Sheltering Chimpanzees

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Introduction

If asked to describe the barest essentials for an individual's survival, it seems likely that most human beings would list water, food and shelter. The first two are straight-forward and apply to all organisms, even plants, but the third varies markedly from simple to complex and has a multitude of functions beyond buffering the weather. Shelter's importance is universally acknowledged, even in song: The Rolling Stones sought it ('Gimme Shelter' 1969), Bob Dylan was offered it ('Shelter from the Storm' 1975), and Bob Marley specified it as 'a roof right over our heads' ('Is This Love' 1984). Most poignantly, Lyle Lovett reprised the cultural history of Texas from the shade of a traditional wrap-around porch ('This Old Porch' 1983) (Figs. 1, 2).

Aims

What follows here is a synthesis of research on the making and use of beds/nests/sleeping platforms (with those terms used interchangeably, as synonyms) and other shelters by wild *Pan troglodytes*. It focusses on the last 15 years, which have seen a burgeoning number of empirical studies with new methods and clarifying findings, some completely unexpected. We have learned more about chimpanzee shelter in these 15 years than from the preceding 75 years, post-Nissen (1931)

Regrettably, what is NOT included in this editorial are studies of sleep or other nocturnal behavior (Fruth et al.

2018; Zamma 2014), the other three great ape species (Fruth and Hohmann 1993; Tutin et al. 1995; Russon et al. 2007; Anderson et al. 2019), chimpanzees in captivity (Videan 2006), and nests as used in censuses or surveys (Plumptre and Reynolds 1997). All of these cognate topics are relevant and important, but to treat them properly would require a monograph.

Biodiversity

Paradoxically for a primatologist, the most wide-spread makers and users of shelters are invertebrates, from caddisfly cocoons to termite mounds. Aunger (2010) dated the earliest animal 'dwellings' to 530 mya as made by primitive invertebrates (Protostomes), which were simple burrows in the ocean floor. Amongst the vertebrates, birds are the acknowledged masters of a wide variety of shelters, principally for housing their eggs and nestlings. Weaver birds (Ploceidae) are the paramount avian shelter-makers. Few mammalian orders construct shelters, and the acknowledged preeminent maker and user is a large rodent, the beaver, with its lodges and dams that can alter the landscape, changing forest to wetland. Compared with them, nonhuman primate shelters are scarce, except for prosimians (Kappeler 1998) and great apes; monkeys may use caves or be highly selective in their choice of overnight roosting sites (Anderson 1984; Anderson and McGrew 1984), but they do not construct them (Fig. 3).

Background

Beds were notable from the earliest field studies of chimpanzees: Nissen (1931) in Guinea described them in details that are useful even 90 years later. When modern field research on chimpanzees emerged in the 1960s, Goodall (1962) devoted her first publication to descriptions of nests and nest-making behavior at Gombe, as did Izawa and Itani (1966) at Kasakati, in Tanzania. The first person to link

'A structure giving protection from rain, wind, or sun: anything serving as a shield or place of refuge from the weather... such as underground, line of trees, wall.' New Shorter Oxford English Dictionary (1993, p. 2822).

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Fig. 1 Alpha male HM lies on his side in scrappy day nest at Gombe (photo by WC McGrew)

Fig. 2 Male JJ lies supine in ample night bed at Bossou (photo by K Koops)

chimpanzee sleeping platforms to the evolutionary origins of human shelter was archaeologist turned primatologist, Jeanne Sept (1992). The role of nests later shifted to their utility in systematic censusing of chimpanzee populations, as pioneered by Kuroda and Tutin (1993) and Plumptre and Reynolds (1997). Early in the twenty-first century, a ‘golden age’ of research on chimpanzee shelters began with four PhDs addressing the topic, Adriana Hernandez-Aguilar (2006), Kathelijne Koops (2011), Fiona Stewart (2011), and David Samson (2013), each of which has led to multiple publications (Fig. 4).

Ecology

Chimpanzee shelters are entities within contexts: They are not randomly spread over the landscape or the seasons; thus ecological study is a necessary foundation for their understanding. Furthermore, as beds are clumped in space and time, individual nest characteristics as well as the sites containing them need investigation, especially given the re-use of both. Adriana Hernandez-Aguilar is the acknowledged expert in this area of chimpanzee research, in work

Fig. 3 Fongoli research team takes data from a bed, with Susana Fulton-Johnson above collecting shed hairs and Mboule Camara and Donde Kante below collecting deposited feces. (photo by WC McGrew)

done at Issa, Tanzania. From a sample of 5354 nests, she analyzed nest and site re-use at 20 sites with 10 matched controls. Nests were highly clumped, all arboreal, and concentrated on slopes, usually hillsides. The apes focussed on woodland (not forest) but not on water sources, even in the late dry season (Hernandez-Aguilar 2009).

Issa chimpanzee nests reflected environmental constraints and affordances. The apes preferred tall trees

and high first branches, which seems to be indicative of anti-predator tactics, as found elsewhere. Nests were non-randomly oriented in direction, reflecting the site's topography: Those built on west-facing slopes also faced west, suggested that long-range viewing of the surroundings was advantageous, especially in a landscape where altitude varied from 900–1800 m (Hernandez-Aguilar et al. 2013). Trees were used non-randomly for sleeping

Fig. 4 Shelter researchers in action: **(a)** Adriana Hernandez-Aguilar swabs a bed for microbes at Issa (photo by Fiona Stewart); **(b)** Kathelijne Koops ascends tree to retrieve insect trap (upper left corner) at Nimba. (photo courtesy of K Koops); **(c)** Fiona Stewart, who slept

overnight in nests, tests the comfort of a nest at Issa. (photo by AK Piel); **(d)** David Samson collects morphological data from a high sleeping platform at Toro-Semliki. (photo by WC McGrew)

platform construction, but raw frequency is not enough. At Semliki, *Cynometra alexandri* is an extreme example, comprising < 10% of trees available for nesting but selected for 74% of nests (Samson and Hunt 2014). Actual versus potential nesting *trees* from all trees in actual versus potential nesting *sites* are necessary to conclude preference (Hernandez-Aguilar 2020). She showed at Issa that site selection was stronger than individual tree selection.

Logistics

Until 15 years ago, studies of chimpanzee bedding were done from the ground looking up through binoculars, which limited the data collected. Close inspection of arboreal nests in situ was rare, but recent research has remedied that.

Koops et al. (2012a) placed meteorological data-loggers at three different altitudes (670 m, 920 m, 1170 m) and

light traps at three tree heights (1.5 m, 5 m, 10 m) for comparison of weather and mosquito impacts on nesting. Nimba chimpanzees preferred to nest above 1000 m but variation in mosquito density had little effect. Samson et al (2013, 2019) also set arthropod traps to test the insect vector hypothesis in various ways, such as forest versus woodland. They used experimental nests to test if Semliki's chimpanzees preferred tree species for nesting that repelled flying insects more than did controls; they did. The follow-up study of insect vectors tested the 'encounter-dilution hypothesis', that nests in groups decreased vulnerability to insects, especially mosquitoes, compared with a nest alone; it did, showing an advantage to social sleeping.

Stewart (2011) went a crucial step further, to participant observation. Overnight, she slept in the canopy or on the ground, either in chimpanzee or self-made nests, or on the bare ground, sometimes in the company of chimpanzees. She did so to self-test three hypotheses to do with sleep quality, exposure to pathogens via insect vectors, and thermoregulation. The measurements were sleep interruptions and their causes, number of insect bites, and body temperature from data-loggers attached to ventrum (exposed) versus dorsum (insulated) while lying supine. Sleep quality was better, insect bites were fewer, and body temperature was less chilled when sleeping arboreally.

Structure

Trees show evolved structural variation, while sleeping platforms show intentional architectural variation. Both are important. Samson (2012) climbed to access 65 nests and described their morphology in 15 variables, which manifested differently across tree species. Structurally, the best fit between nest and tree fit a weight-bearing explanation, with nests providing secure stability for sleeping, which is unnecessary for lighter-bodied monkeys, who can perch on a bough. Samson and Hunt (2014) tested tree structure variation using 23 models across the seven most commonly nested-in species at Semliki, versus one control species. Most nests were made in *Cynometra*, which showed relevant physical properties, such as tripod branching, small leaves, strong and stiff branches, etc.

Zamma and Ihobe (2015) published detailed data on sourcing of vegetation used for bed construction, such as number of twigs per branch, number of leaves per branch, leaf area, strength of leaf attachment, etc., at Mahale. Total area of leaves per unit length of branch was the key to selection of tree species for bed-making, allowing the chimpanzees to make leafier (denser?) mattresses.

Function

The preferred, almost default, explanation for why great apes build nests is to reduce vulnerability to predators (Pruetz et al. 2008; Koops et al. 2012a; Stewart and Pruetz 2013). A host of variables, such as nest height, height of lowest branch, distal location in canopy, etc. are widely considered to be indicators of an anti-predator adaptation. Predation's effect is so compelling in principle that it rarely has been tested in practice: An obvious hypothesis is that the stronger the predator pressure, the greater the expression of buffering variables. Predator pressure can be variously measured, such as presence and abundance of threatening predator species; frequency of encounters or interaction with predators (McGrew et al. 2014); strength of other anti-predator responses, such as alarm calls. Bottom-line, the most telling test is actual predation rate, but that requires long-term data to have a large enough sample of such rare events.

Unfortunately, several other potential reasons exist for nesting higher in the canopy: Fewer sanguinivorous arthropods, especially disease vectors; cooler temperatures, especially evaporative breezes; lower, more comfortable humidity; greater scanning visibility, etc. These aspects too require empirical testing: Koops et al. (2012a) found that humidity but not temperature related to nest height. Such testing requires arboreal access to observers or instruments to record the variables. Modern technology supplies some of the means to expand data collection, especially drones, which have the potential to examine bed-making and -using in action, especially if equipped with low-light, night-vision capacity. Camera traps are of less use, as chimpanzee nesting (unlike much foraging) is nomadic, but some nest sites and locations within trees may be reused often enough for patient, long-term data collection (Stewart et al. 2011).

Many other hypotheses have been proposed for why great apes construct sleeping platforms: thermoregulation, infection/disease by parasites or via vectors, safe elevated sleeping, avoiding terrestrial hazards from army ants to humans, and most challenging of all, cognitive benefits from a good night's sleep. Such factors of mental well-being take various forms, from comfortable posture to memory consolidation to REM sleep to dreaming, all of which may result from a comfortable sleeping substrate (Fruth and Hohmann 1996; Stewart et al. 2007; Coolidge and Wynn 2009; Samson and Nunn 2015).

Each of these factors may be broken down into component variables, that is, breezes can cause wind-chill (bad) or evaporative cooling (good). Some effects (e.g., altitude) are less directly acting than others (e.g., venomous snakes). Others may affect one sex more than the other

(Stewart and Pruetz 2020). Happily, some basic cost–benefit, trade-off complications are not applicable, as beds are universally quick and easy to make, and raw material sourcing is no problem, although it may vary with season (Fig. 5).

Tree or ground

Sleeping platforms vary in vertical range and circadian cycle, that is arboreal versus terrestrial, and diurnal versus nocturnal, and also use, such as short naps versus longer overnight sleeps. Both types have costs and benefits: an ape in a tree nest will not be preyed upon by earth-bound predators (lion, hyena) but may fall to injury or death. An ape in a ground nest is vulnerable to all terrestrial predators but is safe from falling. For other variables, such as in thermoregulation or not, the costs and benefits may be off-setting: bare ground requires little time or effort to construct, but constructed bedding provides insulation. Selection pressures also vary, for example, regarding predation: the stronger the predator pressure, the lower should be the proportion of ground nests made, but overnight and daytime ground nests may differ, tracking predators' activity periods. Beds on the ground are absent in some populations, such as Issa, which has large carnivores, versus common in others, such as Nimba, where it is male-biased (Koops et al. 2007, 2012b).

Ground nesting is not without other costs as well, such as exposure to soil-living gastrointestinal parasites, for example

helminths: Zommers et al. (2012) showed that chimpanzees that spent more time on the ground had more infections and higher-intensity infections. On the other hand, ground nesting provides postural stability and, at least in the dry season, less thermoregulatory stress, plus surprisingly, fewer insects (Samson and Hunt 2012; Samson et al. 2019). However, no study has yet compared ground bedding versus no bedding, that is, sleeping on the bare ground, which occurs in some populations, such as Fongoli.

All of these studies have implications for reconstructing the key transition made by our hominoid ancestors from arboreal to terrestrial sleeping (Sept 1992; Koops et al. 2007; Coolidge and Wynn 2009; Koops et al. 2012a, b).

Human evolution

Evidence for the evolution of human shelter is sketchy and controversial, but the oldest structure may be Mary Leakey's (1931) site DK at Olduvai Gorge, dated at 1.86 mya. It comprises a ring of stones encircling a shallow depression on the landscape. This archaeological find could be all that remains of a windbreak, shade cover, or protective barrier (of thorns?) against predators. Hayden (2008, pp. 125–132) summarised the conflicting debates about the interpretations of these 'artefacts'.

Later, about 175 kya, Neanderthals made annular constructions of stone deep within the shelter of a cave in southwest France (Jaubert et al. 2016). Later, in the Middle Stone Age (ca 77 kya), early *Homo sapiens* bedded down on

Fig. 5 Ground nest at Nimba (photo by K Koops)

aromatic leaves in the Sibudu rock shelter in South Africa (Wadley et al. 2011). Later still, Neanderthals in the Middle Palaeolithic at 50–41 kya in France twisted plant fibers to make cord suitable for mats in the Abri du Maras rock shelter (Hardy et al. 2020). If clothing is considered to be wearable shelter, then both Neanderthals and early modern humans made such portable, personal shelters from selected animal skins between 60 and 24 kya in Europe (Collard et al. 2016). Combinatorial bedding (mattress?) from plants and clay were recovered from a Stone Age Israeli hut of 19 k year age (Nadel et al. 2004).

Chimpanzees provide the foundation for this whole cumulative cultural sequence, which began with the transition of early hominins from arboreal to terrestrial sleeping (Samson and Nunn 2015; Coolidge and Wynn 2009). Apes remain relevant today, epitomized in the Human Evolution Bed, the design of which is based on the chimpanzee nest and is commercially available in Japan (Human Evolution Bed Project Team 2016)!

Variation

Making and using arboreal sleeping platforms is universal in *Pan troglodytes*, throughout the species' wide range from Tanzania to Senegal. Despite nests being recorded at more than 120 chimpanzee field sites (McGrew 2017), both intra- and inter-population comparisons are few. Perhaps it is assumed that all their elevated beds are the same, suggesting that chimpanzee nest behavior is genetically determined. Apes are not deer mice (*Peromyscus* spp.), in which *P. polionotus* and *P. maniculatus* build different types of burrow systems, even after 20 generations of living in cages with no substrate, and when cross-bred, the hybrids build burrows with intermediate characteristics (Weber and Hoekstra 2009). Assumptions are of little use in science!

Baldwin et al.'s (1981) comparison of savanna nests at Mt. Assirik in Senegal with forest nests in Equatorial Guinea was the only *inter-population*, comparative study of beds for more than 30 years (Fig. 6).

Stewart and Pruetz (2013) compared chimpanzee sleeping platforms at two similar savanna sites, Fongoli and Issa, seeking to relate them to predator pressure. Fongoli is essentially predator-free, while Issa has the full complement of large carnivores. The more threatened Issa chimpanzees bunched together, with more individuals nesting in one tree, and they made beds higher and more peripheral in the canopy. Stewart et al. (2018) also compared nest architecture and weather conditions at Fongoli and Issa, using both observational and experimental methods. For the former, fresh chimpanzee nests were measured *in situ*; for the latter, temperature data-loggers were placed in experimental nests with controls nearby to test insulation, while other

data-loggers measured humidity and wind speed. Nests proved to be good insulators, as chimpanzees made thicker lining and mattresses when it was colder and sturdier and deeper nest cups when it was windier.

Intra-population comparisons, especially of neighbouring groups, are common for tool-use in extractive foraging, but few have been done for chimpanzee nests. Whiten et al. (1999, Table 1) compared K-group with M-group at Mahale and found five differences in behaviour between them, but none dealt with beds. Zamma and Makelele (2010) compared the beds of two neighbouring groups, at Myako and Kasoje, at Mahale and found differences in longevity (rate of decay). More than 20 years later, the absence of such comparisons of nests at sites with two or more habituated groups, such as Budongo, Gombe, Tai, etc. is notable. Perhaps there is another unspoken assumption that something that is species-typical and universal does not vary within populations of a species?

Culture

Given that bed-making is a complex behavioural package that is dependent on social learning and not spontaneously learned individually (Videan 2006), it could be cultural. However, the making of 'magic circles', in which a captive-born and -reared chimpanzee sitting on the substrate places objects around its perimeter, suggests that some innate proclivity exists. No data on this behaviour pattern seem to have been published. Given that few wild-born chimpanzees are left in laboratories or zoos, and that no cases of spontaneously invented nest making have been reported, controlled research opportunities in captivity seem unlikely. Perhaps the solution lies in studies in refuges and sanctuaries in habitat countries, such as Chimfunshi in Zambia? (Fig. 7).

Shelter use or construction in nature fare little better in terms of published findings. Few chimpanzees use caves, perhaps because few in central or eastern Africa have the opportunity. Data from Fongoli, in Senegal, suggest that the apes elsewhere would make use of them, at least for relief from high temperatures, if not for overnight sleeping (Pruetz 2007).

Comprehensive, comparative analyses focussed on chimpanzee shelter-related behaviors that are putatively cultural are scarce. Whiten et al. (1999) looked for variation across 65 candidate behavioral patterns at six long-term study sites. Only one of the 65 types related to shelter: Ground night-nest (#25) was classed as 'patterns for which any absence can be explained by local ecological factors'. Perhaps this assignment referred indirectly to inferred vulnerability to predators being present or absent.

When differences do exist between study sites, almost all can be explained, at least in principle, on ecological

Fig. 6 Pioneer nest researcher Pamela Baldwin with an unusually low arboreal sleeping platform at Mt. Assirik (photo by WC McGrew)

grounds, either ultimately or proximally. If trees are shorter in savanna than in rainforest, it is not surprising the chimpanzee nests in savanna are at lower heights. If different plant species are used for beds at different sites, then purported preference must be seen in relation to the relative abundance of those species. And so on. However, a significant change in nesting behaviour over a relatively short time at the same site suggests possible cultural change. Stewart and Pruetz (2013) found at Fongoli that percentage of ground nests increased from 3% in 2001–2 to 12% in 2007–9. Koops et al. (2012a) found at Nimba

that the percentage of ground nests increased from 6% (2003–4) to 12% (2006) to 20% (2007–2008). This apparent trend seems remarkably quick, but reminds us of the importance of long-term data.

Some elements of sleeping platforms' composition are amenable to cultural scrutiny: Leafy, detached twigs are potentially available from all woody vegetation everywhere, but using them as nest lining has been reported as present in some sites but absent in others, which achieve the same result by using more branches (Stewart et al. 2018).

Fig. 7 Captive chimpanzee at Lwiro Primates Rehabilitation Center, Democratic republic of Congo, makes a ‘hyper-nest’ (Photo courtesy of Lwiro Primates Rehabilitation Center)

Comprehensive, multivariate statistical analyses may shed light on which of the many variables are culturally and/or environmentally important.

Future research

The last 15 years have seen a blossoming of knowledge about chimpanzee shelters, on many fronts, but gaps remain. Most of the research has been done on savanna populations of chimpanzees (Assirik, Fongoli, Issa, Semliki), although that eco-type hosts only a minority of wild chimpanzees. Studies of captive chimpanzee sheltering are few. Rain forest sites deserve more attention, despite the challenges of access to tall, multi-layered canopy. Most shelter research has been done on the eastern and western subspecies, with little or none on central or Nigerian-Cameroonian ones. Little research has been done on chimpanzee beds when they are allopatric versus sympatric with gorillas (Sanz et al. 2007). Day-nests and sleeping on bare ground are neglected, yet both may be important. Idiosyncratic variation in bed-building has yet to be explored. The extent to which cultural versus environmental processes contribute to sheltering is unclear. The as-yet unstudied ontogeny of bed-making may

help to elucidate this, as has been done with tool use; matrilineal transmission is likely but needs testing. Finally, more needs doing on emerging topics: Cave-use by Senegalese chimpanzees is ripe for inter-disciplinary investigations by primate archaeologists and palaeo-anthropologists. Much remains to be done, especially as shelter use and construction is such a fundamental skill in chimpanzee daily life.

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