## Title: Insights into the evolution of sleep through study of wild primate sleep ecology

## Introduction:

Sleep is an evolutionary puzzle. During sleep animals do not perform vital activities for life or fitness such as foraging, parental care, or finding mates. Sleeping animals are also vulnerable to predation. The persistence of sleep despite such evolutionary pressures indicates its importance. A burgeoning body of evidence has revealed that sleep is involved in both physiological and cognitive mechanisms supporting a multitude of functions, including energy conservation, growth and repair, thermoregulation, metabolic regulation, immunological enhancement, memory consolidation, emotional regulation, and even adaptive stillness to avoid predation (Sampson & Nunn, 2018; Siegal, 2005).

Behavioral ecology research has advanced sleep research through phylogenetic comparisons of sleep across species to better understand how natural selection has shaped sleep and sleep-related behavior. Research has covered a diversity of topics including sleeping site selection, predation effects on circadian rhythms, and variation in sleep architecture, defined as the quantitative structure and pattern of sleep. In mammals, this includes non-rapid eye movement (NREM) and rapid eye movement (REM) sleep, which are cyclical). NREM sleep usually dominates the first third of a human's sleeping bout. REM sleep is divided into tonic REM sleep (without actual rapid eye movements) and phasic REM sleep (with acute eye movements but muscle atonia). Human sleepers, when awakened during REM, are able to report coherent dreams with active participation of the dreamer. REM sleep occurs towards the end of a typical sleeping bout and can be identified using video footage of sleep behaviour and potentially through accelerometers that measure movement across multiple planes (Loftus et al. 2022).

## Problem Statement:

Sleep influences life history and results in trade-offs similar to optimal foraging theory. Just as for energy intake, sleeping patterns and sleep architecture follow dynamic and adaptive processes in response to environmental constraints (Fruth et al. 2018). Sleep architecture is variable within and across mammal species and habitats, and is of particular importance when investigating not only animal adaptation to environmental pressures, such as predation, but also the origins of sleep in humans.

A major evolutionary leap occurred in the sleep of the ancestor of the great apes. Lesser apes and other primates typically sleep arboreally, with some small monkeys utilizing tree holes as a fixed-site for sleeping, but most sleep on bare branches, even when predominantly terrestrial in the day (Fruth & Hohmann, 1996). Orangutans, chimpanzees, bonobos, and gorillas universally build nests in which to sleep at night and sometimes during the day. Nest building is an obligate behaviour in great apes, constructions are built nightly and never serve as a place for caching young. Structures are commonly built within trees, selected for stable and resilient biomechanical properties (Sampson & Hunt, 2014).

Nest-building is arguably the most pervasive form of material culture in great apes reflecting their ability for environmental problem solving and skilled object manipulation considered crucial for hominization (Fruth et al. 2018). Nest building in great apes is a phylogenetically conservative behaviour likely to have evolved in the Miocene (Fruth & Hohmann, 1996), somewhere between 18–14 mya (Duda & Zrzavý, 2013). Nest building may have been an evolutionary response to increasing body size, which would have made branch sleeping more precarious (Sampson & Nunn, 2015). Nests also function as shelters to repel, or mask odors that attract, biting insects (Samson et al. 2012; Stewart 2011), provide inaccessibility or crypsis from predators (Stewart & Pruetz 2013), insulation to keep warm (Stewart et al. 2018), and a stable and secure sleeping environment (Sampson & Hunt, 2014; Stewart et al. 2018). As the climate cooled and habitat dried from the middle to late Miocene, great ape nests likely functioned as shelters to buffer apes against increasingly stressful environmental conditions, including changing climate, habitat loss, and varying predator guilds (Fruth et al. 2018).

Nest building may also have evolved as a consequence of feeding competition with quickly radiating and better-adapted monkeys (Fruth & Hohmann, 1996). These "proto-nests" may have led to the "feeding nests" that can be regularly observed in great apes (Fruth & Hohmann, 1996). Feeding nests may then have turned into resting platforms, providing support for the increasing body weight of apes. These originally proximate functions of early nests may have improved quality of sleep through better thermoregulation, and a recumbent posture in a safe and secure location, ultimately resulting in a "great leap forward" in the evolution of great ape cognition (Fruth & Hohmann, 1996).

This "sleep quality hypothesis" is contrasted with the "engineering hypothesis", which suggests conversely that the greater cognitive performance of great apes enables them to build nests (Baldwin et al. 1981; Sampson & Nunn, 2015; Samson & Schumaker, 2013). These hypotheses may not be mutually exclusive in that increased complexity of nest architecture may have enhanced cognition through improved sleep, which in turn enhanced nest building skill, resulting in a positive feedback loop (Sampson & Nunn, 2015). Few studies have investigated how nests and sleep enhance cognition in great apes. Complexity of captive orangutan beds (made with hay, blankets or boxes) correlates with reduced night-time motor activity, less fragmentation, and greater sleep efficiency (Samson & Schumaker, 2013). Sleep has been demonstrated to enhance performance of captive apes participating in cognitive testing experiments (Martin-Ordas & Call, 2011). Whilst nest construction likely contributed to the “great leap forward” in the evolution of great ape cognition, the transition from tree-to-ground sleep may have resulted in a further leap forward in sleep quality and cognition in hominins (Coolidge & Wynn, 2006).

Comparative data to test these hypotheses, particularly of primate sleep architecture, are limited and only one study of wild populations has measured sleep in wild primates (Loftus et al., 2022). Such studies are difficult because of the invasive nature of established methods using polysomnography to record brain wave activity; however videography and accelerometers have been shown to be effective in detecting sleep and sleep disturbance (Loftus et al. 2022; Sampson & Shumaker, 2013). Comparative data reveal that relative to other mammals primates have greater sleep intensity (deeper sleep), generally consolidate sleep into a single inactive period, and nocturnal species sleep longer than diurnal ones (Nunn et al., 2009). Greater sleep site security and comfort result in deeper sleep in diurnal lemurs, suggesting an evolutionary relationship between sleep safety and cognition in a wild primate (Sampson et al., 2018). Relative to other primates, humans are an evolutionary outlier, spending a much shorter time asleep and a higher proportion of sleep in REM than predicted by their body and brain size, risk of predation, foraging requirements, sexual dimorphism, and diet (Nunn & Sampson, 2018; Sampson & Nunn, 2015). Humans have achieved this unique sleep architecture by eliminating NREM, whilst maintaining similar REM duration, despite evolutionary pressure to shorten overall sleep duration (Nunn & Sampson, 2018). Such changes are proposed to have occurred due to evolutionary shifts in human sleep environments allowing greater sleep quality through deeper sleep, similar to the transition from branch to nest in the great apes(Nunn & Sampson, 2018).

An emerging literature on the nocturnal activity of diurnal primates, especially chimpanzees (Tagg et al., 2018) now intersects with methodological innovations in our ability to measure sleep quality in nonhumans. Here I propose to apply these new methods to transformative questions about the evolution of cognition and sleep in primates from the wild.

**General Objective:**

*Comparative data on sleep is necessary to investigate how natural selection has shaped sleep across species, including humans. I aim to document sleep architecture in wild primates and* ***investigate the influence of sleep ecology on wild primate sleep architecture, quality, and intensity***. I will test ecological trade-offs in sleep decisions by investigating the influence of climate, predation, and food availability on sleep ***architecture, quality, and intensity*** in three sympatric primate species.

**Specific Objectives:**

1. I will test the influence of sociality and whether chimpanzee sleep is less affected by climatic conditions and predator activity given the greater security of nest sleeping, and whether across primates low food availability is likely to disrupt sleep by reducing sleep duration.
2. I will test the “sleep quality hypothesis” and “sleep intensity hypothesis” (described above) in wild chimpanzees. My previous research has documented considerable variation in chimpanzee nest architecture within and across populations and individuals.
3. I will assess whether more complex, compliant, or cushioned nests result in a greater proportion of time in REM and higher sleep quality, together with less time in NREM, awake and with fewer behavioural measures of sleep fragmentation and arousability.

**Methods:**

***Measuring sleep architecture and quality in wild primates:*** I aim to measure sleep architecture, quality, and intensity of baboons and red-tailed monkeys, using accelerometer biologging collars, and of chimpanzees using infra-red videography. The recent methodological developments for measuring sleep in nonhumans have not yet been applied to wild primates. Although the gold standard for measuring sleep is polysomnography, which measures brain waves among other metrics, it is invasive, time-limited, and not appropriate for wild subjects. Analogous data, however, can be captured by accelerometers (e.g. actigraphy), which can be attached to animal collars and use algorithms to determine sleep duration and fragmentation based on animal movement (Loftus et al., 2022; Sampson et al., 2019). Accelerometer bio-loggers have also been used to determine wild baboon daytime foraging and locomotion behaviour (Fehlmann et al., 2017). I will deploy accelerometers on ten individuals each in study troops of yellow baboons and red-tail monkeys for one year in order to measure their sleep architecture, quality, and intensity. I will use algorithms to determine sleep duration, quality (sleep duration/time in sleep site; Videan et al., 2006), fragmentation (the number of awakenings greater than 2 min per hour) and arousability (number of motor activity bouts per hour; following

Sampson & Shumaker, 2013) based on animal movement data from these accelerometers and following established methods (Loftus et al., 2022; Sampson et al. 2019). Individuals will be darted following all COSTECH and TAWIRI protocols by an experienced veterinarian.

Second, infra-red videographic data will allow me to categorise sleep states, document subtle body movements during sleep, and ultimately determine the duration of time asleep versus awake, in REM versus NREM, and behavioural measures of sleep fragmentation, arousability and sleep quality. Darting wild chimpanzees is inadvisable and normally, capturing sleep data of wild chimpanzees would be logistically prohibitive due to their arboreal nesting patterns. However, the Issa study site is characterised by open vegetation and mountainous topography. That Issa chimpanzees preferentially sleep on woodland slopes allows for remarkable visibility and access into their nests for nocturnal monitoring of sleep activity (Stewart & Pruetz, 2013).

***Influence of climate, predation, and food availability:*** Long term climatic data (temperature, relative humidity, wind speed, and rainfall) are recorded at 30min intervals in different vegetation types at the Issa Valley field site. Presence of predators is recorded on 50 camera traps deployed long term within the home ranges of all three primates and further recorded ad-lib by direct sightings, vocalisations, or tracks and feces. Chimpanzees, baboons, and red-tail monkeys at Issa are currently followed during the day to record direct observations of foraging (e.g. food type and species, feeding rates), ranging (habitat and GIS) and social (grooming, proximity, aggression and affiliation) behaviour. All of these data will be used to build linear mixed models to investigate relative influence on sleep within and across species and individuals.

***Measuring nest architecture of wild chimpanzees:*** During my PhD I developed new methods for assessing chimpanzee nest shape and architecture (Stewart, 2011). I will build on these methods to provide data on the comfort (Stewart, 2007), compliance (van Casteran et al., 2012), and complexity of the nest structure that can be compared to measures of sleep architecture within and across individuals.

**Expected outputs:**

I hope to have the opportunity to involve Tanzanian B.Sc interns in this research, which will result in one to two academic publications. This study is designed to increase our understanding in the evolution of sleep and the selective factors that may shape variation in sleeping patterns in primates. On completion of the research a report will be provided to TAWIRI and COSTECH and any necessary footage and relevant data will be made available to the relevant authorities upon request.

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