studies of farm livestock have indicated that soft flooring and substrates are preferred over harder surfaces such as concrete or wooden floors (e.g., cattle: Manninen et al. 2002; sheep: Gordon & Cockram 1995). When given the choice of cages with or without nesting materials (paper towels and tissues), laboratory mice (n = 6) spent significantly more time in the bedding cage (90% of observation time) compared to areas without bedding substrate (van de Weerd et al. 1998). The authors concluded that bedding material are beneficial to welfare by promoting species-typical nesting behaviours, and giving animals greater control over their living conditions. There is also evidence that some nesting materials are preferred over others. Laboratory-housed rats (n = 24) and mice (n = 20) showed preferences, when given a choice, for shredded paper and wood shavings over sawdust (Blom et al. 1996). The former substrates were also preferred over sawdust in another colony of laboratory rats (n = 24) (van de Weerd et al. 1996). This led authors to conclude that large-particle materials (e.g., paper, woodchips) are more suitable than others (e.g., sawdust) for nest building, at least for rodents.

However, there are several limitations concerning the use of preference tests. For example, it must be considered that welfare need not be adversely affected if preferences are not met (Duncan 1992; Fraser 1996) - do animals necessarily suffer if a preferred resource is unavailable? It has also been pointed out that choices offered to animals may be equally acceptable, or equally deficient (Fraser 1996).

Study aims and hypotheses

Although nest construction techniques have been described in free-living apes, descriptions of nest building patterns in captive apes are lacking. Therefore the first aim of the present study was to describe the nest building techniques of a captive group of chimpanzees that have regular access to nesting materials. Based on existing descriptions, it was hypothesised that:

a. Techniques described in other captive populations, such as gathering materials toward the body and arranging materials around the body would also be evident in this group (along with individual variations).

The second aim of this research was to assess preferences among different potential nesting materials. Bernstein (1962) and Videan (2006a) have already shown that certain materials are preferred over others for nest building. Although similar from a methodological point of view, the current study sought to expand on previous findings by presenting nesting materials that are more widely used by zoos and wildlife parks, including browse, hay, wood wool, straw and sacking (see chapter 2). If preferences do exist, these findings may have practical consequences for the types of nesting substrates given to captive apes. Following from reports of free-ranging apes and laboratory-based studies, it was predicted that:

b. Chimpanzees would show a preference for softer (presumably more comfortable) nesting materials.

c. More time would be devoted to nest building when presented with preferred materials.

5.2 Methods and analyses

Chimpanzees and housing

The chimpanzees in the this study were the 11 mixed-age and -sex group of chimpanzees housed at Budongo Trail, Edinburgh Zoo, previously described in chapters 3 and 4.

Data collection

During April-May 2009, the EZ chimpanzees were presented with four sets of nesting materials. Each set contained two bedding materials. Material set one consisted of straw and eucalyptus branches - the standard nesting materials presented to the chimpanzees. Set two consisted of wood wool and cotton materials (e.g., blankets, towels and clothes). Set three contained hessian sacks and browse (branches and foliage collected from areas around the zoo). Set four consisted of hay and paper sacks. Rather than introduce all eight materials simultaneously, each set was presented separately, as this was in keeping with the zoo’s usual practice of providing two choices of bedding material.

Appropriate amounts (for each group member to have access) of one material set were distributed throughout pods 1, 2 and 3 in the indoor exhibit at the beginning of each observation week. The materials were left in the pods for one week; replenished as needed by staff. After one week, any remaining materials were cleared from the pods, and a different material set was introduced. This continued for a total of four weeks, until all four material sets had been introduced. The same material sets were then presented in random order (as they became available for use) for another four weeks, using the same procedure outlined above. Therefore, at the end of eight weeks, each material set had been presented twice (table 5.1). This procedure was used to assess if initial preference for nesting materials continued into their second presentation.

Table 5.1. Order of materials presented

Week of study	Materials presented
1	Straw & eucalyptus (set 1)
2	Woodwool & cotton (set 2)
3	Browse & hessian sack (set 3)
4	Hay & paper sack (set 4)
5	Browse & hessian sack (set 3)
6	Woodwool & cotton (set 2)
7	Hay & paper sack (set 4)
8	Straw & eucalyptus (set 1)

On each day of observations, members of staff or a zoo volunteer were requested to randomly select a focal pod. As time of nest building was variable, there was no set time for the beginning of observations. Rather, each chimpanzee within the selected pod was subject to one-minute scan sampling from the moment they touched or manipulated nesting material(s) in any way. The materials each chimpanzee used in nest construction (e.g., straw, eucalyptus, or both materials) were recorded, along with time taken to nest build (in minutes), and nest building technique(s)[9]. A simple technique (ST) consisted of transporting nesting material, but either failing to construct a nest (simply lying on the material), or, if a nest was made, it had no discernable form or shape. A complex technique (CT) included transporting material, gathering it around the legs/lower torso, pressing /tucking material around the body to form a recognisable nest of oval/circular shape, with defined ‘cup’ (centre of nest) and ‘rim’ (outside edge of nest). If no nest building was observed, any manipulation of nesting material (such as covering the body with material) was noted. When possible, individual episodes of nest construction were filmed using a hand-held camcorder (‘Sony Handycam DCR-SR78E’) to allow later detailed description of nest building techniques. Scans of each individual within the focal pod continued until 18.30hrs. These scans generated data on a total of 51 nests. At the end of daily focal pod scans, I also recorded the materials that all observable group members had used.

When each material set was introduced, each randomly selected pod was used as focal pod for one day. The data from individual chimpanzees within each pod across each presentation of material sets were used in analysis of nest building techniques and duration of nest construction. After each pod had been used as a focal pod (at the end of three days), I returned on the fourth day to record additional data on materials used in nest construction. These data, in conjunction with focal pod data and the data on nesting material use at the end of each observation day, generated data on material preferences from 170 chimpanzee night nests.

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[9] Individual retirement times and general and specific sleep site selection were also recorded, but are detailed elsewhere (chapter 6).

Data analyses

Kolmogorov-Smirnov tests indicated that data were not normally distributed, and so the non-parametric Wilcoxon signed ranks test was used to test for differences in nest building techniques, frequency of techniques used, comparison of nest construction within each material set, and number of nests built in the 1st and 2nd presentation of sets. Tests for preferred materials and duration of nest construction dependent on material were one-tailed, all remaining tests were two-tailed. Data were analysed using SPSS 17.0, with alpha set at 0.025.

5.3 Results

Nest construction techniques

A total of 51 nest-building episodes were directly observed and recorded during focal pod sampling. Individuals differed in nest construction techniques - several group members (e.g., Qafzeh, Louis: table 5.2) only used simple techniques, where others invariably used more complex techniques (e.g., Lyndsey, Emma).

Table 5.2 Frequencies of using a simple technique (ST), a complex technique (CT), and making no attempts at nest building

Chimpanzee	No. times in focal pod	No. times used ST	No. times used CT	No attempt
Cindy	8	3	0	5
Lyndsey	8	0	8	0
Kilimi	3	0	2	1
Emma	7	0	7	0
Lucy	6	3	2	1
Qafzeh	6	4	0	2
Louis	8	3	0	5
David	7	2	3	2
Kindia	8	1	6	1
Liberius	8	6	1	1
Ricky	8	3	0	5

Generally, nest building consisted of using the simple or complex techniques previously described. Seven of the most frequently occurring behaviours are described in table 5.3; less frequently occurring behaviours are discussed later. Each nest building episode invariably began with the transportation of nesting material, most frequently in the arms, but using the mouth was also occasionally observed in males Louis and Liberius.

Table 5.3 Most frequently used nest building techniques

Technique and abbreviation	Description
Depression (D)	Using hands, substrate is pushed outwards to form a small (usually circular) depression in the substrate
Gather-tuck (GT)	Nesting material is gathered towards the body, and loosely tucked around the torso/legs
Arrange-tuck (AT)	Nesting material is arranged around the body, and folded/tucked more tightly around the torso/legs
Press (PR)	Nesting material is pressed firmly downwards into the nest rim using either knuckles or wrists
Turn (TUR)	Chimpanzee turns while in the nest, forming the nest shape around it as it turns (in sitting/standing position)
Throw (THR)	Nesting material is thrown above and behind the chimpanzee (see plate 5.2)
Separate materials (SEP)	Clumps of nesting materials (only applicable for straw, wood wool and hay) are separated with the fingers to form smaller strands

After nesting material transportation, what happened next could vary. For example, a substrate depression might be made, followed by gathering and tucking material around the torso (in either a sitting or standing posture). Some chimpanzees then turned around in the nest, pressed material down with the back of the hands or knuckles, or even tossed material over the head (plate 5.2). See table 5.4 for individual and group frequencies of technique use.

Plate 5.2 Kindia demonstrating the ‘throwing’ technique with straw

Table 5.4 Individual and group frequencies of using each technique, plus median value and IQR[10]

Chimpanzee	D	GT	AT	PR	TUR	THR	SEP
Lyndsey	7	10	13	13	13	3	5
Kilimi	1	5	5	5	2	0	0
Emma	1	7	10	10	6	3	5
Lucy	0	3	2	1	2	1	1
Qafzeh	0	1	1	0	0	0	0
Louis	0	0	1	1	1	0	0
David	0	2	5	4	2	0	1
Kindia	1	5	4	7	5	8	2
Liberius	0	2	4	0	0	0	0
Ricky	0	0	2	1	1	0	1
Group frequency	**10**	**35**	**47**	**42**	**32**	**15**	**15**
Median (IQR)	**0 (1)**	**2.5 (5)**	**4 (5)**	**2.5 (7)**	**2 (5)**	**0 (3)**	**1 (3)**

The only behaviour that was observed at least once in each chimpanzee was ‘arrange-tuck’, in which nesting materials were arranged toward the body and tucked around the torso and/or legs. This was the most frequently observed technique, used significantly more than turn (z = -2.05, p = 0.02) throwing (z = -2.25, p = 0.01) and separate materials (z = -2.83, p = 0.01), but not significantly more than gather-tuck (z = -1.98, p = 0.03) or press materials (z = -1.19, p = 0.06).

Most chimpanzees used gather-tuck; however, it was only used significantly more frequently than separate (z = -2.45, p = 0.01). All other comparisons failed to reach significance (versus press z = -1.14, p = 0.13; versus turn z = -0.65, p = 0.26; versus throw z = -1.83, p = 0.03).

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[10] Elderly female Cindy was excluded from analysis as she was never observed to use any of the described techniques

Pressing nesting material with the knuckles or wrists was recorded in eight individuals. It occurred significantly more frequently than throw ($z = -2.04$, $p = 0.02$) and separate ($z = -2.21$, $p = 0.02$), but not turn ($z = -1.76$, $p = 0.04$). Turning around in the nest during construction occurred more frequently than separate materials ($z = -1.62$, $p = 0.01$), but not throw ($z = -1.52$, $p = 0.05$). There was no significant difference in frequency of throw or separate materials ($z = -0.68$, $p = 0.24$).[11]

Less frequently used techniques – individual variations

In conjunction with the seven more frequently occurring techniques, several other techniques were recorded, but relatively infrequently, and so were not included in table 5.3. Louis, for example, was the only individual to hold down hay with his foot and 'stamp' on it, whilst arranging the remaining nesting material. Using the technique of pushing nesting material away from the body and into the nest rim was only observed in four individuals. Females Lyndsey and Lucy did this during 2 nest-building episodes, Emma once. David was the only male chimpanzee to do this, which he did during two nest-building episodes. Lyndsey was observed to both chew and snap eucalyptus twigs before incorporating them into the nest on two separate occasions. She was the only individual to manipulate any materials orally, although her male offspring Kindia was also observed to snap twigs before nest building with them. Lyndsey was also the only chimpanzee observed to 'scoop' floor substrate toward the nest - incorporating it into the nest rim.

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[11] The technique of making a depression in substrate prior to nest construction was excluded from analysis as several chimpanzees only ever retired to nest baskets.

Preferred materials within each set

Data from focal pod observations, from all observed nest builders after focal observations, plus records from the additional days of data collection (totalling records of 170 nests) revealed preferences between materials presented in each set.

Material set 1

When given a choice of straw and eucalyptus, most chimpanzees used only straw, never attempting to nest build using eucalyptus only. However, some individual variations were apparent. Lyndsey, and to a lesser extent Emma, sometimes incorporated both straw and eucalyptus into their nests (table 5.5). Group analysis showed that straw alone was used significantly more frequently than eucalyptus alone (z = -2.69, p = 0.01). Although straw alone was also used more frequently than materials combined, this failed to reach significance (z = -1.84, p = 0.04).

Table 5.5 Individual frequencies, plus group frequency, of nest construction using material set 1

Chimpanzee	Straw	Eucalyptus	Both materials
Cindy	0	0	0
Lyndsey	2	0	6
Kilmi	2	0	0
Emma	4	0	3
Lucy	2	0	0
Qafzeh	1	0	0
Louis	1	0	0
David	6	0	0
Kindia	8	0	0
Liberius	2	0	0
Ricky	0	0	0
Group frequency	**28**	**0**	**9**

Material set 2

As with material set 1, preferences for specific materials varied among individuals. With the exception of one female (plate 5.3), all chimpanzees used only wood wool when retiring. See table 5.6 for individual and group frequencies.

Plate 5.3 Lyndsey, who most frequently used a combination of materials, incorporates a cotton shirt into her wood wool nest.

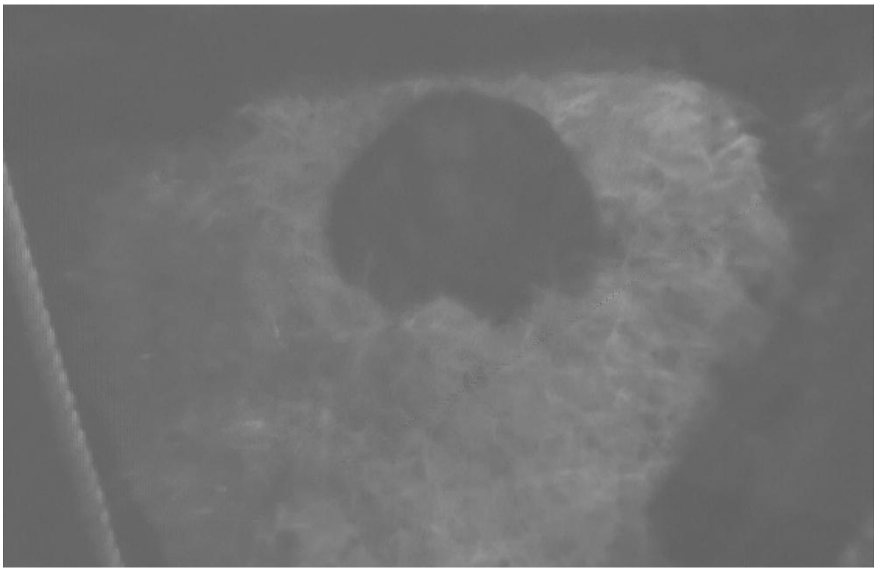
Comparison of use of wood wool only and cotton materials showed only that wood wool was used significantly more frequently ($z = -2.55$, $p = 0.01$). Wood wool only was used more frequently than both materials combined, although this difference fell short of significance ($z = -1.49$, $p = 0.07$). Using both materials to nest build occurred more frequently than using cotton only ($z = -1.98$, $p = 0.02$).

Table 5.6 Individual frequencies, plus group frequency, of nest construction using material set 2

Chimpanzee	Wood wool	Cotton	Both materials
Cindy	0	0	0
Lyndsey	1	0	7
Kilmi	0	0	1
Emma	4	0	3
Lucy	3	0	3
Qafzeh	6	0	0
Louis	3	0	2
David	5	0	0
Kindia	7	0	1
Liberius	5	0	2
Ricky	2	0	0
Group frequency	**36**	**0**	**19**

Notably, wood wool was used to construct by far the largest nest seen during the study. Lucy typically used simple techniques, but she used more complex techniques to construct a nest that was estimated (from direct observation and confirmation by staff) to be 2.5-3 meters in diameter (plate 5.4).

Plate 5.4 The largest observed nest constructed by Lucy.



Material set 3

Table 5.7 shows a general group trend toward using browse only for nesting. Use of hessian only was infrequent.

Table 5.7 Individual frequencies, plus group frequency, of nest construction using material set 3

Chimpanzee	Hessian	Browse	Both materials
Cindy	0	0	0
Lyndsey	1	1	6
Kilmi	0	2	1
Emma	0	1	3
Lucy	0	2	1
Qafzeh	0	1	0
Louis	0	3	0
David	0	1	0
Kindia	1	3	0
Liberius	0	1	0
Ricky	0	0	0
Group frequency	**2**	**15**	**11**

Browse only was used significantly more frequently than hessian only (z = -2.59, p = 0.01). There was no significant difference between frequency of using hessian only and both materials combined (z = -1.29, p = 0.10), or between use of browse and both materials combined (z = -0.91, p = 0.19).

Material set 4

All chimpanzees showed a marked preference for using hay only; this included Lyndsey, who in all other conditions most frequently used a combination of materials. Nests constructed from paper sacks only or the two materials combined were rare (see table 5.8).

Table 5.8 Individual frequencies, plus group frequency, of nest construction using material set 4

Chimpanzee	Hay	Sacks	Both materials
Cindy	0	0	0
Lyndsey	6	1	1
Kilmi	0	0	0
Emma	5	0	1
Lucy	6	0	0
Qafzeh	4	0	0
Louis	5	0	0
David	7	0	0
Kindia	8	0	0
Liberius	3	0	0
Ricky	3	0	0
Group frequency	**47**	**1**	**2**

The frequency of nest building episodes using hay only was significantly greater than using paper sack only (z = -2.81, p = 0.01), and using a combination of both materials (z = -2.81, p = 0.01). The difference between use of combined materials and paper sacks alone was not significant (z = -1.00, p = 0.16).

Duration of nest construction

To test for differences in the duration of nest construction, data from focal observations of nest building were used. The durations of each nest-building episode during each presentation (1st and 2nd) of material sets were summed to give a total nest construction time for each chimpanzee per presentation of material sets.

Overall, more time was taken to nest build using material sets 4 (median time: 3.9 min, IQR: 5.4) and 2 (median: 2.5 min, IQR: 4.9) (see figure 5.1). For material sets 1 and 3, median times of nest construction were 1 minute (IQR: 1.6) and < 1 min (IQR: 1.6), respectively.

These differences were not significant between sets 1 and 2 (z = -1.19, p = 0.05) or sets 1 and 3 (z = -1.27, p = 0.08). However, significantly more time was spent nest building using set 4 compared to set 1 (z = -2.14, p = 0.01), and using set 2 compared to set 3 (z = -2.10, p = 0.01). Finally, significantly more time was spent nest building with set 4 than 3 (z = -2.67, p = 0.01), but there was no difference between sets 4 and 2 (z = -0.97, p = 0.17).

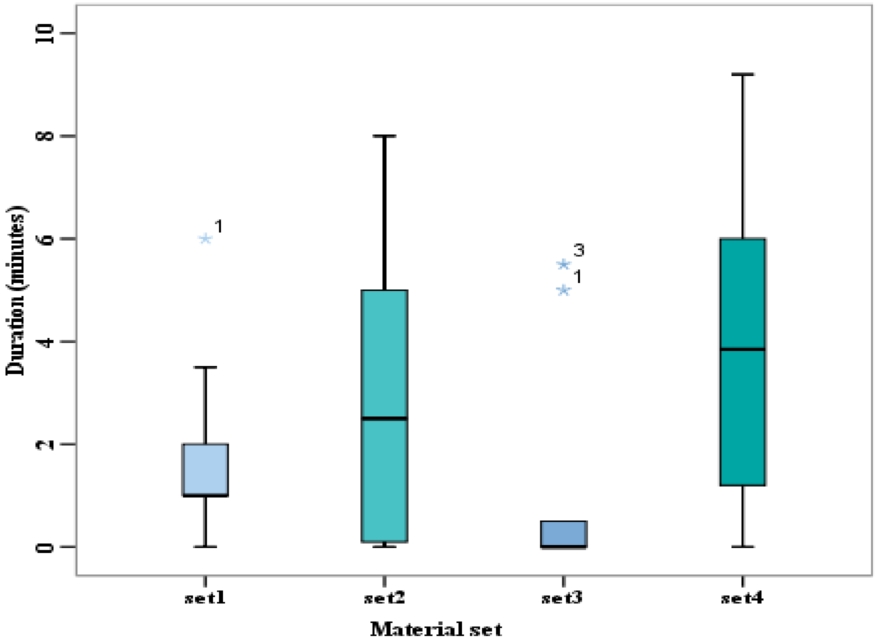


Figure 5.1 Group duration of nest building using each set of materials.

Frequency of nest construction in each presentation of material sets

To test if the number of nests constructed varied between each presentation of materials, the numbers built in each presentation were compared. For set 1, a total of 37 nests was constructed (see table 5.9), 16 of which were built on the 1st presentation of materials, with 21 being built during the 2nd presentation, a non-significant difference (z = -1.52, p = 0.13). With set 2, 55 nests were constructed, 28 on the 1st presentation of materials, 27 during the 2nd presentation, a non-significant difference (z = -0.45, p = 0.66).

For set 3, only 28 nests were constructed, 14 on each presentation of materials. For set 4, a total of 50 nests were constructed, 26 of which were built on the first presentation, with 24 being built during the 2nd presentation; this again was a non-significant difference (z = -1.00, p = 0.31).

Table 5.9 Individual data for number of nests built in the 1st and 2nd presentation of materials

Condition	**1**		**2**		**3**		**4**	
Presentation	**1st**	**2nd**	**1st**	**2nd**	**1st**	**2nd**	**1st**	**2nd**
Chimpanzee								
Lyndsey	4	4	4	4	4	4	4	4
Kilimi	0	2	1	0	2	1	0	0
Emma	4	3	3	4	2	2	3	3
Lucy	0	2	3	3	1	2	3	3
Qafzeh	0	1	3	3	1	0	2	2
Louis	0	1	2	3	2	1	3	2
David	3	3	3	2	0	1	4	3
Kindia	4	4	4	4	2	2	4	4
Liberius	1	1	4	3	0	1	1	2
Ricky	0	0	1	1	0	0	2	1
Nests built per presentation	**16**	**21**	**28**	**27**	**14**	**14**	**26**	**24**

5.4 Discussion

Since the publication of early accounts of ape nest building (e.g., Bolwig 1959; Goodall 1962; MacKinnon 1974; Nissen 1931), interest in the actual motor patterns involved in the daily behaviour of nest construction appears to have waned, with the exceptions of Bernstein (1962, 1967, 1969) and more recently Videan (2006a). Therefore, one of the aims of this study was to provide a detailed description of nest building behaviour, to help fill this gap in the sleep-related literature (Fruth & Hohmann 1996)

Comparable to observations of free-living chimpanzees (Goodall 1962; Nissen1931), gorillas (Bolwig 1959) and orangutans (MacKinnon 1974), the gathering and arranging of nesting materials around the body were typically the first and most frequently observed techniques of nest construction in this captive group. Similar descriptions from laboratory housed apes, such as Bernstein's (1962) description of chimpanzees 'winding' materials around themselves, and Morimura and Mori's (2010) description of chimpanzees 'shaping' materials around the body, also suggest that these techniques are the basic requirements for making a nest that will provide comfort and/or warmth.

Similarly, the pressing of materials into the nest rim is reminiscent of MacKinnon's (1974) descriptions of nest building in free-living orangutans; it is also observed in captive apes – hay was 'pounded' into position by chimpanzees, gorillas, and orangutans (Bernstein 1969). Pressing and turning in the nest are probably the simplest way to form the outside rim of the nest while ensuring that materials are distributed evenly around the body, again presumably to provide thermoregulatory benefits and comfort during sleep. Although comprehensive descriptions of nest building behaviour are lacking from the field and in captivity (McGrew 2004), there do seem to be striking resemblances in techniques across ape taxa, despite differences in environmental conditions, age, sex, and available nesting materials. This uniformity in construction techniques shared by wild-living apes suggests that this particular behavioural trait evolved in their common ancestor several million years ago (e.g., Baldwin et al. 1981), possibly to facilitate a comfortable, relaxed sleep (Fruth & Hohmann 1996).

However, one construction technique frequently observed in free-living apes was notably absent in the EZ chimpanzees, even when appropriate materials (eucalyptus branches and browse) were available. Several authors (e.g. Bolwig 1959; Goodall 1962; Nissen 1931) have described how twigs and branches are broken, bent and inter-woven to form the outside rim of the night nest. This complex weaving of materials was never observed in the EZ group, although it was documented in Videan's (2006a) report on laboratory-housed chimpanzees. Although firm conclusions cannot be drawn from a study of one population, it should be considered that such differences in nest building techniques might represent a cultural variation in nest building behaviours. Inter-group variations in tool-use have long been heralded as evidence of primate culture (e.g., McGrew & Tutin 1978; van Schaik et al. 2003; Whiten et al. 2001), yet disparities in nest building behaviour have been overlooked in this regard. Given the difficulty in collecting data on wild apes, studies focusing on nesting in captive populations could be a valuable tool in adding to our general knowledge of chimpanzee cultures.

The paucity of data on cultural variation in nest building has been partly attributed to a perceived homogeneity in nest construction (see McGrew 2004). Recently, however, Sousa and colleagues (2011) reported 2 distinct and easily distinguishable chimpanzee night nest types constructed in oil-palm trees in the Cantanhez National park (Guinea-Bissau). The authors concluded that differing sequences of leaf handling led to either ‘nests of bent leaves’ or ‘nests of broken leaves’. There were, unfortunately, no direct observations of nest construction in this field research, but it nonetheless highlights that nests are not necessarily constructed in a homogenous pattern.

Although some construction patterns do appear somewhat universal, the data from this group have also demonstrated some marked within-group differences in nest building behaviour. Captive-born females Emma and Lyndsey, for example, invariably used a range of complex techniques to construct recognisable, well-formed nests, whereas other group members either failed to construct nests (e.g., Cindy), or typically used simple techniques to form rudimentary, poorly constructed nests (e.g., Louis, Ricky). Of interest is that the latter three chimpanzees were the only wild-born individuals in the group, contrasting with previous reports of wild-born chimpanzees making more nests than captive-born counterparts (Bernstein 1962, 1969; Videan 2006a), and also using more complex construction techniques. It is conceivable that the three wild-born chimpanzees were removed from their mothers during an important phase for socially learning and practicing precise nest-building techniques (see Goodall 1962, 1968), and so lacked more complex nest building skills. However, it should also be noted that, when constructing a nest, Cindy’s offspring (Lyndsey) and grand-offspring (Kindia, Kilimi) generally used complex techniques. It is therefore possible that Cindy at one time was a proficient nest builder, and these skills were imitated and practised by Lyndsey, and later her offspring. As the eldest group member, it is plausible that diminishing physical abilities (as with elderly humans: Laurentani et al. 2003) have made it more difficult for Cindy to manipulate materials into a recognisable nest.

There were also instances of idiosyncratic nest building behaviours, restricted to one group member. Adult male Louis, for example, was the only individual to hold material down with his foot - a variant also documented in wild chimpanzees (Goodall 1962) and in one population of laboratory housed chimpanzees (Bernstein 1962). Lyndsey was the only chimpanzee to chew eucalyptus twigs before incorporating them into the nest, and to lean out of the nest to ‘scoop’ the floor substrate into the nest rim. It thus appears that individuals may expand upon the ‘standard’ nest building techniques to suit their own requirements. These deviations may be examples of ‘innovative’ behaviours – spontaneous behaviours that emerge for solving a particular problem (Kummer & Goodall 1985). The construction of ‘leaf-cushions’ by chimpanzees at Bossou to sit on when the ground is wet (and so presumably improve comfort) is one example of an innovative behaviour (Hirata et al.1998); this population has been studied since the mid-1970s yet the behaviour had not been observed during the first twenty years of research.

The nest modifications shown by Lyndsey may have been spontaneous, innovative acts to improve the comfort of the nest. Twigs may have been chewed, for example, to remove uncomfortable, sharp ends. The incorporation of floor substrate into the nest rim may have strengthened the nest, again promoting more comfortable rest.

Without further research, however, it is impossible to be sure how rare this behaviour was. Only one sleeping area per night was scanned, leaving the possibility that similar behaviours performed by other individuals were missed. The issue of innovativeness in nesting certainly warrants further research; with their reputation for innovation (e.g., Lehner et al. 2010), captive orangutans would be worthy subjects from this perspective.

As expected, the chimpanzees showed a preference for soft (thus presumably more comfortable) nesting substrates - the highest rates of nest building were observed with (in descending order) hay, wood wool and straw. It is reported that captive primates rapidly become habituated to some enrichment items (see Honess & Marin 2006a,b). The group studied here did not appear to lose interest in the preferred materials they were given; initial preference for nesting materials continued into their second presentation. Longitudinal studies, however, would be needed before firm conclusions can be drawn for possible habituation rates to bedding materials.

When given a choice, materials such as hay, wood wool and straw were consistently chosen over simultaneously presented alternatives such as paper sacks, cotton and eucalyptus. These data are in keeping with previous studies, where softer nesting materials such as hay produced a greater number of nests than browse or paper (e.g. gorillas: Lukas et al. 2003; chimpanzees: Videan 2006a). Similarly, substrate preference tests on domestic farm animals (Manninen et al. 2002; Gordon & Cockram 1995) and laboratory rodents (Blom et al. 1996; van de Weerd et al. 1996) have shown that soft substrates are preferred for resting and nesting. Moreover, the degree of physical comfort is hypothesised to affect both nest site selection (e.g., bonobos: Fruth & Hohmann 1993) and nest building behaviour (e.g., chimpanzees: Nissen 1931) in wild apes.

Data from the questionnaire distributed to zoos and wildlife parks (chapter 2) showed that 9 facilities regularly provide one type of nesting substrate (straw, wood wool, paper only) to captive great apes. The data from the present study indicate that these materials are preferred over simultaneously presented alternatives. However, it should be noted that some individuals in the EZ group consistently used a combination of these materials when nest building – this was particularly marked when chimpanzees were provided with wood wool and cotton items (material set 2) and hessian sacks and browse (set 3). Zoos should therefore consider providing at least two nesting materials to ensure that all group members have access to resources they apparently ‘want’ (Dawkins 2004, 2006) for nest building. Survey data showed that more than half of zoos (14/23) do regularly provide a combination of nesting materials. This is recommended in light of the present findings. The presentation of two nesting substrates also allows apes to ‘line’ the nest with additional materials, as with Lyndsey in this study, which is in keeping with nest construction techniques documented in free-living apes (e.g., Bolwig 1959; Nissen 1931), and so provides opportunity for species-typical nest building behaviour. It is further noteworthy that nest construction times using the preferred materials (hay, wood wool) more closely resembles those typical of free-living chimpanzees (Bolwig 1959: 3 minutes; Goodall 1962: up to five minutes). This should be considered if aiming to promote behavioural repertoires and time budgets comparable to those of wild species.

In the light of Stewart et al.'s (2007) work on comfort of nests, future researchers could usefully consider evaluating the softness/comfort of nests built using different materials, adding an extra insight into comfort levels dependent on nesting substrate.

Bernstein's (1962) research into nesting materials included providing chains and rope. The suitability of these materials as nesting substrate is clearly questionable. The current study has also indicated some other materials that may be of limited value for nest building. Although they were incorporated into nests, eucalyptus branches and cotton items were never used as a single nesting material. These data may be surprising, given that branches and twigs form the basis of free-ranging chimpanzees' nests (Goodall 1962), and we might expect that cotton items are soft and comfortable. It could be that the EZ chimpanzees lacked the learned nest construction technique (Bernstein 1962; Videan 2006a) of bending and weaving branches to form a substantial nest rim, as is typical of their wild counterparts (e.g. Nissen 1931). Although cotton items could be arranged into an existing nest (e.g., Lyndsey), or draped over the legs (as with a blanket, e.g., Cindy), they were not used to initially form the outside rim of a nest (pers. observation). The preferred materials, hay, wood wool and straw, in contrast, could be easily arranged, tucked and pressed to form a defined nest rim. The ease with which materials can form a substantial nest structure should be taken into account; cotton clothes/towels and similar items should only be used in conjunction with other material that is known to facilitate the construction of a nest.

Preference tests can be used as a tool to gauge which resources are important to captive animals (Yeates & Main 2008), and give indications of the resources animals like and want (Dawkins 2004). However, it has been argued (e.g., Duncan 1992; Fraser 1996) that welfare is not necessarily poor if preferred resources are not available. It is also possible that captive apes may prefer a missing resource (e.g., Fraser 1996) that has not been used in the present study nor used across zoos and wildlife parks across the UK. Nonetheless, the use of simple preference tests for nesting materials may be beneficial for welfare in a number of ways, and have implications for husbandry practices.

As discussed in chapter 1, there have traditionally been three conceptualisations of animal welfare, in terms of how animals feel, their ability to express natural behavioural repertoires, and their biological fitness (Fraser et al. 1997). According to Dawkins (1990), positive affective states, including comfort, enhance animal welfare. During the present study, the provision of preferred materials appeared to stimulate nesting behaviour in a chimpanzee that failed to nest build with materials most frequently presented to the group. Although the nests were not well constructed, the aged male Ricky attempted to build nests with both wood wool and hay. In accordance with the natural living approach, this emergence of species-typical behaviour is indicative of improved welfare.

It seems likely that nesting on a softer, more comfortable material may promote better quality of sleep in captive apes; human sleep quality can be adversely affected by uncomfortable sleeping surfaces (Bader & Engdal 2000; Lee & Park 2006). As sleep is vital in maintaining physical and mental health (Savage & West 2007) and individual fitness (Webb 1975), the provision of preferred, soft nesting substrate may also be beneficial in terms of biological health and welfare.

Many zoos currently provide a combination of nesting materials to captive apes, but without the realization that some materials (for example paper sacks in the present study) are rarely used in nest construction. It may therefore be more cost effective to ascertain which materials are most frequently used for this purpose. This could be done by conducting a series of simple choice tests (as in the present study), or alternatively by simultaneously presenting a greater number of materials and observing which produce the greatest number of nests, which was not possible in the present study.

Conclusions and recommendations

This group of chimpanzees showed several nest building techniques that are comparable to those described in free-living apes and others housed in captive conditions. Given their ubiquitous nature, these techniques are probably the simplest way to form a physically comfortable nest. When compared with previous descriptions of nest building behaviour, these data also raise the possibility of cultural differences in nesting patterns – a question that has so far not been considered in the study of primate cultures, and so which merits further investigation.

In keeping with previous observations, the captive chimpanzees here consistently preferred soft nesting materials such as hay, wood wool and straw for constructing nests, although additional materials were incorporated. Facilities that house captive apes should consider these materials to facilitate nest construction. Eucalyptus and cotton items were used less frequently, suggesting limited suitability for nest building if presented as a single bedding substrate. These should therefore be used in conjunction with a more suitable substrate. Providing several materials can have multiple benefits for welfare: providing a comfortable sleeping site and thus enhanced sleep quality, facilitating nesting behaviour, and allowing the freedom to choose preferred substrate(s). These factors should all be taken into consideration when presenting captive apes with nesting materials.

Chapter 6

Seasonal and environmental influences on nesting behaviours

"It's a cruel season that makes you get ready for bed while it's light out" ~ Bill Watterson

6.1 Introduction

The effect of seasonality on multiple aspects of primates' daytime behaviour and ecology is widely acknowledged (e.g., Matsumoto-Oda 2002; Watts 1998; White 1998). Birth rates and party size, for example, vary according to season in wild bonobos (Furuichi et al. 1998; Mulavwa et al. 2008). Western lowland gorillas show seasonal variations in feeding, resting and travelling behaviours (Masi et al. 2009), and free-ranging orangutans demonstrate changes in both group and travelling party size (Buij et al. 2002; Sugardjito et al. 1987).

Field studies have shown that multiple behaviours vary across seasons in chimpanzees, including reproductive behaviours (Lodwick et al. 2004; Nishida et al. 1990; Wallis 2002), active periods (Doran 1997; Lodwick et al. 2004), and feeding and ranging behaviours (Doran 1997; Matsumoto-Oda 2002). Group party size and composition are also subject to seasonal changes (Furuichi et al. 2001a). Predation pressure and presence of oestrous females can affect seasonal variations in chimpanzee party size (Boesch 1996b; Boesch 1991a; Goodall 1986). Fluctuations in food availability and quality can account for variations in reproductive cycles (Anderson et al. 2006), grouping patterns (Boesch 1991a; Furuichi et al. 2001a; Moscovice et al. 2007) and ranging distance (Doran 1997).

In conjunction with ecological variables such as predation pressure and food availability, both day and nighttime behaviours of free-ranging primates can change as a direct consequence of seasonal fluxes in air temperature, levels of rainfall, and light conditions. For example, savanna chimpanzees (*P.t. verus*) at Fongoli, Senegal used caves significantly more frequently at the peak of the dry season, when air temperatures rose to a mean of almost thirty-five degrees Celsius (Pruetz 2007); the caves were significantly cooler than the surrounding woodland and gallery forest. The Sonso chimpanzee community at Budongo Forest also showed behavioural thermoregulatory strategies in response to temperature (Kosheleff & Anderson 2009). As daytime temperatures peaked, chimpanzees spent more time on cooler forest floors versus warmer tree canopies, with concurrent decreases in foraging (active) behaviour and increases in daytime resting.

Whereas Fongoli chimpanzees use caves to shelter from extreme heat, longitudinal observations of free-ranging chacma baboons have shown that caves are used more frequently in cold nighttime temperatures (Barrett et al. 2004). Although external temperatures could fall to extremely low levels (minimum of 1.9°C), temperatures inside caves remained fairly constant, varying by only 1.5°. The authors concluded that these sleeping caves provided protection from cold temperatures and wind.

Huddling behaviour is perhaps the most well known behavioural strategy to facilitate thermoregulation, and so comfort, around a sleeping site. Two populations of Japanese macaques huddled more frequently in winter (December-March) than in autumn months (October-November) (Hanya et al. 2007). Season-dependent increases in huddling behaviours have been documented across several other primate taxa (e.g., rhesus macaques: Southwick et al. 1965; howler monkeys: Gaulin & Gaulin 1995; see also chapter 1). In all of these species, sleeping cluster size increased during colder months. Changes in social behaviours as a result of climatic variables were reported in captive group-living stump-tailed macaques (n = 36, Dahl & Smith 1985). Combined measurement of thermal criteria (wind speed and air temperature), light condition (sunny versus cloudy) and behavioural componenents indicated that affiliative social behaviours (including huddling) generally increased under cooler, cloudy conditions, with a decrease in frequency of solitary activities. As with free-ranging populations, huddling behaviour appears to provide thermoregulatory benefits in captivity.

Vessey's (1973) report on the nocturnal behaviours of free-ranging rhesus monkeys stated that times of sunset and sunrise influenced activities around the sleep site. During summer, when sunset was approximately forty minutes later than in winter, there was a delay in movement into the mangroves. That is, retirement was delayed in periods of extended hours of sunlight. It was also noted that, regardless of time of year, vocalisations and movements increased forty minutes before dawn, and so these behaviours seemed dependent on sunrise. Kummer (1968 cited in Vessey 1973) also reported a correlation between morning activity patterns and sunrise in wild baboons.

In the great apes, seasonal and environmental variables also influence sleep-related behaviours. Generally, ape sleep site selection may vary from season to season, usually attributed to synchronised changes in resource availability (e.g., vegetation: Yamagiwa 2001; preferred fruit: Iwato & Ando 2007; abundant nesting material: Rayadin & Saitoh 2009). Basabose and Yamagiwa (2002) reported that chimpanzees in the Kahuzi-Biega National Park (DRC) showed season-dependent changes in nest site selection. During the dry season, chimpanzees mainly nested in secondary forest, with primary forest being significantly favoured during the latter stages of the rainy season.

Although not much studied, climatic variables such as rainfall, temperature, and light exposure have all been documented to exert influence on several nesting behaviours. Wild bonobos, for example, construct nests that are covered (by a canopy layer) more frequently during the rainy season than the dry season (Fruth & Hohmann 1994), thus protecting them from rainfall. Previous research showed that, following rain, day nests were built at higher levels than night nests, possibly as bonobos could dry off faster by exposing themselves to the sun (Fruth & Hohmann 1993). Schaller (1965) observed that gorillas in the Virunga Volcano region of DRC more frequently constructed night nests under the shelter of leaning tree trunks in rainy conditions. Later research on lowland gorilla communities in Equatorial Guinea also found that the frequency of nest building under cover increased during the rainy season (Groves & Sabater-Pi 1985).

Tutin and colleagues (1995) reported that the frequency of arboreal gorilla nests in the Lope Reserve (Gabon) was positively correlated with amount of rainfall. Nests constructed by chimpanzees in both Senegal and Equatorial Guinea were generally higher, and more open (not covered by a layer of vegetation) during the wet season (June-September/October). This may appear odd, as chimpanzees would thus be exposed to rain and wind. However, by building higher and uncovered nests, chimpanzees could avoid water dripping onto them from overhead vegetation during the night, and would also dry more quickly in the morning sunlight (Baldwin et al. 1981). At Gombe, a juvenile female was observed to construct a nest with a rainproof ‘roof’, by standing up and pulling palm fronds over herself and the nest (Goodall 1968). MacKinnon (1974) similarly reported that orangutans constructed ‘roofs’ or ‘umbrellas’ as protection from both rain and sunshine, by placing branches above the nest, or simply holding the branches above themselves.

Free-living apes typically build nests prior to sunset (see also chapter 3). Wild orangutans have been reported to nest build approximately 30 minutes prior to sundown (e.g., Harrison 1962; MacKinnon 1974). Chimpanzees also typically nest before sunset (e.g., Farmer 2002; Goodall 1962). There are, however, exceptions to these general findings. Both Goodall (1968) and Nissen (1931) observed that chimpanzee night nests could be constructed after dark. Similarly, gorillas have been documented to construct nests as night falls, when light was failing (Groves & Sabater-Pi 1985).

There is evidence that seasonal changes in lighting conditions influence retirement times in apes, similar to Vessey’s free-ranging macaques (1973). During the rainy season (between December and May), nests made by the Gombe chimpanzees were generally constructed one and a half hours before sundown, at approximately 18.00h. In contrast, during the dry season (June-October), nests were constructed later - between 18.45 hrs and 19.15 pm. ‘False dusks’ (low cloud resulting in low light conditions) and heavy rain outwith the rainy season also resulted in early nest construction (Goodall 1962). Time of leaving the nest was also affected by season, with chimpanzees rising much later during the rainy season, sometimes up to one hour after sunrise. MacKinnon (1974) reported similar patterns in free-ranging orangutans, with the onset of nesting generally being earlier in November than April. Temperature also appeared to also affect time of arising in these apes; on colder mornings, they stayed in nests for longer.

The effect of light on retirement times is of particular interest as sleep-related behaviours of diurnal primates and humans are regulated by both endogenous and environmental mechanisms. The circadian rhythms (‘biological clocks’) that regulate phasing of daily sleep-wake cycles change according to seasonal variations in day length and light (Cardinali 2000), and so the phasing of sleep-wake cycles is also subject to seasonal variation (Aujard & Vasseur 2001; Usui 2000). This change in light is one of the key environmental cues (known as ‘zeitgebers’) that influences daily patterns of wakefulness and sleep (Duffy et al. 1996; Kunz & Herrmann 2000; Mistleberger & Skene 2004; Monk & Welsh 2003; Stanley 2005).

Exposure to bright light in the evening (versus morning or afternoon), for example, delayed sleep onset by a mean of 1.62 hours in human participants (n = 23) (Carrier & Dumont 1995). After participants (n = 8) had been exposed to bright light or dim light prior to sleep onset, sleep duration was significantly shorter after exposure to bright light (Dijk et al. 1987).

Although there appear to be no studies on captive populations to specifically address the effects of seasonal changes in light, temperature and humidity on nesting-related behaviours of apes, some evidence indicates that variations in several aspects of nesting behaviour can be attributed to environmental and seasonal fluctuations.
In laboratory-housed chimpanzees (n = 20) ambient temperature and humidity levels affected several sleep-related behaviours. As maximum relative humidity increased from 61% to 100%, both sleep duration and sleep quality significantly decreased. Minimum humidity levels (from 32% to 90%) did not significantly affect sleep quality, but did result in increased total time in bed and sleep duration. As overnight temperature increased (ranging from 20°C to 31°C), chimpanzees typically spent less

time in bed, both retiring and arising later. Further, chimpanzees preferred sleeping on concrete floors than elevated platforms, which the author suggested may be due to the summer heat (the research was conducted between May and September, Videan 2006b). However, no cross-seasonal comparison was made, and so it is unknown whether frequency of ground nesting was subject to seasonal change.

Human studies have reported comparable findings. EEG and EoG measurements showed that higher levels of humidity (80% vs. 50%) resulted in decreased levels of slow wave and REM sleep and increased wakefulness in male participants (n = 9) (Okamoto-Mizuno & Tsuzuki 2003). Okamoto-Mizuno et al. (2005) reported that increased humidity increased adult males' (n = 8) heat stress during sleep, leading to increased bouts of nocturnal wakefulness. Measures of bedroom temperature and humidity, and wrist actigraph readings showed that summer time rises of temperature and humidity resulted in more disturbed sleep in elderly participants (n = 19) (Okamoto-Mizuno et al. 2010). Compared to autumn and winter, there were significantly more nocturnal awakenings during summer months. Okamoto-Mizuno et al. (2004) reported that higher levels of ambient temperature (32°C vs. 26°C) resulted in decreased duration of REM sleep and an increasing number of periods of wakefulness in elderly adult males (n = 10).

Cross-seasonal research on zoo-housed gorillas (n = 17) has also demonstrated that climatic variables influence nesting behaviours. During summer months, when indoor temperatures averaged approximately 27°C, gorillas spent over fifty percent of total scans lying in a sleeping posture on a bare floor, making no attempts to nest build. During winter observations (November-December, with an average approximate temperature of 21°C), the number of bare-floor nests decreased significantly, with a concurrent increase in elevated nests (Lukas et al. 2003). The techniques used in nest building also appeared to be affected by decreases in temperature; during winter months there was a significant increase in the amount of time ‘fluffing’ nesting material (hay) around the torso. Furthermore, the gorillas showed more habitual use of the same sleeping sites during winter than summer. This could be due to some areas being warmer than others, but unfortunately no details were given. In another study of zoo-housed gorillas (n = 16-21) during summer (July-August), one specific room (room 1) was used as a sleep site more frequently than any other (of a total of seven potential sleep sites) (Weiche & Anderson 2007). This room afforded the most open view of outside space, and an opening for fresh air to circulate. During colder months (September-October, January-April), another sleep site (room 5) was used more frequently than any other area. This room was the closest to the heated keeper area.

Appropriate lighting and thermal conditions may improve comfort, and so be important in maintaining welfare for captive animals (Gonyou 1994; see also chapter 5). Indeed, legislation dictates that species-appropriate lighting and temperature conditions are required for the comfort and well being of captive species (e.g., Animal [Scientific Procedures] Act 1986, cited in Wolfensohn & Honess 2005; Secretary of State’s Standards of Modern Zoo Practice 2004, Section 2). It has also been suggested that zoo animals should be given a choice of enclosures that feature differing light, humidity and temperature levels (Wickins-Drazilova 2006), potentially allowing them to express the environmental needs and preferences that are important to them (e.g., Dawkins 2004, 2006; Yeates & Main 2008). However, with the exception of the studies cited above, research that specifically focuses on the effects of environmental variables on ape nighttime behaviours is negligible, despite having implications for husbandry practices and welfare.

Study aims and hypotheses

In free-ranging apes, time of retirement, sleep site selection, and nesting behaviours are influenced by a number of seasonal and environmental factors, including rainfall, temperature and light conditions. However, little attention has been paid to environmental features that may influence nesting and sleep-related behaviours in captive groups. The aim of the present study was to compare several aspects of nest-related behaviours in zoo-housed chimpanzees over two seasons. This not only adds to our knowledge of factors that can influence this important facet of chimpanzee daily life, it can also lead to practical considerations for enclosure design, management practices and welfare. In keeping with reports from both wild and captive apes, it was predicted that:

a. Time of retirement will be later during lighter spring months.

b. During winter the warmest sleeping sites will be more frequently utilised - the inverse was expected during warmer spring months

6.2 Methods and analyses

Data collection

The data presented here were obtained during two studies of the chimpanzee group (n = 11) housed at Budongo Trail exhibit, Edinburgh Zoo. The first set of observations (chapter 4) was conducted in winter (December 2008 through January

2009). Times of sunset in Edinburgh during these observations ranged from a minimum time of 15.38 h to a maximum of 16.44 h (median time: 15.54h, IQR: 0.74). The second study (chapter 5), took place in April through May 2009. Times of sunset for the duration of this study ranged between 19.44 h and 21.00 h (median time: 20.26 h. IQR: 0.4).

Although these studies addressed different aspects of nest-related activities, details of retirement times and sleep site selection[12] for each chimpanzee were recorded in each study. Thus, retirement times, sleep site selection and nesting groups could be compared across season. Median retirement times were determined from winter group scans (excluding nights where chimpanzees were not directly observable) and focal-pod scans during springtime data collection (see chapters 4 & 5). Details of pod temperatures and humidity levels are from records kept by primate care staff at Budongo Trail[13]. Although these records do not extend to the off-exhibit (OE) area, it is known that this area is heated (pers. comm. with EZ staff), as it is always accessible to chimpanzees and used by staff during working hours.

Data analyses

Kolmogorov-Smirnov tests showed that the data were not normally distributed, and so non-parametric Wilcoxon signed-ranks tests were used for all group and individual analyses. All data were analysed in SPSS 17.0. Tests were one-tailed, with alpha set at 0.025.

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[12] There are 5 potential sleep sites at Budongo Trail – 3 pods, off exhibit (OE) area and connecting tunnels (Tun). See also chapter 3.

[13] Temperature and humidity data are not kept for the OE area, and so only data for pods 1, 2, and 3 are available for comparison.

6.3 Results

Seasonal variation in retirement times

During winter, group median time of retirement was 16.35h (IQR: 0.85); this increased to 17.20h (IQR: 0.6) during spring months. For nest builders' retirement was defined as the first indication of the onset of nest building (gathering of nesting materials), for non-nest builders, retirement was the adoption of a rest posture on substrate/nest basket (see chapter 3 for descriptions). This increase in latency to retire was significant (z = -2.94, p = 0.01).

The majority of chimpanzee retired before 17.00h during winter, but all group members retired later than 17.00h during spring observations. Adult female Lucy showed the greatest variation, retiring over almost one and a half hours later during spring. See table 6.1 for individual median retirement times in winter versus spring months.

Table 6.1 Individual median retirement times across season

Chimpanzee	Winter	Spring
Cindy	16.47 (n = 26)	17.17 (n = 8)
Lyndsey	16.30 (n = 26)	17.17 (n = 8)
Kilmi	16.40 (n = 5)	17.29 (n = 3)
Emma	16.33 (n = 26)	17.20 (n = 7)
Lucy	16.23 (n = 4)	18.02 (n = 6)
Qafzeh	16.08 (n = 2)	17.20 (n = 6)
Louis	16.23 (n = 8)	17.12 (n = 8)
David	16.33 (n = 25)	17.23 (n = 7)
Kindia	16.45 (n = 13)	17.23 (n = 8)
Liberius	17.33 (n = 12)	17.19 (n = 8)
Ricky	16.25 (n = 29)	17.16 (n = 8)

Seasonal variation in sleep site selection

Table 6.2 shows that only four chimpanzees (Cindy, Lyndsey, Kilimi, Kindia) tended to retire to the same sleeping site in both winter and spring. For the others, choice of sleeping site was more varied between the seasons. Several individuals who had most frequently retired to the off-exhibit area and pod 3 during winter most frequently retired to pod 1 during the spring. Emma, who preferred pod 3 during winter, most frequently retired to pod 2 in the spring. During winter, David preferred pod 1, but he mainly nested in the connecting tunnels during spring. Of further interest is that Cindy, Lyndsey and Ricky invariably retired to one specific sleeping location only (Cindy: nest basket 2, pod 2; Lyndsey: highest floor level, pod 2; Ricky: nest basket 5, pod 1). All other group members retired to at least 2 different sleeping areas.

Table 6.2 Comparison of individual most frequently used sleep site, plus percentage of total nights at this site, across season

	Winter		**Spring**	
Chimpanzee	**Frequently used site**	**% total nights**	**Frequently used site**	**% total nights**
Cindy	Pod 2 (n = 13)	45%	Pod 2 (n = 32)	100%
Lyndsey	Pod 2 (n = 25)	86%	Pod 2 (n = 32)	100%
Kilimi	OE (n = 24)	83%	OE (n = 22)	69%
Emma	Pod 3 (n = 17)	59%	Pod 2 (n = 15)	47%
Lucy	OE (n = 25)	86%	Pod 1(n = 13)	41%
Qafzeh	OE (n = 27)	93%	Pod 1 (n = 12)	38%
Louis	OE (n = 21)	72%	Pod 1 (n = 28)	88%
David	Pod 1 (n = 9)	31%	Tun (n = 17)	53%
Kindia	Pod 3 (n = 15)	52%	Pod 3 (n = 28)	88%
Liberius	Pod 3 (n = 18)	62%	Pod 1 (n = 25)	78%
Ricky	Pod 3 (n = 24)	83%	Pod 1 (n = 32)	100%

Seasonal variation in nest group composition

As the majority of chimpanzees changed sleep site between seasons, the composition of nest groups also showed variation. During winter observations (see also chapter

4), Qafzeh, Louis, Kilimi and Lucy frequently formed a nesting group in the off-exhibit area during winter (41% of total nights), but there were no occurrences of this nest group during spring. During the same period, the most commonly observed nest group (14% of total nights) in pod 2 comprised of Emma, Lyndsey, Cindy and Kindia. With Kindia favouring pod 3 during spring, this nest group was never observed during spring observations. Cindy, who had frequently shared pod 3 with Emma and Ricky (41% of total nights) during winter only ever retired to pod 2 during spring, invariably sharing this sleep site with her adult daughter Lyndsey.

Seasonal variation in sleep site occupancy

Table 6.3 shows that pods 1, 2, and the connecting tunnels were used more frequently during spring observations. This between-season difference was significant for pod 1 (z = -4.592, p = 0.01) and the connecting tunnels (z = -1.94, p = 0.025), but the increase of use of pod 2 fell just short of significance: z = -1.92, p = 0.03. Compared to winter, significantly fewer individuals slept in the off-exhibit area and pod 3 (z = -4.75, p = 0.01; z = -3.27, p = 0.01, respectively) during spring.

Table 6.3 Minimum, maximum and median number of chimpanzees in each sleeping site per night across season

	Winter (n = 29)			**Spring (n = 32)**		
Sleep site	**Median**	**IQR**	**Range**	**Median**	**IQR**	**Range**
Pod1	0	1	0-4	3	1	2-5
Pod2	2	1	1-4	3	1	2-5
Pod3	3	2	0-6	2	1	0-5
OE	4	1	2-6	2	1	0-3
Tun	0	1	0-3	1	2	0-4

Temperature, humidity and sleep site occupancy

As they are under human control, the temperatures of each pod did not vary to a great extent between seasons (see table 6.4). Pod 1 temperatures and humidity levels were very similar across both seasons. Similarly, pod 2 median temperatures varied by only 1°C, although humidity levels did increase in spring months. Median temperatures in pod 3 decreased in spring, with a concurrent increase in humidity levels by almost 10%.

Table 6.4 Median temperature (in degrees Celsius) and humidity levels in pods 1, 2 and 3 during winter and spring

Sleep site	**Winter (n = 29)**		**Spring (n = 32)**	
	Median temp (plus IQR)	**Median humidity (plus IQR)**	**Median temp (plus IQR)**	**Median humidity (plus IQR)**
Pod 1	21.2 (1.6)	43% (5)	22.0 (3.2)	43% (4)
Pod 2	24.8 (1.4)	47% (17)	25.8 (1.5)	55% (19)
Pod 3	23.2 (1.6)	48% (12)	19.0 (3.4)	57% (10)

During winter, pod 1 was the coolest and least humid pod, and was not often used as a sleep site (median number of chimpanzees per night: 0), suggesting that that coldest sleeping area was avoided. Although not typically the warmest area, pod 3 had the highest humidity levels, and was the most frequently used of all the pods (median number of chimpanzees: 3). The warmest area with medium humidity levels, pod 2, was used by a median of 2 chimpanzees per night. These data indicate the warmest pods with the highest humidity levels were generally favoured during winter months.

In contrast to winter data, pod 1 was frequently used during spring (median number of chimpanzees: 3). Although humidity levels remained lower than in other pods, this area was no longer the coolest. During spring, the lowest temperatures were generally in pod 3, which also had the highest humidity levels. There was a significant decrease in the number of individuals retiring in this pod. As in winter, pod 2 was the warmest sleeping area during spring, and there was a slight increase in the number of individuals retiring to this area. These data indicate that the warmest, least humid, areas were favoured during spring.

Seasonal variation in frequency of elevated nesting

Table 6.5 shows that, for several individuals, there was no difference in the frequency of retiring to an elevated/substrate location from season to season[14]. Elderly individuals Cindy and Ricky habitually retired to an elevated platform during both seasons. Similarly, David invariably retired to an elevated nest basket or the elevated connecting tunnels. Female Lyndsey consistently nested on the ground during both observation periods. During winter, Emma also made only ground nests; she built only one elevated nest during spring (pod 3, nest basket one).

Only the youngest males, Kindia and Liberius showed between-season variation in elevated retirement/nesting. During winter, Kindia retired to elevated areas in approximately half of total observations, whereas in spring only one elevated nest was constructed. In contrast, Liberius retired to elevated locations more frequently in spring compared to winter.

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[14] Males Qafzeh and Louis and females Lucy and Kilimi were excluded from analysis as they most frequently retired to the off-exhibit area during winter.

Table 6.5 Individual frequencies of elevated nesting/sleeping in winter versus spring (plus % of total observations across each season)

Chimpanzee	Winter		Spring	
	Frequency of elevated nesting/retirement	% of total observations	Frequency of elevated nesting/retirement	% of total observations
Cindy	26	100%	32	100%
Lyndsey	0	/	0	/
Emma	0	/	1	4%
David	25	100%	29	100%
Kindia	13	46%	1	4%
Liberius	12	41%	26	93%
Ricky	29	100%	32	100%

6.4 Discussion

There is a plethora of data indicating that several primate daytime behaviours vary across seasons (Doran 1997: Lodwick et al. 2004; Matsumoto-Oda 2002; Nishida et al. 1990; Wallis 2002). With regard to nighttime behaviours, seasonal decreases in temperature have been shown to influence huddling behaviours in monkeys (e.g., macaques: Southwick et al. 1965; Wada et al. 2007), and seasonal rainfall levels can alter the nesting patterns in great apes (e.g., chimpanzees: Baldwin et al. 1981). Relatively little attention has been paid to the seasonal and environmental factors that may influence the same behaviours in captive apes, despite the fact that environmental variables are important in attempts to promote captive animal welfare (e.g., Honess & Marin 2006b; Morgan & Tromborg 2007).

Although scarce, field data show that free-living apes show seasonal variation in retirement times, generally nesting earlier in rainy versus dry seasons (e.g., chimpanzees: Goodall 1962; gorillas: Groves & Sabater-Pi 1985; orangutans: MacKinnon 1974). As predicted, this species-typical nesting pattern was also observed in the EZ chimpanzees, with the group retiring significantly later during spring versus winter months. Typically ranging between 17.00 and 18.00hrs during spring, these retirement times are also broadly in keeping with those of wild apes. Groves and Sabater-Pi (1985), for example, reported that gorillas usually nested between 17.30h and 18.30h. Farmer (2002) similarly reported a mean nest building time of 17.47h in four rehabilitant chimpanzees.

However, it is notable is that the EZ chimpanzees retired approximately thirty minutes *after* sunset during winter, contradicting reports that wild apes typically nest build before darkness (e.g., Harrison 1962; MacKinnon 1974), and at earlier times during inclement weather conditions (e.g., Goodall 1968). In captive settings, apes are freed from environmental variables such as encroaching darkness and inclement weather by the use of artificial lighting systems and indoor shelter from the elements. This may explain why nests were constructed after the onset of darkness. If zoos intend to approximate the sleeping habits of free-ranging apes, factors such as light levels should be taken into consideration. During winter, bright lighting around the time of retirement is not recommended; rather, low-level lighting systems could be used to encourage early nest building that is typical of wild apes. Given that human-controlled light cycles that do not reflect natural circadian activity can cause stress (Morgan & Tromborg 2007), light levels should be considered in terms of welfare.

Seasonal variation in the nesting behaviour of great apes is often attributed to factors such as abundance of nesting substrate (Rayadin & Saitoh 2009) and proximity to preferred foods (Iwato & Ando 2007). Nonetheless, the present study has shown that even when these variables are under human control, there is still evidence of seasonal differences in nesting patterns. Pod 1, for example, was used significantly more frequently in spring than winter, whereas the inverse was true for the OE area and pod 3.

Previous research (see chapter 4) had indicated that social factors (e.g., presence of kin, daytime associations) had little impact on these chimpanzees’ choice of sleeping site. Rather, the majority of the EZ group habitually returned to a preferred sleeping area, in keeping with reports of wild bonobos and chimpanzees (Fruth & Hohmann 1994; Sept 1998). In the present study, most (7/11) chimpanzees altered their choice of sleep site from winter to spring. In keeping with recommendations from previous chapters, this demonstrates the importance of providing multiple sleeping sites to captive apes to allow them to express individual preferences for different microclimates and light levels (e.g., Ross 2006; Wickins-Drazilova 2006). As wild conditions flux with environmental changes, it has been suggested that captive animals should have comparable opportunities to seek, and exercise control over, environmental conditions that bests suits their environmental and behavioural needs (Coe 1992).

Appropriate thermal conditions may improve comfort, and so can also be regarded as an important factor for maintaining welfare in captive animals (e.g., Gonyou 1994). Early experimental work showed that shaved adult chimpanzees exposed to temperatures above their ‘thermoneutral zone’ of 20-29°C displayed symptoms indicative of physiological stress (e.g., sweating, panting, signs of heat stroke: cited in Kosheleff & Anderson 2009). In this study, as expected, seasonal changes in sleep site occupancy was partly influenced by temperature. Heat was more relevant in winter, when the heated OE area and the warmest pods (3 and 2, respectively) were preferred as sleep sites. Previous research on zoo-housed gorillas reported similar findings: during colder months the warmest indoor area was preferred (Weiche & Anderson 2007). Although high levels of humidity are known to be detrimental to both human (e.g., 80% humidity: Okamoto-Mizuno & Tsuzuki 2003) and chimpanzee (e.g., up to 100%: Videan 2006b) sleep quality, the EZ chimpanzees appeared to prefer sleeping areas with relatively high humidity (pods 3 and 2, respectively) during winter. Although humidity levels in the EZ facility were much lower than in facilities described above, further attention should be paid to this factor, particularly as sleep deprivation is known to have several detrimental effects on physical and psychological health (e.g., lowering immune function Carskadon 2004; leading to depression: Kahn-Greene et al. 2007).

These findings are also relevant for individuals that do not habitually construct nests, as nests themselves are thought to provide warmth and comfort throughout the night (e.g., Nissen 1931; Stewart et al. 2007; see also chapter 5). Elderly female Cindy, for example, was never observed to construct a night nest, and so it is notable that she retired to the warmest areas in winter (pod 2, and less frequently in pod 3). During spring she invariably retired to pod 2, which was the warmest and most humid of all the sleep sites. Although laboratory and zoo-housed apes typically construct night nests, some rarely or never do (e.g., captive- born chimpanzees: Bernstein 1962). In the absence of nest construction, care should be taken to provide adequate heating and humidity levels to ensure comfort and to avoid thermoregulatory distress.

During winter, the coolest sleeping site (pod 1) was typically avoided. This pod also had a door to the outside enclosure. Although it was closed in the evening, cold draughts could have further lowered ambient temperature, and so further inhibited this pod’s use. These observations are broadly in keeping with field studies that have shown nesting patterns varying with inclement weather (e.g., bonobos: Fruth & Hohmann 1994 and gorillas: Groves & Sabater-Pi 1985 nesting under shelters during rains). By choosing the warmest areas and avoiding the coolest, the EZ chimpanzees used comparable thermoregulatory strategies to increase warmth and comfort during winter.

However, the prediction that the coolest sleeping area (pod 3 in the present study) would be preferred in spring was not supported. Contrary to expectation, the pods (1 and 2) with the highest temperatures during this period were used by most chimpanzees. Data from field research and captive groups have indicated that primates will utilise areas that provide shelter from extreme temperatures, such as Pruetz’s (2007) report of increased cave use by savanna chimpanzees in temperatures of around 35°C. Similarly, zoo-housed lowland gorillas (n = 19) spent more time in indoor shaded areas with concrete floors when temperatures increased during summer (Stoinski et al. 2002). Chacma baboons used caves to shelter from extremely low nighttime temperatures of approximately 2°C (Barrett et al. 2004).

In the present study, the variation in indoor temperature between winter and spring may not have been marked enough to necessitate relocating to regulate body temperature. Future studies would do well to measure temperature and record sleep site selection during summer months. Increased variability in temperatures might lead to more discernable effects on choice of retirement areas, as reported in laboratory chimpanzees (Videan 2006b) and zoo-housed gorillas (Weiche &

Anderson 2007). Given that pod 3 was always the most humid, it does appear that temperature was more of a defining factor in sleep site choice during spring.

There was little evidence of seasonal changes in elevated versus ground nesting. Only one chimpanzee (Kindia), made fewer elevated nests during spring. Conversely, another sub-adult male, Liberius, made more elevated nests in spring than in winter. Lyndsey and Emma almost invariably constructed ground nests, whereas David, Ricky and Cindy exclusively constructed elevated. These data contrast with research on zoo-housed gorillas (Lukas et al. 2003), which showed more elevated nests during winter, and more sleeping on bare ground during warmer months. Similarly, laboratory-housed chimpanzees slept on concrete floors during summer (Videan 2006b), despite the fact that elevated areas were available. Conceivably, the Edinburgh spring was not warm enough to increase the incidence ground nesting. It is also possible that individual preferred heights for sleeping are resistant to environmental changes. Survey data (chapter 2) and observations of the BD group (chapter 3) indicate that there are both inter- and intra-group differences in frequencies of ground nest construction.

The significant increase in the use of pod 1 from winter to spring could have been due to the increase in temperature. However, it is noteworthy that this area features a partially glass-covered wall (plate 6.2) that provides visual access to the outdoor enclosure. Weiche & Anderson (2007) reported that in summertime captive gorillas favoured a room that circulated cool, fresh air, and also had the most open view. Free-living chimpanzees are known to base their choice of sleep-site on the view they provide of the surrounding area (e.g., Baldwin et al. 1981; Kortland 1992; see also chapter 1). It is therefore difficult to determine exactly which factors contributed to sleep site selection in the present study.

Plate 6.2 Pod 1 with exterior glass wall. Adult male Louis is lying in the wire basket (nest basket one) on the far right of the picture.

With the onset of spring several chimpanzees (Liberius, Louis, Lucy, Ricky and Qafzeh) frequently retired to pod 1, although they had all previously favoured pod 3 and the off-exhibit area. This general shift appeared to have an effect on nest group composition. Seasonal changes are known to influence nest group size in free-ranging chimpanzees (Goodall 1968). In Senegal, number of nests per group and number of nests per tree both increased during the rainy season (Baldwin et al. 1981). At Gombe, the largest nest group documented was seventeen; with the largest number in one tree being ten (Goodall 1968). Seasonal variations were attributed to the presence of oestrus females and the availability of food and nesting resources.

It is less clear what factors drove the changes in nest party composition observed here, given that food and nest-related resources were always available. Winter nest groups such as Qafzeh, Louis, Kilimi and Lucy did not continue to retire together during spring. Conversely, mother-adult offspring dyad Cindy and Lyndsey, increased their sleep site sharing in spring, and were the only two individuals to spend every night of observations in the same site. These seasonal changes may reflect individual preferences for environmental conditions in certain areas, again showing the necessity of numerous sleeping areas. It should be noted, however, that the series of aggressive encounters documented at the end of winter observations might also have influenced nest group composition (chapter 4). No observations were carried out between March and April, and so it remains unknown if disruptions to the social structure of the group affected nighttime grouping patterns.

Conclusions and recommendations

Seasonal and environmental fluxes in temperature and weather conditions are known to affect the nesting behaviour of wild apes. The present study is one of the few to directly compare several aspects of nesting behaviour across seasons. The findings from this study are complex and subject to a large degree of intra-group variation; longitudinal research that incorporates summer and autumn data is required before firm conclusions can be drawn about how environmental variables influence sleep-related behaviours of captive chimpanzees. Nonetheless, these data can be used to make several husbandry recommendations that are relevant for the welfare of captive apes.

If possible, lighting should be adjusted to reflect seasonal dusk patterns, thus encouraging species-typical retirement times. Given the seasonal and individual variations in choice of sleep site, it is recommended that numerous sleeping areas of varying temperatures and humidity levels be provided (as done at EZ), allowing individual apes to choose their sleep sites according to their own welfare needs. Previous research has shown that extreme temperatures and humidity levels can have adverse effects on both sleep quality and sleep duration. Although the same levels are not applicable here, these factors should be considered for the comfort and biological welfare of captive apes. In the current study, sleeping areas of temperatures above 22°C (within chimpanzees' natural thermoneutral zone) were typically preferred during winter and spring, and areas with the highest humidity were more frequently used in winter, with the least humid area used in spring. Without further research, however, optimal levels of temperature and humidity that are preferred by captive apes will remain unknown.

Chapter 7

Population differences in nest construction techniques: Nest building cultures?

"Sometimes the clues to culture are in the nuances of a universal habit" ~ McGrew 1998

7.1 Introduction

Several primate taxa, such as Japanese macaques, chimpanzees and orangutans, are known to have unique, population-typical behavioural traditions (van Schaik et al. 2003; Whiten et al. 1999, 2001, 2007); these have been widely cited as evidence of primate cultures (e.g., McGrew & Tutin 1978; McGrew 1998; Reynolds 1990; Whiten 2000). Although the definition of culture itself is problematic, and variable across academic disciplines (Whiten et al. 1999), the term 'culture' can be broadly defined as a population-specific behaviour that is acquired and transmitted via social learning mechanisms (McGrew 1998; Mobius et al. 2008).

Of all non-human primates, chimpanzees show the largest degree of inter-population behavioural diversity (Fowler & Sommer 2007; Whiten et al. 1999, 2001). Some behavioural patterns are frequently shown by chimpanzee communities at some study sites, yet are rare or absent in others. Chimpanzees on the western side of the Sassandra-N'Zo river (Cote d'Ivoire), for example, are known to crack nuts, yet the community on the eastern side fail to do so, despite having access to the same resources (Boesch et al. 1994). At Bossou (Guinea), chimpanzees detach fronds from oil-palms and use them to smash the crown of the plant, producing pulp which is then consumed (Yamakoshi & Sugiyama 1995). This behaviour has yet to be documented at any other study site (Lycett et al. 2010). The well-known 'grooming handclasp', first documented by McGrew and Tutin (1978), was a frequently performed behaviour in the 'K' chimpanzee community at Mahale. Since this first report, the same grooming posture has been observed at Kibale and Tai (Boesch &

Tomasello 1998), yet has never been documented at Bossou or Gombe (McGrew 1998).

Several aspects of tool use behaviours are known to vary greatly between populations. Compared to Bossou, the chimpanzees at Tai (both in west Africa) use significantly shorter dipping tools when preying on the same ant species (Mobius et al. 2008). Similarly, Gombe chimpanzees use a long tool when gathering army ants, and then use their free hand to collect ants on the stick before consuming them. At Tai, as well as using shorter tools, fewer ants are gathered, and these are directly consumed from the tool (cited in Boesch 1996a).

Three populations of *P.t. verus* have been recorded using different tools for nut cracking. Sapo forest chimpanzees (eastern Liberia) used stone ‘hammers’ to crack open several species of nut (Anderson et al. 1983), whereas Tai forest chimpanzees also used wooden ‘clubs’ for the same purpose (Boesch & Boesch 1983). Although Sapo forest chimpanzees used both stone, and less frequently, wooden, anvils, at Bossou, it was reported that stone is the *only* material ever utilised as an anvil (Matsuzawa 1994).

In the absence of determinant ecological factors, such inter-population behavioural variations may be attributed to cultural differences, which have most likely arisen through social learning (Boesch 1991b, 2002; Lycett et al. 2007; McGrew 2004; Whiten et al. 1999, 2001). These findings raise questions about the evolution of human cultural processes, and aid our understanding of the extent to which chimpanzee and human cultures are underpinned by the same cognitive and social mechanisms (Horner et al. 2010).

Several decades of field research at study sites across Africa have indicated that numerous behavioural patterns are customary in some populations of chimpanzees, yet absent in others (Whiten et al. 1999, 2001). Boesch and Tomasello (1998) described some population-specific behaviours observed in the longest-studied free-ranging chimpanzee groups. These included foraging, communicative, and body orientated behaviours. Whiten and colleagues (2001) extended this data set considerably, reporting cultural variation in thirty-nine behavioural patterns of *P.t. verus*, *troglodytes* and *schweinfurthii* across nine different study sites. Again, many of the behavioural patterns are body-and foraging/tool-related. It is well documented that chimpanzee nest building is a daily (Fruth & Hohmann 1994, 1996; Goodall 1962, 1968), socially facilitated (Bernstein 1962, 1969; Goodall 1962, 1968; Videan 2006a) behaviour, yet there appears to be no specific cross-cultural comparison of nest building in chimpanzees (McGrew 2004). Given the number of isolated populations across Africa, it would seem reasonable to expect some inter-population variation in nesting behaviours which, if ecological conditions could be ruled out, may also be considered as cultural.

Although not subject to a large amount of research, there are conflicting views on the extent to which nesting behaviours are ecologically or socially/culturally determined. Baldwin et al. (1981) compared several features of nests built by *P.t. troglodytes* in Equatorial Guinea and *P.t. verus* in Senegal. Features such as height of nests, nest group patterns and openness of nests appeared to be related to environmental factors

- predation pressures, availability of food and water, seasonality, and availability of vegetation used in nest construction. In contrast, Koops et al. (2007) reported that environmental variables could not explain the construction of ground nests by chimpanzees in the Nimba Mountain region of Guinea. It was expected that ground nests would more frequently be built in high altitude areas during the dry season, where high winds may prevent tree nesting. However, the number of ground nests did not vary according to season or altitude. Further, ground nests were constructed even when trees of appropriate species and size were nearby, suggesting that cultural or social factors determined this aspect of nesting behaviour in this population. Similarly, Matsuzawa and Yamakoshi (1996) proposed that the high frequency of ground nests recorded at Nimba (35% of 464 nests counted) indicated a "…remarkable behavioral variation in chimpanzee housing" (p224), when compared to areas such as Gombe, where ground nesting was mainly attributed to illness (Goodall 1962).

Maughan and Stanford (2001) recorded several thousand nests in a Ugandan National Park. Although ground nests represented a low percentage of total night nests, most ground nests were concentrated into small groups in one specific area. This could indicate a cultural variation within a small population. However, the authors were unable to eliminate the possibility that the ground nests might be explained by ecological factors, such as low predation pressure in this specific region. Of four neighbouring regions (Bossou, Seringbara, Yeale and Diecke), chimpanzee ground nests has been documented in only three areas (Humle & Matsuzawa 2001), again suggestive of inter-group variation in nesting patterns.

Boesch (1995) reported a significant increase in the frequency of arboreal day nest construction in Tai chimpanzees during a two-year period which coincided with an increase in group nesting (individuals building nests in the same group of trees at the same time). Given that there was no discernable change in environment, it was concluded that these changes were innovations that were socially transmitted to other group members, and so could be regarded as a cultural ‘fashion’.

Comparative data from three separate study sites also hint at cultural differences in nesting behaviours among free-ranging bonobos (Fruth & Hohmann 1993). Nests and nesting trees were higher in Lomako than in Lake Tumba and Yalosidi (all located in Zaire). Ground nests were constructed by both Lake Tumba and Yalosidi populations, but not by the Lomako population. Integrated nests (i.e. nests constructed across two or more treetops or in the junction of a treetop and side branch) were more frequent in Lomako than Yalosidi.

Observations on several populations of orangutans have shown that the ‘raspberry’ vocalisation (a spluttering sound associated with nest construction) is absent in three populations in Borneo, yet habitual in others. Similarly, this vocalisation is customary in one Sumatran population yet absent in another. Moreover, the ‘raspberry’ is performed in the final phases of nest building in Sumatra but prior to nesting in Borneo (van Schaik et al. 2003). Wild orangutan ‘leaf-carrying’ (when nesting materials are collected before reaching the nest site) has been observed at only one site out of seven, suggesting regional differences in this specific behaviour. This behaviour has been labelled as customary or habitual at several orangutan rehabilitation sites, but rare or absent in several others (Russon et al. 2007). At one site leaf-carrying appeared to be influenced by social factors, with juveniles copying the behaviour after seeing an adult female doing it. Further, the majority of leaf-carriers shared nests and made nests in close proximity to fellow leaf-carriers, supporting the view that this specific behaviour was socially transmitted.

Data collected during the course of this research also indicate that some nest-related behaviours differ between captive groups. For example, survey data (chapter 2) showed a disparity in the frequency of ground nest construction across both orangutan and chimpanzee groups housed in different facilities. Survey data also indicated that several groups of zoo-housed gorillas used browse for nest building, contradicting Lukas et al. (2003), who reported that browse was never utilised by the zoo-housed gorillas during their research. Data from the preceding chapter showed that, despite having access to the same bedding materials (straw and eucalyptus), and also despite the presence of wild-born individuals in both studies, the EZ chimpanzees were never observed bending or weaving browse in the manner of Videan's (2006a) captive chimpanzees.

Study aims and hypotheses

Although scant, data indicate that there may be inter-population, or cultural, variations in nest building behaviour, yet there have been no attempts to investigate this possibility. Therefore, the current study aimed to be the first to compare the nest building techniques of two captive-housed chimpanzee groups. Based on evidence from the field and from comparisons of captive ape data, it was expected that there would be inter-group variation in both:

a. nest-building techniques
b. the construction of ground (floor level) nests

7.2 Methods and analyses

Data collection

Ten nest-building episodes were randomly chosen for each individual in the Blair Drummond (BD) group (n = 4) between December 2007 and January 2008. For comparison, ten random episodes were chosen for the four most frequent nest builders in the Edinburgh Zoo (EZ) group between December 2008 and January 2009 (see chapter 3 for details of chimpanzees and housing in both groups). Observations of both groups had recorded the nest building technique(s) used by each individual within each group. During these periods, straw was provided as nesting material to both groups, although the EZ chimpanzees also had access to eucalyptus branches. The enclosures at BD and EZ offer numerous potential sleep sites, including substrate-covered floors and elevated structures (BD – wooden platforms, rubber-hose nest baskets; EZ – wire nest baskets).

Data analyses

Kolmogorov-Smirov tests showed that data were not normally distributed; therefore non-parametric Mann-Whitney U-tests were used for between-group comparisons of nest building techniques, duration of nest construction, and frequency of ground nest building. All tests were analysed using SPSS 17.0, and were two-tailed with alpha set at 0.025.

Details of chimpanzees used in comparisons

The four BD chimpanzees were Blossom (female, estimated age 50+, assumed wild-born), her male offspring Chippy (19 years, captive-born), Pansy (female, estimated late 50s, assumed wild-born), and Rosie (19 years, captive-born). The four EZ chimpanzees were David (male, 33 years), Emma (female, 27 years), Kindia (male offspring of David and Lyndsey, 11 years) and Lyndsey (female 25 years), all captive-born.

Definitions of nest building techniques

Previous research on the EZ group (chapter 5) showed that a range of techniques could be used during nesting construction (table 7.1). These techniques were used to compare the nest building patterns between the two groups. Techniques previously seen in the EZ group but not the BD group (e.g. making depressions in substrate, separating materials) were excluded from the current analysis.

Table 7.1 Nest construction techniques used by both groups, based on data from previous observations of the EZ group

Technique	Description
Gather-tuck (GT)	Nesting material is gathered towards the body, and loosely tucked around the torso/legs
Arrange-tuck (AT)	Nesting material is arranged around the body, and folded/tucked more tightly around the torso/legs
Press (PR)	Nesting material is pressed firmly downwards into the nest rim using either knuckles or wrists (see plate 6.2)
Turn (TUR)	Chimpanzee turns while in the nest, forming the nest shape around it as it turns (in sitting/standing position)
Throw (THR)	Nesting material is thrown above and behind the chimpanzee

Plate 7.2 An example of the 'press' technique. Emma (EZ group) presses straw downwards into the rim of her nest using the back of the hands.

7.3 Results

Nest construction techniques

Table 7.2 shows intra-and inter-group frequencies of nest construction techniques observed at least once during the randomly chosen nest building episodes.

Table 7.2 Individual and group frequencies of techniques used during nest construction (see table 7.1 for technique descriptions and codes)

Group and individuals	**G/T**	**A/T**	**PR**	**TUR**	**THR**
BD					
Blossom	10	10	0	0	0
Chippy	10	10	0	1	0
Pansy	10	10	1	0	0
Rosie	10	10	1	0	2
Group total	**40**	**40**	**2**	**1**	**2**
EZ					
Lyndsey	10	10	10	9	0
Emma	10	10	10	10	4
Kindia	10	10	6	1	0
David	10	10	8	2	0
Group total	**40**	**40**	**34**	**22**	**4**

The technique of gathering material toward the torso and then more closely arranging it around the body to form the outside rim of the nest was observed in all individuals, and so was not analysed for inter-group differences. There was a group difference in use of the technique of pressing nesting material into the nest rim. Only 2 BD chimpanzees used this technique (median frequency: 0.5, IQR: 1), whereas all 4 EZ chimpanzees did (median frequency: 9, IQR: 4). This difference was significant (U = 0.00, z = -2.35, p = 0.02).

Similarly, only 1 BD chimpanzee was recorded to turn around while forming the basic nest shape (median frequency: 0, IQR: 1), whereas all EZ chimpanzees did this, particularly the females, at least once (median frequency: 5.5, IQR: 9). This difference was also significant (U = 0.50, z = -2.23, p = 0.02).

The throwing technique was performed infrequently; it was observed in only one individual per group (BD median frequency: 0, IQR: 2; EZ median frequency: 0, IQR: 3), yielding a non-significant difference ($U = 7.50$, $z = -0.19$, $p = 0.85$).

Using a combination of techniques during nest construction

The number of techniques used per nest building episode (table 7.3) also showed inter-group variation.

Table 7.3 Individual and group data for median (plus IQR and range) number of techniques used per nest building episode

Group and individuals	Median (IQR)	Range
BD		
Blossom	2 (0)	/
Chippy	2 (0)	2-3
Pansy	2 (0)	2-3
Rosie	2 (1)	2-3
Group median (IQR) and range	**2(1)**	**2-3**
EZ		
Lyndsey	4 (0)	3-4
Emma	4 (0)	/
Kindia	3 (1)	2-4
David	3 (1)	2-4
Group median (IQR) and range	**4 (0)**	**3-4**

The BD chimpanzees typically used only two techniques during nest construction (gather-tuck followed by arrange-tuck). Indeed, these were the only techniques used by Blossom in the current study. The remaining group members all used an additional technique (e.g., Rosie: throwing technique; Pansy: pressing material) during at least one nest building episode. In contrast, the EZ chimpanzees typically used four techniques when constructing each nest. Lyndsey and Emma typically used a combination of gather/arrange-tuck, followed by turning in the nest and pressing materials into the rim. Turning during construction was less frequent in David and Kindia, but these chimpanzees did generally incorporate one more technique into the standard gather/arrange-tuck pattern (e.g., Kindia: throwing; David: pressing material). The EZ group used significantly more nest construction techniques than the BD chimpanzees (U = 128.00,z = -6.99, p = 0.01).

Duration of nest construction

Despite individual variation (table 7.4), EZ chimpanzees typically had a longer duration of nest construction than BD, with medians of 2 min and 1 min, respectively (see figure 7.1). Some individuals in the EZ group could take 5 minutes to nest build, compared with a maximum nest construction time of 3 minutes in the BD group. The inter-group difference in nest construction time was significant (U = 565.5, z = -2.45, p = 0.02).

Table 7.4 Individual nest construction times (in minutes) according to group

Group and individuals	Median time (IQR)	Range
BD		
Blossom	1 (0.5)	1-2
Chippy	1 (1)	1-2
Pansy	1 (1)	1-2
Rosie	1 (1)	1-3
EZ		
Lyndsey	2.5 (2)	1-5
Emma	3 (2)	1-5
Kindia	1.5 (1)	0.5-2
David	1 (0)	1-2

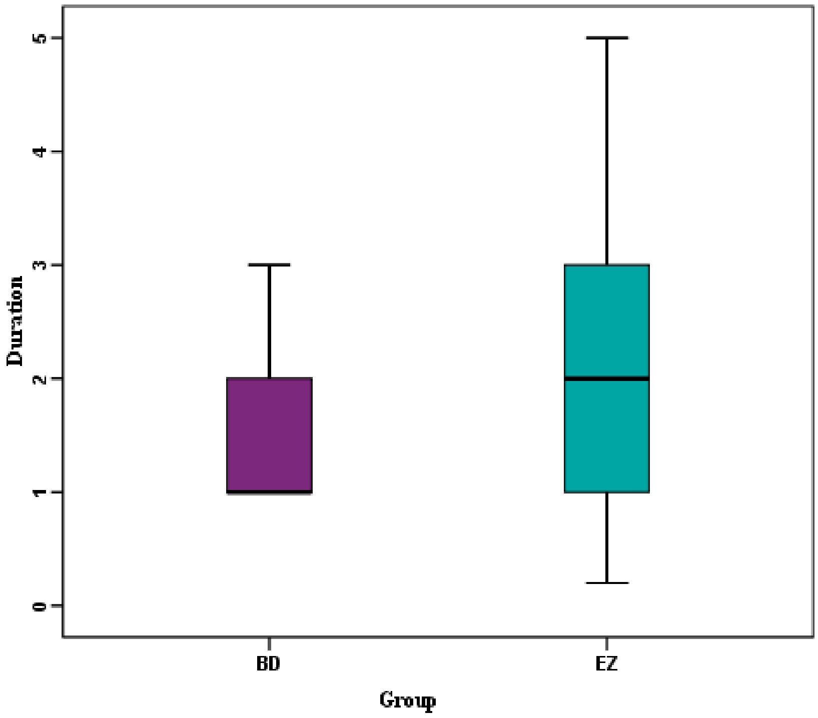

Figure 7.1 Median duration of nest construction per group

Frequency of ground nest construction

Nests constructed by the BD were exclusively elevated (table 7.5); ground nesting was never observed. Although there was intra-group variation between males and females in the EZ group, ground nests were built significantly more frequently than at BD (U = 0.00, z = -2.48, p = 0.01).

Table 7.5 Individual and group frequency of ground versus elevated nesting

Group and individuals	Ground nests	Elevated nests
BD		
Blossom	0	10
Chippy	0	10
Pansy	0	10
Rosie	0	10
Group total	**0**	**40**
EZ		
Lyndsey	10	0
Emma	10	0
Kindia	4	6
David	1	9
Group total	**25**	**15**

7.4 Discussion

Long-term field research at multiple sites has demonstrated that patterns of behaviour are customary or habitual in some ape communities, yet absent in others, which primatologists have proposed as evidence of culture (e.g., McGrew 1998; Ramsey et al. 2007; Whiten et al. 1999; van Schaik et al. 2003). Group differences in grooming techniques (McGrew & Tutin 1978), nut cracking (Boesch et al. 1994; Lycett et al. 2010; Whiten 2000), and foraging (Mobius et al. 2008; Whiten 2000; Whiten et al. 2001) are also increasingly considered as evidence of chimpanzee cultures.

Despite its prevalence in chimpanzee daily life, nesting behaviour is not generally considered in the context of the culture debate, reflecting an underlying belief that nest construction is homogenous across populations (McGrew 2004). In the present study, the techniques of gather-tucking and arrange-tucking bedding materials were common to both study groups. Free-ranging chimpanzees are reported to follow a structured behavioural sequence when nest building: they first construct the outside nest rim, followed by a central mattress, and finally add a lining of softer twigs and leaves (e.g., Bolwig 1959; Goodall 1962; Nissen 1931). The captive groups studied here also showed a quite standard technique of starting their nest by gathering, arranging and tucking straw around their torso to form the basic shape, a behaviour also recorded in other groups of laboratory-housed chimpanzees (e.g., Bernstein 1962; Morimura & Mori 2010; Videan 2006a).

However, even with this small sample size, several inter-group differences were notable. EZ chimpanzees typically employed construction techniques (e.g., turn, press) rarely seen in the BD group. Previous analysis (chapter 5) showed that EZ would separate strands of materials such as straw, but this behaviour was never observed in the BD group. For the EZ group, these techniques were frequently used in combination with the common gather/arrange tuck sequence, while the BD used additional techniques less frequently. This difference in the number of techniques used most likely accounts for the difference in nest building duration between the groups. It is possible that the EZ chimpanzees used a fuller range of complex techniques as they had access to an extra nesting substrate (eucalyptus branches). Field research has shown that the use of additional materials can influence the complexity of nest building techniques (Stewart et al. 2007). Thus, the range of techniques used by the BD group may have been constrained by the fact that only one material was presented. As discussed in the preceding chapter, the provision of at least two nesting substrates is recommended to encourage species-typical nest ‘lining’ behaviour (e.g., Nissen 1931) and durations of nest construction (e.g., Goodall 1962). However, it is noteworthy that the EZ chimpanzees used the techniques of turning and pressing even if straw was the only material used (pers.

obs.), suggesting that the number of materials presented was not the only factor in differences in nest building techniques.

As with field reports of free-ranging bonobos (e.g., Fruth & Hohmann 1993) and chimpanzees (e.g., Matsuzawa & Yamakoshi 1996), the frequency of ground versus elevated nesting varied between the captive groups studied here. BD chimpanzees invariably nested on an elevated platform. Ground nesting was frequent in the EZ group, with most of these nests were constructed by females Lyndsey and Emma. As with the pod floors at Edinburgh, the enclosure floor at Blair Drummond is covered with substrate, but also features an under-floor heating system (see chapter 3). Given that ambient temperature appears to affect sleep site selection in zoo-housed gorillas (e.g., Lukas et al. 2003), it seems surprising that ground nests were never constructed on this warm surface. Both Blossom and Pansy in the BD group were wild-born, and so could have been expressing patterns of arboreal nesting generally characteristic of free-living chimpanzees (e.g., Goodall 1968), although there are exceptions (e.g., Koops et al. 2007) as previously discussed. This nesting pattern could then have been learned and adhered to by their offspring, in keeping with the hypothesis that nest building behaviour is socially influenced (e.g., Goodall 1962; Videan 2006a).

Differences in enclosure layout may also account for the group difference in substrate nesting. Although the EZ chimpanzees constructed substrate nests, these were invariably on the highest floor levels, and so furthest from any potential draughts from the connecting doorways located at the lowest floor levels. At BD, the doorway to the kitchen area could potentially allow cooler air to circulate at floor level, which could account for the BD chimpanzees’ preference for sharing the elevated sleeping areas. Zoo-based research has indicated that gorillas select elevated sleeping sites more frequently in winter months (Lukas et al. 2003), suggesting that the colder floor area was avoided. Free-living chimpanzees are known to disperse into small groups when nesting (Goodall 1962), and it has been suggested that there is an ‘optimal distance’ of four meters between night nests (Baldwin et al. 1981, see also chapter 4). Restricted access to the floor[15] may therefore have reduced the BD group’s ability to disperse in a species-typical nesting pattern. With zoos emphasising the need for allowing natural behaviours to be expressed (e.g., Carlstead 1996; Markowitz 1997), these factors should be considered when designing ape enclosures.

It is also conceivable that the BD group had a strong preference for sleeping in proximity to kin, a phenomenon which has occasionally been documented in free-ranging chimpanzees (Riss & Goodall 1976) and zoo-housed gorillas (Weiche & Anderson 2007). Frequency of sharing with kin or non-kin was not analysed here, as the BD chimpanzees had only one general area (the night enclosure) for sleeping, whereas the EZ group had multiple areas. However, it is notable that the former group typically slept in very close proximity on the same platform. Although mother-adult offspring pair Cindy and Lyndsey at EZ retired to the same area, they slept at least five metres apart (a conservative estimate), with Lyndsey nesting on the floor and Cindy on one of the highest nest baskets. The proximity of nests/retirement areas in the EZ group is in keeping with chimpanzee nesting arrangements in Senegal and Equatorial Guinea (approximately four meters: Baldwin et al. 1981), but markedly different to the mother-adult offspring dyads in the BD group.

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[15] BD chimpanzees were also provided with multiple sleeping pods (hose baskets in the centre of the night enclosure), although these are also not used for nesting (see chapter 3)

Coupled with the sparse evidence of inter-population variation in nest-related activities in other ape species - nest height and frequency of ground nest construction in bonobos (Fruth & Hohmann 1993), and vocalisations and leaf carrying behaviour in orangutans (van Schaik et al. 2003; Russon et al. 2007) - these data illustrate that some aspects of nest-related behaviours vary across populations. Moreover, the rarity of direct observations and descriptions of nest building behaviours of free-ranging apes may lead to the assumption that nest-related behaviours are uniform across groups. Studies on captive apes can therefore inform us about inter-population variations in nesting behaviours.

Field research on free-living primates has shown that the behavioural patterns that form the basis of group-specific cultural traditions gradually disseminated among related and non-related group members (e.g., sweet potato washing in Japanese macaques: McGrew 1998). Research on captive chimpanzees is further contributing valuable empirical data on the cultural transmission of behaviours. Laboratory studies have shown that, by observing conspecific ‘models’, tool-use techniques can be socially transmitted among group members (e.g., Celli et al. 2004; Horner et al. 2010; Whiten et al. 2005, 2007). The grooming handclasp, observed in wild chimpanzees (McGrew & Tutin 1978), has also been documented in a group at Yerkes Primate Research Centre (Bonnie & deWaal 2006; de Waal & Seres 1997). Initiated by a captive born adult female, this behaviour was adopted by all other group members, irrespective of their relationship to the innovator. Despite living under almost identical conditions, a second group at this facility has never been observed to perform the handclasp, suggesting that the behaviour is population-specific. Laboratory-based research on chimpanzee nest building (see also preceding chapter) has provided additional evidence that nest construction skills are socially influenced. Early work by Bernstein (1962) showed that, with few exceptions, wild-born chimpanzees constructed more nests compared to captive-born individuals. Videan’s (2006a) more recently reported similar findings: mother-reared chimpanzees produced more nests and used more complex nest building techniques than nursery reared chimpanzees. Taken together, these results indicate that social learning may influence nest building behaviour and nest construction techniques. The current data add some weight to this hypothesis. Although idiosyncratic techniques were recorded (Rosie, for example, was the only BD individual to throw material during nest building), there does appear to be within-group conformity in nest construction techniques, with all of the BD chimpanzees typically using only the minimum techniques required to form the outside rim of the nest. Similarly, Kindia was the only EZ group member to use the throwing technique in the current study, although several other EZ chimpanzees also employed this technique during observations described in chapter 5; thus this method is not restricted to one individual. Moreover, all four members of the EZ group turned in the nest and pressed nesting material during construction, again showing group-wide conformity in an aspect of nest building. Conceivably, nest building, like tool-use and grooming, can be socially transmitted and maintained in captive groups. At the very least, captive conditions can facilitate long-term documentation of population-specific nest-related behavioural patterns and traditions.

Conclusions and recommendations

The present data set is too restricted to conclude that the different nest building techniques in the two groups constitute long-term behavioural patterns, or ‘cultures’.

Some factors that may affect nest building, such as birth status (wild- versus captive-born), and age and sex classes were not controlled. Nonetheless, these data have indicated that two captive groups of chimpanzees show variation in both nest building techniques and frequency of ground nesting. These findings demonstrate that nest construction techniques are not homogenous across populations, although it is acknowledged that further research is needed in this area. With 23 facilities across the UK and Ireland housing separate groups of chimpanzees, gorillas and orangutans, research into the nesting patterns of the great apes can add a new dimension to the long-standing primate culture debate.

Although not the specific focus of this study, these findings can also be used to reiterate recommendations based on previously discussed data. Multiple sleeping areas, including substrate flooring, should be provided to promote species-typical nest dispersal patterns. Thought should also be given to the positioning of doorways and potentially draughty areas that preclude terrestrial nesting. It is possible that the BD group’s lack of complex nest building techniques was a result of restricted nesting material. Again, it is recommended that at least two bedding materials be provided to encourage species-typical nest construction behaviours and nest construction durations.

Chapter 8 Part 1

Does nest equal rest?: Analysis of nighttime behaviours using continuous video recording

"What hath night to do with sleep?" ~ Milton

8.1.1 Introduction

Sleep is not an inert, passive state, but rather an active brain process that reflects circadian rhythms - the diurnal and seasonal 'biological clock' that regulates the sleep-wake cycle (Cardinali 2000) - and homeostatic mechanisms that are influenced by prior amounts of sleep and wakefulness (Dijk et al. 2000). As with humans and multiple monkey species (see chapter 1), the great apes are naturally diurnal (e.g., Campbell & Tobler 1984; Kappeler 1998), being active during daylight and sleeping in a nest throughout the night.

Across all mammals sleep consists of two broad phases, non-rapid (NREM) and rapid (REM) eye movement sleep (Capellini et al. 2008), distinguishable by a distinct set of associated neurological, physiological, and psychological characteristics. At sleep onset, NREM sleep progresses through four stages – from light, drowsy sleep (in stage one), to deep, slow wave (SWS) sleep in stages three and four (Stanley 2005). REM sleep occurs increasingly as night progresses, being predominant in the latter half of the sleeping period (Stanley 2005). Throughout the sleeping bout, human NREM and REM phases alternate in cycles of approximately ninety minutes (Zepelin 1989).

Although broadly similar across mammals, there are some particularly notable similarities between human and nonhuman primate sleep patterns. Early research showed that sleep architecture of sub-adult pig-tailed macaques (*Macaca nemestrina*, n = 6) was comparable to that of humans (Reite et al. 1965). Sleep cycle durations lasted between seventy-five and eighty-five minutes and, as in humans, 'paradoxical'

(REM) sleep was more frequent in the latter stages of the night. Studies on adult baboons (n = 16) (Bert et al. 1975) and rhesus monkeys (n = 5) (Weitzman et al. 1965) also showed that NREM and REM sleep progress in cycles throughout the night. Reite et al. (1965) and Weitzman et al. (1965), however, were unable to reliably distinguish stage one NREM sleep from a state of drowsy wakefulness in their macaque subjects.

Like the previously cited monkey examples, chimpanzees progress through the four stages of NREM sleep to REM sleep (Adey et al. 1963; Bert et al. 1970), but the sub-division of NREM sleep into four progressive stages is applicable only to humans and their nearest evolutionary relatives (chimpanzees, Tobler 1995). Bert et al. (1970) showed that three adult chimpanzees had well-defined stage 1 NREM EEG patterns. Freemon et al. (1970) documented several similarities between chimpanzees and humans in the duration of the first and last REM periods, the number of eye movements in the first and last periods of REM, and also the number of body movements in the first and last REM periods.

As with sleep architecture, sleep duration and sleep cycles are broadly similar amongst humans and great apes. Although subject to individual variation, the natural duration of human sleep is approximately eight hours (Stanley 2005). Early EEG measurements recorded chimpanzee sleep duration as 9.6 hours (Bert et al. 1970), with more recent data reporting 8.8 hours (Videan 2006b). Duration of sleep cycles, approximately 90 minutes in humans and 85 in chimpanzees (Tobler 1995) is also comparable, as is the concentration of sleep into one ‘monophasic’ bout per day (Ball 1992; Tobler 1995; Zepelin et al. 2005).

The data on which these similarities between human and primate sleep architecture are based typically originates from controlled laboratory conditions and electroencephalogram (EEG) measures (e.g., chimpanzees: Bert et al. 1970; Freemon et al. 1970) or electro-oculagraphy (EoG) (e.g., Reite et al. 1965), often coupled with some form of physical restraint (for example baboons: Bert et al. 1975; rhesus macaques: Weitzman et al. 1965; chimpanzees: Adey et al. 1963). However, the scientific validity of data from restrained animals, with resulting problems in recording EEG for extended periods, has been questioned, and welfare issues also arise with the use of such methods (Crofts et al. 2001). Therefore, less invasive techniques, such as telemetry transmitters (e.g., common marmosets, *Callithrix jacchus*: Crofts et al. 2001) and actigraphy systems (e.g., cotton-top tamarins, *Saguinus oedipus*, and squirrel monkeys, *Saimiri sciureus*: Kantha & Suzuki 2006) are increasingly being employed to measure sleep cycles and sleep durations in laboratory-housed primates. Following from the tradition of the 1960s and 70s, studies have continued to focus on architectural aspects of primate sleep, including the staging of sleep patterns (e.g., macaque spp. Hsieh et al. 2008; Kaemingk & Reite 1987), sleep time and sleep episode length (e.g., *Callithrix* spp.: Kantha & Suzuki 2006).

Due to its association with the end of a sleep cycle, particularly REM sleep (Stanley 2005), nocturnal awakening is a frequently reported aspect of human and primate sleep (Capellini et al. 2008; Freemon et al. 1970; Reite et al. 1965). Some infant pig-tailed macaques (n = 11) were found to spend over 3 hours per night awake (Kaemingk & Reite 1987). Crofts et al. (2001) reported that laboratory housed marmosets (n = 4) were generally awake for two out of twelve hours of darkness. Laboratory housed rhesus macaques also spent up to two hours per night awake

(Balzamo et al. 1998). Zoo-housed gelada baboons, *Theropithecus gelada,* showed approximately forty-two waking episodes per night (Noser et al. 2003). Bert et al. (1970) reported that three adult laboratory-housed chimpanzees were awake for at least five minutes out of every hour. More recently, it was reported that chimpanzees (n = 20) awakened three to five times per night (Videan 2006b). Human studies have indicated that up to ten percent of a sleep bout can be interrupted by spontaneous nocturnal awakenings (Dijk & Kronauer 1999). Some individuals may waken up to fourteen times per night, for durations of up to six minutes (Barbato et al. 2002).

While physiological measures of sleep, such as EEG and EoG, can elucidate structural aspects of sleep, direct observations and non-invasive video recording can provide detailed descriptions of nocturnal behaviours – an aspect of sleep-related activity that has not been the subject of much scientific attention (Anderson 1984, 2000). The human bed is not used exclusively for sleep and rest, and so, given the number of similarities between human and primate sleep structure, it seems reasonable to propose that other primates also perform other activities during the night.

Vessey (1973) employed an image-intensifier night scope to document nocturnal behaviours in free-ranging rhesus monkeys. This population demonstrated a wide range of nighttime behaviours - vocalisations and movements, ‘tantrums’ by infants and juveniles, and occasional bouts of aggression. The presence of bright moonlight facilitated several activities, adding play to the nighttime behavioural repertoire. Chimpanzees living semi-free on an island were reported as frequently being active during the hours of darkness, playing and occasionally fighting throughout the night (Gale [date not provided], cited in Riss & Goodall 1976).

Laboratory-based research has yielded similar results. Using video recording, Munoz-Delgado et al. (1995) showed that stump-tailed macaques (*M. arctoides*, n = 9) engaged in several non-sleep related activities (self-directed and social grooming) during bouts of wakefulness. Subsequent research in the same laboratory confirmed and extended these results, with individuals of the same species (n = 10) showing a variety of intermittent social (social grooming, play, change of huddling partners) and non-social (locomotor activity, scratching) behaviours, although such activities were more frequent in the evening (19.00-20.00hrs) and in early morning (05.00-06.00hrs). Individual variations in nocturnal activity reflected age and gender, with females showing more play, and older females generally performing more social behaviours (Munoz-Delgado et al. 2004a). Peer-reared pigtail macaque infants occasionally aroused each other from sleep and played throughout the night (Kaemingk & Reite 1987). Videan (2006b) reported that laboratory housed chimpanzees (n = 20) also woke up frequently, changed sleeping locations, monitored the surrounding environment, and foraged or drank. Although infrequent, social grooming was observed between closely affiliated individuals.

These reports make it clear that free-ranging and captive primates engage in multiple social and non-social nighttime activities. However, some data are inconsistent. Overnight video recording showed that, in stark contrast to Vessey's (1973) observations of the same species, laboratory housed rhesus monkeys (n = 18) remained largely inactive during the night, irrespective of whether they were single, paired, or group-housed (Erffmeyer 1982). Although spontaneous awakening occurred, self-directed and social behaviours gradually decreased in frequency throughout the night, with highest levels in the evening and the following morning.

Only low levels of activity accompanied nocturnal awakenings, such as scratching, or changing posture then returning to sleep. Chimpanzees housed in a research centre (n = 6) were reported to move infrequently during the night, whether they slept indoors with access to three separate sleeping areas, outdoors, or indoors with access to only one sleeping site (Riss & Goodall 1976). These data, however, were based on point sampling just after chimpanzees retired and then at midnight, so it is likely that nighttime behaviours were underrepresented.

The literature is generally skewed in favour of human-primate similarities in sleep patterns. Although physiological studies have aided our understanding of primate sleep architecture, non-invasive studies are starting to broaden our knowledge, not only of primate sleep, but also of primate nighttime behaviour - an area that has hitherto been neglected.

Study aims and hypotheses

The aim of the present study was to detail the nighttime behaviours of four individual chimpanzees. Based on previous observations (chapter 3) that this group remained relatively active after retirement, and reports that nighttime activity levels are generally higher in the evening (e.g., Erffmeyer 1982; Munoz-Delgado et al. 2004a), it was predicted that:

a. The chimpanzees would engage in some social and non-social behaviours throughout the night.

b. These behaviours would occur predominantly during the first night phase (17.00h to 24.00h), compared to the second (00.00h to 07.00h).

8.1.2 Methods and analyses

Data collection

Throughout the month of February (2008), light-sensitive cameras linked to a hard drive recording device monitored the overnight behaviours of the same adult group of chimpanzees that were observed in a previous study, namely mother-adult offspring dyads Blossom and Chippy and Pansy and Rosie (see chapter 3 for details of individual chimpanzees and housing). Direct observations showed that the chimpanzees regularly constructed nests on two elevated wooden platforms (platforms A and B). Based on this information, a low-light-sensitive camera (‘Voltek night vision’) was mounted above each platform. A dim (70W) light (‘Thorn Sonpak LX7-15’) was mounted above the night enclosure’s wire mesh ceiling opposite to the sleeping platforms to allow enough light for recording without disrupting the chimpanzees’ sleep. The light and the cameras were mounted one week prior to recording to habituate chimpanzees to their presence. Over twenty-nine nights (throughout the month of February, 2008), data from each camera were recorded onto a ‘Western Digital’ 40-gigabyte hard drive. Recording was continuous from approximately 17.00h each day until approximately 07.00h the following morning, totalling approximately four hundred and six hours of overnight data.

The resulting data were analysed using a ‘Voltek’ 4-channel digital recorder and 18” JVC monitor. The time (hour, minute and second) was inlaid on each night’s recording. Analysis incorporated all social and non-social[16] behaviours performed between 17.00h and 07.00h the following morning (see table 8.1.1). All behaviours

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[16] Duration of nest construction was recorded, but has been reported elsewhere (chapter 9)

were coded *ad-libitum*. Sleeping partner combinations were also noted, as these were typically associated with social behaviours[17].

Table 8.1.1 Description of retirement behaviours and post-retirement social and non-social behaviours

Behaviour	**Description**
Retirement behaviours	
Retirement	For nest builders: First indication of the onset of nest building (gathering of nesting materials) For non-nest builders: The adoption of a rest posture (lying on left/right side, or in a prone/supine position) on sleeping platform
Nest construction	Using available materials to arrange a recognisable circular/oval nest around the body that is subsequently used to rest in
Post-retirement non-social behaviours	
Nest amendment	Manipulations to materials that have already formed an apparently completed nest
Self-directed behaviours	Manipulation of own body: autogrooming, picking at hair, foot-clasp, inspection of body parts
Post-retirement social behaviours	
Affiliative social	Allogroom: examine/pick through the skin of another individual Touch: using the hand to touch another individual in any part of the body
Agonistic social	Aggressive (non-contact): Charging/lunging at one or more group members without physical contact Aggressive (contact): Charging/lunging at one or group members with subsequent physical attack (e.g. hit, bite)

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[17] Data on rest postures, frequency of changes in rest postures, and orientation changes were also derived from overnight recording. These are detailed in part 2.

As behaviours on the video recording were easily identifiable, gross body movements and independently timed on the recording equipment, inter-observer reliability measures were not used. Instead, the behaviour of an individual chimpanzee was viewed 5 times. The first 2 viewings established an exact timeframe of behaviour, first approximating a time and then establishing the exact time frame on the second viewing (minutes and seconds). Procedures for recording behaviours were broadly similar. Behaviours were first preliminary identified and coded, viewed again, and finally transcribed onto manual check sheets along with corresponding timeframes.

Data Analyses

Although randomisation tests can be used for small *n*'s, they are most appropriate for studies incorporating randomised experimental designs (Plowman 2008). With no experimental procedures in the present study, non-parametric tests that are also appropriate for small sample were used (Siegel 1956) as Kolmogorov-Smirnov tests showed that the data were not normally distributed. Wilcoxon signed-rank tests were used for individual analyses, and Kruskal-Wallis and Mann-Whitney U tests for between-chimpanzee comparisons. Tests for frequency of behaviours in the first versus second night phase were one-tailed; all remaining tests were two-tailed. Statistical tests were conducted using SPSS 17.0, with alpha set at 0.025.

8.1.3 Results

Time of retirement

In general, the chimpanzees retired shortly after 17.00h (group median time: 17.29hrs, IQR = 0.31). On nights when the chimpanzees were not in a nest but lying on the sleeping platforms, retirement time was defined as when each chimpanzee adopted a rest posture (for example lying right/left side; lying prone or supine). Individual retirement times are shown in table 8.1.2.

Table 8.1.2 Individual median (plus IQR) retirement times, plus earliest and latest observed times

Chimpanzee	Median time (plus IQR)	Range
Blossom	17.23 (0.31)	17.07 –17.55
Chippy[18]	17.37 (0.79)	17.01 – 19.42
Pansy	17.26 (0.31)	17.02 – 19.42
Rosie	17.27 (0.14)	17.05 – 18.15

There were no significant differences in time of retirement between any of the chimpanzees. (Between female analysis: Blossom vs. Pansy U = 90.0, p = 0.41; vs Rosie U = 98.5, p = 0.80. Pansy vs Rosie U = 167.5, p = 0.53). The male, Chippy, typically nested later than females, but not significantly so: Chippy vs Blossom U = 59.5, p = 0.23; vs Pansy U = 136.0, p =0.64; vs Rosie U = 111.5, p= 0.28.

Rosie was the only chimpanzee observed to spend every night in a nest. Both Chippy and Pansy were seen to spend 3 nights on a platform without any evidence of nest construction. Blossom spent 1 night without nesting. Although nest building usually occurred after 17.00h, on several occasions the chimpanzees were already in their night nests prior to the start of analysis. On 17 occasions Blossom was observed in a nest built prior to 17.00hrs; for Chippy and Rosie this happened on 11 nights, and for

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[18] Chippy was observed on one occasion to briefly nest build at 02.42hrs – this outlier was excluded from analysis

Pansy, 8 nights. Thus, a group total of 62 nest-building episodes were recorded and analysed.

Nest amendments

Nest amendments were not evenly distributed over the study period; Blossom, Chippy, and Rosie failed to make any amendments on 4, 5 and 2 nights, respectively. Pansy spent 11 nights in a nest that was not amended. As expected, nests were more frequently amended during night phase 1 (between 17.00h and 24.00hrs) than night phase 2 (between 00.00 and 07.00hrs**)** (see table 8.1.3), particularly for the eldest female, Pansy, who performed the least nest amendments during both night phases. This decrease was significant for all females: Blossom (z = -3.27, p = 0.01); Pansy (z = -3.70, p = 0.01); Rosie (z = -3.96, p = 0.01), but just failed to reach significance for the male, Chippy (z = -2.99, p = 0.03).

Table 8.1.3 Total frequency, median (plus IQR), of nest amendments during both night phases

Chimpanzee	**Night phase**					
	1 (17.00-24.00h)			**2** (00.00-07.00h)		
	total	**median (IQR)**	**range**	**total**	**median (IQR)**	**range**
Blossom	45	1.00 (1)	0-5	15	0 (1)	0-7
Chippy	37	1.00 (2)	0-4	17	0 (1)	0-3
Pansy	27	1.00 (2)	0-4	5	0 (0)	0-2
Rosie	45	1.00 (1)	0-4	15	0 (1)	0-2

During night phase 1, Pansy made significantly fewer nest amendments than Blossom and Rosie (U = 285.00, z = -2.21, p = 0.02; U = 266.00, z = -2.51, p = 0.01, respectively). There was no significant difference between Blossom and Rosie (U = 405.00, z = -0.25, p = 0.81). There was no significant male-female variation in frequency of nest amendments in this time period: Chippy vs. Blossom (U = 395.50, z = -0.99, p = 0.32), vs. Pansy (U = 355.00, z = -1.07, p = 0.29), vs. Rosie (U = 345.00, z = -1.21, p = 0.23).

During night phase 2, Pansy made significantly fewer nest amendments than any other chimpanzee: vs. Blossom and Rosie (U = 292.50, z = -2.50, p = 0.01), vs. Chippy: U = 302.00, z = -2.35, p = 0.02. There was no significant difference between Blossom and Rosie, U = 361.00, z = -1.09, p = 0.28), or between Chippy and these females (Blossom: U = 367.00, z = -0.99, p = 0.33; Rosie: U = 420.00, z = -0.01, p = 0.99).

Leaving the nest without leaving the sleeping platform

All chimpanzees left their nests after completion, although this was very infrequent for both Pansy and Rosie during both night phases (see table 8.1.4). The only recorded instances of leaving the nest in the latter night phase concerned mother-adult offspring pair Blossom and Chippy.

Table 8.1.4 Total frequency, plus median and range, of leaving the nest during both night phases

Chimpanzee	**Night phase**					
	1 (17.00-24.00h)			**2** (00.00-07.00h)		
	total	**median (IQR)**	**range**	**total**	**median (IQR)**	**range**
Blossom	8	0 (0)	0-3	8	0 (0)	0-2
Chippy	17	0 (1)	0-2	15	0 (1)	0-3
Pansy	2	0 (0)	0-1	0	/	/
Rosie	4	0 (1)	0-1	0	/	/

There was no significant difference among the females in frequency of leaving the nest during night phase 1 (χ_2 = 0.57, df = 2, p = 0.75), but Chippy left the nest significantly more frequently than each female (vs. Blossom: U = 302.00, z = -2.30, p = 0.02; vs. Pansy: U = 268.00, z = -3.03, p = 0.01; vs. Rosie: U = 292.00, z = -2.46, p = 0.01).

Although only one female left the nest in the latter night phase, there was no significant variation among females (χ_2 = 6.14, df = 2, p = 0.06). As with night phase 1, the male chimpanzee left his nest significantly more than Pansy (U = 261.00, z = -3.64, p = 0.01) and Rosie (U = 261.00, z = -3.64, p = 0.01), but not Blossom (U = 313.00, z = -2.24, p = 0.03).

Leaving the sleeping platform

Although all individuals left the sleeping platform between 17.00 and 24.00hours, these forays decreased in the second night phase (table 8.1.5). Indeed, Rosie was the only chimpanzee to leave the sleeping platform at any time after 00.00hrs[19]. This decrease in frequency was significant for each individual: Blossom: z = -3.169, p = 0.01; Chippy: z = -2.64, p = 0.01; Pansy – z = -2.71, p = 0.01; Rosie: z = -2.71, p = 0.01.

Table 8.1.5 Total frequency, plus median and range, of leaving the sleeping platform during both night phases

Chimpanzee	**Night phase**					
	1 (17.00-24.00h)			**2** (00.00-07.00h)		
	total	**median (IQR)**	**range**	**total**	**median (IQR)**	**range**
Blossom	19	0 (1)	0-3	0	/	/
Chippy	13	0 (1)	0-4	0	/	/
Pansy	10	0 (1)	0-2	0	/	/
Rosie	11	0 (1)	0-2	1	0 (1)	0-1

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[19] All chimpanzees left their sleeping platforms on nights 23 & 24. These were coded as a response to the male's charging displays (discussed later). They were therefore considered outliers, and so excluded from analyses

After leaving the sleeping platform in the first night phase, chimpanzees often returned with extra nesting material. Thus, 47.4% of all platform departures by Blossom were to gather material; corresponding scores for Chippy and Pansy were 53.8% and 40%, respectively. Blossom was the only chimpanzee to return with extra nesting material after 18.00h, and this only happened only once (at 18.01h). There was no significant between-chimpanzee variation in frequency of leaving the platform between 17.00 and midnight (χ_2 =2.39, df = 3, p = 0.50) or between midnight and 07.00h (χ_2 = 3.00, df = 3, p = 0.39).

Nighttime self-directed, affiliative and agonistic social behaviours

Self-directed behaviours were infrequently recorded, and always observed during night phase 1 (17.00-24.00h). Rosie self-groomed on one occasion, for approximately 1 min. Blossom self-groomed 3 times over 2 nights, totalling approximately 3.5 min. Chippy once self-groomed for approximately 3 min, and once appeared to manipulate his feet playfully for 2 min. Pansy was the only chimpanzee never observed to perform any self-directed behaviours.

Affiliative social behaviours were also rarely observed, and generally restricted toward a sleeping partner (those sharing a sleeping platform). Blossom showed 13 instances of social behaviour over 9 nights. Over 75% of these behaviours were directed toward Chippy, and included brief touches to the arm, grooming, play and an embrace. Another 15% of social acts (all grooming) were directed toward Pansy. Only one social interaction occurred between Blossom and Rosie, the former briefly touching the latter. Again, these behaviours were restricted to the first night phase. Chippy initiated only 2 affiliative behaviours; both consisted of grooming his mother, and occurred after his charging displays on night 23.

Rosie’s two social interactions consisted of grooming Blossom and embracing her mother, Pansy, during Chippy’s charging displays on night 23. Pansy initiated only three social behaviours, briefly touching and grooming Rosie. For her remaining social act she moved from the central pods up to sleeping platform A and briefly kissed Chippy. This occurred shortly after 17.00hrs on night 24; there had been a charging display on the previous night. This was the only social act not directed towards a platform-sharer.

Two instances of non-contact aggressive behaviours were recorded, both initiated by the male. On night 23, Chippy initiated a charging display at approximately 06.00h. Displays occurred intermittently for approximately nine minutes, after which Chippy returned to his nest on platform A. On the following night, charging displays began at approximately 03.00h, and continued sporadically until approximately 06.30h, when again Chippy returned to settle in his nest.

Sleeping partners

Table 8.1.6 shows the most frequently used platforms, and the most frequent sleeping partner combinations. In contrast to the male, the females shared a sleeping site with at least one other individual each night – there were never any observations of a female sleeping alone on a platform. Mother-offspring dyads were the most frequent sleep partner combinations, accounting for 62% of all combinations, although all three females shared a sleeping platform on ten nights.

Table 8.1.6 Number of nights spent on each sleeping platform, individually and with sleeping partner(s)

Individual, plus partner(s)	Platform A	Platform B
Blossom	0	0
Chippy	0	10
Pansy	0	0
Rosie	0	0
Blossom, Chippy	18	0
Blossom, Pansy	0	0
Blossom, Rosie	1	0
Blossom, Pansy, Rosie	10	0
Pansy, Chippy	0	1
Pansy, Rosie	0	18

8.1.4 Discussion

The structural aspects of primate sleep and their similarity to human sleep patterns (Tobler 1995) have been the conventional focus of sleep-related research. Like humans, nonhuman primates are known to spontaneously awaken during the sleeping bout, yet there are relatively few descriptions of primate behaviour throughout the night (e.g., Anderson 1998; Fruth & Hohmann 1994). In spite of the small sample size, the results from this month-long study provide new information on the nocturnal behaviours of captive chimpanzees. The emphasis of this research was not on sleep itself, but rather on the range of behaviours that occurred throughout the night.

Early reports of free-living chimpanzees indicated that, subsequent to nest building, there was minimal nighttime activity (e.g., Goodall 1962). Later observations by the same author (Goodall 1968), however, indicated that some individuals mated in night nests, and travelled from their nests to feed during the night. Nighttime vocalisations were also heard in these Gombe chimpanzees, with similar reports of post-retirement vocalisations in wild gorillas (e.g., Groves & Sabater-Pi 1985). Other reports of nighttime activity in a range of captive-housed apes (e.g., Videan 2006b) and monkeys (Munoz-Delgado et al. 1995) indicate clearly that nighttime is not exclusively devoted to sleep. Direct observations of the BD and EZ chimpanzees (chapter 3), and video data from the current study broadly concur – there were instances of leaving the nest and sleeping site to collect nesting materials or to forage, and amending nests throughout the night. Although infrequent, affiliative and agonistic behaviours were also recorded. As expected, the frequency of these behaviours generally decreased during the second night phase, in keeping with reports of activity levels from laboratory housed macaques (Erffmeyer 1982; Munoz-Delgado et al. 2004a). These similarities are likely due to both chimpanzees and macaques being naturally diurnal species; decreasing activity levels as night progresses.

Compared with social activities and instances of leaving the nest or sleeping platform, making amendments to the nest was the most frequently occurring behaviour performed in the second night phase. Similar behaviour has been documented in wild chimpanzees. Goodall (1962), for example, described an adult female amending a nest 15 minutes after apparent completion, by relocating used twigs and then resting her head on them as if constructing a twig ‘pillow’. Given the body weight of an adult chimpanzee, it is likely that nesting substrate is compressed during the course of the night, and so amendments may be a means of reconstructing areas that have been compacted – perhaps similar to the way in which humans ‘fluff’ their pillow to increase comfort. As previously discussed (see chapters 3 and 5), institutions that house apes should consider providing at least two types of appropriate nesting material that promote comfort and species-typical nest lining behaviours. Having only straw as a nesting substrate during this time period could have inhibited complex nest building behaviour in the BD group. This in turn could lower comfort levels, and potentially be a welfare issue (e.g., Dawkins 1990).

However, it is also notable that amendments were not made every night. It is conceivable that well constructed nests require fewer amendments than poorly constructed nests; future studies could test potential relationships between initial nest construction effort and duration and the incidence of subsequent amendments. Of further interest is a possible age-related difference in the frequency of nest amendments. Pansy, the oldest chimpanzee, spent eleven nights on non-amended nests, and also made the fewest amendments during each night phase. Perhaps this was a reflection of reduced strength and muscle mass, thus physical mobility, as in elderly humans (Laurentani et al. 2003).

Overnight recordings of laboratory housed chimpanzees (Videan 2006b) showed that nighttime activities included changes in sleeping location within the enclosure – although no specific details were given. Similarly, laboratory housed stump-tailed macaques, particularly young males, changed huddling partners throughout the night (Munoz-Delgado et al. 2004a). Zoo-housed gelada baboons also frequently left sleeping huddles, changed position, and even left the sleep site (Noser et al. 2003). Contrary to these reports, the chimpanzees in this group never changed sleeping location or sleeping partner after retirement. This may indicate preferred sleeping areas, a factor known in sleep site selection in free-ranging chimpanzees (e.g., Hernandez-Aguilar 2009), and which also appeared to influence the nesting behaviour of the EZ group (chapter 4). This hypothesis is supported by the fact that each chimpanzee used a specific sleeping platform more frequently than another. Of interest here is that, in contrast to survey data (chapter 2) and the EZ group (chapter 3), substrate (ground) nesting was not observed in the BD group. This could potentially be a cultural inter-group difference, or a strategy to avoid a potentially draughty floor area (see chapter 6). However, it is notable that the BD group had access to another set of elevated sleeping sites, a series of circular sleeping ‘pods’ of various heights and depths stemming from a central vertical pole in the middle of the enclosure (see chapter 3). These pods consisted of a metal rim with an attached heavy-duty canvas lattice mattress, but were never used as a sleep site.

Notably, the BD sleeping pods are deeper (over 50cm at lowest depth) than the nest baskets at EZ (15cm at lowest depth), and feature large gaps in the lattice, compared to the more compact wire mesh of the EZ baskets. The lack of a firm and stable foundation may have inhibited nesting on these pods, as stability and security are factors known to influence sleep site selection in wild apes. Large-bodied (e.g., flanged male) Bornean orangutans, for example, built nests in more stable locations (at lower heights) than smaller individuals (Rayadin & Saitoh 2009), as did females that were co-sleeping with infants. Bonobos (Fruth & Hohmann 1993) were reported to use ‘integrated’ nests (built over branches of two adjacent trees) if one tree was insufficient to hold the weight of the nest. Similarly, Gombe chimpanzees nested on a “firm foundation” (van-Lawick Goodall 1971 p 41) of a fork or two horizontal branches. For captive facilities, it is therefore recommended that elevated nesting sites feature a secure base to support large-bodied apes, particularly as survey data showed that *potentially* unstable (although unconfirmed) cargo nets, hammocks and firehose are provided as sleeping structures in 7, 4, and 1 captive facilities, respectively.

If choices of sleeping location were indeed restricted by avoiding draughty and unstable sleeping locations, this could explain the finding of consistent co-sleeping partners. As previously discussed, wild-living chimpanzees typically split into small groups when nesting (see chapter 4), sleeping at ‘optimal’ distances of several meters from other individuals (e.g., Baldwin et al. 1981). This again recalls the previous recommendation that several areas are provided that allow apes a choice of sleeping site and nearest nesting neighbours. However, it is possible that the BD simply preferred to sleep in close proximity to other group members. As sleep increases vulnerability (e.g., Lima et al. 2005, see chapter 1), sleeping in close proximity to a family member may promote a sense of security, also known to affect the sleeping arrangements of human families (Troxel et al. 2007). Additionally, these findings are in keeping with other studies of captive apes. Videan (2006b) reported that a female mother-offspring pair was the most frequent sleeping partners, followed by two adult females with a close social bond. Riss and Goodall (1976) also found sleeping partner preferences in laboratory housed adolescent chimpanzees. Prior to being merged into a group of six, the chimpanzees had lived in several subgroups. Two unrelated females from one subgroup continued to be frequent sleeping partners, while a male and female from another subgroup did likewise. However, unless zoos, wildlife parks and laboratories provide multiple sleeping areas, it will remain unknown is apes choose to co-sleep, or only do so as a result of restricted sleeping spaces.

Affiliative social behaviours were infrequent in the present study, and typically limited to sleep site sharers. With the exception of co-sleeping mother-infants (Goodall 1968), this lack of nighttime social behaviour appears typical of wild chimpanzees, but has also been documented in laboratory housed chimpanzees (Videan 2006b) and macaques (Munoz-Delgado et al. 2004a). Nighttime agonistic encounters have also been reported in free-living (Vessey 1973) and captive (Munoz-Delgado et al. 2004a) macaque species. I was unable to establish any motive for the charging displays by the male chimpanzee, possibly as the cameras above the night enclosure recorded visual information only. It is therefore possible that the displays were a response to external, auditory stimuli that remain unknown. But it seems likely that such an extreme response would occur only if the noises were unfamiliar and unexpected.

The only other report of nocturnal aggression in captive chimpanzees (see de Waal 1986) describes the fatal wounding of a male, presumably by two other high-ranking males after a period of social tension. In the current study, there was no physical contact with any of the females during Chippy’s charging displays, and so it seems unlikely that the displays were a continuation of daytime conflicts, unlike observations of the EZ group (chapter 4). As data on nocturnal behaviour of chimpanzees are so rare, it is possible that intra-group aggression is widespread but undocumented. It is worth reiterating here that numerous sleeping areas allow subordinates to avoid social stressors by allowing them avoid and flee social tensions, as has been previously recommended.

The present study has so far flagged several issues (e.g., comfort, stability of nest sites) that are relevant to housing recommendations and welfare of captive apes. Sleep itself should be considered from a welfare perspective. Long-term sleep deprivation on laboratory rats has been implicated in a host of physiological changes such as decreases in cerebral function, metabolic rate (resulting in hypothermic symptoms) and resistance to infection. This immunosuppression can be a lethal complication of long-standing sleep loss (see Everson 1995 for reviews). Human studies have also shown that psychological health can be negatively affected by sustained sleep deprivation; it can reduce problem-solving and decision-making skills, and affect memory (Killgore et al. 2008). Adequate sleep is also imperative for biological health in a number of ways, including repairing tissue, controlling thermoregulation and for regulating the immune system (Walker 2008). Extended periods of wakefulness have been implicated in increased cardiovascular risk (Sforza et al. 2004), elevated blood pressure, and to increased likelihood of obesity (Banks & Dinges 2007). This latter point is of particular interest here as obesity has increasing being acknowledged as a growing health problem in captive chimpanzee populations (e.g., Lee & Guhad 2001; Videan et al. 2007). Non-invasive recording could potentially be used to assess sleep duration to ensure that sleep deprivation does not become detrimental to welfare.

During this research, all members of the BD group were invariably still in a nest/in a rest posture on a platform at 07.00h; there was no evidence of arising earlier than this time. Taking the median retirement time of 17.29, conservatively estimating latency to sleep as 5 minutes (after Videan 2006b), and accounting for the nighttime behaviours observed, total sleep time can be approximated as 13 hours. This estimation is approximately 3 hours longer than laboratory data reported by Bert and colleagues (1970), and approximately 5 hours longer than Videan's (2006b) estimations. Observations of free-ranging apes, although scarce, showed that chimpanzees spent up to 14 hours in nests during the rainy season (Goodall 1968). Groves and Sabater-Pi (1985) similarly reported that gorillas could spend up to 12 hours in nests; often extending time in bed during fog and low-cloud conditions, and during the rainy season. Thus, time spent in nests or at a sleep site in the BD group are more strongly aligned with free-ranging data than data from laboratory studies.

Studies using non-invasive technology (e.g., low-level lighting, CCTV), or a combination of invasive and non-invasive recoding equipment and (e.g., radiotelemetry systems and infra-red cameras) have shown that primate nighttime behaviours can be successfully documented with minimal sleep disturbance (e.g., Crofts et al. 2001; Munoz-Delgado et al. 1995). Given that long-term sleep disruption can deleterious to health and welfare, the methodology used for overnight recording should be carefully considered. In the present study, retirement times were slightly later during February than they had been during December and January (see chapter 3 for details). However, it is notable that 47 nests were constructed prior to 17.00hrs when video analysis began, suggesting that the low-level lighting used here was not disturbing typical nesting patterns

It should also be considered that, with further research, non-invasive technology has the potential to be used as an alternative to invasive procedures typically used in sleep research (e.g., restraining chair: Adey et al. 1963). For example, human (Stanley 2005) and primate studies (Freemon et al. 1970; Reite et al. 1965) have shown that nocturnal awakenings are most prevalent at the end of a sleep cycle, in particular the end of the REM cycle. The approach used here that clearly revealed periods of nocturnal wakefulness could be incorporated in non-invasive studies of scoring sleep cycles. Simultaneous use of EEG measurements and video recording has been employed for scoring nocturnal sleep-wake cycles in adult rhesus monkeys (n = 6: Balzamo et al. 1998; n = 6: Lagarde et al. 1996), with generally high levels of concordance between video and EEG analyses for bouts of wakefulness and sleep stages. However, both studies also showed that video analysis is not infallible; difficulties in reliably categorising sleep stages were noted. Some bouts of wakefulness were missed, and mistakenly categorised as NREM sleep.

There were also methodological issues in the current study. The positioning of the cameras directly above the night enclosure was adequate for recording noticeable occurrences of wakefulness, such as making nest amendments and social agonistic and affiliative behaviours. However, it is also possible that the chimpanzees were awake during the night but failed to perform any noticeable behaviour. The ‘bird’s-eye’ view provided by each camera meant that I was unable to reliably determine if the chimpanzees were awake while lying in a lateral position. Future studies could employ multiple cameras at varying angles to remedy this. Nonetheless, the use of non-invasive recording technology can be of value for providing data on primate post-retirement behaviour, avoiding the methodological problems of lack of light and observer fatigue (e.g., Kantha & Suzuki 2006).

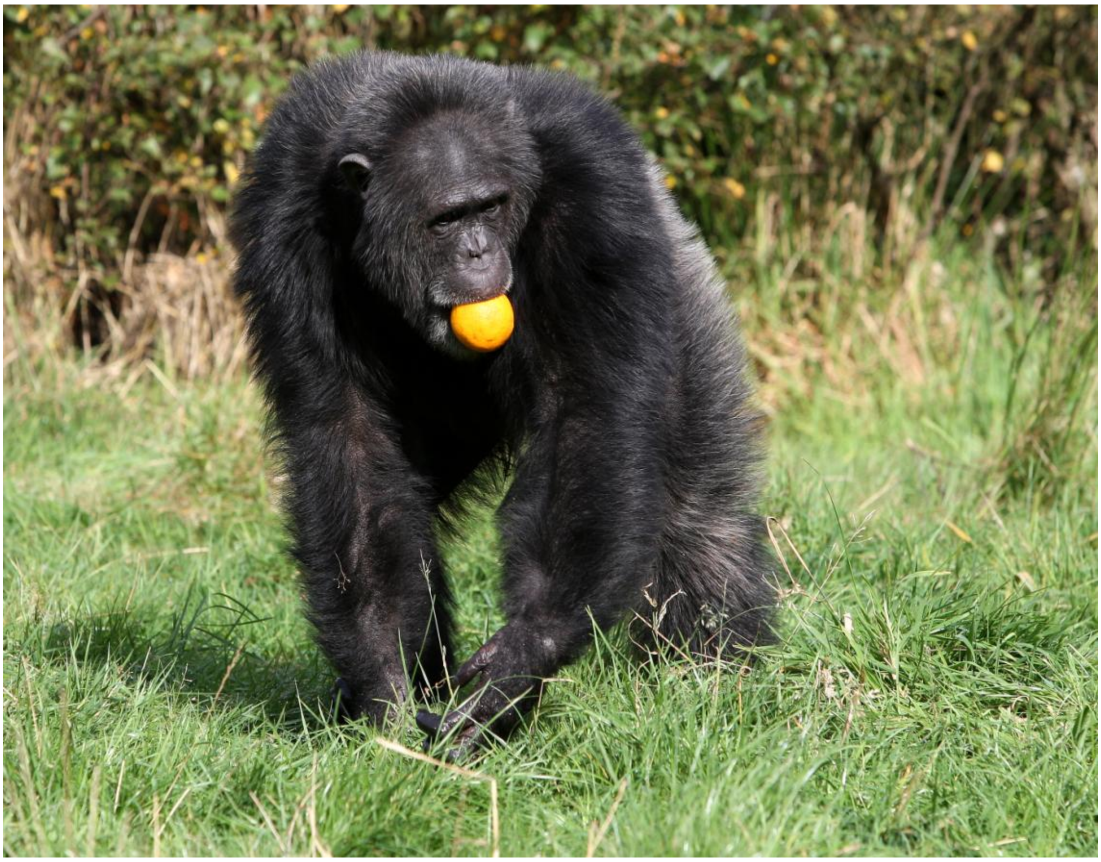
Conclusions and recommendations

In keeping with reports from free-living apes and captive housed primates, the chimpanzees in the present study performed non-social (e.g., amending nests) and social (e.g., allogrooming) behaviours even after nests had been constructed and the group had seemingly retired. These data add to a growing body of literature that diurnal primate activity can continue throughout the night. These findings can also be used to further emphasise recommendations based on previous studies, such as providing additional nesting substrate and numerous sleeping sites to improve comfort and allow escape from stressful social situations. Nesting surfaces, like the deep sleeping pods in the BD enclosure, that may be perceived as unsubstantial are not likely to be used as sleeping sites, and so more stable locations such as shallow baskets or platforms should be provided.

The use of a low-lighting system and continuous video recording can be beneficial to the study of ape nighttime behaviour in a number of ways. Although arduous to code and analyse, individual chimpanzees and their behaviours are readily identifiable and recognisable, and all behaviours can be recorded, thereby eliminating the possibility of some behaviours being under-represented. In addition to documenting nighttime activities and aspects of the captive environment that could be improved, this approach could be used to estimate sleep frequency and duration, and potentially reduce the need for surgical procedures and implantations for laboratory-housed primates used in sleep-related research. Similar non-invasive procedures have potentially far-reaching implications for the welfare of many captive-housed primates.

Chapter 8 Part 2

Nighttime postural shifts and orientation changes



> "As far as I could determine, the chimpanzee sleeps in his nest lying on his back or side; legs and arms are probably drawn up close to the body" ~ Nissen 1931, p45

8.2.1 Introduction

Although primate sleep has mainly been defined through electroencephalographic (EEG) recordings (for example Adey et al. 1963; Bert et al 1970, 1975; Freemon et al. 1970; Reite et al. 1965; Weitzman et al. 1965; see also part 1), several behavioural criteria also characterise the sleep state - behavioural quiescence, reduced responsiveness to external stimuli, rapid reversibility of the state with stimulation, and the adoption of a species-typical sleeping posture (Campbell & Tobler 1984; Lima et al. 2005; Tobler 1995; Zepelin et al. 2005).

Small New World monkeys (e.g., common marmosets) sleep in crouched or 'curled up' postures (Crofts et al. 2001), whereas the typically larger Old World monkeys adopt squatting or sitting positions (e.g., baboons: Anderson & McGrew 1984; macaques: Erffmeyer 1982; Vessey 1973). These postures are generally held to be adaptations to conserve body heat, thus affording thermoregulatory benefits (Nissen 1931); they may also serve to maintain physical stability during sleep (Anderson 2000).

Unlike monkeys but like humans, great apes lie down to sleep at night (Goodall 1962; Lukas et al. 2003), typically drawing their limbs toward the body in a similar manner to human 'foetal' sleeping positions (Dunkell 1977). According to Goodall (1962), during inclement weather chimpanzees may sit up in the nest, drawing the knees close to the torso and wrapping their arms around them – as humans might. However, as with nighttime behavioural research generally, detailed accounts of primate sleeping postures are scarce. Observations on resting positions are rarely continuous throughout an entire sleeping bout, but usually are limited to postures adopted immediately upon retirement. Goodall (1962, 1968), for example, described how free-ranging chimpanzees may initially lie in a supine position before turning onto one side. Early observations of free-ranging orangutans revealed that they would sometimes sit in their nests, but they were usually observed in prone or supine positions (MacKinnon 1974). Zoo-housed gorillas (n = 17) more readily adopted reclining, versus sitting or crouching, postures after nest construction, although again these descriptions are based on positions adopted just after retirement (Lukas et al. 2003).

Adult laboratory-housed chimpanzees (n = 3) were recorded as sleeping most frequently in a lateral position (on the right or left side), with legs drawn up in an almost foetal posture. Although supine positions were observed, these were less frequent than reclining laterally (Bert et al. 1970). Unrestrained juvenile chimpanzees again reportedly preferred lateral sleeping positions although, contrary to the adult chimpanzees cited above, they also frequently adopted prone postures (Freemon et al. 1970), suggesting a potential age difference in preferred sleeping positions. Of further interest is that the sleeping postures of the juveniles were related to sleep stages – prone postures mostly occurred in the first stages of REM sleep but were less frequent in the latter REM stages. Videan (2006b) reported similar findings in another laboratory setting. Although lateral sleeping positions were favoured (accounting for approximately 62% of total sleep duration), there was no significant preference for either the right or left side when sleeping. Older chimpanzees slept longer than younger ones, with fewer arousals, and males spent significantly more sleeping time supine, thus indicating possible age- and sex-related variation in sleep positions. Individual variations in sleeping postures should be expected; although baboons typically sleep in a sitting position (Anderson & McGrew 1984), two male zoo-housed gelada baboons were observed to sleep in a reclining position over six nights (Noser et al. 2003).

The factors that can influence the sleeping postures of primates – gender, preferred positions, age, and sleep stages – are also hypothesised to affect human sleep positioning. Similar to Videan's (2006b) report on male chimpanzees, human males have been reported to spend more total sleep time in the supine position than females (Gordon et al. 2007). Human infants first begin to show a specific sleep position at approximately three months of age, and show a distinct preference for a particular sleeping posture by seven years (Gordon et al. 2004). Self-reporting and overnight video recording of adult humans has shown that, as in chimpanzees, the most common sleeping position is the side-lying position (DeKoninck et al. 1983; Gordon et al. 2004, 2007; Gordon & Buettner 2009; Johnson et al. 1930), although preferences may vary across the lifespan. Elderly participants (aged sixty-five to eighty) showed a marked preference for sleeping on the right hand side; this accounted for almost 60% of total sleep time (DeKoninck et al. 1992). Laboratory studies have yielded similar results. Compared with 8- to 12-year olds, who only showed slight variation in time spent in prone, supine, and lateral sleeping postures, 35- to 45-year-olds slept mostly in lateral positions, and spent the least amount of time in the supine position. The amount of time spent in the prone position was almost negligible for 65- to 80-year-olds. Although approximately 30% of sleep time was spent lying either supine or on the left side, almost 60% was spent on the right side (Lorrain & De Koninck 1998). Gordon and Buettner (2009) reported that 40- to

59-year-olds and older participants (60 years plus), spent less time in the prone position than any other posture. Again, the largest percentage of total sleep time was spent on the right side for those of 60 years and above.

As the ageing process appears to affect the expression of preferred postures, it also appears to affect the number of postural changes performed throughout the night. EEG and video recordings across various age ranges revealed a marked decrease in the number of postural changes with age (De Koninck et al. 1992). Eighteen- to 24-year-olds, for example, changed posture on average 27 times over two nights, compared to approximately 20 times in 35- to 45-year-olds. Comparisons of elderly (61-75 years) and very elderly (76-98 years) humans revealed a significant decline in the number of body movements in the latter; the respective mean rates for the two groups were 0.25 per minute and 0.09 per minute, respectively (Giganti et al. 2008).

Although much research has emphasised the role of development in human sleeping postures, there are several other factors that affect this behavioural aspect of sleep. As in juvenile chimpanzees (Freemon et al. 1970), human sleep postural changes and periods of immobility vary with sleep cycle stages. EEG recordings and time-lapse photography demonstrated that in human adults (n = 6) periods of sleep immobility were characteristic of stage two and three NREM sleep, with postural shifts beginning in the transition from NREM to REM sleep (Hobson et al. 1978). ‘Good’ sleepers spent more time immobile compared to ‘poor’ sleepers. Using the same methodology, Aaronson et al. (1982) reported that most major nocturnal movements in four adults were highly correlated with specific sleep stages; namely the ascending phases of NREM into REM sleep, and the termination of the REM cycle. Eighty three percent of all movements were associated with a phase change in these participants.

In contrast to the relatively scarce literature on sleep positions in both humans and nonhuman primates, how primates position themselves around a sleeping site is well documented; it often reflects social organisation (e.g., monogamous male-female pairing in sportive lemurs: Rasoloharijaona et al. 2003), minimising risk of falling (e.g., choice of solid boughs in the heavy-bodied snub-nosed monkeys, *Rhinopithecus roxellana*: Li et al. 2006), and anti-predation strategies (e.g., preference for tall trees in bonobos: Fruth & Hohmann 1993; choosing sites that are inaccessible to predators in baboons: Hamilton 1982) (see also chapter 1). Socially dominant individuals may remain more vigilant throughout the night; free-ranging adult male bonnet macaques selected the highest sleeping location (Ramakrishnan & Coss 2001). Sleeping on the periphery of the group (e.g., stump-tailed and rhesus macaques: Munoz-Delgado et al. 2004b; Vessey 1973; chimpanzees: Goodall 1962) may also facilitate monitoring of the environment, or interposition between predators and more vulnerable group members (Anderson 1984, 1998). Sleeping postures themselves can also be used to avoid detection; by lowering their heads and forming a tightly packed huddle, Geoffroy’s tamarins (*Saguinus geoffroyi*) appeared to camouflage themselves against predators (Dawson 1979 cited in Anderson 1984).

A recent study of sleep site selection in humans (n = 138) further demonstrates the vulnerability associated with sleep, and the consequent importance of monitoring the surrounding environment (Sporrle & Stich 2010). When asked to place beds on the floorplan of a room, most participants (all adults) placed the bed so as to facilitate direct observation of the door. Further, they also placed the bed on the side of the room to which the door would open. In keeping with primate data, these results suggest choice of a sleeping site that allows vigilance and readiness to act against potential danger.

As previously discussed (see part 1), sleep plays an essential role in physiological restoration, and also has consequences for psychological welfare. The postures that facilitate sleep are therefore also important considerations for welfare. As noted by Fraser (1989), "…appropriate position and postures are involved in all the forms of rest and sleep for comfort and relaxation. The latter is the essential feature of this vital behaviour." (p184). Although comfort has been implicated in promoting positive affective states (e.g., Dawkins 1990), and comfort is an important feature of ape nesting habits (Stewart et al. 2007, see also chapter 5), the sleeping postures and sleeping surfaces of captive apes have not been subject to investigation, typically being only briefly mentioned in wider studies of sleep architecture (e.g., Bert et al. 1970; Freemon et al. 1970).

Human studies, although limited, have shown that sleeping on rigid, uncomfortable sleeping surfaces generally gives rise to more nocturnal body movements (e.g., Suckling et al. 1957), which may in turn affect sleep quality. DeKoninck et al. (1983), for example, reported that high frequencies of body movements and postural changes were more typical of poor sleepers (those unsatisfied with sleep quality) than 'good' sleepers. The presence of a partner may also influence postural shifting during the night. Nightlong video records indicated a strong correlation between frequency of movements, and also synchronicity in movements between members of a couple during a 7-night period (Aaronson et al. 1980). Given the similarities between chimpanzee and human sleep, and as most captive apes in the UK are housed communally and with access to elevated sleeping surfaces that are presumably rigid (e.g., shelves, platforms, benches – see chapter 2), the study of sleep positions and postures may have implications for sleep site considerations and welfare in captive-housed apes.

Study aims and hypotheses

There has been little interest in primate resting/sleeping postures *per se*, although there have been a few attempts to describe resting positions immediately after nest construction (e.g., Goodall 1962, 1968; Lukas et al. 2003). Sleeping postures are also sometimes briefly mentioned in overnight studies of sleep stages (e.g., Freemon et al. 1970), sleep duration (Videan 2006b), and in the wider context of nocturnal behaviour (Erffmeyer 1982). As with humans (DeKoninck et al. 1992; Gordon et al. 2007, 2009), there appear to be age- and sex-related differences in chimpanzee resting postures (e.g., Videan 2006b) - these have yet to be subject to systematic investigation. Research on sleep site selection by primates (Anderson 1984, 1998) and humans (Sporrle & Stich 2010) indicate that sleeping positions may be chosen to facilitate monitoring of the surrounding environment; again however, this requires empirical testing. Based on the available information, it was predicted that, during sleep:

a. Lateral positions would be favoured over prone or supine postures.
b. Older chimpanzees would show fewer nocturnal postural shifts than younger chimpanzees.

c. Chimpanzees would most frequently be orientated toward the open area of the enclosure.

d. The male chimpanzee in particular would spend more time orientated toward the open area of the enclosure.

8.2.2 Methods and analyses

Data collection

The data analysed here were taken from the overnight recordings of the four Blair Drummond chimpanzees during February 2008 (see preceding section). As described in part 1, analyses began at 17.00hrs and ended at 07.00hrs. Between these hours, the resting postures (prone, supine, right side, left side), changes in resting postures (coded as any postural shift of the entire body, e.g., right side to left side) and the direction in which each chimpanzee was orientated (coded as enclosure centre, sleeping partner, and enclosure wall) were recorded ad-libitum. As in the preceding chapter, each postural shift was repeatedly viewed to code and manually record and the event, orientation, and the precise timing.

Data analyses

Kolmogorov-Smirnov test showed that data were not normally distributed; therefore non-parametric analyses were used. Wilcoxon signed-ranks tests were used for individual analyses, and Kruskal-Wallis and Mann-Whitney U tests were used for group analyses. SPSS 17.0 was used for all analyses, with alpha set at 0.025. Tests relevant to the hypotheses (favouring lateral positions, age differences in posture shifts, orientation data) were one-tailed, all others were two-tailed.

8.2.3 Results

Changes in rest postures

Over the duration of the study, the male chimpanzee changed resting posture more frequently than any of the females (see figure 8.2.1), although this difference was not as marked in comparison to his mother, Blossom.

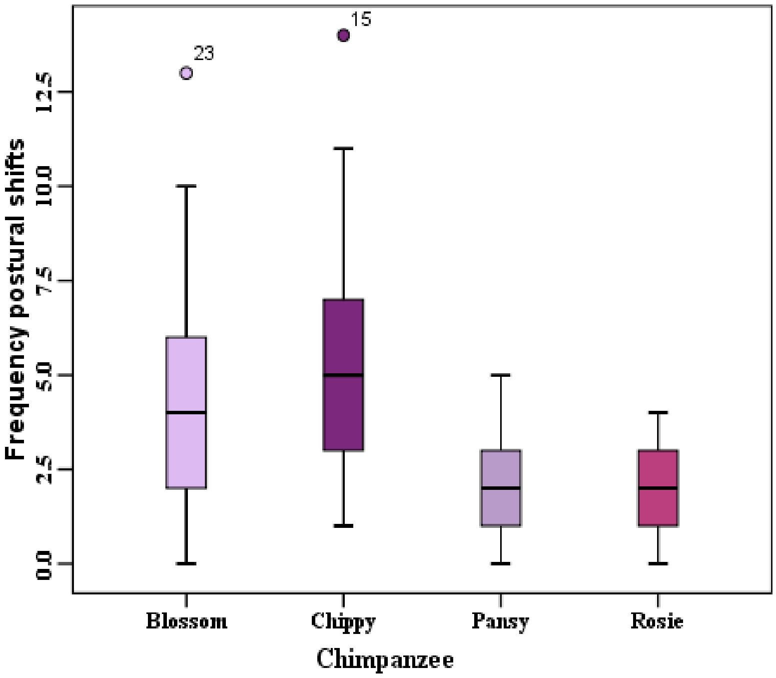


Figure 8.2.1 Individual median frequencies of postural shifts across 29 nights.

Table 8.2.1 Total frequency, plus median, IQR, and range, of postural changes in the first and second night phases

Chimpanzee	**Night phase**					
	1 (17.00-24.00h)			**2** (00.00-07.00h)		
	total	**median (IQR)**	**range**	**total**	**median (IQR)**	**range**
Blossom	165	5 (4)	1-13	85	3 (4)	0-7
Chippy	187	6 (5)	3-14	114	3 (2)	1-9
Pansy	73	2 (1)	0-5	39	1 (2)	0-4
Rosie	81	3 (3)	0-5	57	2 (2)	0-4

The decrease in frequency of postural shifts according to night phase was significant for all group members: Blossom: z = -3.93, p = 0.01; Chippy: z = -3.42, p = 0.01; Pansy: z = -3.32, p = 0.01; Rosie z = -2.15, p = 0.02.

Intra-group analyses showed that Chippy changed posture significantly more frequently than Pansy and Rosie (U = 64.00, z = -5.60, p = 0.01; U = 102.50, z = -4.99, p = 0.01, respectively) during night phase 1, but not Blossom (U = 363.00, z = -0.90, p = 0.19). Blossom also changed posture significantly more frequently than both Pansy and Rosie (U = 117.50, z = -4.76, p = 0.01; U = 152.50, z = -4.20, p = 0.01, respectively). There was no significant difference between Pansy and Rosie (U = 389.50, z = -0.49, p = 0.62).

Between 00.00 and 07.00hrs, Chippy continued to show significantly more postural changes than Pansy and Rosie (U = 114.00, z = -4.83, p = 0.01; U = 171.00, z = -3.96, p = 0.01), but again not his mother, Blossom (U = 311.50, z = -1.71, p = 0.09). Pansy changed posture less frequently than Blossom and Rosie (U = 238.50, z = -2.88, p = 0.04; U = 281.50, z = -2.24, p = 0.03, respectively); with no difference between the latter two (U = 323.00, z = -1.55, p = 0.12).

Postural changes and sleeping partners

Table 8.2.2 shows that the number of postural changes was generally similar irrespective of sleeping partner(s)[20].

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[20] Instances where Blossom and Rosie were co-sleepers (1 night) and Chippy and Pansy were co-sleepers (also 1 night) were considered outliers and excluded from analysis.

Table 8.2.2 Median number of postural shifts according to sleeping partner(s)

Individual (plus sleeping partner[s])	**Median postural shifts**	**IQR**	**Range**
Blossom (Chippy)	8	6	2-14
Blossom (Pansy, Rosie)	8	4	2-11
Chippy (no partner)	9	5	6-17
Chippy (Blossom)	9.5	8	6-17
Pansy (Rosie)	2.5	3	1-9
Pansy (Rosie, Blossom)	4.5	2	2-7
Rosie (Pansy)	4	3	1-10
Rosie (Pansy, Blossom)	5.5	2	2-7

Analysis confirmed this; there were no significant differences in the numbers of posture changes according to platform sharer(s): Blossom ($z = -0.42$, $p = 0.68$), Chippy (9.9; $z = -0.06$, $p = 0.95$), Pansy ($z = -0.70$, $p = 0.48$), Rosie ($z = -1.32$, $p = 0.18$).

Is postural adjustment related to measures of nest building?

Spearman’s Rho correlation co-efficients were used to determine if the time at which nest construction started (when known) was related to the number of postural changes shown by each chimpanzee. There was no significant relationship for any of the chimpanzees: (Blossom: $n = 26$, $r_s = -0.37$, $p = 0.06$; Chippy: $n = 25$, $r_s = -0.29$, $p = 0.16$; Pansy: $n = 27$, $r_s = 0.19$, $p = 0.34$; Rosie: $n = 29$, $r_s = 0.06$, $p = 0.76$).

The same co-efficient was used to assess whether duration of nest building was related to the number of postural changes of each chimpanzee. Again, there was no significant relationship for any individual (Blossom: $n = 19$, $r_s = -0.23$, $p = 0.34$; Chippy: $n = 21$, $r_s = -0.01$, $p = 0.96$; Pansy: $n = 21$, $r_s = -0.30$, $p = 0.20$; Rosie: $n = 25$, $r_s = -0.26$, $p = 0.20$).

Individual preferred postures

For all group members the most common postures were lateral ones. Prone and supine postures were generally less favoured (see table 8.2.3 for individual details). For females, more time was spent on the right than left side. Although medians were similar, the inverse was true of Chippy.

Table 8.2.3 Median (plus IQR) times spent in each rest posture (in minutes)

Chimpanzee	Posture							
	Prone		Supine		Right		Left	
	median	IQR	median	IQR	median	IQR	median	IQR
Blossom	30	79	0	0	484	294	206	322
Chippy	34	87	3	18	320	239	329	171
Pansy	0	21	0	0	428	282	289	333
Rosie	0	41	0	9	508	328	231	290

As predicted, all individuals spent significantly more time on lateral versus prone or supine positions (detailed in table 8.2.4).

Table 8.2.4 Wilcoxon (z) statistic and probability (p) values for time spent in lateral versus prone and supine postures

Chimpanzee	Right vs. prone	Right vs. supine	Left vs. prone	Left vs. supine
Blossom	4.55, p=0.01	-4.70, p=0.01	-3.23, p=0.01	-4.55, p=0.01
Chippy	-4.14, p=0.01	-4.70, p=0.01	-4.42, p=0.01	-4.70, p=0.01
Pansy	-4.68, p=0.01	-4.66, p=0.01	-4.51, p=0.01	-4.68, p=0.01
Rosie	-4.70, p=0.01	-4.70, p=0.01	-4.44, p=0.01	-4.70, p=0.01

Although all chimpanzees spent more total rest time in the prone versus supine position, this only reached significance for Blossom and Chippy (table 8.2.5). Chippy generally favoured the left side, but this also failed to reach significance. All of the females favoured the right side, but this only reached significance for Blossom and Rosie.

Table 8.2.5 Wilcoxon (z) statistic and probability (p) values for time spent in prone versus supine postures, and time spent on right versus left side

Chimpanzee	Prone vs. supine	Right vs. left
Blossom	-3.73, p = 0.01	-3.31, p = 0.01
Chippy	-4.14, p = 0.01	-0.24, p = 0.81
Pansy	-1.35, p = 0.18	-1.55, p = 0.12
Rosie	-1.35, p = 0.18	-2.11, p = 0.04

Intra-group comparisons of time spent in each posture

Prone

Chippy spent significantly longer prone than Pansy or Rosie (U = 199.00, z = -3.56, p = 0.01; U = 232.00, z = -2.98, p = 0.03, respectively), but not Blossom (U = 348.500, z = -1.23, p = 0.26). Although Blossom spent longer in this posture than the other females, the difference was only significant compared to Pansy: U = 276.50, z = -2.39, p = 0.02 (Blossom vs. Rosie: U = 329.50, z = -1.48, p = 0.14). Pansy and Rosie did not differ in this respect (U = 368.00, z = -0.91, p = 0.36).

Supine

The younger chimpanzees spent significantly more time supine than the older females (Rosie vs. Blossom: U = 287.00, z = -2.58, p = 0.01; Rosie vs. Pansy: U = 318.50, z = -1.94, p = 0.05; Chippy vs. Blossom: U = 209.50, z = -3.76, p = 0.01; Chippy vs. Pansy: U = 249.50, z = -3.01, p = 0.03). There was no significant difference between Rosie and Chippy (U = 333.50, z = -1.42, p = 0.15), nor between the older females (U = 399.50, z = -0.52, p = 0.60).

Right side

All females spent more time on the right side than any other posture, with no significant variability among them ($\chi 2$ = 2.67, df = 2, p = 0.26). Chippy spent significantly less time on his right side than Blossom and Rosie (U = 208.00, z = -3.31, p = 0.01; U = 263.00, z = -2.45, p = 0.02, respectively), but did not differ from Pansy (U = 311.50, z = -1.70, p = 0.09).

Left side

Chippy spent more time lying on his left side than any of the females, but the only difference to reach significance was between Chippy and Blossom: U = 253.00, z = -2.61, p = 0.01 (Chippy vs. Pansy: U = 367.50, z = -0.68, p = 0.49; Chippy vs Rosie: U = 297.50, z = -1.91, p = 0.06). There was no significant variation between females (χ_2 = 3.61, df = 2, p = 0.17).

Individual orientations

As predicted, all four chimpanzees were more commonly orientated toward the centre of the night enclosure than toward a sleeping partner or the enclosure wall (table 8.2.6), although this only reached significance for Chippy and Pansy (see table 8.2.7). Similarly, all chimpanzees spent more time orientated toward the centre of the enclosure than a platform sharer, although this difference only reached significance for Rosie. Only Pansy orientated more toward a platform sharer than the enclosure wall, although this failed to reach significance. The remaining three chimpanzees spent more time facing the wall than their sleeping partner, although this was significant only for Rosie.

Table 8.2.6 Median time, plus IQR, spent orientated toward the centre of the enclosure, sleeping partner(s), or enclosure wall (in minutes)

Chimpanzee	**Orientation**					
	Enclosure		**Partner**		**Wall**	
	median	IQR	median	IQR	median	IQR
Blossom	291	315	35	458	261	395
Chippy	426	208	104	267	175	181
Pansy	311	322	134	340	171	345
Rosie	397	409	33	129	231	349

Table 8.2.7 Wilcoxon (z) statistic and probability (p) values for orientation toward centre of enclosure, sleeping partner(s), or enclosure wall

Chimpanzee	**Enclosure vs. wall**	**p**	**Enclosure vs. partner**	**p**	**Sharer vs. wall**	**p**
Blossom	-0.44	0.33	-1.40	0.08	-0.97	0.17
Chippy	-3.60	0.01	-1.65	0.05	-0.56	0.29
Pansy	-2.48	0.01	-1.87	0.03	-0.27	0.50
Rosie	-1.89	0.03	-3.28	0.01	-2.16	0.02

Chippy spent more time orientated towards the centre of the enclosure than any of the females. This difference, however, failed to reach significance ($\chi2$ = 4.55, df = 3, p = 0.11). Pansy, the eldest female, spent the least time orientated toward the wall. Again, however, there was no significant intra-group difference ($\chi2$ = 3.01, df = 3, p = 0.39). Although there was some individual variation in the amount of time orientated toward a platform sharer, this also failed to reach significant levels ($\chi2$ = 3.01, df = 3, p = 0.39).

8.2.4 Discussion

Even though such a small sample size makes findings difficult to generalise across populations, this study is the first to focus on changes in rest postures, preferred resting postures and orientation changes in a captive primate group. As there are no systematic studies of primate sleeping postures for comparison, these data must be viewed as preliminary. However, the overnight recordings have revealed some similarities and differences between chimpanzee and human nocturnal postures that are of interest in the wider study of sleep-related behaviours. Further research that focuses on sleeping positions and sleeping surfaces can be of practical use in terms of providing a comfortable sleeping area for captive apes.

Early overnight recordings of human sleep revealed between 20 and 45 changes of sleeping posture per night (Johnson et al. 1930). However, more recent reports have questioned such large numbers of postural shifts; several studies have concluded that humans average 11-13 postural changes per night (Dzvonik et al. 1986, Gordon et al. 2004). In the present study, median numbers of postural changes were much lower than in these reports, and generally decreased in the second night phase.

The male chimpanzee performed the greatest number of postural changes, possibly a reflection of sexually dimorphic sleep-related behaviour documented in both free-ranging and captive primates that is usually linked to anti-predation strategies. Dominant silverback gorillas, for instance, typically choose and lead their group to their sleeping site (e.g., Reynolds 1965). Adult male rhesus monkeys move to the periphery of sleeping groups on reaching maturity (Vessey 1973), as do maturing chimpanzee males (Goodall 1962). Dominant individuals in a zoo-housed baboon group (Noser et al. 2003) remained more alert during the night, adopting less relaxed postures than their subordinate counterparts. Laboratory housed pig-tailed macaque infants of dominant mothers had shorter sleep latencies compared to infants of mid/low-ranked females (Reite et al. 1976), attributed to dominant mothers being more able to select a secure space than lower-ranked individuals. Laboratory-housed stump-tailed macaques also remained vigilant throughout the night, with two males selecting a sleeping site away from other group members (Munoz-Delgado et al. 2004b). From their vantage point the two males alternated rest and activity cycles with each other: when one rested, the other remained vigilant, and vice versa. It has been proposed that males may move away from the group and occupy the highest sites available in order to observe the surrounding environment (Anderson 1984), thus facilitating early detection of predators.

This hypothesis receives support from the finding that, as predicted, Chippy spent the most time orientated toward the centre of the enclosure. Of course the captive setting of this study presented no predation risk, and it is possible that orientation preferences may be unrelated to any need to choose a safe sleeping site. Also, Chippy and Rosie were captive-born and thus had no direct experience of predators or predation risk. Previous research has shown that vigilance behaviours around a sleep site are present even in captivity. After presentation of a mock predator, Geoffroy’s marmosets alarm-called and retired later than in baseline periods (Hankerson & Caine 2004). One possible experimental approach might be to briefly introduce a similar mock predator, and record subsequent choice of the sleeping sites and behaviours throughout the night.

The hypothesis that lateral sleeping postures would be favoured was also supported, comparable to reports from both humans and chimpanzees. Self-reports have indicated that men and women habitually adopt a lateral sleeping position (e.g., Gordon et al. 2007). The reliability of this method can be questioned; however, research comparing self-reported versus video recorded sleep positions demonstrated high levels of concordance between the two, again favouring lateral positions (Gordon et al. 2004; Kubota et al. 2003). Sleeping on the right or left side is the most commonly adopted posture among humans, accounting for the largest amounts of total sleep time (DeKoninck et al. 1992; Lorrain & DeKoninck 1998; Gordon et al. 2004). Laboratory housed chimpanzees also appear to show this trend (Freemon et al. 1970; Videan 2006b), more frequently sleeping on the left or right side than sleeping prone or supine.

The supine posture was the least favoured by all group members, a similar finding to that of Bert et al. (1970). This is of interest as sleeping supine has been implicated in poor sleep quality in humans (e.g., DeKoninck et al. 1983), and also has been associated with sleep disorders such as sleep apnoea (Oksenberg & Silverberg 1998). Thus, it appears that the BD chimpanzees favoured postures that facilitated a ‘good’ sleep. However, in the absence of comparative data and physiological measures of sleep, this conclusion must remain speculative. Also in keeping with reports of human (Gordon et al. 2007) and chimpanzee (Videan 2006b) males preferring the supine posture, the male in this group also spent more time supine compared to females, although generally this position was not adopted for extended amounts of time.

In contrast to Videan’s (2006b) findings, all of the females favoured a specific lateral posture – namely, lying on the right side. The same preference has been reported for elderly humans (DeKoninck et al. 1992; Gordon & Buettner 2009; Lorrain &

DeKoninck 1998). This would be applicable to both Blossom and Pansy (estimated to be in their fifties), but not Rosie, who was not yet 20 years old at the time of research. Conceivably, age-related differences may not be as marked in chimpanzees as in humans. Typically, postural shifting decreases with age, as does the amount of time spent in REM sleep – the stage most associated with fluctuations in body movements (DeKoninck et al. 1992; Lorrain & DeKoninck 1998). Although comparative primate data are lacking, research on humans indicates that frequency of body movements (Giganti et al. 2008) and postural shifts decrease (DeKoninck et al. 1992) whereas periods of immobility increase (Aaronson et al. 1982) with advancing age. For this chimpanzee group, the predicted relationship between frequency of postural changes and age was only partly supported. Although the oldest chimpanzee, Pansy, did perform the fewest postural changes, the second oldest (Blossom) changed posture more frequently than the youngest female.

This may be attributable to Blossom and Chippy's sleeping arrangements. It is notable that these individuals were frequent co-sleepers, and also had higher frequencies of postural shifts compared with the other mother-adult offspring dyad. Bed-sharing in human mother-infant dyads has been correlated with a higher frequency of infant nocturnal arousals (e.g., Richard et al. 1996), and so it is possible that the proximity and movements of her offspring increased the frequency of Blossom's position shifts. This would also be in keeping with Aaronson et al.'s (1980) observations of a human couple's synchrony in frequencies of movement and periods of immobility. More recently, a study of 46 pairs of bed partners confirmed a substantial degree of concordance in sleeping partner movements (Pankhurst & Horne 1994).

In conjunction with age (DeKoninck et al. 1992), presence of a sleeping partner (Aaronson et al. 1980), and possibly gender (these data), the comfort afforded by sleeping surfaces is known to affect nighttime movements and sleep quality. Four men made significantly more movements when sleeping on a hard surface (plywood covered with carpet), compared to a soft or medium-hard surface (Suckling et al. 1957), although there were also individual differences in sensitivity to the three sleep surfaces. Women (n = 12) preferred to sleep on comfortable surfaces, scoring soft, hard, and foam-covered mattresses as significantly more comfortable than a wooden sleeping surface (Buckle & Fernandes 1998). A more recent study reported that the sleep quality of a group of nine men did not differ as a function of sleep surface; however, within-subject analysis indicated that measures of sleep structure, sleep continuity and self-reports of sleep quality were affected by the substrate (Bader & Engdal 2000). Subjective scoring and EEG recordings demonstrated that sixteen adults sleeping on comfortable (versus uncomfortable) mattresses had higher levels of sleep efficiency (Lee & Park 2006). Damn et al. (2003) showed that postural shifts were more frequent in crate-housed sows versus sows in substrate-enriched pens.

Animal studies have also shown that comfortable surfaces are preferred for resting. Cows (n = 32) and sows (n = 47) showed preference for lying on rubber wood chips and rubber mats, respectively, over concrete surfaces (Fisher et al. 2003; Tuyttens et al. 2008), with the former spending significantly longer resting on wood chips than concrete. In the absence of the BD chimpanzees’ use of alternative sleeping surfaces (e.g., the substrate covered floor), it remains unknown how comfortable or uncomfortable the wooden sleeping platforms were for them. However, given the low frequency of postural shifts and the approximately 13.5 hours per night on the sleeping platforms (part 1), it appears that the rigid sleeping surfaces were comfortable enough for this captive group. Nests of free ranging apes have been described as “springy” (Nissen 1931) and “comfortable” (Groves & Sabater-Pi 1985) although they are constructed on stable, firm, surfaces (e.g., Rayadin & Saitoh 2009; van-Lawick Goodall 1971). It is therefore possible that, in comparison to humans, chimpanzees prefer solid sleeping surfaces as they provide a secure base for arboreal sleeping. All of the zoos and wildlife parks that were surveyed (chapter 2) reported that elevated platforms, shelves and benches featured in apes’ night enclosures. These may be preferred as a secure sleep site, but this also demonstrates the need to provide suitable nesting substrates to avoid contact pressure, and so discomfort, from lying on firm surfaces. These should facilitate comfort and sleep, both of which may be beneficial to welfare (Dawkins 1990; Fraser 1989; Roder & Timmermans 2002).

Given evidence from wild chimpanzees that the amount of effort invested in nest building is positively correlated with how comfortable the completed nest is (Stewart et al. 2007), it might be predicted that the longer nests take to construct, the more comfortable they would be, which in turn might lead to fewer postural changes during the night. However, for the chimpanzees in this study there appeared to be no significant relationship between the two variables. However, it must be considered that nest-building records were incomplete; some nests were completed before the start of analysis. Future research should incorporate direct observations of nest building and recordings of nighttime behaviours to question the relationship of nest quality and sleep quality in more depth.

The findings from this non-intrusive study have implications for enclosure design and captive primate welfare. The relative infrequency of postural shifts in general, coupled with finding that postural changes did not vary according to platform sharer(s), suggests that sleep was not disrupted by the presence of a platform sharer. Nonetheless, several other studies have shown that primate sleep can be disturbed by other group members. Observations of laboratory-housed marmosets and juvenile macaques, for example, showed that individuals could often be woken by the movements of others in close proximity (Crofts et al 2001; Kaemingk & Reite 1987).

Data has shown that, in conjunction with increased nighttime arousals, co-sleeping can influence sleep architecture, reducing stage 4 NREM sleep (i.e. deep) and increasing stage 1 and 2 light NREM sleep in human infants (McKenna 1996; Mosko et al. 1996). It is still recommended that several sleep sites be made available to captive apes (discussed in chapter 4) to avoid the possible detrimental effects of long-term sleep deprivation (Sforza et al. 2004; Walker 2008). It should also be considered that sharing a nest or sleep site is contrary to species-typical nesting behaviours (Fruth & Hohmann 1994), although there are exceptions (e.g., adult male chimpanzees co-sleeping: Riss & Goodall 1976). Facilities that house apes should therefore incorporate at least one suitable sleeping area for each individual.

As discussed in the preceding section, the focus of this research was not to score sleep phases or cycles. However, as with periods of wakefulness, video recording of nocturnal postural shifts could potentially be used as indicators of primate sleep phasing. Movements during sleep are differently distributed across sleep stages: major body movements occur predominantly in transitions to and from REM sleep, with the longest periods of immobility being associated with specific phases during NREM sleep (Aaronson et al. 1982). Video records of sleeping humans have allowed reliable measures of sleep cycles (Aaronson et al. 1982; Hobson et al. 1978). Alternative methods are largely able to reduce invasive, neurological measurements of primate sleep. Moreover, given the similarities between human and chimpanzee sleep organisation, non-invasive observation of chimpanzee sleep-related behaviours may provide information on evolutionary factors underlying human sleep patterns, including safety at sleep sites, sleeping postures and social aspects of sleep-related behaviours (Anderson 2000).

Conclusions and recommendations

This study is the first to specifically focus on the nighttime sleeping postures of captive chimpanzees, adding to our current scant knowledge of sleep-related behaviours. As in humans, lateral positions are the most frequently adopted sleeping postures. In terms of frequency of postural shifts, there is some evidence that, like humans, these are age- and sex-related, although further research is needed before firm conclusions can be drawn.

Unlike humans, chimpanzees may prefer a rigid sleeping base to increase feelings of security while sleeping in an elevated location. This has implications for sleep site design, and comfortable nesting materials should always be provided to prevent discomfort through contact pressure on such surfaces. Although not the case here, human and primate data have indicated that co-sleepers and proximate group members can increase nocturnal awakenings and affect sleep architecture. To avoid sleep deprivation captive apes should be allowed the opportunity to sleep at distance from other group members, at least one sleep site per individual should be provided.

Non-invasive recording of nocturnal sleeping positions could potentially used in conjunction with nighttime awakenings and behaviours as an alternative method of scoring sleep phases. This in turn may have consequences for all primates used in sleep-related research.

Chapter 9

Nesting and nighttime behaviours following the peaceful death of an elderly group member

"Death, so called, is a thing which makes men weep,
And yet a third of life is passed in sleep." ~ Lord Byron

9.1 Introduction

Responses to the loss or death of an attachment figure can take many forms (often involving multiple systems): affective (emotional), psychological (behavioural and cognitive) and physiological (for example, appetite reduction and sleep disturbance) (Waldrop 2007). Grief – a response to loss through separation or death – is a natural and ubiquitous human reaction, which also occurs to some degree in a wide range of social mammals (Archer 1999), including the highly social non-human primates.

Research on attachment in both humans and primates, has contributed to our understanding of grief (Shear & Shair 2005). Mother-infant separation studies have generally reported a biphasic response pattern in monkeys and apes, similar to Bowlby's (1960) ethological model of grief reactions in human children after being separated from a caregiver (usually the mother). Immediately following separation, children enter the so-called 'protest' phase, showing high levels of distress and agitation. Within days, social interactions decrease and the child becomes dejected – the 'despair' phase.

Studies have shown that the behavioural responses of primate infants to maternal separation are broadly comparable to grief reactions in human children. Kaufman and Rosenblum (1967) reported the behavioural consequences for four pigtail macaques (mean age 5.6 months) of involuntary separations from their mothers. Initially, both mothers and infants emitted distress vocalisations, and infants engaged in agitated locomotor behaviours (pacing, frequent trips to the cage door), with no sleep occurring throughout the first day of separation. Although the infants remained in the social group in which they had been reared, up to thirty-six hours after the removal of the mothers self-clasping behaviours increased, with a concurrent decrease in social interactions and play. After five to six days of separation, ‘depressive’ behaviours were still apparent, but had lessened; exploration of the environment and interactions with conspecifics increased. By the third and fourth weeks of separation, social play had reached levels similar to those prior to separation. Upon reunion, all infants showed increases in ventral-ventral physical contact with mothers for one month, to the extent that explorative and play behaviours fell to levels lower than those prior to separation.

Eight Tonkean macaque infants (age range 5-9 months) showed separation-induced increases in several behaviours including distress vocalisations and clinging to unrelated group members. Decreases in social play were also recorded (Drago & Thierry 2000). Similar responses have been documented in apes. Three captive infant gorillas (aged 27 months) were experimentally separated from their mothers and the silverback male for a total of 24 weeks (Hoff et al. 1994). The infants were housed together in an unfamiliar cage. Upon separation, infants made distress calls for two days, before showing several symptoms of ‘behavioural depression’ for the following month. Frequency of mutual huddling increased, along with self-clasping. Caretakers also recorded reductions in appetite and feeding. A 33-month-old gorilla infant in a wildlife park showed decreased activity and an increase in affiliative behaviours with the silverback male when its mother was temporarily separated from the group for a surgical procedure (Nakamichi et al. 2001).

Grief responses to loss are not restricted to mother-infant pairs (Hofer 1984); the term is broadly applicable to the reaction seen following the loss of any significant attachment figure, or those with whom we share ‘affectional bonds’ (Bowlby 1980 in Archer 1999). Adult rhesus monkeys (n = 10) were physically removed from their family unit and placed into one of three environments: caged with familiar subjects (members of the same family group, n = 4), caged with unfamiliar subjects (from different family groups, n = 4), or housed individually (n = 2). Macaques housed with both familiar and unfamiliar peers showed little behavioural reaction to separation from the larger family unit. However, over the experimental period of separation (126 days), the two individuals that were individually housed showed significant increases in self-clasping and stereotypic behaviours (although no exact details of stereotypies were provided: Suomi et al. 1975).

The severance of attachment bonds results in grief reactions in several primate species. Death of course is the ultimate disruption to an attachment bond. Although understandably scarce, there are an increasing number of reports from both free-ranging and captive environments detailing primates’ responses to the death of related and unrelated group members. The transportation of dead infants, even into the latter stages of decomposition, or indeed to mummification, has been observed in several free-ranging primate populations (e.g., gelada baboons: Fashing et al. 2010; ring-tailed lemurs: Nakamichi et al. 1996; Japanese macaques: Sugiyama et al. 2009; chimpanzees: Biro et al. 2010; Cronin et al. 2011; Hosaka et al. 2000; Matsuzawa 1997; gorillas: Warren & Williamson 2004), and is indicative of the strong mother-infant attachment bond across several primate taxa.

Physiological and behavioural responses to stress and death have been measured in free-ranging female chacma baboons in Botswana (Engh et al. 2006), who are known to retain life-long, close social bonds with matrilineal kin (Silk et al. 1999). The GC (glucocorticoid – a hormonal response to stress) levels in females increased after known/suspected predation on group members. GC levels of females who had lost a close relative to predation were significantly higher than of those who were not closely bonded to the dead individual(s). These responses however, were relatively short in duration. After two months, GC levels had returned to baseline levels. Of interest is that behavioural focal data showed that grooming diversity and number of grooming partners increased in those affected by the death of a relative, which may have been a strategy to compensate for the loss of an attachment figure.

On the death of his mother, a juvenile male chimpanzee (eight years old) was described as falling into a "deep depression", behaving lethargically and losing his appetite (Goodall 1990). Probably due to his lack of feeding and subsequent weakening of the immune system, the young male died. The behavioural responses of sixteen chimpanzees to the accidental death of an adult male at Gombe National Park were reported in some detail by Teleki (1973). The adult male fell out of a tree and broke his neck. Immediate responses included alarm calls, male charging displays, general "frenzied activity", and frequent submissive and reassurance behaviours. Some individuals also sat near the corpse (within several meters), but had no physical contact with it. Although all stared at the body, there was no physical contact until approximately one hour after death, when an adolescent male approached the corpse and examined/sniffed an area near the dead male's head.

Social grooming among group-members resumed approximately twenty minutes after the death, and continued until the body was abandoned almost four hours later.

In contrast to this account, Boesch and Boesch-Achermann (2000 cited in Anderson 2011) reported that chimpanzees of the Tai forest did make physical contact with a dead female, shaking and grooming the corpse, and even dragging it during displays. Fawcett and Muhumuza (2000) reported that an adolescent female chimpanzee “gently shook” the body of an adult male that had been fatally attacked in the Sonso chimpanzee community (Budongo Forest, Uganda). As also reported by Teleki (1973), several males displayed around the vicinity of the corpse, with one adult male leaping on and violently shaking the body.

A recent report on the death of a silverback gorilla (Volcanoes National Park, Rwanda), found dead in his night nest after a brief illness, indicted that the remaining group members were clearly affected by the death. A juvenile male who was reported to have a strong affiliative relationship with the silverback remained close to the body, while a young blackback male manipulated and sniffed the body (http://gorillafund.org/Page.aspx?pid=494, 499). The only female group member was described as ‘very stressed’ – although no behavioural descriptions accompany this. In the days following the death, there was an increase in display behaviours and vocalisations by the remaining male group members. The group stayed in relatively close proximity to the body, ranging within 200 meters of the body until field-tracking staff removed it.

Brown (1897) described the behaviour of a young male captive chimpanzee following the death of a long-term cage-mate, with whom he had a strong bond.

Immediately after her death, the male was reported to make attempts to rouse her – manipulating the head and hands and pushing the body. On failing to rouse her, the male ‘snatched’ at his hair and made distress vocalisations. Several behavioural changes were also reported in the period following the death, including stronger attachment to the keeper and a change in sleep site selection. Both chimpanzees had slept in close proximity on a blanket on the floor prior to the female’s death, but the male moved to sleep at the top of the enclosure following her death. Written three years later, a similar anecdote describes the reactions of a chimpanzee to the deaths of two of his cage-mates (Garner 1900 cited in Pollock 1961). In both instances, the chimpanzee stayed in close proximity to the body, and showed increased attachment behaviour to the author.

A mixed age-sex group of zoo-housed gorillas (n = 6, 3 adult females, two with juvenile male offspring, and another silverback adult male) were observed for three months prior to, and following, the death of a silverback male. Post-death observations revealed an increase in aggressive display behaviours by the remaining male. A mother-infant pair showed increased spatial proximity and close physical contact in the month immediately following the death of the male, gradually decreasing over a further two months to pre-death levels (Hoff et al. 1998).

Using similar methodology, Less et al. (2010) recorded the responses to the death of a silverback in two separate zoo-housed gorilla groups. In the first group (n = 10) there was no significant effect on hourly rates of affiliative, agonistic or displacement behaviours. However, from pre to post-death conditions, there were significant increases in social distance, and also in self-directed behaviours, which may be indicative of elevated stress (e.g., Davenport et al. 2008). Conversely, the second group (n = 3) showed increases in agonistic and displacement behaviours, and also increases in social proximity. These studies strongly suggest within and between population differences in grief responses.

Similar to the second group of zoo-housed gorillas described above, an infant orang-utan showed an increase in close physical contact with several adult females, especially a maternal aunt, following the death of her mother (Whilde & Marples 2010). Notably, the aunt allowed the infant to share her night nest. As with several other recent studies, this group (n = 5) was zoo-housed, allowing researchers to record pre and post-death behaviours of group members. As well as the recorded increase in social proximity, the infant showed more object manipulation and locomotion, with a concurrent decrease in resting.

Although most behavioural data are biased toward daytime observations, a few of the above-cited accounts allude to the fact that grief responses can affect multiple aspects of primate sleep-related behaviour. Brown’s (1897) young chimpanzee changed his sleep site after the death of his cage-mate. Kaufman and Rosenblum (1967) noted that infant macaques did not sleep on the first day of maternal separation, and Whilde and Marples (2010) observed that an infant orangutan shared the night nest of a maternal aunt after the death of her mother. A respondent to the questionnaire in the course of this research (chapter 2) also reported that two females co-slept for a short time (one week) after the death of a male group member. Sleep disturbance is a well-documented response to the loss of an attachment figure in humans (Laurence & Weikart 1984; Schechtman et al. 1997).

The effects of the death of a spouse on sleeping patterns have been subject to much research. In the first week following the loss of a spouse, 77% of widows (total n = 22) reported sleep disturbances. The severity of the insomnia (difficulty initiating or maintaining sleep) decreased gradually in the following three months (Parkes 1970). Similarly, laboratory based research showed that sleep patterns were impaired for spousally bereaved participants (n = 94), but not elderly control subjects (n = 45) (Brown et al. 1996). Baglioni et al. (2010) conducted a longitudinal study on the effects of bereavement on 22 widows. As with the previous studies, insomnia was prevalent factor during the grieving process. The majority of widows reported suffering from some type of sleep disruption, with symptoms of insomnia ‘marked’ in 14 (64%) of the participants. Self-report data from a larger sample of widows (n = 173) also showed that a large proportion (23%) suffered from some type of sleep disturbance (Kowalski & Bondmass 2008).

Although many studies have focused on the death of a spouse, sleep disturbance is known to affect all age/sex classes following the death of an attachment figure. A questionnaire study involving bereaved (n = 508) and non-bereaved (n = 307) university students showed that symptoms of insomnia were significantly more prevalent in the bereaved group versus the control group (Hardison et al. 2005). Self-report data revealed that bereaved adults (n = 105) suffered from low levels of sleep quality and impaired sleep duration (Germain et al. 2005). Only 11% of the total participants reported that they suffered from minimal sleep disruption. Grief-related thoughts were associated with impaired sleep (as measured by self-report data and EEG-assessed sleep patterns) in 29 individuals being treated for bereavement-related depression (Hall et al 1998), and 108 adult sufferers of ‘complicated’ grief (acute, prolonged grief) reported poor sleep quality, poor sleep duration, and high levels of sleep disturbance (Maytal et al. 2007). These symptoms were also reported by caregivers of terminally ill relatives (n = 30) one year after their bereavement (Waldrop 2007). There is also evidence that sleep disturbance is not dependent on the type of loss suffered. Miyabayashi and Yasuda (2007) reported that sleep disturbance was frequent in bereaved parents and spouses (n = 215) that had suffered loss through suicide, accidents, or short and long illnesses.

Numerous studies have shown that the perceived loss or death of an attachment figure can result in grief reactions in several primate species. Although human studies unequivocally demonstrate that sleep disturbance accompanies grief, there appears to be no systematic data on the effects of loss or death on sleep-related behaviours of primates. Early laboratory-based studies on infant pig-tailed macaques that were reared in isolation on cloth surrogate mothers (Reite & Short 1977) concluded that rearing conditions (isolated versus mother-reared group living infants) did not affect sleep physiology (sleep stages and sleep cycles). However, behavioural quantifications of sleep-related disturbances after death are lacking.

In the present study, events preceding the death of a captive adult female chimpanzee, the moment of her death, and the subsequent nesting and nocturnal behaviours of the remaining group members were recorded on camera. Pansy, an elderly female, had been in ill health for several weeks prior to death (see supplemental data – appendix 2). Approaching the time of death, care staff decided not to remove Pansy from the night enclosure, allowing the other group members (Rosie, Pansy's female offspring; Blossom, an unrelated elderly female, and Chippy, Blossom's male offspring) to remain with her throughout the night (see also

Anderson et al. 2010 - appendix 5). On sleeping platform B (her most frequently used sleep site), Pansy died at 16.24hrs.

Study aims

As the recordings from this night are unique, there are no specific hypotheses to be tested. Rather, all events and behaviours have been described in timelines (appendices 3 and 4). Where possible, nesting and nocturnal behaviours on the night of Pansy's death are compared to data on nesting and nocturnal behaviours of this same group in a previous study (chapter 8). In this way, some tentative conclusions can drawn on how the death of Pansy affected the nesting and sleep-related behaviours of the remaining group members.

9.2 Methods and analyses

Data collection

The four chimpanzees in this study were housed at Blair Drummond Safari Park, a small group whose nesting and nocturnal behaviours had previously been observed and recorded (see chapter 3 for details of housing, chapter 8 for details of camera positions and recording equipment). On the night of death (December 7th 2008), the same cameras and recording equipment were *in situ* over sleeping platforms A and B from previous nocturnal research undertaken in February 2008. Cameras were activated by staff at 16.13hrs, recording all events on each platform onto the hard drive until recording was terminated at 08.53hrs the following morning.

Data analyses

Data recorded onto the hard drive were analysed ad-libitum. Based on previous behaviours (described in chapter 8.1), and also incorporating behaviours specific to these data (e.g., shaking of Pansy's shoulder/arm), the behaviour(s) of each chimpanzee prior to Pansy's death, at the moment of death, their subsequent retirement to sleeping platforms, their nocturnal behaviours, and their behaviour on awakening were coded and recorded manually. This was then converted into timelines (appendices 3 and 4).

Although recording of the night of death was not terminated until 08.53, I have only included data up to 07.00hrs, in order to compare it to data from the 29-night study in February 2008. All the behaviours performed by each chimpanzee between 07.00 and 08.43hrs are available in the timelines, although not used in the comparisons here. As one chimpanzee (Rosie) nested later than observed in the previous study, data on nest amendments, leaving the nest and sleeping platform etc. have been matched for this timeframe. As only one night of data was available, no statistical comparisons were made.

9.3 Results

Effect of death on retirement times and duration of nest building

Table 9.1 shows that the time of retirement on the night of Pansy's death did not differ greatly from retirement times during the February study for Blossom and Chippy. Although Blossom did make her nest earlier on the night of death, previous data shows that she frequently built her nest prior to 17.00 hrs (see table 9.2). However, there is a large discrepancy in time of nest building for Rosie. During the February study, median time of nest building was approximately 17.30 hrs, with the majority of her nests being built between 17.00 and 18.00 hrs. The latest recorded time of nest building by Rosie during the 2008 study was 18.15 hrs. On the night of her mother's death, Rosie did not construct a nest until almost eight o'clock in the evening.

Table 9.1 Median time (plus IQR) of retirement/nest building compared to the night of Pansy's death

Chimpanzee	**February study**		**Night of Pansy's death**
	Median time	**IQR**	**Time**
Blossom	17.23	0.31	16.53
Chippy	17.37	0.79	17.35
Rosie	17.27	0.14	19.47

Table 9.2 Data from February 2008 study. Percentage of nests built before 17.00 hrs, between 17.00-18.00 hrs, and between 18.00-19.00 hrs

Chimpanzee	**% nests prior to 17.00hrs**	**% nests between 17-18.00hrs**	**% nests between 18 - 19.00hrs**
Blossom	61.5	38.5	0
Chippy	42.3	42.3	15.4
Rosie	34.5	55.2	10.3

For all chimpanzees, the median duration of nest building during the February 2008 study and on the night of death were similar, indicating that this behaviour was unaffected by the death. All durations of nest building fell within the normal ranges of construction time during the February study (table 9.3).

Table 9.3 Comparison of median duration (plus IQR) of nest building during the February study, and duration of nest building on the night of Pansy's death (in minutes)

Chimpanzee	February study		Night of Pansy's death
	Median duration	**IQR**	**Duration**
Blossom	2	0.8	2.2
Chippy	2	1.8	1.5
Rosie	3	1.0	2.2

Effect of death on general and specific sleep site selection

On the night of Pansy's death, Blossom and Chippy (mother and adult male offspring dyad) slept on platform A. This was the most common sleeping area and sleeping partner combination recorded during the previous observations (18/29 nights: 62% of total nights). Rosie (adult female) and her mother demonstrated an identical sleeping arrangement on sleeping platform B (also 18/29: 62% of total nights). Rosie also spent most of the night on platform B after the death of her mother. As all chimpanzees returned to their most frequently used platforms, it appears that the death of a group member did not affect general sleep site selection.

During February, Pansy spent 90% of total nights against the back wall, approximately halfway across the platform - also the approximate location where she died (see plate 9.2). For 10% of the time she was in Rosie's usual position – against the left hand wall in the middle/left bottom corner.

Plate 9.2 The area where Pansy died was in the general area where she usually slept when on platform B.

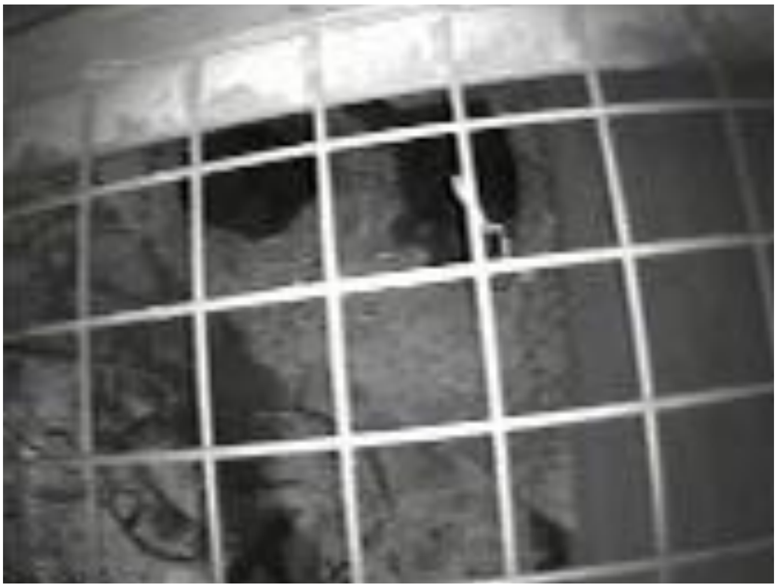
During February, Rosie spent 90% of time on this platform against the right hand wall, near the bottom left hand corner (see plate 9.3). For 5 % of the time she nested against the back wall, approximately half way across the platform. The remaining 5% of the time she was against the left wall, but further up the platform toward the back wall.

Plate 9.3 Rosie (left side of picture) is sitting in the general area where she nested during February. Blossom (right of picture next to horizontal ladder) is sitting in the area where Rosie nested on the night of her mother's death.

At 19.47 Rosie constructed her nest close to the horizontal ladder at the top right hand side of the platform. At 01.21 she moved further down the diagonal of the platform (still on the right hand side). There was no attempt to construct a nest, but straw was scattered over the platform. In February, Rosie most frequently nested in the bottom left corner of platform B, and less frequently at the top end of the platform. On the night of her mother's death, she nested in two areas that she had never previously been seen to use for this purpose – the top right hand corner of the platform and the diagonal edge of the platform. The presence of Pansy's body may have prohibited Rosie nesting at the bottom left hand side of the platform

During the February study, Blossom spent invariably retired to the same area (against the right hand wall, approximately mid-way up the platform) (100% of total nights on platform A). During the February study, Chippy spent 60% of total nights on platform A in the top left corner close to the horizontal ladder, and 40% of total nights at the bottom right corner of the platform. In contrast to Rosie, Blossom and Chippie made their nests in their typical preferred nesting areas when Pansy died (plate 9.4).

Plate 9.4 Blossom (on the right of the picture) and Chippy (on the left of the picture near the platform diagonal) nested in their generally preferred areas.



Effect of death on leaving the nest, leaving the sleeping platform, and on nest amendments

The chimpanzees rarely left their nest during the previous study (median frequency Blossom: 0, IQR 0; Chippy: 0, IQR: 1; Rosie: 0, IQR: 0). This typical tendency of all the chimpanzees to remain in their nest during the night also applied on the night of Pansy's death. Blossom did not leave her nest on the night of Pansy's death; corresponding frequencies for Chippy and Rosie were 2 and 1, respectively.

As with leaving the nest, leaving the sleeping platform was an infrequent behaviour during February 2008 (median frequency Blossom: 0, IQR 0; Chippy: 0, IQR: 0; Rosie: 0, IQR: 0). On the night of Pansy's death, none of the chimpanzees left the sleeping platform after retirement.

Frequency of making amendments to nests was also in keeping with data from February 2008 (table 9.4) in terms of median frequency and in the normal nightly ranges, again indicating that this nesting pattern was unaffected by Pansy's death.

Table 9.4 Median frequency (plus IQR) of nest amendments during the February study, and frequency on the night of death.

Chimpanzee	February study		Night of Pansy's death
	Median frequency	IQR	Frequency
Blossom	1	2	2
Chippy	1	2	1
Rosie	1	2	2

Effect of death on postural shifts and orientation

Comparison of the median number of postural changes during February and the number of postural shifts on the night of Pansy's death shows an increase for each chimpanzee (see figure 9.1). Blossom showed the most marked increase, with posture changes increasing over ten-fold from February data. Rosie showed over twice as many changes on the night of death compared with the maximum previously recorded. Chippy also showed more postural changes compared to his median frequencies, but the number was similar to the maximum number from February.

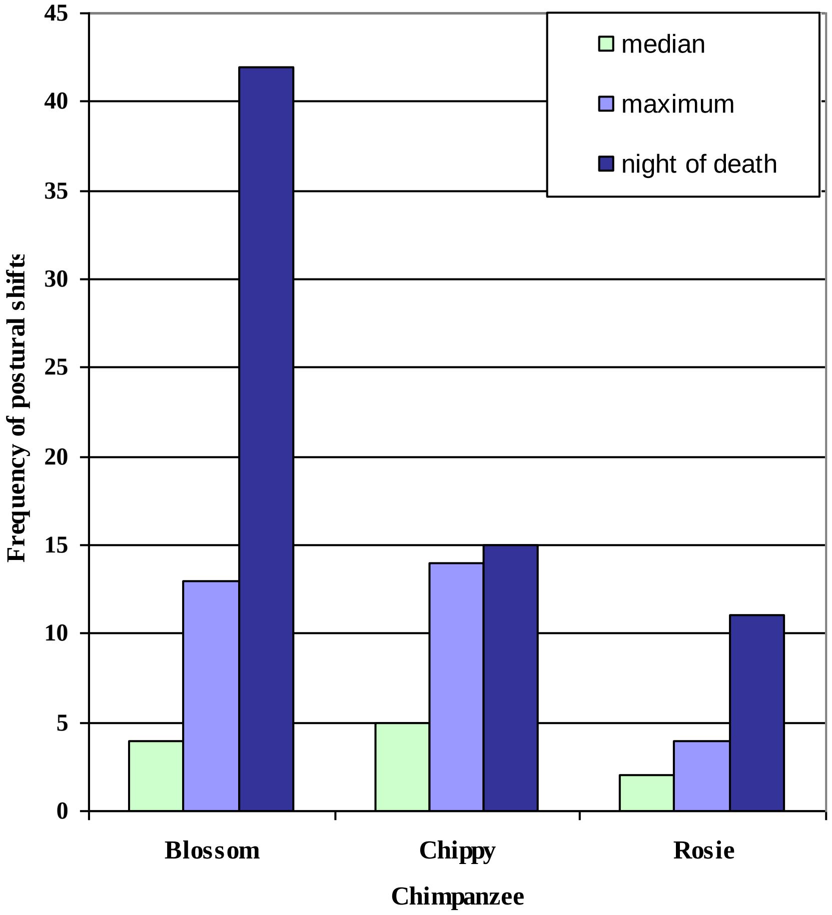


Figure 9.1 Median frequency and maximum number of postural changes recorded during February, and frequency on the night of Pansy's death.

Data from the previous study also indicated that the chimpanzees had preferred resting/sleeping postures, measured by the amount of time spent in these postures. Table 9.5 shows that Blossom preferred sleeping on her right side. She spent less time in a prone position on the night of Pansy's death, with an increase in the time spent in the supine position. Chippy slept preferentially on his left side, with an increase in time spent supine and a marked decrease in the time spent prone on the night of Pansy's death. Rosie was never observed either prone or supine on the night of her mother's death, although she was (infrequently) observed in these positions in the earlier study. During that study she spent more time on her right side, but when her mother died she spent more time on her left side.

Table 9.5 Median time (plus IQR) spent in each rest posture during February and on the night of Pansy's death (after nest building)

Chimpanzee	February study				Night of Pansy's death			
	prone	**supine**	**right**	**left**	**prone**	**supine**	**right**	**left**
Blossom	30 (79)	0 (0)	484 (294)	206 (322)	39	28	378	371
Chippy	34 (87)	3 (18)	320 (239)	329 (171)	0	31	250	518
Rosie	0 (41)	0 (9)	508 (328)	231 (290)	0	0	267	396

On the night of Pansy's death, all chimpanzees spent more time orientated toward the middle of the enclosure than facing a platform sharer or the enclosure wall (see table 9.6). In general, Chippy followed the same pattern of orientation on the night of Pansy's death as he did during the February study. The majority of time was spent orientated toward the middle of the enclosure, less time was spent orientated toward an enclosure wall, and the least amount of time was spent orientated toward a platform sharer. Blossom broadly followed this trend, spending most time in both recordings orientated toward the enclosure wall, and less frequently orientated toward the platform sharer.

However, there is contrast in the amount of time Blossom orientated toward her platform sharer. In the February study, the median time of facing a sharer was approximately 35 minutes, but this fell to only 8 minutes on the night of Pansy's death. Rosie spent a similar amount of time facing the wall in both the February study and on the night of Pansy's death. As with Blossom, there was a change in the amount of time orientated toward a platform sharer. In February Rosie faced a platform sharer for a median of 33 minutes, but although she shared the platform with her dead mother, she never orientated herself toward Pansy's body; instead she spent time orientated toward the middle of enclosure.

Table 9.6 Median time (plus IQR) each chimpanzee spent orientated toward enclosure centre, platform sharer(s) and enclosure wall during February 2008 and on the night of death after nest building (in minutes)

Chimpanzee	**February study**			**Night of Pansy's death**		
	enclosure	**sharer**	**wall**	**enclosure**	**sharer**	**wall**
Blossom	291 (315)	35 (458)	261 (395)	457	8	317
Chippy	426 (208)	104 (267)	175 (181)	359	191	231
Rosie	397 (409)	33 (129)	231 (349)	423	0	230

Effect of death on aggressive and social behaviours

Over the 29-night duration of the February study, only 3 aggressive behaviours were observed (see also chapter 8.1). On night 23, the adult male performed charging displays at 06:00hours, lasting approximately 9 minutes. He also performed displays on the following night, starting at 03:00hrs and continuing sporadically until 06:34hrs. Blossom also performed aggressive behaviours on this night, including charging and foot stamping. Although Chippy ran across platform B, where Pansy and Rosie were sleeping, he made no physical contact with either of them. On the night of Pansy's death, however, Chippy performed 3 separate charging displays, once shortly after the death, and twice the following morning (detailed in appendix 3). In contrast to the February data, the charging displays all involved contact aggression, with Chippy repeatedly bringing both fists down and ‘thumping’ Pansy’s torso.

Social behaviours around the time of nest building and during the night were infrequent during February 2008 (chapter 8:1). Around the time of Pansy’s death she was the recipient of numerous positive social contacts immediately prior to, and at the moment of, death. All chimpanzees groomed and touched her prior to death, with Blossom and Chippy also manipulating her body at the time of death (details on timelines). In February 2008 only 3 instances of Pansy being the recipient of a positive social contact were observed – she was twice groomed by Blossom, and once embraced by Rosie. Between 16.14hrs and 16.24hrs (time prior to death), 11 positive contacts were directed toward Pansy, including grooming, brief touches, and arranging straw around her. At the moment of death (16.24hrs), three additional positive contacts were recorded while the chimpanzees gathered around Pansy (plate 9.5): Blossom manipulated and groomed the body, with Chippy also manipulating the body.

Plate 9.5 Left to right: Rosie, Chippy and Blossom gathered round Pansy at the moment of her death.

Although there were no positive social contacts directed at Pansy after 16.25h, Blossom and Chippy interacted 6 times throughout the night. During February, only 12 social contacts were recorded for this dyad over the total recording period. The duration of these affiliaitive contacts is also of interest. Over 29 nights, the total duration of social contacts lasted approximately 20 minutes, although 7 minutes of these social behaviours occurred after a charging display, and so may be data outliers. On the night of Pansy's death, the duration of affiliative social contacts between this mother-offspring dyad was approximately 18 minutes.

9.4 Discussion

This chapter has compared several aspects of the nesting and nocturnal behaviours in a small group of chimpanzees on the night of the death of a group member, and data on nesting and nocturnal patterns from a previous study. This may be the first such research of its kind, providing a unique opportunity to more fully understand the behaviour of apes in the hours following the peaceful death of a long-term group member.

Primates’ grief responses to loss through maternal separation have been well documented in monkey and ape species. Both infant and adult monkeys show abnormal behaviours when separated from their mothers and family groups (pigtail macaques: Kaufman & Rosenblum 1967; rhesus macaques: Suomi et al. 1975). Infant gorillas show similar behavioural disturbances (Hoff et al. 1994) and reductions in social behaviours on separation from their mother (Nakamichi et al. 2001). Observations on the responses to the death of a group member are fewer, although they are exceptions (e.g., Biro et al. 2010; Boesch & Boesch-Achermann 2000; Fawcett & Muhumuza 2000). In recent years there has been an increase in reports on the behaviours of captive apes preceding and following the death of a group member (e.g., Hoff et al. 1998; Less et al. 2010; Whilde & Marples 2010), although these typically focus on changes on daytime behaviours.

The number of social affiliative contacts (such as touches, grooming, manipulations) directed toward Pansy approaching the time of death was more frequent than previously documented, yet none of the remaining chimpanzees made any attempts to touch or manipulate the body after death. This contrasts with previous reports of wild chimpanzees that manipulated the corpses of dead infants, touching them and lifting their limbs (Biro et al. 2010). Sub-adult males and juveniles also touched and manipulated the corpse of a newborn infant chimpanzee at Mahale Mountains (Kooriyama 2009), and some chimpanzees at Gombe (Teleki 1973) showed ‘persistent and intense’ interest in the corpse of an adult male. As well as the mother, an unrelated adult male and adolescent female groomed (for several minutes) the body of an infant chimpanzee two days after its death (Cronin et al. 2011).

It is unclear why the chimpanzees in this study did not display the same ‘interest’ in Pansy’s body that has been documented in free-ranging populations. This could be related to age; juveniles and sub-adult chimpanzees generally exhibit more investigative behaviours (Teleki 1973), and the chimpanzees reported to most frequently manipulate the corpse of an infant at Mahale were also juveniles and adolescent males (Kooriyama 2009).

Increases in aggressive behaviour have also been observed in captive gorillas (Hoff et al. 1998; Less et al. 2010) and free-ranging chimpanzees (Hosaka et al. 2000; Teleki 1973) following a death. The adult male in this study previously never made physical aggressive contact with the females during nocturnal charging displays, yet after Pansy’s death made three physical assaults on her body. Disruptions to the social structure are known to lead to aggressive behaviours (see for example de Waal 1998); the death of a group member may also cause this type of responses, especially in males. It is notable that several reports of free-living chimpanzees indicate that it is predominately male group members that show aggressive charging displays and physical attacks on corpses (e.g., Fawcett & Muhumuza 2000; Hosaka et al. 2000; Teleki 1973). Further published reports, however, are needed to confirm this potential sex difference.

Captive gorillas (Hoff et al. 1998) and an infant orangutan (Whilde & Marples 2010) showed an increase in social behaviours after the death of an attachment figure. In the BD chimpanzees, mother-adult offspring pair Blossom and Chippy spent a similar duration in social grooming following Pansy's death as they had throughout the entire previous month of February, indicating a marked increase in affiliative behaviours in response to death. Teleki (1973) described a comparable trend in free-ranging chimpanzees: social grooming rates increased during the four hours subsequent to the male's accidental demise. Free-living baboons (Engh et al. 2006) also increased rates of social grooming following the deaths of group members.

Apes' reactions to death show within- and between-population differences. Some individuals show increases in social behaviours (e.g., Hoff et al. 1998; Whilde & Marples 2010), while others show increases in aggressive behaviours (e.g., Lee et al. 2010) after the death of a group member. The responses of this group were broadly typical of those described in free-living apes, including manipulation the body, increased grooming, and male displays toward the body. The remaining group members also showed individual differences in nocturnal behaviours following the death.

The death of a close friend or relative is a psychological stressor, with grief causing disruptions to several daily functions, including sleep (Averill 1968; Bonanno & Kaltman 2001). Nighttime actigraph recordings of school-age children (n = 140), for example, showed that total time asleep decreased and frequency of nocturnal awakenings increased during periods of familial stress such as illness and loss (Sadeh et al. 2000). There is an abundance of human studies citing the effects of grief on sleep, but this study appears to be the first to describe disrupted sleep-related behaviours in our nearest evolutionary neighbours. Several nest-related behaviours (e.g., duration of nest construction, frequency of nest amendments) and active behaviours (e.g., leaving the nest and sleeping platforms) were consistent across the two periods, indicating that they were unaffected by Pansy’s death. However, several other nighttime behaviours did appear to be influenced, some of which were broadly parallel to human data.

Symptoms of insomnia, including difficulty initiating sleep, are well documented in human grief research (e.g., Baglioni et al. 2010; Hardison et al. 2005; Parkes 1970). One of the most striking observations made here concerns Rosie’s latency to nest build. On the night of her mother’s death, Rosie delayed building a nest until almost 20.00 hrs, approximately one and a half hours later than the latest observed time during the February study. Although it is possible that she made an earlier nest on a lower platform (platform ‘L’, see chapter 3) that was not within range of the cameras, this seems unlikely, as she was never observed to use this platform during previous observations (chapters 3 and 8).

As well as disturbed sleep onset time; there was also an effect on sleeping location, with Rosie nesting in two areas where she had never previously slept. In earlier observations, Rosie most frequently slept against the left enclosure wall, and less frequently against the back wall. When Pansy died Rosie did not sleep against back wall probably because that is where the body lay, but the reasons for her choice of sleeping locations on that night remain unclear. Brown (1897) also reported that an adult male chimpanzee altered his sleep site after the death of his cage-mate. The two remaining chimpanzees in the group studied here both returned to their habitual nesting areas.

Pansy's death also resulted in changes in orientation for each chimpanzee during the night, although again it is the reaction of Pansy's daughter Rosie that is of particular interest. In contrast to the earlier study Rosie never orientated toward Pansy's body, but instead spent most time orientated toward the middle of the enclosure. This change is difficult to interpret. Given that all chimpanzees orientated toward a platform sharer at some point during each night of the February study, Rosie's orientation away from Pansy appears deliberate. However, although Rosie appeared to avoid visual contact with her dead mother she did nest in close proximity to her, despite the availability of several alternative nesting areas within the enclosure. This suggests that Rosie chose to spend the night near her mother's body. The mother-offspring bond is known to be strong across primates, as demonstrated by the carrying of dead infants by chimpanzee mothers (see for example Biro et al. 2010; Cronin et al. 2011). Goodall (1990) described a young male chimpanzee as being lethargic and depressed after the death of his mother. Even unrelated individuals can remain close to the dead body of a group member. After the death of a silverback with whom he had a strong social bond, a juvenile male gorilla was found by field staff lying next to the body, and remained lying next to him for several hours before leaving to feed (http://gorillafund.org/Page.aspx?pid=494).

The number of postural shifts during the night also reveals disruption and individual differences in the responses of the remaining group members. The number of postural shifts by Chippy and Rosie was similar to their maximum number previously recorded. Blossom, however, showed a marked increase in shifts of posture on the night of Pansy's death. Captive chimpanzees are known to waken infrequently during the night (Videan 2006b), and human studies have shown that increases in nocturnal movements and postural shifts are indicative of poor sleep quality (e.g., DeKoninck et al. 1983). Reduced sleep duration and frequent sleep disturbances are common humans following bereavement (Germain et al. 2005; Maytal et al. 2007). Interestingly, disturbed sleep and insomnia are more prevalent in the elderly humans (Drake et al. 2003), which is consistent with the higher frequency of postural shifts made by Blossom, compared to the younger chimpanzees.

The nighttime data presented here do indicate that the sleeping patterns of the remaining 3 chimpanzees were disturbed. However, as these recordings were only made for 1 night, it remains unknown if the sleep disturbances reported here were long or short-term and if these could have negatively affected welfare, as in humans (e.g., Sforza et al. 2004; Walker 2008). Data from free-living baboons indicated that stress after death was relatively short-lived (Engh et al. 2006), as were the behavioural changes in zoo-housed gorillas (Hoff et al. 1998). The changes in sleeping arrangements provided by the survey respondent showed that chimpanzees resumed normal arrangements one week after the group member’s death. As the BD chimpanzees resumed normal (pre-death) activity levels a few weeks after Pansy’s death (Anderson et al. 2010), it seems likely that changes to nighttime activities would also be short-term.

The following should also be considered for welfare. In captive situations, corpses are usually removed shortly after death, thus forcing a separation that is traumatic to other group members, and which may be detrimental to their welfare (Warren & Williamson 2004). The data presented here should be considered in routine procedures of removing captive apes for veterinary treatment and/or euthanasia (see also Anderson et al. 2010). By allowing her to remain within her social group, Pansy was able to receive a number of affiliative social contacts at the time of her death. In light of the psychological and health-based welfare consequences of separating primates from their social groups, it may be less stressful to allow dying individuals to remain with other group members, as long as there is no evidence of suffering (Mason & Veasey 2010). Several zoos (e.g., Columbus, Taronga zoos cited in Warren & Williamson 2004) remove dead infants only after 1-2 days, to allow a period of 'natural mourning' if there is no evidence of infectious disease.

Conclusions and recommendations

Daytime observations of primate responses to the death of a group member, although still rare, are increasing. An opportunistic recording of immediate and nighttime behavioural responses of captive chimpanzees to the death of a group member has given us additional insight into this inevitable event.

Some nest-related and post-retirement active behaviours appeared unaffected by the death, although increased latency to retire and an increase in postural changes did indicate that sleep was disrupted by this event. Such phenomena are also true of human bereaved. In keeping with reports from free-living and captive apes, affiliative behaviours increased. Those directed at Pansy at the time of her death were more frequent than previous observations, and those between two remaining chimpanzees also increased. Also comparable to wild ape reports was the male's physical attack on the body. These data not only add to the growing body of literature on primate responses to death, but also have implications for welfare. In the absence of suffering, it may be less stressful to allow dying apes to remain with their social groups.

Chapter 10

Nesting and nighttime behaviours of captive chimpanzees: Conclusions, recommendations and future research directions

"Sleep is the best meditation" ~ Dalai Lama

Both free-ranging and captive great apes will engage in nest building activities if provided the opportunity (Berle et al. 1995; Bernstein 1962, 1969; Goodall 1962, 1968; MacKinnon 1974; Videan 2006a). The data presented here were generated from a nation-wide survey of zoos and safari parks holding three species of great apes, and direct observations/ video recordings conducted on two captive chimpanzee groups. It is acknowledged that the relatively small sample size limits generalizing the findings to the broader captive ape or chimpanzee population; instead the results must be viewed as preliminary.

Nonetheless, this research has provided data on a species-typical behaviour that has traditionally been neglected and is poorly understood (Fruth & Hohmann 1994, 1996); it has implications for sleeping facilities that have hitherto been overlooked as a factor in captive ape welfare (e.g., Anderson 1998). In this final chapter, I will briefly reiterate the main findings of the current research, consider their implications for chimpanzee housing and management from a number of welfare perspectives, and highlight areas for further research.

Nest building as a natural behaviour

Modern zoos place a high emphasis on the expression of wild-type behaviours as a means to maintaining welfare, as summarised by Markowitz (1997 p2):

> "…the conservation of behavior is essential to the most important and widely-expressed goals of zoos and aquariums."

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 (chapter 2) 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). Direct observations (chapter 3) of the BD and EZ chimpanzees showed similar inter – and intra-group variation in this respect. These same observations also highlighted several other 'wild-type' nesting behaviours.

As reported at several sites across Africa (e.g., DRC: Farmer 2002; Gombe: Goodall 1962; Western French Guinea: Nissen 1931), retirement times of the two captive groups here were broadly in keeping with times of sunset and dusk, although this was more notable for the BD group. There was also evidence of sex differences in the frequency and duration of nest construction, with females generally nest building more frequently and for a longer time. Although comparative data for night nests are lacking, studies of chimpanzee day nests have also shown that females construct day nests more frequently than males (Hiraiwa-Hasegawa 1989; Plumptre & Reynolds 1997). Both the BD and EZ group also performed several post-retirement behaviours reported in wild apes (e.g., feeding: Goodall 1968; infrequent social behaviours: Nissen 1931).

When forming a nest group, free-living chimpanzees generally separate (fission) into smaller groups than daytime parties (although there appear to be resource-based exceptions e.g., Goodall 1962), but do not necessarily sleep in close proximity to affiliated group members or kin (Goldberg & Wrangham 1997). Likewise, the study on the larger EZ group (chapter 4) showed that, when given access to a number of different areas, nesting groups contained similar numbers to those of wild communities, and they were not always influenced by these social factors. Rather, individual preferences for specific sites appeared to be the determining factor in sleeping site choice for this group. Again, this is characteristic of free-living chimpanzees (e.g., Pruetz et al. 2008; Sept 1992). These preferred sleeping sites might also be influenced by factors such as security from dominant group members and social tensions (discussed below).

Further research on this group (chapter 5) showed that the motor patterns used in nest construction, such as gathering materials and arranging and shaping around the body, were broadly similar to those used by wild chimpanzees (e.g., Goodall 1962; Nissen 1931) and other captive groups (Bernstein 1962; Morimura and Mori 2010). The apparently universal nature of some techniques suggests that these are the basis of forming a comfortable, secure overnight sleeping place.

Nest building to promote positive affective states

The natural behaviour approach to enhancing animal welfare, although advocated by modern zoos, has been subject to criticism (e.g., Dawkins 2003). However, this approach need not be the only welfare-relevant aspect of nest building behaviour. Positive affective states, such as feelings of security and physical comfort, are also hypothesised to influence welfare.

Several authors (e.g., Dawkins 2004, 2006; Ross et al. 2009) have suggested that the positioning of captive animals in relation to other group members and their environment can reliably inform of what they prefer (i.e., what they ‘like’ and ‘want’). The frequent positioning of low-ranking members of the EZ group (chapter 4) in areas separate from the highest-ranked males may be indication that sleeping sites are based partly on the security they afford from social tensions and dominant group members, as been documented in zoo-housed low-ranked gorillas (Weiche & Anderson 2007). In light of survey data that show that apes are typically housed communally, in conjunction with promoting natural socio-spatial arrangements, zoos should consider providing separate sleeping areas to allow subordinate chimpanzees to avoid/flee from dominant group members.

In terms of physical comfort, in agreement with previous findings (Bernstein 1962; Videan 2006a), data from chapter 5 showed that soft bedding materials were preferred over others, typically resulting in higher rates of nest building, even in individuals that rarely constructed night nests. Zoos and other facilities should note that the provision of two bedding substrates could encourage species-typical nest lining behaviours (e.g., Nissen 1931). The majority of survey respondents did report that combinations of materials are given to captive apes; the findings here suggest that this enrichment practice be continued. The few facilities that reported providing only one material regularly should take these findings into consideration. Although preference tests have several limitations (e.g., Fraser 1996), these findings support the view that comfort is one of the fundamental functions of ape night nests (e.g., Baldwin et al. 1981; Stewart et al. 2007).

Cross-seasonal research on the EZ chimpanzees (chapter 6) indicated that thermoregulatory comfort might have influence choice of sleep site. In both winter and spring months, the warmest sleeping areas (above 22 degrees Celsius at the time of research) were generally favoured. However, sleep site selection was subject to intra-group variation. Nonetheless, species-appropriate environmental conditions such as light, temperature and humidity are widely thought to contribute to comfort and welfare (Gonyou 1994; Secretary of State's Standards of Modern Zoo Practice 2004). Providing choice of environmental conditions within a captive setting can allow individual environmental needs and preferences to be expressed (Wickins-Drazilova 2006; Yeates & Main 2008). Human studies (e.g., Dijk et al. 1987) have indicated that lighting conditions that do not replicate natural variations in day length and light can reduce sleep duration. Furthermore, failure to regulate enclosure temperature and humidity levels can negatively impact on sleep quality and duration, as demonstrated by Videan's (2006b) laboratory-based chimpanzee study, and so may become detrimental to biological health.

Nest building from a biological health perspective

Adequate quality and duration of sleep have been implicated in biological health in a number of ways, including repairing tissue, controlling thermoregulation and to regulate the immune system (Walker 2008). Human (e.g., Walker 2008) and animal (e.g., Everson 1995) studies have long shown that long-term sleep deprivation can be detrimental to physiological and psychological health, resulting in depression (Kahn-Greene et al. 2007), memory impairment (Killgore et al. 2008), increased blood pressure and increased likelihood of obesity (Banks & Dinges 2007).

Of interest was the finding that BD chimpanzees (chapter 8) frequently co-slept (shared the same sleeping platform). Although unusual in free-living chimpanzees (Fruth & Hohmann 1996), these data concur with proximal sleeping arrangements documented in Riss and Goodall’s (1976) and Videan’s (2006b) laboratory chimpanzees. However, it is also possible that a lack of suitable alternative sites contributed towards frequent co-sleeping. Wild chimpanzees build nests on solid, firm foundations (Nissen 1931; van-Lawick Goodall 1971); the relatively deep and unstable pods available to this group may have negated their use. Survey respondents indicated that firehoses and hammocks are sometimes provided as nesting sites. It is possible that these may lack a sufficiently firm foundation for nest construction. In light of human sleep-surface studies (Bader & Engdal 2000; Lee & Park 2006), the structures that are provided as sleep sites should be reviewed, with the aim of providing comfortable resting sites that can promote adequate durations and quality of sleep.

Nest building from an integrated perspective

As discussed in chapter 1, the three main approaches to defining and assessing animal welfare all have shortcomings. Several authors (e.g., Bracke & Hopster 2004; Maple 1979), and indeed legislature (Secretary of State’s Standards of Modern Zoo Practice 2004), have pointed out that the performance of species-typical behavioural patterns, how animals feel, and the maintenance of physiological health are not mutually exclusive factors in terms of captive animal welfare. I suggest that integrating these approaches should be extended to environmentally enrich the sleeping facilities of captive apes. The provision of appropriate nesting material and sleeping structures, for example, improves comfort, encourages natural nest construction behaviour, potentially enhancing sleep quality. The provision of several separate sleeping areas and sleeping structures can add elements of choice and control into sleeping areas, whilst also avoiding overcrowding and potential social stressors. These factors may also be conducive to maintaining/improving welfare standards of captive apes (e.g., Morgan & Tromborg 2007; Swaisgood 2007). Based on the findings of this research, the following recommendations are made to promote wild-type nesting profiles, comfort, and potentially enhance sleep quality.

Recommendations for enclosure/sleeping area design

- Multiple separate sleeping rooms should be provided.

These would encourage naturalistic socio-spatial sleeping arrangements (formation of nighttime sub-groups or isolation, if preferred), provide alternative nesting sites in cases of nest usurping and abandonment, minimise competition for sleeping structures, and allow subordinates to withdraw from socially stressful situations. If it is not feasible to provide multiple sleeping rooms, screens or partitions could be used. Multiple sleeping areas would also permit individual control over nesting sites, and also allow expression of seasonal changes in preferred nesting areas and individual preferences for microclimates. Therefore:

- If possible, sleeping areas should incorporate varying light, temperature and humidity levels.
- Consideration should be given to lighting conditions with a view to promoting species-typical retirement times and sleep quality.

Recommendations for sleeping/nesting structures

To facilitate intra-group variation in terrestrial versus elevated nesting:

- Sleeping areas should incorporate elevated structures and substrate-covered flooring.

In light of the BD chimpanzees' lack of use of potentially insecure sleeping structures,

- Elevated sleeping structures should be stable and firm.

Survey data showed that structures such as hammocks and fire-hose are sometimes provided to captive apes. As direct observations of what structures are used are lacking, it is possible (although unconfirmed), that these are not used. Based on inter-group differences between the EZ and BD chimpanzees, nesting structures should be:

- adequately spaced to allow optimal sleeping distances from other group members.

In instances of co-sleeping:

- Structures should be large enough to accommodate more than a single individual.

Recommendations for nesting materials

Although individuals in both the BD and EZ groups constructed nests with any available materials, data from the EZ chimpanzees indicated that soft, easily manipulable materials were preferred.

- These, and similar materials, should be used to encourage nest building.

It should also be noted that some materials (paper sack in the present research) are rarely used. To avoid wasting money on materials that may not be be utilised:

- Direct observations of which materials actually facilitate nesting should be carried out.

To encourage species-typical nest-lining behaviour:

- At least 2 materials should be simultaneously presented.

Directions for future research

The second broad aim of this study was to document aspects of nest-related behaviours that are rarely studied in captivity, despite the fact that nest-related behaviours are more visible in these settings compared to chimpanzees' natural environments. Field data (see for example Fruth & Hohmann's 1996 review), and nighttime recordings of the BD group (this research), demonstrate that chimpanzees can spend up to half their lifetime, or more, at their sleeping site. To generate a more comprehensive understanding of chimpanzee life, more research is needed that focuses on the social and behavioural biology of nighttime behaviours.

Kinship has previously been used to explain daytime affiliative patterns in wild chimpanzees (e.g., Goodall 1986). In contrast to most available captive data (chimpanzees: Videan 2006b; gorillas: Lukas et al. 2003), data from the EZ group showed that social factors had a relatively weak influence on nighttime behaviours – neither relatedness nor daytime associations was a reliable predictor of sleep site selection. These findings can be added to an increasing amount of field evidence that maternal relatedness does not necessarily influence day or nighttime sociality (e.g., daytime social bonds in female bonobos: Hashimoto et al. 1996; nesting groups of wild chimpanzees: Goldberg & Wrangham 1997). This study is also the first to show that the daytime social bonds shared by unrelated male chimpanzees (Mitani et al. 2000, 2002) can extend into nighttime. Further studies on mixed-age, -sex, and related/unrelated groups would further clarify the impact of social relationships and social events on the sleeping arrangements of captive apes.

In general, little is known of the sleep-related behaviours of free-ranging and captive primates after they have retired, and so the overnight video-based records of the BD group described in chapter 8 enrich the existing literature on diurnal primates' nocturnal behaviours. As with Videan's (2006b) laboratory-based research, these data showed that captive chimpanzees show more complex nocturnal behavioural profiles than might be commonly assumed.

The same recordings also highlighted some apparent age-and sex-related differences in nocturnal behaviour, although the small sample size again renders this finding preliminary. Sex differences in nesting behaviours are relatively well documented (e.g., female chimpanzees nesting at higher heights and more frequently constructing day nests than males: Brownlow et al. 2001; males sleeping at the periphery of the nest group: Goodall 1962). The male chimpanzee in the BD group was typically more 'active' than females throughout the night, more frequently leaving the nest, changing posture, and performing displays. Similarly, species-specific postures characterise the sleep state, yet there has been no systematic research on this topic. The present study thus contributes to our understanding of a largely neglected area, showing that, like humans, individual chimpanzees have preferred resting postures. Potential age- and sex-related differences within the small study group show the value of further research in order to more fully understand factors that might underlie differences in sleep-related adaptations and nocturnal activity patterns. With further research, the use of non-invasive nighttime recording equipment that clearly shows bouts of wakefulness, night time activities and postural changes, could potentially be a tool in assessing and scoring sleep-cycles and stages in a variety of laboratory-housed primates, as has already been done with some degree of success (e.g., Balzamo et al. 1998; Lagarde et al. 1996).

The opportunistic recording of the death of a chimpanzee in this same group has given insight into another aspect of chimpanzee social biology that is (understandably) singular. With few exceptions (e.g., Brown 1897; respondent to survey) chimpanzee behavioural responses to death have typically been observed during daytime. For the first time, continuous overnight recording showed that the death of a group member also affected nighttime activities. Frequencies of postural changes increased from previously documented levels (particularly in the case of the aged female, Blossom), indicating that sleep was disrupted, reminiscent of humans' reactions to bereavement (Parkes 1970). Frequencies of social affiliative behaviours with other group members and aggressive charging displays by the male in the BD group recall some responses reported in wild chimpanzees (e.g., Fawcett & Muhumuza 2000; Teleki 1973). As no such research has ever been conducted before now, it is impossible to make definite statements regarding how universal these responses are across populations, or how the death of an attachment figure affects long-term sleeping behaviours. Moreover, there are obvious shortcomings to research of this type. Statistical analysis, for example, was not possible as there was only one night of data available. Further, the data from the February research were collected during only one month, and so the nesting and nocturnal behaviours of the group may have been subject to change. Nonetheless, the behaviour of the chimpanzees in the sixteen hours following death give a rare and unique insight into how the death of a group member affected nesting and nocturnal behaviours, and so the record adds to the growing body of literature of how non-human primates respond to death.

Daytime behaviours (e.g., production and use of tools that result in a functional outcome) are a reflection of chimpanzees' extensive motor and cognitive skills (e.g., McGrew 1992). Although there is some debate as to whether nest building can be included in the realm of tool use (Fruth & Hohmann 1996), both free-living (Stewart et al. 2007) and captive apes (with individual exceptions, the BD group in this research) can use a variety of complex manipulatory, and less frequently, innovative, patterns to produce a night nest. Comparative data between the chimpanzee groups studied here also highlighted the group-specific nature of nest construction techniques.

For many years, socially learned, group-specific behaviours (e.g., tool use: Boesch & Boesch 1983; grooming postures: McGrew & Tutin 1978) have been the cornerstone of our understanding of primate cultures. Despite evidence that nest building is also a socially transmitted behaviour (Bernstein 1962; Videan 2006a) and the suggestion that nest-related behaviours may be specific to particular ape populations (e.g., the chimpanzee cultural 'fashion' of nesting in oil palm trees: Goodall 1968; orangutan leaf-carrying prior to nest building: Russon et al. 2007), nest construction techniques have not been included as a behaviour indicative of cultural differences. The data presented here (chapter 7) showed that the EZ group had higher levels of skilled, complex nest building techniques than the BD group. It is acknowledged, however, that the additional material given to the EZ group may have facilitated more complex nest building skills, as in wild chimpanzees (Stewart et al. 2007). At the very least, these data can tentatively be used to extend the range of behaviours that can be considered cultural. As captive settings are relatively free from confounding ecological variables such as predation pressure and fluctuating resources, they may be more likely to reveal cultural aspects of nesting and resting. The large number of ape populations across the British Isles, as gleaned by survey data, could be a valuable resource for more thoroughly researching this issue.

Concluding comment

Given the inherent hardship in documenting overnight behaviours of wild apes, captive studies can add to the existing literature of this neglected topic, and highlight future research directions. Chimpanzees have individual preferences for nesting and resting sites that can vary according to season and environmental change, and show preference for certain nesting materials and sleeping partners. These should be considered in sleeping area design and management policies if zoos aim to promote biologically relevant behaviours, positive affective states and biological health. It is time to awaken to the significance of these factors in terms of captive ape welfare.

References

Aaronson ST Rashed S Biber MP Hobson JA 1980 (Abstract) Sleeping together: A video tape look at a couple's sleep. Sleep Res 9: 120

Aaronson ST Rashed S Biber MP Hobson JA 1982 Brain state and body position: A time-lapse video study of sleep. Arch Gen Psychiat 39: 330-335

Adey WR Kado RT Rhodes JM 1963 Sleep: Cortical and sub cortical recordings in the chimpanzee. Science 141: 932-933

Ancrenaz M Calaque R Lackman-Ancrenaz I 2004 Orangutan nesting behaviour in distributed forest of Sabah, Malaysia: implications for nest census. Int J Primatol 25: 983-999

Anderson DP Nordheim EV Boesch C 2006 Environmental factors influencing the seasonality of estrus in chimpanzees. Primates 47: 43-50

Anderson JR Williamson EA Carter J 1983 Chimpanzees of Sapo forest, Liberia: Density, nests, tools and meat-eating. Primates 24: 594-601

Anderson JR 1984 Ethology and ecology of sleep in monkeys and apes. Adv Study Behav 14: 165-229

Anderson JR McGrew WC 1984 Guinea baboons (*Papio papio*) at a sleeping site. Am J Primatol 6: 1-14

Anderson JR 1998 Sleep, sleeping sites and sleep-related activities: Awakening to their significance. Am J Primatol 46: 63-75

Anderson JR 2000 Sleep-related behavioural adaptations in free-ranging anthropoid primates. Sleep Med Rev 4: 355-373

Anderson JR Gillies A Lock LC 2010 *Pan* thanatology. Curr Biol 20: R349-R351

Anderson JR 2011 A primatological perspective on death. Am J Primatol 71: 1-5

Animal (Scientific Procedures) Act 1986. London: Her Majesty's Stationery Office

Archer J 1999 The nature of grief: The evolution and psychology of reactions to loss. London: Routledge

Aujard F Vasseur F 2001 Effect of ambient temperature on the body temperature rhythm of male grey mouse lemurs (*Microcebus murinus*). Int J Primatol 22: 43-56

Averill JR 1968 Grief: Its nature and significance. Psychol Bull 70: 721-748

Bader GG Engdal S 2000 The influence of bed firmness on sleep quality. App Ergonom 31: 487-497.

Baekland F Hoy P 1971 Reported vs recorded sleep characteristics. Arch Gen Psychiat 24: 548-551

Baglioni C Speigelhalder K Lombardo C Rieman D 2010 Sleep and emotions: A focus on insomnia. Sleep Med Rev 14: 227-238

Baldwin PJ Sabater Pi J McGrew WC Tutin CEG 1981 Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). Primates 22: 474-486

Baker KC 1997 Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. Zoo Biol 16: 225-236

Baker KC Weed JL Crockett CM Bloomsmith MA 2007 Survey of environmental enrichment programs for laboratory primates. Am J Primatol 69: 377-394

Ball NJ 1992 The phasing of sleep in animals. In: Stampi C (ed). Why we nap. Boston: Birkhauser pp31-49

Balzamo E Van Beers P Lagarde D 1998 Scoring of sleep and wakefulness by behavioural analysis from video recordings in rhesus monkeys: Comparison with conventional EEG analysis. Electro Clin Neurophysiol 106: 206-212

Banks S Dinges DF 2007 Behavioral and physiological consequences of sleep restriction. J Clin Sleep Med 3: 519-528

Barbato G Baker C Bender C Wehr TA 2002 Spontaneous sleep interruptions during extended nights. Relationships with NREM and REM sleep phases and effects on REM sleep regulation. Clin Neurophysiol 113: 892-900

Barber JCE 2009 Programmatic approaches to assessing and improving animal welfare in zoos and aquariums. Zoo Biol 28: 519-530

Barnard CJ Hurst JL1996 Welfare by design: The natural selection of welfare criterion. Anim Welf 5: 405-433

Barnett JL Hemsworth PH 1990 The validity of physiological and behavioural measures of animal welfare. Appl Anim Behav Sci 25: 117-187

Barrett L Gaynor D Rendall D Mitchell D Henzi SP 2004 Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*). J Hum Evol 46: 215-222

Basabose AK Yamagiwa J 2002 Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: Influence of sympatric gorillas. Int J Primatol 23: 263-282

Berle A Fruth B Van Elsacker E 1995 Nest building behavior in captive bonobos (*Pan paniscus*). Prim Rep 42: 43-45

Bernstein IS 1962 Response to nesting material of wild born and captive born chimpanzees. Anim Behav 10: 1-6

Bernstein IS 1967 Age and experience in chimpanzee nest building. Psychol Rep 20: 1106

Bernstein IS 1969 A comparison of nesting patterns among the three great apes. Behaviour 1: 393-402

Bert J Kripke DF Rhodes J 1970 Electroencephalogram of the mature chimpanzee: twenty-four hour recordings. Electro Clin Neurophysiol 28: 368-373

Bert J Balzamo E Chase M Pegram V 1975 The sleep of the baboon, *Papio papio*, under natural conditions and in the laboratory. Electro Clin Neurophysiol 39: 657-662

BIAZA 2000 Zoo research guidelines: Research sampling guides for zoos. London: BIAZA

Biro D Humle T Koops K Sousa C Hayashi M Matsuzawa T 2010 Chimpanzee mothers at Bossou, Guinea carry the mummified remains of their dead infants. Curr Biol 20: R351-R352

Bishop N 1979 Himalayan langurs: temperate colobines. J Hum Evol 8: 251-281

Blom HJM van Tintelen G van Vorstenbosch CJAHV Baumans V Beyen AC 1996 Preferences of mice and rats for types of bedding material. Lab Anim 30: 234-244

Bloomsmith MA Alford PL Maple TL 1988 Successful feeding enrichment for captive chimpanzees. Am J Primatol 16: 155-164

Bloomsmith MA Else JG 2005 Behavioral management of chimpanzees in biomedical research facilities: The state of science. ILAR 46: 192-201

Boe KE Andersen IL Buisson L Simensen E Keksrud WK 2007 Flooring preference in dairy goats at moderate and low ambient temperature. Appl Anim Behav Sci 108: 45-57

Boesch C Boesch H 1983 Optimisation of nut-cracking with natural hammers by wild chimpanzees. Behaviour 83: 265-286

Boesch C 1991a The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117: 220-242

Boesch C 1991b Teaching among wild chimpanzees. Anim Behav 41: 530-532

Boesch C Marchesi P Marchesi N Fruth B Joulian F 1994 Is nut cracking in wild chimpanzees cultural behaviour? J Hum Evol 4: 325-338

Boesch C 1995 Innovation in wild chimpanzees. Int J Primatol 16: 1-16

Boesch C 1996a The emergence of cultures of among wild chimpanzees. In: Runciman WG Maynard-Smith J Dunbar RIM (eds). Evolution of social behaviour patterns in primates and man. Oxford: Oxford University Press pp251-268

Boesch C 1996b Social grouping in Tai chimpanzees. In: McGrew WC Marchant LF Nishida T (eds). Great Ape Societies. Cambridge: Cambridge University Press pp101-114

Boesch C Tomasello M 1998 Chimpanzee and human cultures. Curr Anthropol 39: 591-604

Boesch C 2002 Behavioural diversity in *Pan*. In: Boesch C Hohmann G Marchant LF (eds). Behavioural diversity in chimpanzees and bonobos. Cambridge: Cambridge University Press pp1-8

Bolwig N 1959 A study of the nests built by mountain gorilla and chimpanzee. S Afr J Sci 55: 286-291

Bonanno GA Kaltmann S 2001 The varieties of grief experience. Clin Psychol Rev 21: 705-734

Bonnie KE de Waal FBM 2006 Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. Primates 47: 27-34

Bourgeois SR Brent L 2005 Modifying the behaviour of singly caged baboons: Evaluating the effectiveness of four enrichment techniques. Anim Welf 14: 71-81

Bowlby J 1960 Grief and mourning in infancy and early childhood. Psychoanal Study Child 15: 9-52

Bracke MBM Hopster H 2006 Assessing the importance of natural behavior for animal welfare. J Agricult Environ Ethics 19: 77-89

Brambell FWR 1965 Report of the technical committee to enquire into the welfare of animals kept under intensive livestock husbandry systems. London: Her Majesty's Stationery Office

Brent L 1992 Woodchip bedding as enrichment for captive chimpanzees in an outdoor enclosure. Anim Welf 1: 161-170

Broom DM 1986 Indicators of poor welfare. Brit Vet J 142: 524-526

Broom DM 1988a The scientific assessment of animal welfare. Appl Anim Behav Sci 20: 5

Broom DM 1991 Animal welfare: Concepts and measurement. J Anim Sci 69: 4167-4175

Broom DM 1996 Animal welfare defined in terms of attempts to cope with the environment. Acta Agric Scandin 27: 22-28

Broom DM 2010 Cognitive ability and awareness in domestic animals and decisions about obligations to animals. Appl Anim Behav Sci 126: 1-11

Broom DM Johnson KG 1993 Stress and animal welfare. London: Chapman & Hall

Brown AE 1897 Grief in the chimpanzee. Am Nat 13: 173-175

Brown DL Gold KC 1995 Effects of straw bedding on non-social and abnormal behavior of captive lowland gorilla (*Gorilla gorilla gorilla*). Proc 2nd Int Conf Environ Enrich 2: 24-38

Brown LF Reynolds III CF Monk TH Priegerson HG Dew MA Houck PR Mazumdar S Buysse DJ Hoch CC Kupfer DJ 1996 Social rhythm stability following late-life spousal bereavement: Associations with depression and sleep impairment. Psychiat Res 62: 161-169

Brownlow AR Plumptre AJ Ward R 2001 Sources of variation in the nesting behavior of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo forest, Uganda. Am J Primatol 55: 49-55

Buckle P Fernandes A 1998 Mattress evaluation – assessment of contact pressure, comfort and discomfort. Appl Ergonom 29: 35-39

Buij R Wich SA Lubis AH Sterck EHM 2002 Seasonal movements in the Sumatran orangutan (*Pongo pygmaeus abelli*) and consequences for conservation. Bio Cons 107: 83-87

Caine NG Potter MP Mayer E 1992 Sleeping site selection by captive tamarins (*Saguinus labiatus*). Ethology 90: 63-71

Campbell SS Tobler I 1984 Animal sleep: a review across phylogeny. Neuro Biobehav Rev 8: 269-300

Capellini I Nunn CL McNamara P Preston BT Barton RA 2008 Energetic constraints, not predation, influence the evolution of sleep patterning in mammals. Funct Ecol 22: 847-853

Cardinali DP 2000 The human body circadian: how the biological clock influences sleep and emption. Neuroendo Lett 21: 9-15

Carlstead K Shepherdson D 1994 Effects of environmental enrichment on reproduction. Zoo Biol 13: 447-459

Carlstead K 1996 Effects of captivity on the behavior of wild mammals. In: Kleiman DG Allen ME Thompson KV Lumpkin S (eds). Wild mammals in captivity: Principles and techniques. Chicago: University of Chicago Press pp317-333

Carrier J Dumont M 1995 Sleep propensity and sleep architecture after bright light exposure at three different times of day. J Sleep Res 4: 202-211

Carskadon MA 2004 Sleep deprivation: Health consequences and societal impact. Med Clin N Am 88: 767-776

Casimir MJ 1979 An analysis of gorilla nesting sites of the Mt. Kahuzi region (Republique du Zaire). Folia Primatol 24: 290-308

Celli ML Tomonaga M Udono T Teramoto M Nagano K 2003 Tool use task as environmental enrichment for captive chimpanzees. Appl Anim Behav Sci 81: 171-182

Celli ML Hirata S Tomonaga M 2004 Socioecological influences on tool use in captive chimpanzees. Int J Primatol 25: 1267-1281

Chamove AS 1989a Assessing the welfare of captive primates: A critque. Lab Anim Welf Res: Primates 39-49

Chamove AS 1989b Environmental enrichment: A review. Anim Technol 40: 155-178

Chapman CA 1989 Spider monkey sleeping sites: Use and availability. Am J Primatol 18: 53-60

Clarence WM Scott JP Dorris MC Pare M 2006 Use of enclosures with functional vertical space by captive rhesus monkeys (*Macaca mulatta*) involved in biomedical research. J Am Assoc Lab Anim Sci 45: 31-34

Clubb R Mason GJ 2007 Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. Appl Anim Behav Sci 102: 303-328

Coe JC 1992 Plan ahead for behavioral enrichment. AAZPA National Convention: Environmental enrichment kaleidoscope: Research, management and design pp120-123

Crofts HS Wilson S Muggleton NG Nutt DJ Scott EAM Pearce PC 2001 Investigation of the common marmoset (*Callithrix jacchus*) using radiotelematry. Clin Neurophysiol 112: 2265-2273

Cronin KA Van Leeuwen EJC Mulenga IC Bodamer MD 2011 Behavioral response of a chimpanzee mother toward her dead infant. Am J Primatol 73: 1-7

Cui LW Quan RC Xiao W 2006 Sleeping sites of black and white snub nosed monkeys (*Rhinopithecus bieti*) at Baimi Snow Mountain, China. J Zool 270: 192-198

Dahl JF Smith EO 1985 Assessing variation in the social behavior of stumptail macaques using thermal criteria. Am J Phys Anthropol 68: 467-477

Damn BI Lisborg L Vestergaard KS Vanicek J 2003 Nest building, behavioural disturbances and heart rate in farrowing sows kept in crates and Schmid pens. Livest Prod Sci 80: 175-187

Davenport MD Lutz CK Tiefenbacher S Novak MA Meyer JS 2008 A rhesus monkey model of self injury: Effects of relocation stress on behavior and neuroendocrine function. Biol Psychiat 63: 990-996

Dawkins MS 1977 Do hens suffer in battery cages? Environmental preferences and welfare. Anim Behav 25: 1034-1046

Dawkins MS 1980 Animal suffering: The science of animal welfare. London: Chapman & Hall

Dawkins MS 1983 Battery hens name their price: Consumer demand theory and the measurement of ecological ‘needs’. Anim Behav 31: 1195-1205

Dawkins MS 1988 Behavioural deprivation: A central problem in animal welfare. Appl Anim Welf Sci 20: 209-225

Dawkins MS 1990 From an animal’s point of view: Motivation, fitness, and animal welfare. Behav Brain Sci 13: 1-61

Dawkins MS 2003 Behaviour as a tool in the assessment of animal welfare. Zoology 106: 383-387

Dawkins MS 2004 Using behaviour to assess animal welfare. Anim Welf 13: S3-7

Day RT Elwood RW 1999 Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: The role of predation risk, proximity to feeding sites, and territorial defence. Ethology 105: 1035-1051

De Koninck J Gagnon P Lallier S 1983 Sleep positions in the young adult and their relationship with the subjective quality of sleep. Sleep 61: 52-59.

De Koninck J Lorrain D Gagnon P 1992 Sleep positions and position shifts in five age groups: an ontogenetic picture. Sleep 15: 143-149.

de Waal FBM 1986 The brutal elimination of a rival among captive male chimpanzees. Ethol Sociobiol 7: 237-251 de Waal FBM Seres M 1997 Propagation of handclasp grooming among captive chimpanzees. Am J Primatol 43: 339-346

de Waal FBM 1998 Chimpanzee politics: Power and sex among apes (rev. ed). Baltimore: John Hopkins University Press

Di Bitetti MS Luengos Vidal EM Baldovino MC Benesovsky V 2000 Sleeping site preference in tufted capuchin monkeys (*Cebus apella nigritus*). Am J Primatol 50: 257-274

Dickie L 1998 Environmental enrichment for Old World primates with reference to the primate collection at Edinburgh Zoo. Int Zoo Yrbk 36: 131-139

Dijk DJ Visscher C Bloem G Beersman D Daan S 1987 Reduction of human sleep duration after bright light exposure in the morning. Neurosci Lett 73: 181-186

Dijk DJ Kronauer RE 1999 Commentary: Models of sleep regulation: Successes and continuity challenges. J Biol Rhythms 14: 569-673

Dijk DJ Duffy JF Czeisler CA 2000 Contribution of circadian physiology and sleep-related homeostasis to age-related changes in human sleep. Chronobiol Int 17: 285-311

Doran DM Hunt KD 1994 Comparative locomotor behavior of chimpanzees and bonobos: Species and habitat differences. In: Wrangham RW McGrew WC deWaal FBM Heltne PG (eds). Chimpanzee Cultures. Cambridge: Harvard University Press pp93-106

Doran D 1997 Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. Int J Primatol 18: 183-206

Drago L Thierry B 2000 Effects of six-day maternal separation on Tonkean macaque infants. Primates 41: 137-145

Drake CL Roehrs T Roth T 2003 Insomnia causes, consequences, and therapeutics: An overview. Depress Anxiety 18: 163-176

Duffy JF Kronaeur RE Czeisler CA 1996 Phase-shifting human circadian rhythms: Influence of sleep timing, social contact and light exposure. J Physiol 295: 289-297

Duncan IJH 1970 Frustration in the fowl. In: Freeman BM Gordon RF (eds). Aspects of Poultry behavior. Edinburgh: British Poultry Science Ltd. Pp15-31

Duncan IJH 1992 Measuring preferences and the strength of preferences. Poultry Sci 71: 658-663

Duncan IJH 1993 Welfare is to do with what animals feel. J Agric Environ Ethics 6(Supp 2): 8-14

Duncan IJH Fraser D 1997 Understanding animal welfare. In: Appleby MC Hughes BO (eds) Animal Welfare. Wallingford: CAB International pp19-31

Duncan IJH 2006 The changing concept of animal sentience. Appl Anim Behav Sci 100: 11-19

Dunkell S 1977 Sleep positions: The night language of the body. New York: William Morrow

Dytham C 2003 Choosing and using statistics: A biologist's guide (2nd ed). Oxford: Blackwell Publishing

Dzvonik ML Kripke DF Klauber M Ancoli-Israel S 1986 Body position changes and periodic movements in sleep. Sleep 9: 484-491

Engh AL Beehner JC Bergman TJ Whitten PL Hoffmeier RR Seyfarth RM Cheney DL 2006 Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus)*. Proc R Soc B 273: 707-712

Erffmeyer ES 1982 The nocturnal behavior of caged rhesus monkeys (*Macaca mulatta*). Folia Primatol 38: 240-249

Estrada A Estrada R 1976 Establishment of a free-ranging colony of stumptail macaques (*Macaca arctoides*): Relations to the ecology. Primates 17: 337-355

Everson CA 1995 Functional consequences of sustained sleep deprivation in the rat. Behav Brain Res 69: 43-54

Farmer K 2002 The behaviour and adaptation of reintroduced chimpanzees (*Pan troglodytes troglodytes*) in the Republic of Congo. Unpublished PhD Thesis, University of Stirling

Fashing PJ Nguyen N Barry TS Goodale CB Burke RJ Jones SCZ Kerby JT Lee LM Nurmi NO Venkataraman VV 2010 Death among geladas (*Theropithecus gelada*): A broader perspective on mummified infants and primate thanatology. Am J Primatol 71: 1-5

FAWC (Farm Animal Welfare Council) 1992 FAWC updates the five freedoms. Vet Record 131: 357

Fawcett K Muhumuza G 2000 Death of a wild chimpanzee community member: Possible outcome of intense sexual competition. Am J Primatol 51: 243-247

Fisher AD Stewart M Verkerk GA morrow CJ Matthews LR The effects of surface type on lying behaviour and stress responses of dairy cows during periodic weather-induced removal from pasture. Appl Anim Behav Sci 81: 1-11

Fowler A Sommer V 2007 Subsistence technology in Nigerian chimpanzees. Int J Primatol 28: 997-1023

Franklin SP Miller KE Baker AJ Dietz JM 2007 Do cavity-nesting primates reduce scent marking before retirement to avoid attracting predators to sleeping sites? Am J Primatol 69: 255-266

Fraser AF 1989 Animal welfare theory: The keyboard of the maintenance ethosystem. Appl Anim Behav Sci 22: 177-190

Fraser D 1983 Curious idling. Appl Anim Ethol 10: 159-164

Fraser D 1996 Preference and motivational testing to improve animal well-being. Lab Anim 25: 27-31

Fraser D Weary DM Pajor EA Milligan BN 1997 A scientific conception of animal welfare that reflects ethical concerns. Anim Welf 6: 187-205

Fraser D 2009 Assessing animal welfare: Different philosophies, different scientific approaches. Zoo Biol 28: 507-518

Freemon FR McNew JJ Adey WR 1970 Sleep of unrestrained chimpanzee: Differences between first and last rapid eye movement periods. Folia Primatol 13: 144-149

Fruth B Hohmann G 1993 Ecological and behavioural aspects of nest building in wild bonobos (*Pan paniscus*). Ethology 94: 113-126

Fruth B Hohmann G 1994 Comparative analyses of nest building behavior in bonobos and chimpanzees. In: Wrangham RW McGrew WC de Waal FBM Heltne PG (eds). Chimpanzee cultures. London: Harvard University Press pp109-127

Fruth B Hohmann G 1996 Nest building behavior in the great apes: the great leap forward? In: McGrew WC Marchant LF Nishida T (eds). Great ape societies. Cambridge: Cambridge University Press pp225-240

Fruth B McGrew WC 1998 Resting and nesting in primates: behavioural ecology of inactivity. Am J Primatol 46: 3-5

Fuller G Sadowski L Cassella C Lukas KE 2009 Examining deep litter as environmental enrichment for a family group of Wolf's guenons, *Cercopithecus wolfi*. Zoo Biol 28: 1-7

Furuichi T Takasaki H Sprague D 1982 Winter range utilization of a Japanese macaque troop in a snowy habitat. Folia Primatol 37: 77-94

Furuichi T Inagaki H Angoue-Ovono S 1997 Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: Employing a new method to distinguish between nests of the two species. Int J Primatol 18: 1029-1046

Furuichi T Idana G Ihobe H Kuroda S Kitamura K Mori A Enomoto T Okayasu N Hashimoto C Kano T 1998 Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. Int J Primatol 1029-1043

Furuichi T Hashimoto C 2000 Ground beds of chimpanzees in the Kalinzu Forest, Uganda. Pan Afr News 7: 26-28

Furuichi T Hashimoto C Tashiro Y 2001a Extended application of a marked-nest census method to examine seasonal changes in habitat use by chimpanzees. Int J Primatol 22: 913-928

Furuichi T Hashimoto C Tashiro Y 2004 Botanical and topographical factors influencing nesting-site selection by chimpanzees in Kalinzu forest, Uganda. Int J Primatol 25: 755-765

Garcia JE Braza F 1993 Sleeping sites and lodge trees of the night monkey (*Aotus azarae*) in Bolivia. Int J Primatol 14: 467-477

Germain A Caroff K Buysse DJ Shear MK 2005 Sleep quality in complicated grief. J Trauma Stress 18: 343-346

Ghiglieri MP 1984 The chimpanzees of Kibale forest: a field study of ecology and social structure. New York: Columbia University Press pp31-51

Giganti F Ficca G Gori S Salzarulo P 2008 Body movements during sleep and their relationship with sleep stages are further modified in very old subjects. Brain Res Bull 75: 66-69

Gilby IC Wrangham RW 2008 Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. Behav Ecol Sociobiol 62: 1831-1842

Gilloux I Gurnell J Shepherdson D 1992 An enrichment device for great apes. Anim Welf 1: 279-289

Goff C Howell SM Fritz J Nankivell B 1994 Space use and proximity of captive chimpanzees (*Pan troglodytes*) mother/offspring pairs. Zoo Biol 13: 61-68

Goldberg TL Wrangham RW 1997 Genetic correlates of social behaviour in wild chimpanzees: Evidence from mitochondrial DNA. Anim Behav 54: 559-570

Gonyou HW 1994 Why the study of animal behavior is associated with the animal welfare issue. J Anim Sci 72: 2171-2177

Goodall JM 1962 Nest building behaviour in the free ranging chimpanzee. Ann NY Acad Sci 102: 455-467

Goodall J 1968 The behaviour of free-living chimpanzees in the Gombe stream reserve. Anim Behav Mono 1: 163-311

Goodall J 1986 The chimpanzees of Gombe: Patterns of behavior. Cambridge: Harvard University Press

Goodall J 1990 Through a window. Boston: Houghton-Mifflin

Gordon GDH Cockram MS 1995 A comparison of wooden slats and straw bedding on the behaviour of sheep. Anim Welf 4: 131-134

Gordon SJ Grimmer KA Trott P 2004 Self-reported versus recorded sleep position: An observational study. Internet J Allied Sci Practice 2: 1-11

Gordon SJ Grimmer KA Trott P 2007 Sleep position, age, gender, sleep quality and waking Cervico-Thoracic symptoms. Internet J Allied Sci Practice 5: 1-8

Gordon SJ Buettner PG 2009 Age and lateral sleep position: a pilot study. Internet J Allied Sci Practice 7: 1-5

Goulart VD Azevedo PG van de Schepop JA Teixeira CP Barcante L Azevedo CS Young RJ 2009 GAPs in the study of zoo and wild animal welfare. Zoo Biol 28: 561-573

Groves P Sabater Pi J 1985 From ape’s nest to human fix-point. Man 20: 22-47

Gygax L Tobler I 2001 Social aspects of sleep cluster formation and sleep behaviour in a mixed group of longtailed macaques (*Macaca fascicularis*). http://www.proximate-biology.ch/down/manu.html

Hall M Baum A Buysse DJ Prigerson HG Kupfer DJ Reynolds III CF 1998 Sleep as mediator of the stress-immune relationship. Psychosom Med 60: 48-51

Hamilton WJ 1982 Baboon sleeping site preference and relationships to primate grouping patterns. Am J Primatol 3: 41-53

Hankerson SJ Caine NG 2004 Pre-retirement predator encounters alter the morning behaviour of captive marmosets (*Callithrix geoffroyi*). Am J Primato. 63: 75-85

Hanya G Kiyono M Hayaishi S 2007 Behavioural thermoregulation of wild Japanese macaques: Comparisons between two subpopulations. Am J Primatol 69: 802-815

Hardison HG Neimeyer RA Lichstein KL 2005 Insomnia and complicated grief symptoms in bereaved college students. Behav Sleep Med

Harrison B 1962 Orangutan. London: Collins pp70-72

Harrison B 1969 The nesting behaviour of semi-wild juvenile orang-utans. Sarawak Mus J 17: 336-384

Hashimoto C Furuichi T Takenaka O 1996 Matrilineal kin relationships and social behavior of wild bonobos (*Pan paniscus*): Sequencing the D-loop region of mitochondrial DNA. Primates: 37: 305-318

Hausfater G Meade BJ 1982 Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. Primates 23: 287-297

Hediger H 1950 Wild animals in captivity. London: Butterworth

Herbert PL Bard K 2000 Orangutan use of vertical space in an innovative habitat. Zoo Biol 19: 239-251

Hernandez-Aguilar RA 2009 Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. J Hum Evol 57: 350-364

Hill SP Broom DM 2009 Measuring zoo animal welfare: Theory and Practice. Zoo Biol 28: 531-544

Hinde RA 1976 Interactions, relationships, and social structure. Man 11: 1-7

Hiraiwa-Hasegawa M 1986 Sex differences in the behavioural development of chimpanzees at Mahale. In: Heltne PG Marquardt LA (eds). Understanding chimpanzees. Cambridge MA: Harvard University Press pp104-115

Hirata S Myowa M Matsuzawa T 1998 Use of leaves as cushions to sit on wet ground by wild chimpanzees. Am J Primatol 44: 215-220

Hobson JA Spagna T Malenka R 1978 Ethology of sleep studied with time-lapse photography: Postural immobility and sleep-cycle phase in humans. Science 201: 1251-1253

Hofer MA 1984 Relationships as regulators: A psychobiologic perspective on bereavement. Psychosom Med 46: 183-197

Hoff MP Nadler RD Hoff KT Maple TL 1994 Separation and depression in infant gorillas. Dev Pyschobiol 27: 429-452

Hoff MP Hoff KT Maple TL 1998 Behavioural responses of a western lowland gorilla (*Gorilla gorilla gorilla*) group to the loss of the silverback male at Zoo Atlanta. Int Zoo Ybk 36: 90-96

Hohmann G Fruth B 2003 Culture in bonobos? Between-species and within-species variation in behavior. Curr Anthropol 44: 563-571

Honess PE Marin CM 2006a Behavioural and physiological aspects of stress and aggression in primates. Neurosci Biobehav Rev 30: 390-412

Honess PE Marin CM 2006b Enrichment and aggression in primates. Neurosci Biobehav Rev 30: 413-436

Hosaka K Matsumoto-Oda A Huffman MA Kawanaka K 2000 Reactions to dead bodies of conspecifics by wild chimpanzees in the Mahale Mountains, Tanzania. Prim Res 16: 1-15 (English summary)

Horner V Proctor D Bonnie KE Whiten A de Waal FBM 2010 Prestige affects cultural learning in chimpanzees. Plos ONE 5:e10625.doi: 10.13715

Hornyak M Cejnar M Elam M Matousek M Wallin BG 1991 Sympathetic muscle nerve activity during sleep in men. Brain 114: 1281-1295

Hosey GR Jacques M Burton M 1999 Allowing captive marmosets to choose the size and position of their nest box. Anim Welf 8: 281-285

Hosey GR 2005 How does the zoo environment affect the behaviour of captive primates? Appl Anim Behav Sci 90: 107-129

Hoy JM Murray PJ Tribe A 2010 Thirty years later: Enrichment practices for captive mammals. Zoo Biol 29: 303-316

Hsieh KC Robinson EL Fuller CA 2008 Sleep architecture in unrestrained rhesus monkeys (*Macaca mulatta*) synchronised to 24-hour light-dark cycles. Sleep 31: 1239-1250

http://gorillafund.org/Page.aspx?pid=494

http://gorillafund.org/Page.aspx?pid=499

Huang C Wei F Li M Li Y Sun R 2003 Sleeping cave selection, activity pattern and time budget of white-headed langurs. Int J Primatol 24: 813-824

Huffman MA 1990 Some socio-behavioral manifestations of old age. In: Nishida T (ed). The chimpanzees of the Mahale Mountains: Sexual and life history strategies. Tokyo: Tokyo University Press pp237-255

Hughes BO Duncan IJH 1988 The notion of ethological ‘need’, models of motivation and animal welfare. Anim Behav 36: 1696-1707

Humle T Matasuzawa T 2001 Behavioural diversity among the wild chimpanzee populations of Bossou and neighbouring area Guinea, and Cote d’Ivoire, West Africa: A preliminary report. Folia Primatol 72: 57-68

Issa EB Wang X 2008 Sensory responses during sleep in primate primary and secondary auditory cortex. J Neurosci 28: 14467-14480

Iwata Y Ando C 2007 Bed and bed-site reuse by western lowland gorilla (*Gorilla g. gorilla*) in Moukalaba-Doudou National Park, Gabon. Primates 48: 77-80

Jensen P Toates FM 1993 Who needs ‘behavioural needs’? Motivational aspects of the needs of animals. Appl Anim Behav Sci 37: 1616-181

Jensen MB Pedersen LJ 2008 Using motivation to assess ethological needs and preferences. Appl Anim Behav Sci 113: 340-356

Johnson HM Swan TH Weigand AB 1930 In what positions do healthy people sleep? J Am Med Assoc 94: 2058-2062

Kaemingk K Reite M 1987 Social environment and nocturnal sleep: Studies in peer-reared monkeys. Sleep 10: 542-50

Kahn-Greene ET Killgore DB Kamimori GH Balkin TJ Killgore WDS 2007 The effects of sleep deprivation on symptoms of psychopathology in healthy adults. Sleep Med 8: 215-221

Kantha SS Suzuki J 2006 Sleep quantitation in common marmoset, cotton top tamarin and squirrel monkey by non-invasive actigraphy. Comp Biochem Phys 144: 203-210

Kappeler PM 1998 Nests, tree holes, and the evolution of primate life histories. Am J Primatol 46: 7-33

Kaufman IC Rosenblum LA 1967 The reaction to separation in infant monkeys: Anaclitic depression and conservation-withdrawl. Psychosom Med 29: 648-675

Kawata K 2008 Zoo animal feeding: A natural history viewpoint. Zool Gart 78: 17-42

Killgore WDS Kahn-Greene ET Lipizzi EL Newman RA Kamimori GH Balkin TJ 2008 Sleep deprivation reduces perceived emotional intelligence and constructive thinking skills. Sleep Med 9: 517-526

Kirkden RD Pajor EA 2006 Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. Appl Anim Behav Sci 100: 29-47

Koops K Humle T Sterck EHM Matsuzawa T 2007 Ground-nesting by the chimpanzees of the Nimba Mountains, Guinea: Environmentally or socially determined? Am J Primatol 69: 407-419

Kooriyama T 2009 The death of a newborn chimpanzee at Mahale: reactions of its mother and other individuals to the body. Pan Afr News 16(2) Paper 4

Kortland A 1992 On chimpanzee dormitories and early hominid sites. Curr Anthropol 33: 399-401

Kosheleff VP Anderson CNK 2009 Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. Am J Phys Anthropol 139: 172-181

Kowalski SD Bondmass MD 2008 Physiological and psychological symptoms of grief in widows. Res Nursing Health 31: 23-30

Koyama N 1973 Dominance, grooming, and clasped-sleeping relationship among bonnet monkeys in India. Primates 14: 225-244

Kubota T Oshima N Kunisawa N Murayama R Okano S Mori-Okamoto J 2003 Characteristic features of the nocturnal sleeping posture of healthy men. Sleep Bio Rhy 1: 183-185

Kummer H Goodall J 1985 Conditions of innovative behaviour in primates. Phil Trans R Soc Land B 308: 203-214

Kunz D Herrmann M 2000 Sleep-wake cycle, sleep-related disturbances, and sleep disorders: A chronobiological approach. Comp Psychiat 41: 104-115

Lagarde D Balzamo E van Beers P 1996 Sleep-wakefulness scoring in rhesus monkeys: a behavior analysis versus EEG. J Sleep Res 5 Supp 1: 115

Laland KN Janik VM 2006 The animal cultures debate. Trends Ecol Evol 21: 542-547

Langergraber K Mitani JC Vigilant L 2009 Kinship and social bonds in female chimpanzees (*Pan troglodytes*). Am J Primatol 71: 840-851

Laurentani F Russo CR Bandinelli S Bartali B Cavazzini C DiIorio A Corsi AM Rantanen T Guralnik JM Ferrucci L 2003 Age associated changes in skeletal muscles and their effect on mobility: An operational diagnosis of sarcopenia. J Appl Physiol 95: 1851-1860

Lee DR Guhad PA 2001 Chimpanzee health care and medicine program. In: Brent L (ed). Special topics in primatology: The care and management of captive chiumpanzees. San Antonio: American Society of Primatologists pp63-117.

Lee H Park S 2006 Quantitative effects of mattress types (comfortable vs. uncomfortable) on sleep quality through polysomnography and skin temperature. Int J Ind Ergonom 36: 943-949

Lehner SR Burkart JM van Schaik CP 2010 An evaluation of the geographic method for recognizing innovations in nature, using zoo orangutans. Primates 51: 101-118

Less EH Lukas KE Kuhar CW Stoinski TS 2010 Behavioral responses of captive western lowland gorillas (*Gorilla gorilla gorilla*) to the death of silverbacks in multi-male groups. Zoo Biol 29: 16-29

Li BG Chen C Ji WH Ren BP 2000 Seasonal home range changes of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Quinling Mountains of China. Folia Primatol 71: 375-386

Li D Grueter CC Ren B Zhou Q Li M Peng Z Wei F 2006 Characteristics of night time sleeping places selected by golden monkeys (*Rhinopithecus bieti*) in the Samage forest, Baima Snow Mountain Nature Reserve, China. Int Zool 1: 141-152

Lima SL Rattenborg NC Lesku JA Amlaner CJ 2005 Sleeping under the risk of predation. Anim Behav 70: 723-736

Lima SL Rattenborg NC 2007 A behavioural shutdown can make sleeping safer: a strategic perspective on the function of sleep. Anim Behav 74: 189-197

Line SW 1987 Environmental enrichment for laboratory primates. J Am Vet Med Assoc 190: 854-859

Liu ZH Zhao QK 2004 Sleeping sites of *Rhinopithecus bieti* at Mt. Fuhe, Yunnan. Primates 45: 241-248

Lodwick JL Borries C Pusey AE Goodall J McGrew WC 2004 From nest to nest – influence of ecology and reporoduction on the active period of adult Gombe chimpanzees. Am J Primatol 64: 249-260

Lorrain D De Koninck J 1998 Sleep position and sleep stages: Evidence of their independence. Sleep 21: 335-340

Ludes E Anderson JR 1996 Comparison of the behaviour of captive white-faced capuchin monkeys (*Cebus capucinus*) in the presence of four kinds of deep litter. Appl Anim Behav Sci 49: 293-303

Lui ZH Zhao QK 2004 Sleeping sites of *Rhinopithecus bieti* at Mt. Fuhe, Yunnan. Primates 45: 241-248

Lukas KE Stoinski TS Burks K Snyder R Maple TL 2003 Nest Building in captive *Gorilla gorilla gorilla* Int J Primatol 24: 103-123

Lycett SJ Collard M McGrew WC 2007 Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. PNAS 104: 17588-17592

Lycett SJ Collard M McGrew WC 2010 Are behavioural differences among wild chimpanzee communities genetic or cultural? An assessment using tool-use data and phylogenetic methods. Am J Phys Anthropol 142: 461-467

MacKinnon J 1971 The orangutan in Sabah today. Oryx 11: 141-191

MacKinnon J 1974 The behavior and ecology of wild orangutan (*Pongo pygmaeus*). Anim Behav 22: 3-74

Mallapur A 2005 Managing primates in zoos: Lessons from animal behaviour. Curr Sci 89: 1214-1219

Mallapur A Waran N Sinha A 2005 Factors influencing the behaviour and welfare of captive lion-tailed macaques in Indian zoos. Appl Anim Behav Sci 91:337-353

Manninen E de Pasille AM Rushen J Norring M Saloniemi H 2002 Preferences of dairy cows kept in unheated buildings for different kinds of cubicle flooring. Appl Anim Behav Sci 75: 281-292

Maple TL 1979 Great Apes in captivity. In: Erwin J Maple TL Mitchell G (eds). Captivity and behavior: Primates in breeding colonies, laboratories, and zoos. New York: van Nostrand Reinhold Company pp239-270

Maple TL Perkins LA 1996 Enclosure furnishings and structural environmental enrichment. In: Kleiman DG Allen ME Thompson KV Lumpkin S (eds). Wild mammals in captivity. Chicago: University of Chicago Press pp212-222

Markowitz H The conservation of species-typical behaviors. Zoo Biol 16: 1-2

Masi S Cipolletta C Robbins MM 2009 Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns according to frugivory. Am J Primatol 71: 91-100

Mason GJ 1991 Stereotypies and suffering. Behav Process 25: 103-115

Mason G Clubb R Latham N Vickery S 2007 Why and how should we use environmental enrichment to tackle stereotypic behaviour? Appl Anim Behav Sci 102: 163-188

Mason GJ Veasey JS 2010 How should the psychological well-being of zoo elephants be objectively inverstigated? Zoo Biol 29: 237-255

McGlone JJ 1993 What is animal welfare? J Agric Environ Ethics 6(Supp 2): 26-36

Matsumoto-Oda A 2002 Behavioral seasonality in Mahale chimpanzees. Primates 43: 103-117

Matsuzawa T 1994 Field experiments on use of stone tools by chimpanzees in the wild. In: Wrangham RW McGrew WC da Waal FBM Heltne PG (eds). Chimpanzee Cultures. Cambridge MA: Harvard University Press pp351-370

Matsuzawa T 1997 The death of an infant chimpanzee at Bossou, Guinea. Pan Afr News 4(1) Paper 3

Matsuzawa T Yamakoshi G 1996 Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In: Russon AE Bard KA Parker S (eds). Reaching into thought: The minds of the great apes. Cambridge: Cambridge University Press pp 211-232

Maughan JE Stanford CB 2001 Terrestrial nesting by chimpanzees in Bwindi Impenetrable National Park, Uganda. Am J Phys Anthropol Suppl 32: 104

Maytal G Zalta AK Thompson E Chow CW Perlman C Ostacher MJ Pollack MH Shear K Simon MN 2007 Complicated grief and impaired sleep in patients with bipolar disorder. Bipol Disord 9: 913-917

McGrew WC Tutin CEG 1978 Evidence for a social custom in wild chimpanzees? Man 13: 234-251

McGrew WC 1992 Chimpanzee material culture: Implications for human evolution. Cambridge: Cambridge University Press.

McGrew WC 1998 Culture in nonhuman primates? Ann Rev Anthropol 27: 301-328

McGrew WC 2004 Chimpanzee material culture. In: The cultured chimpanzee: Reflections on cultural primatology. Cambridge: Cambridge University Press pp103-130

McKenna JJ 1996 Sudden infant death syndrome in cross-cultural perspective: Is infant-parent co-sleeping protective? Ann Rev Anthropol 25: 201-216

Meddis R 1975 On the function of sleep. Anim Behav 23: 676-691

Mehlman PT Doran DM 2002 Influencing western gorilla nest construction at Modika research center. Int J Primatol 23: 1257-1285

Melfi VA 2005 The appliance of science to zoo housed primates. Appl Anim Behav Sci 90: 97-106

Melfi VA 2009 There are big gaps in our knowledge, and thus approach, to zoo animal welfare: A case for evidence-based zoo animal management. Zoo Biol 28: 574-588

Mellen J MacPhee MS 2001 Philosophy of environmental enrichment: Past, present and future. Zoo Biol 20:211-226

Mench J 1998 Environmental enrichment and the importance of exploratory behavior. In: Shepherdson DJ Mellen JD Hutchins M (eds). Second nature: Environmental enrichment for captive animals. Washington: Smithsonian Institution Press pp30-46

Mendl M 1991 Some problems with the concept of a cut-off point for determining when an animal's welfare is at risk. Appl Anim Behav Sci 31: 139-146

Mistleberger RE Skene DJ 2004 Social influences on mammalian circadian rhythms: Animal and human studies. Biol Res 79: 533-556

Mitani JC Merriweather DA Zhang C 2000 Male affiliation, cooperation and kinship in wild chimpanzees. Anim Behav 59: 885-893

Mitani JC Watts DP Pepper JW Merriwether DA 2002 Demographic and social constraints on male chimpanzee behaviour. Anim Behav 64: 727 – 737

Mitani JC 2009 Male chimpanzees form enduring and equitable bonds. Anim Behav 77: 633-640

Miyabayashi S Yasuda J 2007 Effects of loss from suicide, accident, acute illness and chronic illness on bereaved spouses and parents in Japan: Their general health, depressive mood, and grief reaction. Clin Neurosci 61: 502-508

Mobius Y Boesch C Koops K Matsuzawa T Humle T 2008 Cultural differences in army ant predation by western chimpanzees? A comparative study of microecological variables. Anim Behav 76: 37-45

Monk TH Welsh DK 2003 The role of chronobiology in sleep disorders medicine. Sleep Med Rev 7: 455-473

Morgan KN Tromborg CT 2007 Sources of stress in captivity. Appl Anim Behav Sci 102: 262-302

Morimura N Mori Y 2010 Effects of early rearing conditions on problem-solving skill in captive male chimpanzees (*Pan troglodytess*). Am J Primatol 71: 1-8

Moscovice LR Issa MH Petrzelkova KJ Keuler NS Snowdon CT Huffman MA 2007 Fruit availability, chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. Am J Primatol 69: 487-502

Mosko S Richard C McKenna J Drummond S 1996 Infant sleep architecture during bedsharing and possible implications for SIDS. Sleep 19: 677-684

Mulavwa M Furuichi T Yangozene K Yamba-Yamba M Montema-Salo B Idani G Ihobe H Hashimoto C Tashiro Y Mwanza N 2008 Seasonal changes in fruit production and party size of bonobos at Wamba. In: Furuichi T Thompson J (eds). The bonobos: Behavior, ecology and conservation. New York: Springer pp121-134

Mulavwa MN Yangozene K Ymba-Yamba M Motema-Salo B Mwanza NN Furuichi T 2010 Nest groups of wild bonobos at Wamba: Selection of vegetation and tree species and relationships between nest group size and party size. Am J Primatol 72: 575-586

Munoz-Delgado J Luna-Villegas G Mondragon-Ceballos R, Fernandez-Guardiola A 1995 Behavioural characterisation of sleep in Stumptail Macaques (*Macaca arctoides*) in exterior captivity by means of high sensitivity videorecording. Am J Primatol 36: 245-249

Munoz-Delgado J Arenas-Rosas R Santallan-Doherty AM Mondragon-Ceballos R 2004a Nighttime behavior in captive stumptail macaques (*Macaca arctoides*): A preliminary report on age and sex differences. Lab Prim News 43: 5-9

Munoz-Delgado J Moreno CB Talero C Ruiz J Boni J Mier V Varga-Marosi C Chiappa P Santillan-Doherty AM 2004b Possible alternation of rest-activity cycle and vigilance behavior in peripheral male stumptailed macaques (*Macaca arctoides*) in exterior captivity: A preliminary report. Salud Mental 27: 34-39

Murphy PJ Campbell SS 1996 Physiology of the circadian system in animals and humans. J Clin Neorophysiol 13: 2-16

Nakagawa S 2004 A farewell to Bonferroni: The problems of low statistical power and publication bias. Behav Ecol 15: 1044-1045

Nakamichi M Koyama N Jolly A 1996 Maternal responses to dead and dying infants in wild troops of ring-tailed lemurs at the Berenty Reserve, Madagascar. Int J Primatol 17: 505-523

Nakamichi M Silldorff A Sexton P 2001 Behavioral responses of an infant gorilla to maternal separation in a captive social group of lowland gorillas (*Gorilla gorilla gorilla*). Primates 43: 245-252

Newberry RC 1995 Environmental enrichment: Increasing the biological relevance of captive environments. Appl Anim Behav Sci 44: 229-243

Nishida T 1968 The social group of wild chimpanzees in the Mahale Mountains. Primates 9: 167-224

Nishida T Takasaki H Takahata Y 1990 Demography and reproductive profiles. In: Nishida T (ed). The chimpanzees of the Mahale Mountains. Tokyo: University of Tokyo Press pp 63-98

Nissen HW 1931 A field study of the chimpanzee. In: Observations of chimpanzee behavior and environment in Western French Guinea. Comp Psychol Mono (8). Baltimore: John Hopkins Press pp 2-122

Noser R Gygax L Tobler I 2003 Sleep and social status in captive gelada baboons (*Theropithecus gelada*). Behav Brain Res 147: 9-15

Novak M Suomi S 1998 Psychological well-being of primates in captivity. Am Psychol 43: 765-773

Novak MFSX Kenney C Suomi SJ Ruppenthal GC 2007 Use of an animal-operated folding perches by rhesus macaques (*Macaca mulatta*). J Am Assoc Lab Anim Sci 46: 35-43

Official Journal of the European Communities Council Directive 1999/22/EC Relating to the Keeping of Wild Animals in Zoos 1999

Ogawa H Takahashi H 2003 Triadic positions of Tibetan macaques huddling at a sleeping site. Int J Primatol 24: 591-606

Okamoto-Mizuno K Tsuzuki K Mizuno K 2003 Effects of head cooling on human sleep stages and body temperature. Int J Biometeorol 48: 98-102

Okamoto-Mizuno K Tsuzuki K Mizuno K 2004 Effects of mild heat exposure on sleep stages and body temperature in older men. Int J Biometeorol 49: 32-36

Okamoto-Mizuno K Tsuzuki K Mizuno K Iwaki T 2005 Effects of partial humid heat exposure during different segments of sleep on human sleep stages and body temperature. Physiol Behav 83: 759-765

Okamoto-Mizuno K Tsuzuki K Mizuno K Iwaki T 2010 Effects of season on sleep and skin temperature in the elderly. Int J Biometeorol 54: 401-409

Oksenberg A Silverberg DS 1998 The effect of body posture on sleep-related breathing disorders: Facts and therapeutic implications. Sleep Med Rev 2: 139-162

Pankhurst FP Horne JA 1994 The influence of bed partners on movement during sleep. Sleep 17: 308-315

Parkes CM 1970 The first year of bereavement: a longitudinal study of the reaction of London widows to the death of their husbands. Psychiatry 33: 444-467

Peetz A Norconk MA Kinzey WG 1992 Predation by jaguar on howler monkeys (*Alouatta seniculus*) in Venezuela. Am J Primatol 28: 223-228

Pepper JW Mitani JC Watts DP 1999 General gregariousness and specific social preferences among wild chimpanzees. Int J Primatol 20: 613-632

Pizzutto CS Nichi M Geronymo Sgai MGF Corrêa SHR Viau P Beresca AM Alvarenga de Oliveira C Barnabé RC Alcindo de Barros Vaz Guimarães M 2008 Effect of environmental enrichment on behavioral and endocrine aspects of a captive orangutan (*Pongo pygmaeus*). Lab Prim News 47:10-13

Plowman AB 2008 BIAZA statistics guidelines: Toward a common application of statistical tests for zoo research. Zoo Biol 27: 226-233

Plumptre AJ Reynolds V 1997 Nesting behavior of chimpanzees: Implications for censuses. Int J Primatol 18: 475-485

Pollock GH 1961 Mourning and adaptation. Int J Psychoanal 42: 341-361

Pontes ARM Soares ML 2005 Sleeping sites of common marmosets (*Callithrix jacchus*) indefaunated urban forest fragments: a strategy to maximise food intake. J Zool Lond 266: 55-63

Poole TB 1992 The nature and evolution of behavioural needs in mammals. Anim Welf 1: 203-220

Pruetz JD 2007 Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: Implications for thermoregulatory behavior. Primates 48: 316-319

Pruetz JD Fulton SJ Marchant LF McGrew WC Schiel M Waller M 2008 Arboreal nesting as anti-predator adaptation by Savanna chimpanzees (*Pan troglodytes verus*) in Southeastern Senegal. Am J Primatol 70: 393-401

Rahaman H Parthasarathy MD 1969 Studies on the social behaviour of bonnet monkeys. Primates 10: 149-162

Ramakrishnan U Coss RG 2001 Strategies used by bonnet macaques (*Macaca radiata*) to reduce predation risk while sleeping. Primates 42: 193-206

Ramsey G Bastian MC van Schaik C 2007 Animal innovation defined and operationalized. Behav Brain Sci 30: 393-437

Rayadin Y Saitoh T 2009 Individual variation in nest size and nest site features of the Bornean ornagutans (*Pongo pygmaeus*). Am J Primatol 71: 393-399

Reichard U 1998 Sleeping sites, sleeping places, and presleep behaviour of gibbons (*Hylobates lar*). Am J Primatol 46: 35-62

Reite ML Rhodes JM Kvan E Adey WR 1965 Normal sleep patterns in macaque monkey. Arch Neurol 12: 133-144

Reite M Stynes AJ Vaughn L Pauley JD Short RA 1976 Sleep in infant monkeys: Normal values and behavioural correlates. Physiol Behav 16: 245-251

Reite M Short RA 1977 Nocturnal sleep in isolation-reared monkeys: Evidence for environmental independence. Dev Psychobiol 10: 555-561

Remis MJ 1993 Nesting behavior of lowland gorillas in the Dzanga-Sangha Reserve, Central African Republic: Implications for population estimates and understandings of group dynamics. Tropics 2: 245-255

Reynolds V 1965 Some behavioural comparisons between the chimpanzee and mountain gorilla in the wild. Am Anthropol 67: 691-706

Reynolds V Reynolds F 1965 Chimpanzees of the Budongo Forest. In: DeVore I (ed). Primate behavior: Field studies of monkeys and apes. New York: Holt, Rinehart & Winston pp368-424

Reynolds V 1990 Images of chimpanzees. Anthropol Today 6: 1-3

Rial RV Nicolau MC Gamundi A Akaarir M Aparicio S Garau C Tejada S Roca C Gene L Moranta D Esteban S 2007 The trivial function of sleep. Sleep Med Rev 11: 311-325

Richard C Mosko S McKenna J Drummond S 1996 Sleeping position, orientation, and proximity in bedsharing infants and mothers. Sleep 19: 685-690

Riss D Goodall J 1976 Sleeping behavior and associations in a group of captive chimpanzees. Folia Primatol 25: 1-11

Robinson MH 1998 Enriching the lives of zoo animals, and their welfare: Where research can be fundamental. Anim Welf 7: 151-175

Roder EL Timmermans PJA 2002 Housing and care of monkeys and apes in laboratories: Adaptations allowing essential species-specific behavior. Lab Anim 36: 221-242

Rollin BE 1993 Animal welfare, science, and value. J Agric Environ Ethics 6(Supp 2): 44-50

Ross SR 2006 Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*). Behav Proc 73: 117-120

Ross SR Lukas KE 2006 Use of space in a non-naturalistic environment by chimpanzees (*Pan troglodytess*) and lowland gorillas (*Gorilla gorilla gorilla*). Appl Anim Behav Sci 96: 143-152

Ross SR Schapiro SJ Hau J Lukas KE 2009 Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. Appl Anim Behav Sci 121: 42-50

Rothman JM Pell AN Dierenfield ES M McCann CM 2006 Plant choice in the construction of night nests by gorillas in the Bwindi Impenetrable National Park, Uganda. Am J Primatol 68: 361-368

Rushen J 2003 Changing concepts of farm animal welfare: Bridging the gap between applied and basic research. Appl Anim Behav Sci 81: 199-214

Russon AE Handayani DP Kuncoro P Fersia A 2007 Orangutan leaf-carrying for nest building: Toward unravelling cultural processes. Anim Cogn 10: 189-202

Sabater Pi J Vea JJ Serrallonga J 1997 Did the first hominids build nests? Curr Anthropol 38: 914-916

Sadeh A Raviv A Gruber R 2000 Sleep patterns and sleep disruptions in school-age children. Dev Psych 36: 291-301

Sanz C Morgan D Strindberg S Onononga R 2007 Distinguishing between the nests of sympatric chimpanzees and gorillas. J App Ecol 44: 263-272

Savage VM West GB 2007 A quantitative, theoretical framework for understanding mammalian sleep. PNAS 104: 1051-1056

Schaller GB 1963 The Mountain Gorilla - Ecology and Behavior. Chicago: University of Chicago Press

Schaller GB 1965 The behavior of the mountain gorilla. In: DeVore I (ed) Primate behavior: Field studies of monkeys and apes. New York: Holt, Rinehart & Winston pp324-367

Schechtman KB Kutner NG Wallace RB Buchner DM Ory MG 1997 Gender, self-reported depressive symptoms, and sleep disturbance among older community-dwelling persons. J Psychosom Res 43: 513-527

Secretary of State’s Standards of Modern Zoo Practice 2004. Council Directive 1999/22/EC

Seidensticker J Doherty JG 1996 Integrating animal behaviour and exhibit design. In: Kleiman DG Allen ME Thompson KV Lumpkin S (eds). Wild mammals in captivity. Chicago: University of Chicago Press pp180-190

Seigel S 1956 Nonparametric statistics for the behavioral sciences. London: McGraw Hill

Sept JM 1992 Was there no place like home?: A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. Curr Anthropol 33: 187-207

Sept JM 1998 Shadows on a changing landscape: comparing nest patterns of hominids and chimpanzees since their last common ancestor. Am J Primatol 46: 85-101

Sforza E Chapotot F Lavoie S Roche F Pigeau R Buguet A 2004 Heart rate activation during spontaneous arousals from sleep: Effect of sleep deprivation. Clin Neurophysiol 115: 2442-2451

Shear K Shair H 2005 Attachment, loss, and complicated grief. Dev Psychobiol 47: 253-267

Shepherdson DJ 1998 Tracing the path of environmental enrichment in zoos. In: Shepherdson DJ Mellen JD Hutchins M (eds). Second Nature. Washington: Smithsonian Institution Press pp1-12

Shepherdson DJ Carlstead KC Wielebnowski N 2004 Cross-institutional assessment of stress responses in zoo animals using longitudinal monitoring of faecal corticoids and behaviour. Anim Welf 13: S105-113

Shimoji M Bowers CL Crockett CM 1993 Initial response to introduction of a PVC perch by singly caged *Macaca fascicularis.* Lab Prim News 32: 8-10

Shyne A 2006 Meta-analysis review of the effects of enrichment on stereotypic behavior in zoo mammals. Zoo Biol 25: 317-337

Siegel JM 2005 Clues to the functions of mammalian sleep. Nature 437: 1264-1271

Siegel JM 2008 Do all animals sleep? Trends Neurosci 31: 208-213

Silk JB Seyfarth RM Cheney DL 1999 The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. Behav 136: 670-703

Sousa J Barata AV Sousa C Casanova CCN Vicente L 2011 Chimpanzee oil-palm use in southern Cantanhez National Park, Guinea-Bissau. Am J Primatol 73: 1-13

Spinka M 2006 How important is natural behaviour in animal farming systems? Appl Anim Behav Sci 100: 117-128

Sporrle M Stich J 2010 Sleeping in safe places: an experimental investigation of human sleeping place preferences from an evolutionary perspective. Evol Psychol 8: 405-419

Stanford C O'Malley RC 2008 Sleeping tree choice by Bwindi chimpanzees. Am J Primatol 70: 642-649

Stanley N 2005 The physiology of sleep and the impact of ageing. Euro Urol Supp 3: 17-23

Stevens JMG Vervaecke H van Elsacker L 2008 The bonobo's adaptive potential: Social relations under captive conditions. In: Furuichi T Thompson J (eds). The bonobos: Behavior, ecology and conservation. New York: Springer pp 19-38

Stewart FA Pruetz JD Hansell M H 2007 Do chimpanzees build comfortable nests? Am J Primatol 69: 930-939

Stoinski TS Hoff MP Maple TL 2001 Habitat use and structural preferences of captive western lowland gorillas (*Gorilla gorilla gorilla*): Effects of environmental and social variables. Int J Primatol 22: 431-447

Stoinski TS Hoff MP Maple TL 2002 The effect of structural preferences, temperature, and social factors on visibility in western lowland gorillas (*Gorilla gorilla gorilla*). Environ and Behav 34: 493-507

Suckling EE Koenig EH Hoffman BF Brooks CM 1957 The physiological effects of sleeping on hard or soft beds. Hum Biol 29: 274-288

Sugardjito J 1983 Selecting nest sites of Sumatran orangutans, *Pongo pygmaeus abelii* in the Gunung Leuser National Park, Indonesia. Primates 24: 467-474

Sugardjito J Te Boekhonst IJA van Hooff JARAM 1987 Ecological constraints on the grouping of wild orangutans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. Int J Primatol 8: 17-41

Sugiyama Y Kurita H Matsui T Kimoto S Shimomura T 2009 Carrying of dead infants by Japanese macaque (*Macaca fuscata*) mothers. Anthropol Sci 117: 113-119

Suomi SJ Eisele CD Grady SA Harlow HF 1975 Depressive behavior in adult monkeys following separation from family environment. J Abnorm Psychol 84: 576-578

Swaisgood RR Shepherdson DJ 2005 Scientific approaches to enrichment and stereotypies in zoo animals: What’s been done and where should we go next? Zoo Biol 24: 499-518

Swaisgood RR 2007 Current status and future directions of applied behavioral research for animal welfare and conservation. Appl Anim Behav Sci 102: 139-162

Takahashi H 1997 Huddling relationships in night sleeping groups among wild Japanese macaques during winter. Primates 38: 57-68

Tarou LR Bashaw MJ 2007 Maximising the effectiveness of environmental enrichment: Suggestions from the experimental analysis of behavior. Appl Anim Behav Sci 102: 189-204

Teleki G 1973 Group response to the accidental death of a chimpanzee in Gombe National Park, Tanzania. Folia Primatol 20: 81-94

Tenaza R Tilson RL 1985 Human predation and Kloss's gibbon (*Hylobates klossi*) sleeping trees in Siberut Island, Indonesia. Am J Primatol 8: 299-308

Thorpe WH 1965 The assessment of pain and distress in animals. In: Report of the technical committee to enquire into the welfare of animals kept under intensive livestock husbandry systems. London: Her Majesty's Stationery Office

Tobler I 1995 Is sleep fundamentally different between mammalian species? Behav Brain Res 69: 35-41

Traylor-Holzer K Fritz P 1985 Utilization of space by adult and juvenile groups of captive chimpanzees (*Pan troglodytes*). Zoo Biol 4: 115-127

Troxel WM Robles TF Hall M Buysse DJ 2007 Marital quality and the marital bed: Examining the covariation between relationship quality and sleep. Sleep Med Rev 11: 389-404

Tutin CEG Parnell RJ White LJT Fernandez M 1995 Nest building by lowland gorillas in the Lope Reserve, Gabon: Environmental influences and implications for censusing. Int J Primatol 16: 53-76

Tuyttens FAM 2005 The importance of straw for pig and cattle welfare: A review. Appl Anim Behav Sci 92: 261-282

Tuyttens FAM Wouters F Struelens E Sonck B Duchateau L 2008 Synthetic lying mats improve lying comfort of gestating cows. Appl Anim Behav Sci 114: 76-85

U.S.D.A Regulations on Animals in Laboratories and Commercial Facilities 1998

Usui S 2000 Gradual changes in environmental light intensity and entrainment of circadian rhythms. Brain Dev 22: 561-564

van de Weerd HA van de Broek FAR Baumans V 1996 Preference for different types of flooring in two rat strains. Appl Anim Behav Sci 46: 251-261

van de Weerd HA van Loo PLP van Zutphen LFM Koolhaas JM Baumans V 1998 Strength of preference for nesting material as environmental enrichment for laboratory mice. Appl Anim Behav Sci 55: 369-382

van Lawick-Goodall J 1971 In The Shadow of Man. Glasgow: Collins

van Schaik CP Ancrenaz M Borgen G Galdikas B Knott CD Singleton I Suzuki A Utami SS Merrill M 2003 Orangutan cultures and the evolution of material culture. Science 299: 102-105

Vessey SH 1973 Night observations of free-ranging rhesus monkeys. Am J Phys Anthropol 38: 613-620

Videan EN 2006a Bed building in captive chimpanzees (*Pan troglodytes*): The importance of early rearing. Am J Primatol 68: 745-751

Videan EN 2006b Sleep in the captive chimpanzee (*Pan troglodytes*): The effects of individual and environmental factors on sleep quality and duration. Behav Brain Res 169: 187-192

Videan EN Fritz J Murphy J 2007 Development of guidelines for assessing obesity in captive chimpanzees (*Pan troglodytes*). Zoo Biol 26: 93-104

Wada K Tokida E Ogawa H 2007 The influence of snowfall, temperature and social relationships on sleeping clusters of Japanese monkeys during winter in Shiga Heights. Primates 48: 130-139

Waldrop DP 2007 Caregiver grief in terminal illness and bereavement: A mixed methods study. Health Soc Work 32: 197-206

Walker MP 2008 Cognitive consequences of sleep and sleep loss. Sleep Med 9 (Suppl. 1): S29-S34

Wallis J 2002 Seasonal aspects of reproduction and sexual behavior in two chimpanzee populations: a comparison of Gombe (Tanzania) and Budongo (Uganda). In: Boesch C Hohmann G Marchant LF (eds). Behavioral diversity in chimpanzees and bonobos. New York: Cambridge University Press pp 181-191

Warren Y Williamson EA 2004 Transport of dead infants mountain gorillas by mothers and unrelated females. Zoo Biol 23: 375-378

Watters JV 2009 Toward a predictive theory for environmental enrichment. Zoo Biol 28: 609-622

Watts DP 1998 Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*). Int J Primatol 19: 929-948

Watts DP 2000 Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. Int J Primatol 21: 189-210

Webb WB 1975 The adaptive functions of sleep patterns. In: Levin P Koella WP (eds). Proceedings of the 2nd European Congress on Sleep Research. Basel: Karger pp13-19

Webster J 2005 The assessment and implementation of animal welfare: Theory into practice. Rev Svi Tech Off Int Epiz 24: 723-734

Weiche I Anderson JR 2007 Influence of social and environmental factors of nesting behaviour in captive gorillas (*Gorilla gorilla gorilla*). Folia Primatol 78: 154-165

Weitzman ED Kripke DF Pollack C Dominguez J 1965 Cyclic activity in sleep of *Macaca mulatta*. Arch Neurol 12: 463-467

Wells DL 2009 Sensory stimulation as environmental enrichment for captive animals: A review. Appl Anim Behav Sci 118: 1-11

Wemelsfelder F 2003 Animal boredom – A model of chronic suffering in captive animals and its consequences for environmental enrichment. Available on: www.PSYETA.org/hia/vol8/wemelsfelder

Whilde J Marples N 2010 The behavior of a zoo-housed infant orangutan after the death of its mother. Zoo Biol 29: 1-7

White FJ 1998 Seasonality and socioecology: the importance of variation in fruit abundance to bonobo socialty. Int J Primatol 19: 1013-1027

Whiten A Goodall J McGrew WC Nishida T Reynolds V Sugiyama Y Tutin CEG

Wrangham RW Boesch C 1999 Cultures in chimpanzees. Nature: 437: 737-740

Whiten A 2000 Primate culture and social learning. Cog Sci 24: 477-508

Whiten A Goodall J McGrew WC Nishida T Reynolds V Sugiyama Y Tutin CEG

Wrangham RW Boesch C 2001 Charting cultural variation in chimpanzees. Behaviour: 138: 1481-1516

Whiten A Horner V de Waal FBM 2005 Conformity to cultural norms of tool use in chimpanzees. Nature 437-740

Whiten A Spiteri A Horner V Bonnie KE Lambeth SP Schapiro SJ de Waal FBM 2007 Transmission of multiple traditions within and between chimpanzee groups. Curr Biol 17: 1038-1043

Wickens-Drazilova D 2006 Zoo animal welfare. J Agricult Environ Ethics 19: 27-36

Wolfensohn S Honess P 2005 Hand book of primate husbandry and welfare. Oxford: Blackwell Publishing Ltd

Wolff AV 1989 Polyvinyl chloride piping as perch material for squirrel monkeys. Lab Prim News 28:7-8

World Association of Zoos and Aquariums (WAZA) Code of Ethics and Animal Welfare 2006

Wrangham RW Smuts B 1980 Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. J Reprod Fert 28: 13-31

Wrangham RW Clark AP Isabirye-Basuta G 1992 Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T McGrew WC Marler P Pickford M de Waal FBM (eds). Topics in Primatology: Human Origins. Tokyo: Tokyo University Press pp81-98

www.orcadian.co,uk

Yamagiwa J 2001 Factors influencing the formation of ground nests by eastern lowland gorillas in Kahuzi-Biega National Park: Some evolutionary implications of nesting behavior. J Hum Evol 40: 99-109

Yamakoshi G Sugiyama Y 1995 Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behavior. Primates 36: 489-500

Yeates JW Main DCJ 2008 Assessment of positive welfare: A review. The Vet J 175: 293-300

Yerkes RM 1943 Chimpanzees: A laboratory colony. New Haven: Yale University Press pp16-17

Young RJ 2003 Environmental enrichment for captive animals. Oxford: Blackwell Science

Zepelin H 1989 Mammalian sleep. In: Kryger MH Roth T Dement WC (eds). Principles and practices of sleep medicine. Philadelphia: Saunders pp30-49

Zepelin H Siegel JM Tobler I 2005 Mammalian sleep. In: Kryger MH Roth T Dement WC (eds). Principles and practices of sleep medicine (4th ed). Philadelphia: Elsevier Saunders pp 91-100

Zhang SY 1995 Sleeping habits of brown capuchin monkeys (*Cebus apella*) in French Guinea. Am J Primatol 36: 327-335

Appendix 1: Ape nesting questionnaire

PART 1: Background Information:

1. Name of zoo/wildlife park

2. How many studies (if any) been carried out on the nesting behaviours of chimpanzees, either by staff, students or researchers?

Staff: Students: Researchers:

3. Could you please provide brief details of any such studies:

4. Is there an environmental enrichment programme currently in use?

5. If yes, please provide brief details:

PART 2: Sleeping quarters:

6. Do chimpanzees sleep outside in their outdoor enclosures at any point during the year?

7. If yes, during which months?

8. Are indoor night time sleeping areas communal or separate for each chimpanzee?

9. How many elevated sleeping berths/platforms/sleeping pods are available to build night nests on?

Berths/Platforms: Sleeping pods: Other structures:

10. Please provide brief detail on the above:

11. How many of the chimpanzees sleep on the ground at night?

Adult males: Adult females: Juveniles: Infants:

If possible, for each age-sex class above, please estimate the percentage of nights spent on the ground (e.g., 30%, 75 %...)

PART 3: Nesting materials:

12. Is potential nesting material provided in indoor and outdoor (if applicable) sleeping areas?

13. If yes, what type(s) of materials are presented? Please indicate if they get used by the chimpanzees for making night nests

14. Are different types of nesting materials rotated on a regular basis? For example, using straw for one week, wood-wool for the next week etc

15. If yes, please provide brief details below:

PART 4: Additional information If you feel there is any additional information you would like to add regarding nesting materials/behaviours, or if would like to expand on any of the questions, please use the space below:

Many thanks for your kind co-operation.

Appendix 2: Supplemental information for *Pan* thanatology

Supplemental Information
Pan thanatology
James R. Anderson, Alasdair Gillies, Louise C. Lock

Supplemental Experimental Procedures

Early records are non-existent for Pansy, who arrived at the Blair Drummond (BD) Safari Park as an adult in 1970, having been donated by a circus along with Blossom. Both are thought to be wild-born. When SG started working at the Park in 2001, Pansy still had a high social rank in the group. However, with advancing age, she became increasingly arthritic, and occasionally received beatings from Chippy. Pansy’s social rank gradually diminished, and she became more wary and nervous of her surroundings. The fourth member of the group was Pansy’s daughter, Rosie. At the time of events here, the four chimpanzees had lived together with no other chimpanzees for approximately 19 years.

The chimpanzees live on an island during the warmer months of the year, with little human contact apart from cleaning of the indoor quarters by keepers, and passing boats with visitors. They spend the colder months of the year on the mainland, containing a day area and a night area connected by two wire grille doors. For transportation, the chimpanzees are captured after dark by going onto the island and locking the door of their sleeping area. A transport cage is then attached to the holding cage within the sleeping area. The chimpanzees generally enter the transport without fuss, being highly familiar with the routine. Indeed, Chippy has been seen to physically drag Pansy and Rosie into the transport cage if they have loitered outside when the others have been ready to go.

During November 2008 keepers noticed that Pansy was becoming less active and more withdrawn. Several attempts to capture the chimpanzees failed, mostly due to Pansy refusing to enter the holding area despite the others already waiting there to be transported. Ruses such as feeding only indoors, and providing highly prized food items, were unsuccessful. On the night if he 28th a keeper went onto the island and found only 3 of the 4 chimpanzees in the indoor quarters; Pansy was still outside, despite the low temperature.

On the 30th a pulley system was rigged up to enable the door of the island quarters to be closed from the mainland. On December 2nd Blossom, Rosie and Chippy readily came indoors for food, but Pansy refused. Early in the afternoon she lay down in the snow and started to fall asleep. Fearing hat she would catch hypothermia keepers left more food inside and left the island, at which point Pansy entered. At around 4pm, the pulley system was used and all 4 chimpanzees were captured. It was clear that Pansy was unwell. Although eating, she appeared lethargic. She stirred in response to the general noise and activity of the other chimpanzees, and she entered the transport cage without fuss.

Once inside the winter quarters, due to Pansy's continuing lethargy the park's veterinarian was called in. Darting was considered too risky due to Pansy's age and frailty, so it was decided to try and ensure adequate food and fluid intake and to continue monitoring her. In the course of the day she drank about 1 litre of water from bottles given to her through the mesh wall of the enclosure.

December 5th saw little change in Pansy's condition: she ate little and mostly slept, with no attempt to leave the night area, frequently returning to her nest. At this point the other chimpanzees wee confined to the day area in case veterinary intervention was necessary; they could see and communicate with Pansy through wire mesh grilles separating the two areas, and they were allowed in to the night area for nesting. The group was notably quiet during the day.

The following day Pansy barely moved from her nest. The others were again confined to the day area. Pansy's activity was largely limited to turning in her nest; she ate only half a banana and a few grapes, but drank 1.5l of fruit juice through a length of hosepipe suspended from the roof of the night area. She did this by taking hold of the end of the pipe and directing it into her mouth, controlling what she wanted.

On December 7th she stopped eating and was barely moving. The veterinarian was called. As a priority she was again offered juice through the hosepipe, but she soon pushed he hosepipe away. The vet prescribed 50mg of the anti-inflammatory drug Metacam, which AG dripped into her mouth with a syringe form he ceiling. Pansy ingested the full dose, but further efforts to get her to eat or drink were to no avail. She simply remained in her nest without moving. At around 15.00h, she got up and made her way with difficulty across the traversing ladder to platform B, where she lay down again in the nest that Rosie had made the previous night.

Just before 16.00h Pansy's breathing started to become erratic; she started to breathe rapidly and then appeared to stop breathing altogether. A medically trained keeper identified this as Cheyne-Stokes respiration, sometimes seen in patients approaching death. AG decided to open the grille and let the chimpanzees be together. The two video cameras were then switched on.

The following morning the three surviving chimpanzees moved into the day area with no fuss. In spite of several attempts BD staff were unable to find anyone in Scotland willing to do a post mortem on a primate of unknown origin. A local pet crematorium agreed to dispose of the body.

Appendix 3: Timeline for all events on sleeping platform B

16:13$_{15}$ – Cameras mounted above platforms A and B are activated. On platform B, Pansy is lying on her right side facing the back wall of the enclosure.

16:13$_{55}$ – Pansy moves slightly to the left as if to lie supine, but turns back onto her right hand side. She moves her hands and feet.

16:14$_{11}$ – Rosie arrives via the horizontal ladder that connects platform B with platform A. She sits near Pansy’s head, looks at her for a few moments, then reaches out and briefly touches Pansy’s left arm. Rosie then sifts through straw. Pansy’s breathing appears laboured.

16:15$_{01}$ – Rosie leaves platform B. Pansy does not move.

16:15$_{26}$ – Chippy arrives via the horizontal ladder, carrying food. Chippy swaggers slightly and shakes one of the furnishing ropes, as at the onset of a charging display. He stands near Pansy’s head, looking down at her.

16:15$_{32}$ – Rosie returns via the horizontal ladder and stands at Pansy’s rear, crouches over as if sniffing Pansy, then appears to arrange straw round Pansy’s back/rear.

16:15$_{40}$ – Chippy, still at Pansy’s head, touches Pansy’s neck. As he does this, Pansy opens her mouth; Chippy crouches closer to her.

16:15$_{45}$ – Blossom arrives via the horizontal ladder. Chippy, still sniffing/ touching Pansy’s torso, moves towards her head. Blossom is now sitting at Pansy’s head, Chippy is crouching over her head, and Rosie is sitting at her back/rear.

16:16$_{06}$ – Chippy moves away from Pansy and inspects Rosie’s rear. Blossom moves closer to Pansy’s head and grooms her head/neck. Rosie turns away from Pansy but remains next to her.

16:1616 – Chippy leaves platform B, sits on the vertical ladder and eats. Rosie touches Pansy’s back. Blossom still sits at Pansy’s head, sniffing or grooming Pansy’s hands and arms.

16:1641 – Chippy climbs back onto platform B but leaves immediately via the horizontal ladder, Blossom reaching out to touch him as he passes. Blossom and Rosie are no longer in physical contact with Pansy; both are sitting by her and eating.

16:1712 – Rosie moves closer to Pansy, stands over her, and grooms her face/head. She then moves her hands down Pansy’s back toward her rear. Pansy responds with a slight head tilt to the left (toward Rosie) and small movements of her hands and feet. Blossom remains slightly turned away from Pansy, sitting and eating; she turns her head toward Pansy when Pansy moves.

16:1800 – Blossom stands and briefly moves over toward Pansy’s head, then turns away again to sit and eat. Rosie also moves away from Pansy, and sits next to Blossom. Rosie touches Blossom’s face/head – either grooming or food begging (Blossom is eating).

16:1911 – Rosie turns away from Blossom, and leans over toward Pansy’s head, but makes no contact.

16:1917 – Rosie turns away from Pansy, and moves over to Blossom again.

16:1923 – Both Blossom and Rosie move further away from Pansy, and sit at the edge of the horizontal ladder. Blossom is still eating, Rosie orients her head close to Blossom’s – possibly food begging.

16:2005 – Rosie moves away from Blossom (still eating) into the central area of the platform. She then moves to the edge of the platform and looks toward the central area of the enclosure.

16:2134 – Rosie returns to Pansy, crouches low next to her head. Blossom stands, inspects Rosie’s rear.

16:2202 – Rosie moves away from Pansy, sits again at the middle of the edge of the platform B. Blossom also returns to her previous position by the horizontal ladder.

16:2216 – For the first time in approximately 5 min, Pansy makes a slight movement (small twitch of left hand).

16:2225 – Very slight movement of Pansy’s right foot, followed by small movements of hands, torso and head. Breathing appears very laboured. No observable immediate response from the other females.

16:2241 - Blossom moves to Pansy’s head, and grooms her left arm with her mouth.

16:2308 – Rosie also moves toward Pansy’s head. The two females crouch over Pansy’s head.

16:2311 – Rosie moves to Pansy’s back, appears to stroke or groome Pansy’s torso (ribs). Blossom continues grooming Pansy’s arm.

16:2332 – No change in Rosie’s behaviour. Blossom moves slightly to the left and grooms Pansy’s face.

16:2347 – Pansy extends her arms and legs. Rosie remains sitting at Pansy’s back, but Blossom moves away from Pansy toward the platform edge. Again, Pansy’s breathing is very laboured.

16:2358 – Chippy[21], sitting on one of the central pods, orientates s toward platform B. He leaves the pod, swings onto the horizontal ladder and again swaggers and swings the rope.

16:2404 – Chippy arrives on platform B. Rosie is still standing at Pansy’s back, Blossom moves toward the edge of the platform near the horizontal ladder.

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[21] Between leaving platform B at 16:16 and returning at 16:24, Chippy sat on pod 2 manipulating straw (probably looking for small seeds – a behaviour that was frequently performed).

16:24$_{08}$ – Blossom remains oriented away from Pansy, facing the middle of the enclosure. Rosie still stands behind Pansy’s back. Chippy stands over Pansy’s head, and pulls at her left shoulder and arm.

16:24$_{21}$ – Chippy crouches over Pansy’s head then appears to try to open her mouth. Rosie moves toward Pansy’s head.

16:24$_{25}$ –Blossom, Chippy and Rosie simultaneously turn toward Pansy’s head. Chippy and Rosie are crouched over Pansy’s head; Blossom sits and also looks down at Pansy’s head.

16:24$_{36}$ – Rosie moves from Pansy’s head toward her torso. Blossom moves away from Pansy toward the horizontal ladder. Chippy appears to lift and shake Pansy’s left shoulder and arm.

16:25$_{03}$ – Chippy continues to manipulate Pansy’s shoulder/arm. Blossom stands next to Chippy, and also manipulates her left arm. Rosie stands at Pansy’s lower torso, not in contact with Pansy.

16:25$_{06}$ – Blossom sits at Pansy’s head, stroking Pansy’s left hand. Chippy and Rosie leave platform B simultaneously, Chippy via the vertical ladder, and Rosie via a rope.

16:25$_{16}$ – Blossom stops grooming Pansy’s hand but continues to sit next to her.

16:25$_{31}$ – Blossom moves away from Pansy toward the horizontal ladder. She forages through straw there, finds food, then sits and eats.

16:27$_{04}$ – Blossom leans over to gather more food from the centre of platform B, and then returns near the horizontal ladder to sit and eat. Pansy moves very slightly: 2 head ‘nods’, probably a post-mortem twitch. This elicits no response from the others.

16:28$_{39}$ – Blossom leaves platform B via rope.

16:3316 – Chippy arrives on the platform, immediately runs across the platform to the horizontal ladder as if in a charging display; makes no contact with Pansy.

16:3609 – Main lighting is switched off.

16:3656 – Chippy jumps onto the platform in a charging display. He jumps into the air, brings both hands down and pounds Pansy’s torso, then runs across the platform and across the horizontal ladder.

16:4326 – Rosie arrives via the horizontal ladder, carrying a handful of straw. She sits at the edge near Pansy’s head, and pulls small amounts of straw toward her, but does not build a nest.

16:4354 – Rosie leans over Pansy’s head/ upper torso, but does not seem to make physical contact.

16:4359 – Rosie moves back near the edge of platform.

16:4429 – Rosie again pulls a few strands of straw toward her, but stops after a few seconds and sits still.

16:4535 – Rosie forages through straw, collects food, and sits, eats.

16:4634 – Rosie leaves via the horizontal ladder.

16:5309 – Rosie arrives via the horizontal ladder. She stands over Pansy’s head and looks down at her.

16:5319 – Rosie turns away from Pansy, and lies on her right side at the edge of the platform, her head orientated toward the middle of the enclosure. She eats while lying in this position.

16:5714 – Still in this position, Rosie grooms her arm.

16:5843 – Rosie changes posture so is lying supine at the edge of the platform, scratches her neck for a few seconds.

17:0227 – Rosie sits (still with her back to Pansy), looking in the direction of horizontal ladder.

17:0340 – Still in this position, Rosie manipulates straw (not nest building).

17:0435 – Rosie lies prone at the edge of the platform, gaze directed down toward enclosure floor.

17:0502 – Rosie changes orientation and posture. Turns so head is almost level with the horizontal ladder, and lies on her right side (facing Pansy).

17:0530 – Rosie changes orientation again, lying in her right side facing the back wall, with her head at the edge of the platform.

17:0534 – Still in this position, Rosie lies and manipulates straw.

17:0605 – Rosie stops manipulating straw, turns supine momentarily, then lies on her right side again and manipulates straw.

17:0730 – Rosie lies supine, with her head at the edge of the platform.

17:0800 – Rosie turns back onto right side and manipulates straw.

17:0924 – Rosie stands, and moves over to edge of the horizontal ladder, and sits.

17:1035 – Rosie leaves via the horizontal ladder (Not in camera view, so must either stay on ladder or descend to the floor.

17: 1655 – Rosie arrives on platform A (via pods), where Blossom is lying. As she arrives on the middle of the platform, Blossom reaches out and briefly touches

Rosie’s face. Rosie stands beside Blossom, then gathers straw and leaves platform A via the horizontal ladder.

17:1750 – Rosie arrives on with a large handful of straw. She does not make a nest, but places the straw on platform and sits facing Pansy at the edge of the platform.

17:1814 – Rosie leans over toward Pansy’s head, gathers straw from this area, and pulls it toward herself then sits still (no attempt to build complete nest).

17:1929 – Rosie stands and leaves via the vertical ladder.

17:2139 – Rosie arrives via the vertical ladder, stands near Pansy’s head.

17:2208 – Rosie sits at the edge of platform, facing Pansy’s head.

17:2248 – Still in this position, Rosie manipulates straw.

17:2312 – Rosie stretches, then lies on her left side (parallel to edge of platform), facing left wall. Manipulates straw.

17:2349 – Rosie sits and turns to face the horizontal ladder, then turns again to look over the edge of the platform to the enclosure floor.

17:2437 – Rosie lies on her left side at the edge of the platform (facing left wall), manipulates straw.

17:2508 – Rosie stands and leaves via the horizontal ladder (cameras do not show Rosie again until 19:4140, when the camera over platform A shows her on the enclosure floor, then ascending up the pods onto the horizontal ladder).

19:4338 – Rosie arrives on platform B via the horizontal ladder. She sits beside the ladder with her back to wall.

19:4426 – Rosie moves away from horizontal ladder further down the platform. Sits at the edge of platform, facing Pansy (no physical contact).

19:4540 – Still in this position, Rosie sits, manipulates straw, scratches.

19:4614 – Rosie moves back to sit beside the horizontal ladder, with back to wall.

19:4723 – From this position, begins nest building. Rosie uses the usual gather-arrange-tuck technique around her legs and torso then throws straw behind her head to create a ‘pillow’ of straw behind her. Some of this straw lands on Pansy.

19:5023 – Rosie finishes nest-building, remains sitting in the nest (total nest building time: 3 minutes).

19:5036 – Rosie lies on her left side, her head near horizontal ladder and facing the middle of the enclosure.

19:5141 – Rosie sits up and makes nest amendments (she gathers extra straw and arranges and tucks it into the nest).

19:5202 – Rosie lies on her right side (with her back to Pansy), facing the horizontal ladder.

20:0110 – Rosie sits up in her nest, back against the wall, and stretches.

20:0114 – Rosie lies on her left side, her head at edge of platform, her rear at the horizontal ladder (facing left wall).

20:1445 – Rosie lies on her right side, her head at edge of platform, her rear at the horizontal ladder (facing the middle of the enclosure).

20:2020 – Rosie yawns.

20:4328 – Rosie sits up, her back against the wall.

20:4439 – Rosie lies on her left side, her head at the horizontal ladder, facing the middle of the enclosure.

22:4330 – Rosie moves away from back wall further down platform. She lies on her right side (her rear at horizontal ladder, her head at edge of platform facing the middle of the enclosure). There is no nest building at this new location.

23:4916 – Rosie turns so supine, stretches, the lies on her right side as before.

23:5841 – Rosie returns to her nest beside the horizontal ladder; she sits with her back to wall and makes nest amendments.

23:5950 – Rosie finishes her nest amendments. She stands and moves further down the platform. She crouches so that her rear is over the edge of the platform; she appears to defecate then eat the faeces.

00:0222 – Rosie returns to sit in her nest, back against the wall.

00:0310 – Rosie lies on her left side, her head beside the horizontal ladder facing toward the middle of the enclosure.

01:2114 – Rosie moves away from back wall further down the platform but is still lying on her left side (though in a more foetal position), facing toward the middle of the enclosure.

02:5740 – Rosie turns onto her right side to face the back wall.

03:3435 – Rosie turns supine, stretches then lies on her right side again.

03:4829 – Rosie turns supine, stretches twice then turns onto her left side (head at the platform edge, facing toward the middle of the enclosure).

04:5749 – Rosie changes orientation slightly; she lies on her right side, head at the platform edge, facing the middle of the enclosure.

05:20$_{06}$ – Rosie lies on her left side, head at the platform edge, facing the middle of the enclosure.

05:40$_{15}$ – Rosie stretches then turns onto her right side (head at platform edge, facing the horizontal ladder).

08:00$_{46}$ – Rosie turns onto her left side, head still at platform edge, facing the middle of the enclosure).

08:33$_{38}$**, 08:34**$_{41}$**, 08:35**$_{35}$ – Rosie yawns (no other behavioural changes).

08:38$_{49}$ – Rosie leaves platform via the horizontal ladder.

08:39$_{12}$ – Blossom arrives via horizontal ladder. She stands behind Pansy and looks down to her back. Blossom then approaches Pansy's head, brushes straw from Pansy's body and head/neck and continues to look at her.

08:39$_{40}$ – Blossom turns away from Pansy then leaves via the vertical ladder. Sits on the floor under the platform and scratches.

08:41$_{29}$ – Main lighting is switched on.

08:42$_{02}$ – Chippy runs up vertical ladder in a charging display. He jumps at Pansy and pounds her with both fists 3 times. He then sits down at Pansy's back, removes straw from Pansy's back and looks at her.

08:42$_{10}$ – Blossom arrives via horizontal ladder. She sits at Pansy's head and removes straw from her head/face. Chippy, still sitting at Pansy's back, also appears to remove straw from Pansy's back.

08:42$_{59}$**-** Blossom turns and leaves via the horizontal ladder. Chippy moves to be level with Pansy's head, and looks down at her.

08:44$_{05}$ – Chippy leaves via the horizontal ladder.

08:4900 – Blossom and Chippy forage underneath platform B on enclosure floor, both move out of view after approximately 1 min.

08:5117 – Chippy runs up the vertical ladder and jumps at Pansy, pounding her twice with both fists He then stands at her back, leans forward and looks down at her.

08:5125 – Blossom arrives via the horizontal ladder, sits by Pansy’s head, but makes no physical contact with Pansy.

08:5132 – Chippy jumps off platform via ropes, still appearing agitated, hair erect.

08:5136 – Blossom turns away from Pansy, leaves via rope. No chimpanzees return to Pansy or platform B before they are moved into the adjoining day enclosure to allow keepers into the night enclosure at 08:52 (see appendix 4).

Appendix 4: Timeline for all events on sleeping platform A

16:37$_{02}$ – Chippy arrives on platform, (following display). Sits and manipulates straw for few seconds, then descends onto pods.

16:39$_{52}$ – Rosie arrives on platform A via horizontal ladder. Stands at edge of the platform, reaches down to pods and collects straw.

16:40$_{24}$ – Rosie has collected approximately 2 armfuls of straw. Lies prone on platform A and manipulates straw.

16:41$_{22}$ – Rosie turns so lying at the edge of the platform, looking onto the floor.

16:41$_{54}$ – Rosie sits and manipulates straw at edge of platform A.

16:43$_{23}$ – Rosie leaves platform A with handful of straw. Goes to platform B via horizontal ladder.

16:52$_{33}$ – Blossom and Chippy arrive simultaneously on platform A from floor. En route, Blossom collects large armful of straw from pods.

16:52$_{46}$ – Blossom sits and manipulates straw, sitting with back to right wall. Chippy sits and manipulates straw at the edge of the platform.

16:53$_{02}$- Chippy gathers handful of straw from platform and leaves via horizontal ladder.

16:53$_{47}$ – Blossom begins nest building (usual technique of gathering straw toward legs and torso, then arranging and tucking straw round legs and torso).

16: 55$_{22}$ – Blossom stops nest building, sits and manipulates straw.

16:55$_{47}$ – Blossom resumes nest building (technique as above).

16:5629 – Blossom stops nest building and lies left side and manipulate straw (head orientated toward centre of enclosure).

17:1107 – Chippy arrives on platform with armful straw. As he sits, Blossom reaches out and touches his arm, pulls it toward her.

17:1111 – Chippy sits and manipulates straw at back of platform, next to horizontal ladder.

17:1241 - Chippy leaves platform via pods.

17:1655 – Rosie arrives on platform via pods. As she arrives, Blossom reaches out and touches Rosie's face. Rosie stands over Blossom, but has no physical contact with her.

17:1749 – Rosie gathers handful of straw and leaves via horizontal ladder.

17:1806 – Chippy arrives on platform, with straw gathered from floor. Sits at the back wall of the platform next to horizontal ladder and manipulates straw.

17:2742 – Blossom turns onto right side in nest, pushing herself back slightly so nearer the middle of the platform and Chippy.

17:3400 – Chippy stands, looks over edge of platform onto floor.

17:3508 – Chippy sits down (still near the back wall of the platform next to horizontal ladder) and begin nest building (usual technique of gathering straw toward legs and torso, then arranging and tucking straw round legs and torso).

17:3601- Chippy lies left side in nest (orientated toward horizontal ladder).

17:3622 – Chippy sits and resumes nest building.

17:3702 – Chippy stop nest building, shifts slightly in nest and lies left side (orientated toward back wall).

17: 4142 – Chippy lies supine.

17:4729 – Chippy lies left side.

17:5027 – Blossom lies left side, orientated toward enclosure.

17:5448 – Blossom shifts in nest (closer to Chippy), lies prone and grooms Chippy.

17:5640 – Blossom throws right arm over Chippy’s lower torso (as if embracing), moves closer to him and continues grooming with left hand.

17:5858 – Blossom stops grooming, shifts over toward right wall and lies on left side (orientated toward enclosure).

18:0539 – Chippy sticks out right foot, Blossom grooms it.

18:0930 – Chippy withdraws foot, Blossom ceases grooming.

18:1317 – Blossom sits to make nest amendment (gathers some extra straw, incorporates it into existing nest, and arranges it around legs).

18:1349 – Blossom stops nest amendment, lies prone, and resumes grooming Chippy.

18:1652 – Chippy sits and moves away from Blossom, nearer back of platform next to horizontal ladder. Blossom continues to lie prone in the middle area of the platform.

18:1724 – Blossom lies left side (orientated toward enclosure). Chippy lies on left side against back wall.

18:1849 – Blossom lies prone, manipulates straw.

18:2048 – Blossom lies right side (orientated toward wall).

18:5750 - Blossom stretches, then lies left side (orientated toward enclosure).

19:1120 – Blossom shifts in nest so nearer wall (still on left side).

19:1746 – Blossom yawns (no other changes).

19:1933 – Chippy changes orientation. Moves in nest so head is at edge of platform, rear at horizontal ladder. Lies on right side (head orientated toward Blossom).

19:1948 - Blossom shifts in nest so nearer to Chippy. Reaches out with right arm, rests it on Chippy.

19:2235 – Blossom removes hand from Chippy, lies prone and manipulates straw.

19:2606 – Blossom lies on right side (orientated toward wall).

19:4140 – Blossom lies prone (still facing into enclosure), Chippy moves to back wall of platform and lies on right side.

19:4540 – Chippy stands and looks over edge of platform.

19:4734 – Blossom shifts closer to wall and lies left side (orientated toward enclosure).

19:4750 – Chippy lies left side at the edge of the platform where he had been standing, then yawns.

19:5307 –Blossom lies prone, shifts closer to Chippy, and grooms him.

19:5420 – Blossom stops grooming and sits. Chippy lies supine and stretches. Blossom resumes grooming him.

19:59$_{50}$ – Chippy shifts slightly, Blossom stops grooming. Once he is still, Blossom resumes grooming.

20:04$_{50}$ – Chippy shifts again, Blossom moves away, lies prone and manipulates straw. Chippy turns onto right side at the edge of the platform (orientated toward Blossom).

20:07$_{30}$ – Blossom moves further away toward the middle of the platform and lies on left side (orientated toward enclosure).

20:53$_{12}$ –Blossom stretches (no other changes).

20:59$_{02}$ – Blossom stretches arm, then shifts in nest closer to wall (still on left side).

21:30$_{01}$ – Blossom turns so supine, and stretches legs.

21:32$_{20}$ – Blossom lies left side (orientated toward enclosure).

21:33$_{28}$ – Blossom lies supine

21:36$_{33}$ - Chippy lies supine.

21:36$_{36}$ – Blossom lies left side (orientated toward enclosure).

21:37$_{50}$ – Blossom lies supine, stretches, then lies left side.

21:45$_{18}$ – Chippy lies right side (orientated toward Blossom).

21:48$_{50}$ – Blossom reaches over and touches Chippy with right hand.

21:51$_{50}$ – Blossom stands in nest, changes orientation, and lies prone (now facing back wall).

22:0511 – Blossom changes orientation again, lies on right side (orientated toward wall).

22:3408 – Blossom lies left side (orientated toward enclosure).

23:1330 – Chippy lies supine, stretches, scratches, then lies left side (orientated toward enclosure).

23:1950 –Blossom stretches then lies right side (orientated toward wall).

23:5055 – Chippy stretches (no other change).

00:1308 – Blossom lies left side (orientated toward enclosure).

00:3147 – Chippy stretches (no other change).

00:3455 – Chippy changes orientation, lies left side so facing back wall.

01:0000 –Blossom lies supine.

01:2533 – Blossom lies right side (orientated toward wall).

01:3301 – Chippy scratches (no other change).

01:3351 – Blossom turns onto left side, then immediately lies supine.

01:3820 – Blossom lies right side (orientated toward wall).

01:4824 – Chippy stands and looks over edge platform.

01:4940 – Chippy lies back in nest, supine.

01:5520 – Chippy lies on right side (orientated toward back wall).

02:3841 – Blossom lies supine, scratches, stretches, scratches again. Remains supine.

02:3924 – Chippy sits, scratches, and then makes nest amendment (arranges extra straw round legs).

02:4000 – Chippy stops nest amendment and lies left side (orientated toward enclosure).

02:4008 – Blossom lies left side (orientated toward enclosure).

03:1143 – Blossom lies supine.

03:1720 –Blossom stretches the lies right side (orientated toward wall).

04:2400 – Blossom yawns (no other change).

04:2420 – Chippy lies right side (orientated toward back wall).

04:2540 – Blossom lies supine, yawns, scratches (remains supine).

04:3035 – Blossom lies left side (orientated toward enclosure).

04:4110 – Chippy lies left side (orientated toward enclosure).

04:5652 – Blossom lies supine, stretches, then lies left side.

04:5808 – Blossom lies right side (orientated toward wall).

06:1508 –Blossom lies supine, stretches, scratches, them lies right side (orientated toward wall).

06:1644 – Blossom lies left side (orientated toward enclosure).

06:3200 –Chippy, sits, scratches, then lies left side (orientated toward enclosure).

06:5246 – Blossom lies right side (orientated toward wall).

06:5805 – Blossom lies supine, them lies left side (orientated toward enclosure).

07:0038 – Blossom grooms Chippy (no change in rest posture).

07:0501 – Blossom ceases grooming Chippy, moves closer to wall and makes another nest amendment.

07:0859 – Blossom stops amendment and lies left side (orientated toward enclosure).

07:1957 – Chippy lies on left side with head at edge platform, orientated toward back wall.

07:3150 – Blososm lies right side (orientated toward wall).

08:0102 – Chippy lies prone, appears to look over edge of platform onto the floor.

08:0350 – Chippy shifts away from edge of platform, and lies right side (orientated toward back wall).

08:1142 – Chippy lies supine, stretches, and lies right side.

08:2020 - Chippy lies supine, stretches, and lies right side.

08:2120 – Blossom lies supine, scratches, then lies right side (orientated toward wall).

08:2540 – Blossom lies left side (orientated toward enclosure).

08:2800 – Chippy yawns, scratches, and yawns again.

08:2850 –Chippy scratches.

08:2946 – Chippy lies supine.

08:3550 – Chippy lies prone and manipulates straw.

08:3845 – Chippy leaves platform A and begins to descend down pods. Blossom stands immediately after him but moves towards horizontal ladder. Chippy stops descent and follows Blossom to horizontal ladder. Chippy stops at the ladder, turns, crosses platform A and descends down pods onto enclosure floor.

08.3909 – Rosie arrives onto platform A that has been vacated by Blossom and Chippy. Lies on Blossom's nest on her right side facing the enclosure wall, but turns head back toward platform B.

08.4046 – Rosie sits up in nest, then stands – but does not move off of platform A. She then sits back down in the nest.

08.4123 – Blossom arrives back on platform A. Sits at the edge of the platform next to the horizontal ladder.

08.4129 – Enclosure lights are switched on.

08.4157 – Blossom walks over to Rosie (who is still sitting on Blossom's nest). Stands directly over Rosie, but no physical contact is made.

08.4202 – Blossom and Rosie simultaneously vacate platform A, descending down the vertical pods. Blossom stops at the bottom of the pods, then re-ascends them, moves back onto platform A, and crosses onto platform B via the horizontal ladder (data from the camera over platform B shows that this is when Chippy is displaying and 'thumping' Pansy's body – see appendix 4).

08.4225 – Rosie returns onto platform A (while Chippy was displaying, she had remained sitting on one of the vertical sleeping pods). Lies on her left side in Blossom's nest (facing middle of enclosure)

08.4306 – Blossom returns onto platform A via horizontal ladder. Sits at Rosie's right leg and grooms it. Rosie is lying still.

08.4314 – Rosie moves her right leg. Blossom ceases grooming, but remains sitting at Rosie’s feet.

.08.4426 – Chippy arrives on platform A, descends immediately down vertical pods and has no contact with the females.

08.4426 – Blossom leaves platform A, descends onto floor via vertical pods. Rosie continues to lie on her left side in Blossom’s nest.

08.4430 – Blossom and Chippy stand at the door that leads to the keeper kitchen area. Rosie as previous.

08.5004 – Blossom returns onto platform A. Sits next to Rosie (who is still in nest), but no contact is made.

08.5024 – Rosie (still in nest) shifts forwards into a prone position and looks over the edge of the platform. Blossom also turns and looks over the platform edge.

08.5045 – Rosie leaves platform A, descends vertical pods and stands at the door that leads to the keeper kitchen area.

08.5103 – Blossom also leaves platform A. Stands on vertical pods then swings onto horizontal ladder.

08.5136 – Chippy runs across floor from direction of platform B. Bangs on door, apparently in display. Blossom leaves horizontal ladder, also stands at kitchen door.

08.5204 – Blossom, Chippy and Rosie are moved into the day enclosure.

08.53 – Staff enter the night enclosure.

08.5604 – Filming is ceased.

Appendix 5: *Pan* thanatology

Correspondence

Pan thanatology

James R. Anderson[1], Alasdair Gillies[2] and Louise C. Lock[1]

Chimpanzees' immediate responses to the death of a group-member have rarely been described. Exceptions include maternal care towards dead infants, and frenzied excitement and alarm following the sudden, traumatic deaths of older individuals [1–5]. Some wild chimpanzees die in their night nest [6], but the immediate effect this has on others is totally unknown. Here, with supporting video material, we describe the peaceful demise of an elderly female in the midst of her group. Group responses include pre-death care of the female, close inspection and testing for signs of life at the moment of death, male aggression towards the corpse, all-night attendance by the deceased's adult daughter, cleaning the corpse, and later avoidance of the place where death occurred. Without death-related symbols or rituals, chimpanzees show several behaviours that recall human responses to the death of a close relative.

Observations were made on a female chimpanzee, Pansy (estimated age 50+ years) and three other adults: Blossom (female estimated age 50 years), Rosie (Pansy's daughter, 20 years), and Chippie (Blossom's son, 20 years). The group lives on an island in a safari park, but in winter they are moved to heated indoor quarters (see Supplemental Data available on-line with this issue). In November 2008 Pansy became increasingly lethargic. When the group was moved indoors, she immediately lay down on the floor after eating. The others groomed her, and nested near her in the day area instead of on their usual night area platforms. For several days, Pansy received veterinary care alone in the night area, the others being allowed to join her each evening. During this time she rarely left her nest, which had been made by Blossom.

On December 7th, at approximately 15.00h Pansy got up and laboriously moved across to the other platform, where she lay down in Rosie's nest from the previous night. Toward 16.00h she started showing erratic and laboured breathing. Anticipating imminent death, the head keeper (AG) decided to allow the others to join her and to leave the group undisturbed.

Two overhead video cameras recorded the scene until the following morning. Box 1 presents extracts from the video timeline of events around the presumed time of Pansy's death (16:24; see Supplemental Movie S1, and Supplemental Data for the full timeline). In the 10 minutes preceding death the others groomed or caressed Pansy 11 times, which appeared more frequent than following previous daytime separations (no quantitative data available.) Most notably, none of them groomed her after death; however, Rosie remained near her mother's body almost continuously throughout the night, on a part of the platform where she had never slept during a 29-night study of night-time behaviour 1 year earlier. In that study, Rosie's latest nesting time was 18:15h, but when Pansy died Rosie delayed nesting until 19.47h. Once settled in their nests, each chimpanzee usually made four or five postural changes during the night (range 0–14), but on the night Pansy died Rosie, Chippy and Blossom changed posture 11, 15 and 42 times, respectively. Also that night, Blossom groomed Chippy for 18 minutes, similar to during the entire previous 29-night study. Finally, in that study the male displayed only three times in 29 nights, without targeting anyone, but on the night Pansy died he performed three displays, each ending with an attack on the corpse (see Supplemental Movie S2).

The next day the three surviving chimpanzees were profoundly subdued. From the day area they watched silently as two keepers lowered Pansy from the platform, carried her into the exit corridor, placed her in a body bag, and loaded her into a vehicle that was then driven away. They remained subdued the following day as the night area was cleaned and disinfected, and new straw provided. When the connecting doors were opened Blossom and Rosie entered hesitantly, but Chippy refused; instead he showed fear grins and made loud alarm calls, causing the two females to quickly return to him. The doors were left open, but the chimpanzees slept in the day area, and Chippy again refused to enter the night area the following day. For five consecutive nights no chimpanzee nested on the platform where Pansy died, yet this platform had been used for nesting on every evening of the 29-night study. Rosie was the first to resume nesting there. This account differs from two reports of traumatic deaths in wild

Box 1.

Extracts from video timeline of events occurring on platform B, focussing on the presumed moment of death, and an attack on the corpse by the adult male.

- 16:2311 – Rosie moves to Pansy's back, strokes or grooms Pansy's torso. Blossom continues grooming Pansy's arm.
- 16:2404 – Chippy arrives. Rosie is still standing at Pansy's back.
- 16:2408 – Blossom remains oriented away from Pansy. Rosie still stands behind Pansy's back. Chippy stands over Pansy's head, and pulls at her left shoulder and arm.
- 16:2421 – Chippy crouches over Pansy's head then appears to try to open her mouth. Rosie moves toward Pansy's head.
- 16:2425 –Blossom, Chippy and Rosie simultaneously turn toward Pansy's head. Chippy and Rosie are crouched over Pansy's head. Chippy pulls Blossom's face down towards Pansy's.
- 16:2436 – Rosie moves from Pansy's head toward her torso. Blossom moves away from Pansy. Chippy lifts and shakes Pansy's left shoulder and arm.
- 16:2503 – Chippy continues to manipulate Pansy's shoulder/arm. Blossom stands next to Chippy, and also manipulates her left arm. Rosie stands at Pansy's lower torso, not in contact with Pansy.
- 16:2506 – Blossom sits at Pansy's head, stroking Pansy's left hand. Chippy and Rosie leave simultaneously.
- 16:2516 – Blossom stops grooming Pansy's hand but continues to sit next to her.
- 16:2531 – Blossom moves away from Pansy.
- 16:2704 – Pansy moves very slightly: 2 head nods, probably a post-mortem twitch. This elicits no response from the others.
- 16:3609 – Main lighting is switched off.
- 16:3656 – Chippy jumps onto the platform in a charging display. He jumps into the air, brings both hands down and pounds Pansy's torso, then runs across and off the platform.

chimpanzees. At Gombe, when an adult male died after falling from a tree, other chimpanzees present erupted into aggressive displays and alarm calling, with much mutual embracing and touching [5]. They frequently stared at the corpse and some appeared to sniff it, but nobody touched it in the four hours before they left. In the Taï Forest, a fatal leopard attack on an adolescent female also elicited intense mass excitement, but in this case contacts with the corpse were frequent; some displaying males even dragged it over short distances [4]. The corpse was eventually abandoned after 6 hours. In contrast, Pansy's group-members remained generally calm following her death. Several aspects of their behaviour recall those of mothers with dying infants [3], and are strikingly reminiscent of human responses to peaceful death. Below, we summarize key chimpanzee behaviours and indicate in parentheses possible human counterparts.

During Pansy's final days the others were quiet and attentive to her, and they altered their nesting arrangements (respect, care, anticipatory grief). When Pansy died they appeared to test for signs of life by closely inspecting her mouth and manipulating her limbs (test for pulse or breath). Shortly afterwards, the adult male attacked the dead female, possibly attempting to rouse her [7] (attempted rescucitation); attacks may also have expressed anger or frustration (denial, feelings of anger towards the deceased). The adult daughter remained near the mother's corpse throughout the night (night-time vigil), while Blossom groomed Chippy for an extraordinary amount of time (consolation, social support). All three chimpanzees changed posture frequently during the night (disturbed sleep). They removed straw from Pansy's body the next morning (cleaning the body). For weeks post-death, the survivors remained lethargic and quiet, and they ate less than normal (grief, mourning). They avoided sleeping on the deathbed platform for several days (leaving objects or places associated with the deceased untouched).

These behaviours highlight the interest of a comparative evolutionary perspective on death and dying in species without symbolic representations of death or death- related rituals. Chimpanzees show self-awareness [8] empathy [9] and cultural variations in many behaviors [10]. Are humans uniquely aware of mortality? We propose that chimpanzees' awareness of death has been underestimated, as anticipated some 30 years ago on the basis of self-awareness [8]. Although data are likely to accumulate slowly, a thanatology of *Pan* appears both viable and valuable. Finally, such data may have implications for the end- of-life management of captive elderly chimpanzees, an issue of increasing importance as more great apes are retired from research facilities and zoo populations age. In some cases it might be more humane to allow elderly apes to die naturally in their familiar social setting than to attempt to separate them for treatment or euthanasia.

Supplemental Data

Supplemental data are available at http:// www.cell.com/current-biology/supplemental/ S0960-9822(09)xxxxx-x

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References

1. Van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. *1*, 161–311.
2. Goodall, H. (1986). The Chimpanzees of Gombe: Patterns of Behavior, (Cambridge, MA: Belknap Press).
3. Matsuzawa, T. (1997). The death of an infant chimpanzee at Bossou, Guinea. Pan. Afr. News 4 (1), http://mahale.web.infoseek.co.jp/PAN/4_1/4(1)-03.html.
4. Boesch, C., and Boesch-Achermann, H. (2000). The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution, (Oxford: Oxford University Press).
5. Teleki, G. (1973). Group response to the accidental death of a chimpanzee in Gombe National Park, Tanzania. Folia Primatol. *20*, 81–94.
6. Yamagiwa, J. (1998). An ossified chimpanzee found in a tree nest. Pan. Afr. News 5 (2), http://mahale.web.infoseek.co.jp/PAN/5_2/5(2)-03.html.
7. Brown, A. E. (1879). Grief in the chimpanzee. Am. Nat. N.Y. 13, 173–175.
8. Gallup, G. G., Jr. (1979). Self-awareness in primates. Am. Sci. 67, 417–421.
9. De Waal, F. (1996). Good Natured: The Origins of Right and Wrong in Humans and Other Animals, (Cambridge, MA: Harvard University Press).
10. Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E., Wrangham, R.W., and Boesch, C.. (1999). Cultures in chimpanzees. Nature 399, 682–685.

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