

Do chimpanzees (*Pan troglodytes schweinfurthii*) exhibit sleep related behaviors that minimize exposure to parasitic arthropods? A preliminary report on the possible anti-vector function of chimpanzee sleeping platforms

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Abstract Great apes spend half of their lives in a nightly “nest” or sleeping platform (SP), a complex object created by modifying foliage, which functions as a stable substrate on which to sleep. Of the several purported functions of SPs, one hypothesis is that they protect against parasitic infection. Here we investigate the role of SP site choice in avoiding molestation by arthropods. This study presents preliminary data on the insect-repellent properties of preferred sleeping tree species *Cynometra alexandri*. Insect traps were deployed in gallery forest habitats in which chimpanzees typically “nest.” We compared traps placed adjacent to SPs artificially manufactured with *C. alexandri* trees to an open area within the same habitat. Multiple measures of arthropod counts indicate that simulated *C. alexandri* SP sites have fewer arthropods than similar non-SP sites. Volatile compounds secreted by *C. alexandri* foliage are hypothesized to repel annoying arthropods and/or mask chimpanzee olfactory signals. Of the total insects captured ($n = 6,318$), $n = 145$ were mosquitoes. Of the total mosquitoes captured, $n = 47$ were identified as *Anopheles* (female, $n = 12$). The prominent malarial vector *Anopheles gambiae* was identified among the captured mosquito sample. These results suggest that the presence of broken branches of the tree species *C. alexandri* reduce the amount of insects a chimpanzee is exposed to throughout a night’s sleep. This great ape behavioral and socio-technological adaptation may have evolved, in part, to increase quality of sleep as well as decrease exposure to vectors of disease.

Keywords Chimpanzees · Nest · Pathogen · Mosquito · *Cynometra alexandri*

Introduction

“Night nests” or sleeping platforms (SPs) are a signal feature of great ape daily life in which individuals spend up to 12 h a day (Lodwick et al. 2004). These complex constructions (Shumaker et al. 2011), are manufactured each evening from foliage and stems to constitute a stable and comfortable sleeping structure (Goodall 1962, 1968). SP use has been observed in every chimpanzee, bonobo, gorilla, and orangutan population studied to date. The construction of a new SP each day requires time and effort as individuals search for an appropriate site, maneuver into position to construct the SP, and manipulate a large volume of foliage. However, the utility of this substantial investment is still equivocal. Among the proposed functions of SPs are: predation avoidance (Kortlandt 1992; Pruett et al. 2008), thermoregulation (McGrew 2004), disease avoidance (Fruth and Hohmann 1996; Anderson 1998; Nunn and Heymann 2005) and sleep quality (Fruth and Hohmann 1996; Sabater Pi et al. 1997; Anderson 1998). Recently it has been noted that these explanations are yet to be tested rigorously (McGrew 2004), although there are a growing number of investigations (Ancrenaz et al. 2004; Koops et al. 2007; Ogawa et al. 2007; Stewart et al. 2007; Hernandez-Aguilar 2009; Stewart 2011; Koops et al. 2012; Samson 2012; Samson and Hunt 2012). Our present goal was to test the hypothesis that SP use decreases exposure to parasitic arthropods, with a focus on mosquitoes.

Environmental factors can dramatically influence the way animals experience variation in rainfall, temperature and resource availability, and, subsequently, disease risk

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(Nunn and Altizer 2006). For example, susceptibility to disease can increase due to stress caused by a decline in food resources, which can be triggered by seasonal reductions in rainfall (Lloyd 1995; Beisel 2000; Nelson et al. 2002; Nelson 2004). Declining food and water resources can also increase food sharing between and within species, which may further alter patterns of disease transmission. Dunn (1968) showed that repeated use of tree holes among squirrel monkeys increased the risk of infection by fecal parasites and ectoparasites. Yet primates likely adapt to disease risk in complex ways. The classic example includes self-medicative leaf-swallowing in chimpanzees (Wrangham and Nishida 1983; Huffman et al. 1996, 2006; Huffman 2001, 2003). Capuchin monkeys (*Cebus olivaceus*) occasionally anoint themselves with the secretions from millipedes, which are known to possess insect-repellent qualities (Valderrama et al. 2000; Weldon et al. 2003). Red howler monkeys may selectively choose areas in which feces falls to the ground without hitting branches along the way, reducing the potential for coming across feces along arboreal paths or contaminating food resources (Gilbert 1997). Mantled howlers appear to defecate in peripheral areas of the canopy and closer to the ground, suggesting individuals may be avoiding the contamination of food with intestinal parasites (Henry and Winkler 2001).

Arthropod abundance and distribution, and, subsequently, risk of vector-borne disease, are influenced by environmental factors such as temperature and rainfall (Kovats et al. 2001). This is particularly the case for *Anopheles*-borne *Plasmodium*, 19 species of which normally infect nonhuman primates (Garnham 1966; Coatney et al. 1971). Mosquito development and activity are limited by both temperature and rainfall, with seasonal variation in biting and infectivity (Bodker 2003). During times of high mosquito frequency, baboons in Kibale National Park, Uganda appear to participate in more polyspecific associations (Freeland 1977). If the probability of a vector consuming a blood meal does not increase proportionately with group size, then individual infection could be lower in larger groups (Mooring and Heart 2002) (but see Davies et al. 1991; Nunn and Heymann 2005 for contrasting opinion).

As previously noted, disease avoidance (Fruth and Hohmann 1996; Anderson 1998; Nunn and Heymann 2005) is a hypothesized function of sleeping sites and SPs; research has demonstrated that primate sleeping sites can easily become contaminated with parasites (Freeland 1980; Hausfater and Meade 1982) and it has been suggested that sleep siting may be an adaptive behavior for avoiding parasite infection (MacKinnon 1974). Building a new nest each night could reduce ectoparasite exposure in apes (MacKinnon 1974). In addition, the plants used to make

nests may release chemical compounds that may be naturally repellent to arthropods, or might function to mask the odor of the ape (Stewart 2011), as has been illustrated in Borneo orangutans who occasionally cover their SPs with branches from tree species with known mosquito-repellent properties (Largo et al. 2009). It has been observed at Seringbara that the thermoregulatory strategy of humidity avoidance is more predictive of SP site and location than either antipathogen or antipredation factors (Koops et al. 2012); however, at Semliki, sleeping site height selection and intraspecific association during nighttime sleep bouts may also be influenced by the likelihood of parasitic arthropods (Hunt and Samson unpublished data). Few studies have adequately targeted the parasite-vector-host dynamic between *Plasmodium*, *Anopheles*, and chimpanzees (Nunn and Altizer 2006).

At Semliki, *Cynometra alexandri* is the preferred SP species and is chosen 73.6 % (Hunt and McGrew 2002; Samson 2012), similar to Ishasha (Sept 1992) and Budongo (Brownlow et al. 2001). An aim of this research is to test why chimpanzees significantly prefer this species over other, less selected tree species. Our objective was to provide preliminary, comparative data of flying arthropod catches with and without associated artificially manufactured SPs constructed from the preferred tree species of Semliki chimpanzees. We predict that in paired comparisons of traps associated with and without *Cynometra*, fewer insects, lower insect mass, and female mosquitoes will be recorded in traps associated with *Cynometra*.

Methods

Chimpanzees (*Pan troglodytes schweinfurthii*) have been studied in the Toro-Semliki Wildlife Reserve (TSWR) in western Uganda since 1996. TSWR is northwest of Fort Portal, close to the eastern edge of the Great Rift Valley (0°50′–1°05′N, 30°20′–30°35′E) and encompasses 548 km². Semliki consists of strips of dry and hot gallery forest (50–250 m wide) that is bounded and crosscut by water-courses; within these forests emergent trees reach as high as 50 m (Allan et al. 1996; Hunt and McGrew 2002). The chimpanzee study community range includes the Mugiri River and its tributaries, as well as open woodland and bushland on the escarpment near the northeastern reserve boundary. The biome is predominantly dry *Combretum* savanna and *Borassus* palm savanna. The range of the Mugiri chimpanzees is limited to the northeast by tea estates at the top of the escarpment. The chimpanzee community primarily feeds on the fruiting species such as *Beilschmiedia*, *Cynometra*, *Cola*, *Phoenix*, and *Tamarindus* (Hunt and McGrew 2002). Their community home range is the largest known—72.1 km² (measured with the minimum

convex polygon of any area where identified individuals have been observed). There are estimated to be 30 males, which suggests a community size of approximately 104 (estimated using the average sex ratio across *P.t. schweinfurthii* sites) (Stumpf 2007).

Toro-Semliki has an average rainfall of 1,389 mm (KDH records), though rainfall is at historic highs in the rift valley and earlier annual rainfall records were reported to vary between 700 and 1,300 mm (Plumptre 2010; Pratt et al. 1977). Semliki has two rainy seasons: the long rains from August to December and secondary short rains from March to April. Of chimpanzee study sites, only Assirik is hotter (Hunt and McGrew 2002). Relative humidity (RH) daily maxima averaged 95 and 92 %, respectively (Hunt et al. 1999), while the daily mean temperature high was 34 °C and the daily mean low was 20 °C (Hunt and McGrew 2002).

During a 6-month study period (August 2010–January 2011), we employed multiple CDC Miniature Light Trap Model 512 (with PhotoSwitch and Air-Actuated Gate System) within the Semliki gallery forest habitat to capture flying insects. The PhotoSwitch and Air-Actuated Gate System allowed traps to automatically activate at dusk (1905 hours) and deactivate at dawn (0700 hours). For the purpose of this study, we set two paired traps on the same night to test whether the construction of *Cynometra* SPs reduce exposure to flying arthropods. The first trap, hung 1 m from the ground, had a fresh *Cynometra* SP constructed and placed underneath (Fig. 1). The second control trap, placed within the same microhabitat



Fig. 1 Species *Cynometra alexandri* was used as material for artificial SP construction and associated with a CDC Miniature Light Trap within the riverine gallery forest of Semliki, Uganda

approximately 10 m from the first trap, also hung 1 m from the ground and had no associated SP or vegetation. Trapping always took place in the same location and both traps were placed in an open area. Worn polyester socks (used approximately 8 h and stored in a seal tight bag from the previous day) were attached to each trap as bait because natural human volatiles are known attractants to *Anopheles* mosquitoes (Smallegange et al. 2010, 2011). At the time of trap deactivation, nightly trap collections were emptied into killing jars with a small amount of pure ethanol for further specimen processing (total traps collected $n = 34$). On the day of the catch, insects were weighed (by subtracting the mass of the container to the sum of the insects and container, measured with a tension gauge spring scale accurate to 0.1 g), counted and categorized for later identification (total number of insects processed, $n = 6,318$).

To evaluate whether SPs constructed with *Cynometra* reduce exposure to flying arthropods, insect quantity and mass were compared between traps associated with and without manufactured SPs using a paired samples *t* test using PASW Statistics 18 (IBM SPSS). All tests were two-tailed. Data were evaluated for normal distribution, and level of significance was set at 0.05.

Results

Of the total insects captured, $n = 145$ were mosquitoes. Of the total mosquitoes sexed, $n = 41$ were male and $n = 104$ were female. Of the total mosquitoes captured, $n = 9$ were identified as *Aedes* (all female), $n = 47$ were *Anopheles* (female, $n = 12$), $n = 13$ were *Coquillettidia* (female, $n = 12$), $n = 76$ were *Culex* (female, $n = 71$) (Fig. 2). The prominent malarial vector *Anopheles gambiae* (Gillies and Coetzee 1987) was identified among the captured mosquito

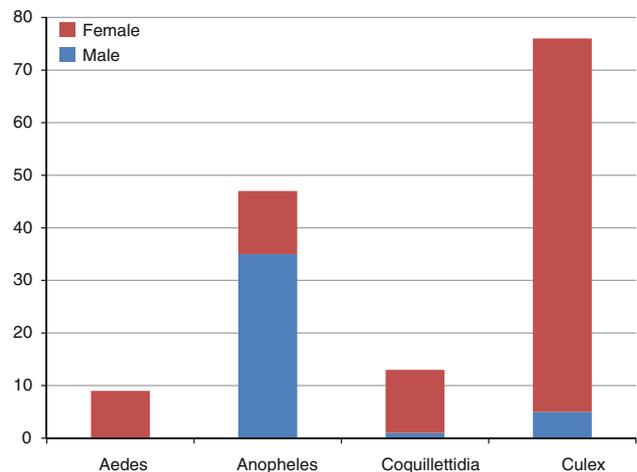
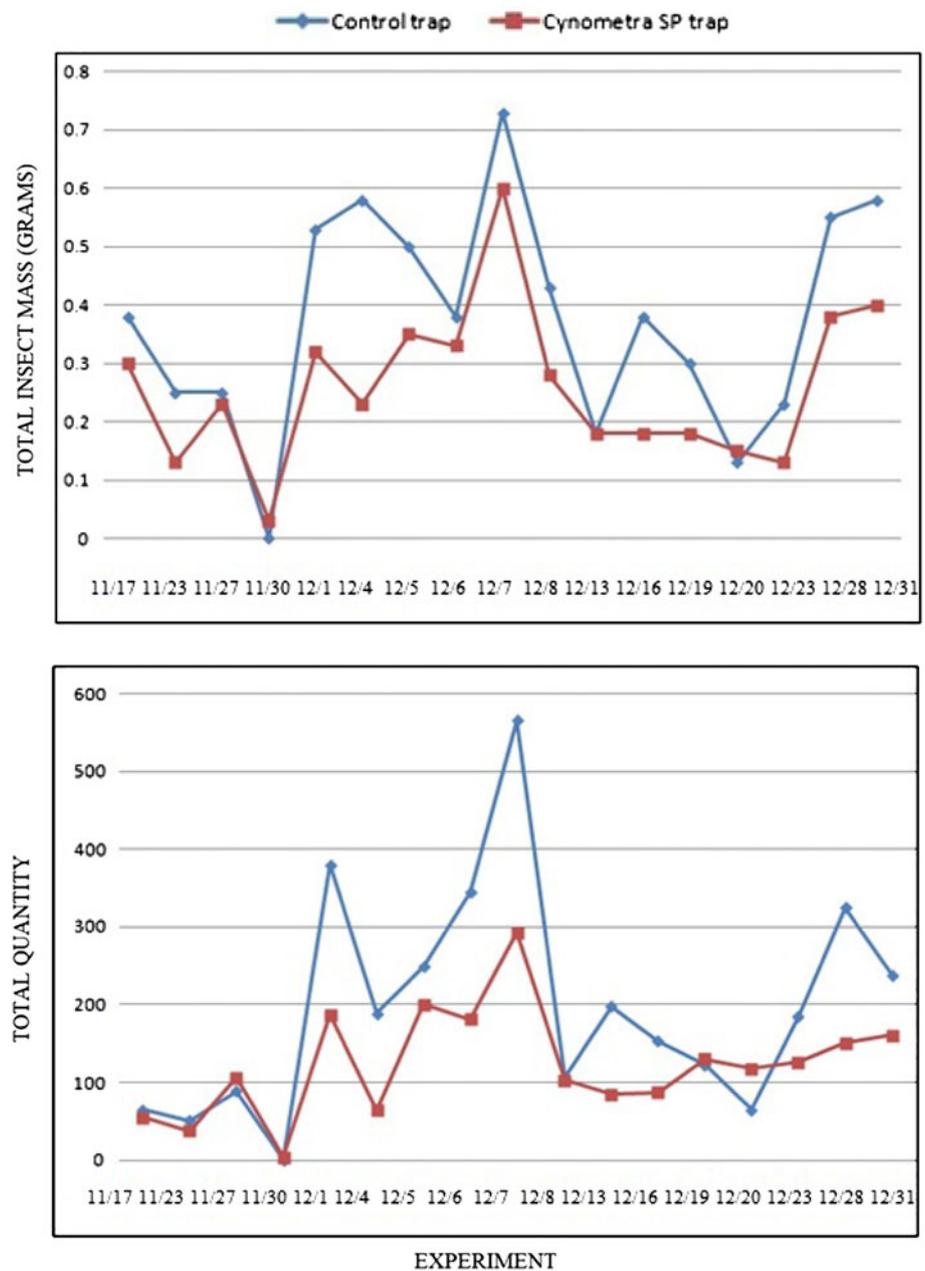


Fig. 2 The distribution of mosquito genera captured during the study, separated by sex

Fig. 3 A comparison of mass and quantity between the *Cynometra* SP trap and the control trap shows that the SP trap yielded significantly less insect mass and total number of insects caught. The *bottom column* shows trails labeled by month and date (2010)



sample. The *Cynometra* SP trap captured significantly less insect mass (control trap = $0.37 \pm \text{SD } 0.19$ (g) vs. *Cynometra* trap = $0.26 \pm \text{SD } 0.14$ (g); $t[16] = 5.00$, $p < 0.001$) and quantity (control trap = $195.8 \pm \text{SD } 144.6$ vs. *Cynometra* trap = $122.9 \pm \text{SD } 69.6$; $t[16] = 3.38$, $p = 0.004$) (Fig. 3). Paired samples correlations reveal a positive significant relationship between (1) control trap total insect mass (g) and *Cynometra* SP trap total insect mass ($n = 17$ trails, Pearson correlation $r^2 = 0.88$, $p < 0.001$) and (2) control trap total number of insects caught and *Cynometra* SP trap total number of insects caught ($n = 17$ trails, Pearson correlation $r^2 = 0.87$, $p < 0.001$). Furthermore, the difference between the number of female

mosquitoes captured by both traps was non-significant (control trap = $1.12 \pm \text{SD } 0.93$ vs. *Cynometra* trap = $1.76 \pm \text{SD } 1.48$, $t[16] = -1.61$, $p = 0.13$). Paired sample correlation was non-significant ($n = 17$, Pearson correlation $r^2 = 0.11$, $p < 0.67$). Finally, the average percentage of mosquitoes to insects caught per trap was 0.015 %.

Discussion

Data support our predictions that SPs constructed with freshly broken *Cynometra* reduce exposure to flying

arthropods. This may be one major reason why these chimpanzees choose to make SPs using *Cynometra*: creating more comfortable sleep (i.e., respite from flying arthropods), and possibly *indirectly* reducing risk of malaria infection. In addition, the prediction that *Cynometra* reduces female mosquito exposure was not supported. Therefore, annoyance towards insects *sensu lato* is hypothesized to be the proximate mechanism guiding avoidance strategies. In fact, it has been suggested that primates allot significant energetic expenditure towards deterrent behaviors that minimize exposure to *Diptera* and *Culicidae* (Dudley and Milton 1990). Behaviors (in this instance, sleeping site selection) that aid in this function while asleep when the body is quiescent, could serve to perform a similar function. It is unknown whether an individual chimpanzee would be able to discriminate between mosquito genera on the basis of the tonal quality of wing beats. Therefore, it is either possible that chimpanzees are psychologically harassed by the frequency of sound emitted by a specific subset of mosquitoes/biting flying arthropods or all mosquitoes/flying arthropods. The possibility that audition may be differentiated between biting insects that do or do not transmit disease is an intriguing one and should be a focus of future research.

Koops and colleagues (2012) did not observe malarial vectors at the Seringbara study site, despite having captured mosquitoes that transmit disease (Yellow fever, First Valley fever and West Nile virus). In contrast, this is the first account of the known malarial vector *Anopheles* recorded in association with a chimpanzee site, which may explain why there was no support for the antipathogen hypothesis at Seringbara. In addition to *Anopheles*—*Aedes*,

Coquillettidia and *Culex* were captured in the sample (Fig. 2). Species among these genera transmit a host of diseases, including Yellow fever, dengue and dengue 2, Chikungunya fever, Arbovirus, and Rift Valley fever (Table 1). Limiting factors in this pilot project include: small sample size, lack of a separate non-*Cynometra* SP (i.e., alternative plant species), and insect capture only 1 m above the ground (instead of in the canopy where chimpanzees typically nest). Although, it should be noted that chimpanzees have been observed constructing sleeping platforms within the range of the trap heights employed in this study (Semliki SP height min = 0.4 m; Hunt unpublished data). Additionally, the trees that were used to anchor the traps were previously observed to be used in SP construction (Hunt unpublished data). Finally, it could be that construction of SPs from any plant may mask the odor of a chimpanzee. Further research should include meteorological analysis, chemical analysis, and comparisons of repellent qualities among trees selected by chimpanzees for sleeping sites other than *Cynometra*.

Putting aside any adaptive benefits of avoiding *Anopheles*-borne *Plasmodium* infection in chimpanzees that use *Cynometra* SPs, simply reducing arthropod activity around the animal (i.e., reducing psychological stress of maintaining vigilance from annoying, biting insects) while attempting to sleep would be advantageous. The importance of the selection of sleep sites that maximize sleep quality must not be underestimated. Preston and colleagues (2009) found that mammalian species that spend more time asleep are able to increase investment in their immune systems, and can, therefore, augment immunocompetence and reduce parasitic infection. Therefore, the relationship

Table 1 Ugandan mosquito species, of the genera captured for this study, considered to be prominent disease vectors found in the AFRICOM (US Department of Defense Unified Command Areas of Responsibility) region

Species	Medical importance	References
<i>Aedes stokesi</i>	Yellow fever	Reinert (1972)
<i>Aedes furcifer</i>	Yellow fever, Dengue 2, Chikungunya fever	Diallo et al. (1999), Germain et al. (1980), Jupp and Kemp (1993)
<i>Aedes aegypti</i>	Dengue, Yellow fever	Christophers (1960)
<i>Aedes africanus</i>	Arbovirus, Yellow fever, Chikungunya fever, Rift Valley fever	Huang (1979)
<i>Anopheles arbiensis</i>	Malaria	Gimnig et al. (2001)
<i>Anopheles funestus</i>	Malaria, <i>Bancroftian filariasis</i>	Gillies and de Meillon (1968)
<i>Anopheles gambiae</i>	Primary malaria vector	Gillies and de Meillon (1968)
<i>Anopheles hancocki</i>	Malaria	Gillies and de Meillon (1968)
<i>Anopheles moucheti</i>	Malaria	Gillies and de Meillon (1968)
<i>Anopheles pharoensis</i>	Malaria	Gillies and de Meillon (1968)
<i>Coquillettidia fuscopennata</i>	Rift Valley fever	Smithburn et al. (1948)
<i>Culex bitaeniorhynchus</i>	<i>W. bancrofti</i> , <i>Burgia malayi</i> , Murray Valley encephalitis, Batai virus	Harbach (1988)

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between insect exposure and sleep comfort could have a powerful effect on individual fitness.

Sleep aids neural processing, neural ontogenesis, and maintenance of neural plasticity (Marks 1995), and plays a central role in improved neural functioning (Hobson 1990). There is substantial experimental evidence to support cognition and memory consolidation as central functions of sleep (Kavanau 1994, 1997; Peigneux et al. 2001; Hobson and Pace-Schott 2002; Walker and Stickgold 2006; Walker 2009). Sleep quality may be of great importance to brain function and cognition (Preston et al. 2009), yet for apes this claim cannot be assessed until sufficient data have been accumulated.

Fruth and Hohmann (1996) suggest multiple benefits from the transition of branch to SP sleep, proposing that sleep architecture among Miocene apes increased in both duration and quality with the transition to more comfortable and stable SP sleep. Furthermore, evidence of middle stone age bedding constructed with foliage characterized by anti-insect properties has been recovered (Wadley et al. 2011). If it is the case that SP site selection and structure are characterized by functional properties that reduce exposure to disease vectors, as well as large bodied predators, then the construction of SPs by large brained apes may have been an important adaptation, shared by the human-ape common ancestor, leading to higher quality sleep environments which augmented waking cognition.

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References

Allan C, Sivell D, Lee T (1996) Semuliki (Toro) Game Reserve, Uganda: results of the Frontier-Uganda Biological Assessment. Report No. 7. The Society for Environmental Exploration, London

Ancrenaz M, Calaque R, Lackman-Ancrenaz I (2004) Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: implications for nest census. *Int J Primatol* 25:983–1000

Anderson JR (1998) Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *Am J Primatol* 46:63–75

Beisel WR (2000) Interactions between nutrition and infection. In: Strickland G (ed) *Hunter's tropical medicine*. Saunders W.B, Philadelphia, pp 967–969

Bodker R (2003) Relationship between altitude and intensity of malaria transmission in the Usambara Mountains, Tanzania. *J Med Entomol* 40:706–717

Brownlow AR, Plumtre AJ, Reynolds V, 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

Christophers SR (1960) *Aedes aegypti*, the yellow fever mosquito: its life history, bionomics and structure. Cambridge University Press, Cambridge

Coatney RG, Collins WE, Warren M, Contacos PG (1971) The primate malarias. National Institutes of Health, Bethesda

Davies CR, Ayres JM, Dye C, Deane LM (1991) Malaria infection rate of amazonian primates increases with body weight and group size. *Funct Ecol* 5:655–662

Diallo M, Thonnon J, Traore-Lamizana M, Fontenille D (1999) Vectors of chikungunya virus in Senegal: current data and transmission cycles. *Am J Trop Med Hyg* 60:281–286

Dudley R, Milton K (1990) Parasite deterrence and the energetic costs of slapping in howler monkeys, *Alouatta palliata*. *J Mammal* 71:463–465

Dunn FL (1968) The parasites of *Saimiri*: in the context of platyrrhine parasitism. In: Rosenblum LA, Cooper RW (eds) *The squirrel monkey*. Academic Press, New York, pp 31–68

Freeland W (1977) Blood-sucking flies and primate polyspecific associations. *Nature* 269:801–802

Freeland W (1980) Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and fecal contamination. *Ecology* 61:1297–1303

Fruth B, Hohmann G (1996) Nest building behavior in the great apes: the great leap forward? In: Marchant LF, Nishida T (eds) *Great ape societies*. Cambridge University Press, Cambridge, pp 225–240

Garnham PCC (1966) *Malaria parasites and other Haemosporidia*. Blackwell Scientific Publications, Oxford

Germain M, Francy DB, Ferrara L, Sanyang Y, Monath TP, Adam C, Salaun JJ (1980) Yellow fever in Gambia 1978–1979: a complementary entomological survey done in October 1979. *Cahiers ORSTOM (Office de la Recherche Scientifique et Technique Outre-Mer) Serie Entomologie Medicale et Parasitologie* 18:3–12

Gilbert K (1997) Red howling monkey use of specific defecation sites as a parasite avoidance strategy. *Anim Behav* 54:451–455

Gillies MT, Coetsee M (1987) *A supplement to the Anophelinae of Africa south of the Sahara*. Johannesburg, South Africa

Gillies MT, de Meillon B (1968) *The Anophelinae of Africa, south of the Sahara*. South African Institute of Medical Research, Johannesburg

Gimnig JE, Ombok M, Kamau L, Hawley WA (2001) Characteristics of larval anopheline (*Diptera: Culicidae*) habitats in western Kenya. *J Med Entomol* 38:282–288

Goodall J (1962) Nest building behavior in the free ranging chimpanzee. *Ann N Y Acad Sci* 102:455–467

Goodall J (1968) *The behaviour of free-living chimpanzees in the Gombe Stream Reserve*. Bailliere, Tindall & Cassell, London

Harbach RE (1988) The mosquitoes of the subgenus *Culex* in southwestern Asia and Egypt (Diptera: Culicidae). *Contrib Amer Entomol Inst* 24:52–61

Hausfater G, Meade B (1982) Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates* 23:287–297

Henry RE, Winkler L (2001) Foraging feeding and defecation site selection as a parasite avoidance strategy of *Alouatta palliata* in a dry tropical forest. *Am J Phys Anthropol Suppl* 32:79

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

Hobson JA (1990) Sleep and dreaming. *J Neurosci* 10:371–382

Hobson JA, Pace-Schott EF (2002) The cognitive neuroscience of sleep: neuronal systems, consciousness and learning. *Nat Rev* 3:679–693

- Huang YM (1979) Medical entomology studies 11. The subgenus *Stegomyia* of *Aedes* in the oriental region with keys to the species (Diptera: Culicidae). *Contrib Am Entomol Inst* 15:1–76
- Huffman MA (2001) Self-medicative behavior in the African great apes: an evolutionary perspective into the origins of human traditional medicine. *Bioscience* 51:651–661
- Huffman MA (2003) Animal self-medication and ethno-medicine: exploration and exploitation of the medicinal properties of plants. *Proc Nutr Soc* 62:371–381
- Huffman MA, Page JE, Sukhdeo MVK, Gotoh S, Kalunde MS, Chandrasiri T, Towers GHN (1996) Leaf-swallowing by chimpanzees: a behavioral adaptation for the control of strongyle nematode infections. *Int J Primatol* 17:475–503
- Huffman MA, Gotoh S, Turner LA, Hamai M, Yoshida K (2006) Seasonal trends in intestinal nematode infection and medicinal plant use among chimpanzees in the Mahale Mountains, Tanzania. *Primates* 38:111–125
- Hunt KD, McGrew WC (2002) Chimpanzees in the dry habitats of Assirik, Senegal and at the Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, Marchant LF (eds) *Behavioral diversity in chimpanzees and bonobos*. Cambridge University Press, Cambridge, pp 35–51
- Hunt KD, Cleminson A, Latham J, Weiss RI, Grimmond S (1999) A partly habituated community of dry-habitat chimpanzees in the Semliki Valley Wildlife Reserve, Uganda. *Am J Phys Anthropol Suppl* 28:157
- Jupp PG, Kemp A (1993) The potential for dengue in south-Africa: vector competence tests with dengue 1 and 2 viruses and 6 mosquito species. *Trans R Soc Trop Med Hyg* 87:639–643
- Kavanau JL (1994) Sleep and dynamic stabilization of neural circuitry: a review and synthesis. *Behav Brain Res* 63:111–126
- Kavanau JL (1997) Origin and evolution of sleep: roles of vision and endothermy. *Brain Res Bull* 42:245–264
- 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
- Koops K, McGrew WC, de Vries H, Matsuzawa T (2012) Nest-building by chimpanzee (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: antipredation, thermoregulation, and antivector hypotheses. *Int J Primatol* 33:356–380
- Kortlandt A (1992) On chimpanzee dormitories and early hominid home sites. *Curr Anthropol* 33:399–401
- Kovats RS, Campbell-Lendrum DH, McMichael AJ, Woodward A, Cox JS (2001) Early effects of climate change: do they include changes in vector-borne disease? *Philos Trans R Soc Lond Ser B Biol Sci* 356:1057–1068
- Largo CJ, Bastian ML, van Schaik CP (2009) Mosquito avoidance drives selection of nest tree species in Bornean orangutans. *Folia Primatol* 80:163
- Lloyd S (1995) Environmental influences on host ecology. In: Grenfell BT, Dobson AP (eds) *Ecology of infectious diseases in natural populations*. Cambridge University Press, Cambridge, pp 327–361
- Lodwick JL, Borries C, Pusey AE, Goodall J, McGrew WC (2004) From nest to nest: influence of ecology and reproduction on the active period of adult Gombe chimpanzees. *Am J Primatol* 64:249–260
- Mackinnon J (1974) The behaviour and ecology of wild orangutans (*Pongo pygmaeus*). *Anim Behav* 22:3–74
- Marks GA (1995) A functional role for REM-sleep in brain maturation. *Behav Brain Res* 69:1–11
- McGrew WC (2004) *The cultured chimpanzee: reflections on cultural primatology*. Cambridge University Press, New York, p 248
- Mooring MS, Hart BL (2002) Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* 123:173–193
- Nelson RJ (2004) Seasonal immune function and sickness responses. *Trends Immunol* 25:187–192
- Nelson RJ, Demas GE, Klein SL, Kriegsfield LJ (2002) Seasonal patterns of stress, immune function, and disease. Cambridge University Press, New York
- Nunn CL, Altizer S (2006) *Infectious diseases in primates*. Oxford University Press, New York
- Nunn CL, Heymann EW (2005) Malaria infection and host behavior: a comparative study of Neotropical primates. *Behav Ecol Sociobiol* 59:30–37
- Ogawa H, Idani G, Moore J, Pintea L, Hernandez-Aguilar A (2007) Sleeping parties and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. *Int J Primatol* 28:1397–1412
- Peigneux P, Laureys S, Delbeuck X, Maquet P (2001) Sleeping brain, learning brain. The role of sleep for memory systems. *Neuro-report* 12:A111–A124
- Plumptre AJ (2010) Long term changes in Africa's rift valley: synthesis of main findings. In: Plumptre AJ (ed) *Long term changes in Africa's rift valley: impacts on biodiversity and ecosystems impacts on biodiversity and ecosystem*. Nova Science Publishers, pp 235–247
- Pratt DJ, Gwynne MD, Blackie JR (1977) *Rangeland management and ecology in East Africa*. Hodder and Stoughton, London, p 310
- Preston B, Capellini I, McNamara P, Barton R, Nunn C (2009) Parasite resistance and the adaptive significance of sleep. *BMC Evol Biol* 9:7
- Pruetz JD, Fulton SJ, Marchant LF, McGrew WC, Waller MSM (2008) Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *Am J Primatol* 70:393–401
- Reinert JF (1972) Contributions to the mosquito fauna of southeast Asia part 15 genus *Aedes meigen*, subgenus *Ayurakitia* Thurman. *Contrib Am Entomol Inst* 9:1–42
- Sabater Pi J, Veà JJ, Serrallonga J (1997) Did the first hominids build nests? *Curr Anthropol* 38:914–916
- Samson DR (2012) The chimpanzee nest quantified: morphology and ecology of arboreal sleeping platforms within the dry habitat site of Toro-Semliki Wildlife Reserve, Uganda. *Primates* (in press)
- Samson DR, Hunt KD (2012) A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. *Am J Primatol* 74:811–818
- 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
- Shumaker RW, Walkup KR, Beck BB (2011) *Animal tool behavior: the use and manufacture of tools by animals*. Johns Hopkins University Press, Baltimore, p 282
- Smallegange RC, Knols BGJ, Takken W (2010) Effectiveness of synthetic versus natural human volatiles as attractants for *Anopheles gambiae* (Diptera: Culicidae) *Sensu Stricto*. *J Med Entomol* 47:338–344
- Smallegange RC, Verhulst NO, Takken W (2011) Sweaty skin: an invitation to bite? *Trends Parasitol* 27:143–148
- Smithburn KC, Haddow AJ, Gillet JD (1948) Rift Valley fever: isolation of the virus from wild mosquitoes. *Brit J Exp Pathol* 29:107–121
- Stewart FA (2011) Why sleep in a nest? empirical testing of the function of simple shelters made by wild chimpanzees. *Am J Phys Anthropol* 146:313–318
- Stewart FA, Pruetz JD, Hansell MH (2007) Do chimpanzees build comfortable nests? *Am J Primatol* 69:930–939
- Stumpf R (2007) Chimpanzees and bonobos: diversity within and between species. In: Campbell CJ, Fuentes A, MacKinnon KC,

- Panger M, Bearder SK (eds) *Primates in perspective*. Oxford University Press, New York, pp 321–344
- Valderrama X, Robinson JG, Attygalle AB, Eisner T (2000) Seasonal anointment with millipedes in a wild primate: a chemical defense against insects? *J Chem Ecol* 26:2781–2790
- Wadley L, Sievers C, Bamford M, Goldberg P, Berna F, Miller C (2011) Middle stone age bedding construction and settlement patterns at Sibudu, south Africa. *Science* 334:1388–1391
- Walker MP (2009) The role of sleep in cognition and emotion. *Ann N Y Acad Sci* 1156:168–197
- Walker MP, Stickgold R (2006) Sleep, memory, and plasticity. *Annu Rev Psychol* 57:139–166
- Walter Reed Biosystematics Unit (2012). <http://wrbu.si.edu/index.html>
- Weldon PJ, Aldrich JR, Klun JA, Oliver JE, Debboun M (2003) Benzoquinones from millipedes deter mosquitoes and elicit self-anointing in capuchin monkeys (*Cebus* spp.). *Naturwissenschaften* 90:301–304
- Wrangham R, Nishida T (1983) *Aspilia* spp. leaves: a puzzle in the feeding behavior of wild chimpanzees. *Primates* 24:276–282