Chimpanzee (*Pan troglodytes schweinfurthii*) Group Sleep and Pathogen-Vector Avoidance: Experimental Support for the Encounter-Dilution Effect

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Abstract

Sleep is essential for survival, yet it represents a time of extreme vulnerability, including through exposure to parasites and pathogens transmitted by biting insects. To reduce the risks of exposure to vector-borne disease, the encounter-dilution hypothesis proposes that the formation of groups at sleep sites is influenced by a "selfish herd" behavior, where individuals dilute risk by sleeping with other group members. To investigate this hypothesis in the context of chimpanzee (*Pan troglodytes schweinfurthii*) sleep site selection, we employed four light traps that we also baited with nontoxic chemical attractants to capture insects throughout the night. Across 74 nights with 294 traps set, we collected 66,545 individual insects. Consistent with the encounter-dilution hypothesis, we found that insect exposure, inferred by absolute numbers of insects caught in nighttime traps, was strongly influenced by the grouping of traps. Specifically, single traps caught more insects—including vector transmitting female mosquitoes—than grouped traps, and the number of insects caught increased with increasing distance between grouped traps. Moreover, ground sleep sites caught fewer insects than arboreal sleep sites. In addition, traps associated with *Cynometra alexandri* trees resulted in significantly lower catch rates than *Pseudospondias microcarpa*–associated traps. Our results suggest wild chimpanzees use group sleep as a strategy to avoid biting insects that serve as hosts for vector-borne diseases.

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Introduction

For most animals, vulnerability to a wide range of threats increases during sleep (Lima *et al.* 2005). A critical factor that influences sleep is the sleep site, which for mammals can function to facilitate social bonds and can reduce thermodynamic stress, predation risk, and exposure to infectious diseases (Capellini *et al.* 2008; Lesku *et al.* 2006; Lima and Rattenborg 2007; Nunn and Heymann 2005). Disease exposure can be viewed as a constraint on group size and a cost to sociality (Nunn 2012; Schülke and Ostner 2012), yet studies report varied associations between parasitism and group size (Rifkin *et al.* 2012); group size (as a proxy for density) is expected to favor the establishment of infections (Altizer *et al*. 2003; Nunn *et al.* 2008), and animals increase interaction with conspecifics in larger groups, resulting in more opportunities for parasite transmission (Dunbar 1991). Importantly, larger groups may attract more vectors, resulting in a greater proportion of individuals being infected with vector-borne parasites and pathogens (Davies *et al.* 1991; Nunn and Heymann 2005).

The encounter-dilution effect (Mooring and Hart 1992; Nunn and Altizer 2006) postulates that group living decreases the probability of attack by mobile parasites. Specifically, barring an increase in the number of insects attracted to a social group, social groups decrease the *per capita* vector-biting rate by distributing the risk of disease exposure across many individuals (Fauchald *et al.* 2007; Krebs *et al.* 2014; Rätti *et al.* 2006). In other words, if the chance of a vector consuming a blood meal does not increase proportionally with group size, then rates of new infections could be lower in larger groups, resulting in a lower prevalence in larger groups. Yet, empirical evidence for the encounter-dilution effect is mostly observational and shows mixed support in the few systems in which it has been studied, including primates, birds, and livestock herds (Krebs *et al*., 2014).

Relative to other mammals, primates are more social sleepers (Nunn *et al.* 2010), including the great apes (Fruth 1995; Fruth and Hohmann, 1996). Chimpanzees (*Pan troglodytes schweinfurthii*) select and manipulate their sleep environments in sophisticated ways that reduce thermoregulatory stress (McGrew 2004; Samson and Hunt 2012). In general, chimpanzees use their sleep environments to avoid predators (Baldwin *et al.* 1981; Pruetz *et al.* 2008; Stewart and Pruetz 2013), reduce exposure to vector-borne pathogens (Anderson 1998; McGrew 2004; Samson *et al.* 2013), and avoid human activity (Tagg *et al.* 2018; Tagg *et al.* 2013). Thus, in response to such ecological pressures, group sleeping and sleep site selection in chimpanzees may be an adaptive behavioral counterstrategy. By decreasing pathogen exposure, individuals could improve sleep quality with significant, positive consequences to daytime energy allocation, health, and cognition (Fruth *et al.* 2018). Ape sleeping platforms provide a barrier between primate hosts and soil parasites (Anderson 1998; Landsoud-Soukate *et al.* 1995). Apes typically make a new sleeping platform each night, which may reduce platform reuse and the buildup of parasites in sleep sites (MacKinnon 1974; Moore and Wilson 2002). Given that mosquitoes often show preferences for foraging at different heights (Lourenço-de-Oliveira and Luz 1996), it has been hypothesized that sleeping sites should be found at heights that avoid overlap with vector-specific microhabitats to reduce contact with arthropods (Nunn and Heymann 2005). However, a study in a wild chimpanzee habitat in the Nimba Mountains of Guinea concluded that mosquito densities were not a significant selection pressure that influenced choice of

sleep sites, finding no evidence that height was predictive of disease vector density (Koops *et al.* 2012). In another study, however, arboreal sleeping platforms were associated with reduced risk of bites from disease vectors (Stewart 2011). Lastly, the tree species used for building a sleeping platform may impact insect biting rates. For example, chimpanzees at the Toro-Semliki Wildlife Reserve prefer building sleeping platforms in the tree species *Cynometra alexandri* (Samson and Hunt 2014), which have insect-repellant properties (Samson *et al.* 2013).

Given there have been few tests of the encounter-dilution effect in natural systems—and none that we are aware of in wild chimpanzees—we conducted an experimental test of the encounter-dilution effect in relation to chimpanzee sleep site configurations and locations. To investigate the links between environmental and social factors that influence insect exposure at sleep sites, we tested a prediction stemming from the encounter-dilution effect hypothesis: sleeping in a group reduces insect exposure. We also tested an ecological hypothesis that is not mutually exclusive of the encounter-dilution effect: sleeping arboreally with protective tree species reduces insect exposure. We used insect light traps to experimentally test the predictions. Thus, based on the encounter-dilution effect hypothesis, we predicted that baited traps placed in groups would catch fewer insects per trap (including female mosquitoes that can vector malaria) than single traps, and that there would be a positive association between catch rate and distance from one trap to another within that trap group. Based on the ecological hypothesis, we predicted arboreal traps would catch overall fewer insects than terrestrial traps and that traps associated with preferred tree species (i.e., *Cynometra alexandri*) would catch fewer insects than traps associated with a less preferred tree species.

Methods

Study Site and Data Collection

The research took place at an established chimpanzee field site to ensure that vectors and forest structure are relevant for applying our findings to chimpanzees. Chimpanzees have been studied in the Toro-Semliki Wildlife Reserve (TSWR) in western Uganda since 1996. Semliki is northwest of Fort Portal, close to the eastern edge of the Great Rift Valley (0°50′ to 1°05′N, 30°20′ to 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 biome is predominantly dry *Combretum* savanna and *Borassus* palm savanna.

During a 12-month study period (July 2014–July 2015), we employed four CDC New Standard Miniature Light Traps (with PhotoSwitch and Air-Actuated Gate System) in the Semliki gallery forest habitat to capture flying insects on 74 data collection nights (total traps deployed $N = 294$). The PhotoSwitch and Air-Actuated Gate System allowed traps to automatically activate at dusk (19:05 h) and deactivate at dawn (07:00 h). We baited traps using a BG-Lure (BioQuip Products), an effective nontoxic chemical mosquito attractant that releases a combination of lactic acid, ammonia, and fatty acids (Roiz *et al.* 2012). We emptied traps into killing jars at the time of trap

deactivation in the morning, with a small amount of pure ethanol for further specimen processing. We preserved insects for later identification (between mosquito and non-mosquito) and sexing.

We sequentially performed three experiments. In the first experiment (July–November 2014; Fig 1), we collected data by setting up four traps within the gallery forest 1 m above the ground in two conditions: a single-trap condition (i.e., one trap) and grouped trap condition (i.e., three traps set up in a triangle formation). We repeated this procedure for 31 nights. To minimize interaction between the single-trap and grouped trap condition the traps were located >20 m from each other. For the grouped traps, each night we randomly assigned one of three possible trap-to-trap distances (1.5 m, 5.2 m, and 8.9 m). We derived the number of traps and trap distances from previous sleeping platform (i.e., nest or bed) distribution data at Semliki (Hunt *unpubl. data*), where the mean number of platforms within a sleep cluster was 3.4 ± 3.1 and the platform-to-platform distance within a sleep cluster was 5.2 ± 3.7 m. Therefore, we used these values to inform the three potential grouped trap distances by using the standard deviation (1.5 m and 8.9 m) and the mean (3.4 m) to inform the per night, randomly assigned trap distances.

The second experiment was identical to the first but was performed in a savanna-woodland habitat at Semliki and repeated for 23 nights between February 2015 and May 2015.

We repeated the third experiment for 20 nights from between June and July 2015 in the gallery forest, but with a different protocol. We paired the traps into two conditions, where one trap was placed terrestrially (1 m from the ground) and the other arboreally (10 m above the ground) in association between either a highly preferred sleep site tree species *Cynometra alexandri* or with the least preferred (but still selected) tree-species *Pseudospondias microcarpa*.

Data Analysis

We conducted analyses in R Development Core Team 2016. We analyzed both biting insects and mosquitoes, as individual chimpanzees may not be able to differentiate between biting species. For experiment 1, we used a Bayes factor (Morey *et al.* 2015)
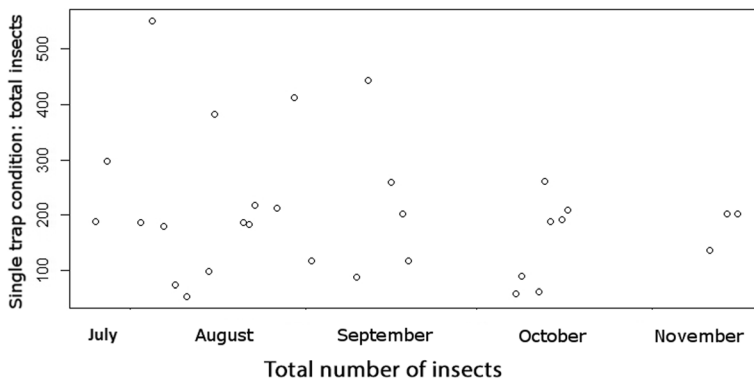

Fig. 1 A distribution of total insects caught in the single-trap condition in the gallery forest in a study of chimpanzee sleep sites at the Toro-Semliki Wildlife Reserve, Uganda, July–November 2014.

analysis to assess the difference in catch loads (while controlling for the date the trap was caught) between single and grouped conditions. We used a general linear model to compare the single-trap condition and the grouped trap condition to evaluate the difference in individual trap catches as a function of trap condition (corrected for distance) based on the change in number of female mosquitoes captured. Specifically, the response variable was calculated as the total number of female mosquitoes caught in the single trap condition subtracted from the average number of female mosquitoes caught in the grouped condition on the same night.

$$\text{Model 0:} \Delta \text{ female mosquito catch} \sim \text{trap condition} + \text{distance}$$

In addition, to assess the predictors of total insect exposure (proxied by insect catch load), we built a linear mixed effects model for the total insects caught using the lme4 package (Bates *et al.* 2015). In this model, we controlled for temporal effects (i.e., seasonal and daily) by identifying trap date (i.e., date on which the trap was set) as a random effect. The fixed effects in the model were predictors of trap condition (single, paired, or grouped), distance between traps (if paired or grouped), habitat (gallery forest or savanna), location (terrestrial or arboreal), and associated tree species (*Cynometra alexandri* or *Pseudospondias microcarpa*).

$$\text{Model 1 : Insect catch} \sim \text{trap condition} + \text{distance} + \text{habitat} + \text{location} + |\text{trap date}|$$

We ran a model without the savanna variable to control for collinearity between habitat and date in which the traps were distributed. However, this did not qualitatively change the results for any of the predictor variables. Thus, we included the savanna variable in the model. We obtained estimates using log-likelihood optimization. To average the models with $\Delta \text{AIC} < 10$, we used the MuMIn package (Bartoń, 2015). Statistical inferences were made using standardized coefficient estimates with shrinkage and 95% confidence intervals.

Ethical Note

At all times, research was conducted in accordance with the laws of Uganda and was approved by Duke University.

Data Availability The data will be provided on reasonable request to the author DRS.

Results

In all, 294 traps collected a total of 66,545 insects, which were classified as mosquitoes ($N = 3690$) or non-mosquitoes ($N = 62,855$). A Bayes factor analysis (BF = 36,386.0, nighttime observation $N = 122$) showed extreme evidence in support of a difference between the gallery forest that captured more total insects in the single traps (mean =
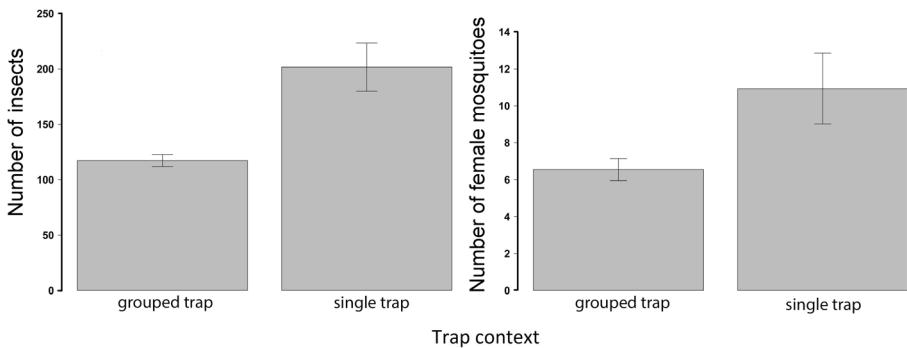
Fig. 2 Mean ± standard deviation trap catches for all insects and female mosquitoes in a single-trap condition and a group trap condition in a study of chimpanzee sleep sites at the Toro-Semliki Wildlife Reserve, Uganda, July 2014–May 2015.

201.6 ± 118.7) than the grouped traps (mean = 117.2 ± 52.9). A similar effect of strong evidence in support of a difference was found for female mosquito catches (BF = 10.1, nighttime observation $N = 122$), as the single traps (mean = 11.0 ± 10.3) captured more than the traps within the group (mean = 6.5 ± 5.7; Fig. 2). When compared to the three distances, single traps always caught more insects and female mosquitoes compared to individual traps within the group (Table I).

The distance between lures significantly predicted catch size (Table II and Fig. 3). This difference was predicted by distance (Table II). In other words, a grouped trap condition that involved traps placed closer together attracted fewer female mosquitos, as compared to traps that were spaced farther apart. Thirty percent of the variance in trap catches within the group condition was explained by distance ($R^2 = 0.30$).

The linear mixed-effects model, encompassing all experiments, showed several influences on total insect capture numbers (Table III). The confidence intervals on the estimates for grouped traps, trap distance, habitat, location, and associated tree species did not overlap with zero, suggesting they have a consistent effect on insect exposure. Based on the standardized coefficient from the model (Fig. 4), overall insect exposure was lower in grouped trap contexts and when associated with tree species *Cynometra alexandri alexandri*. In contrast, exposure was higher in grouped traps that were placed farther apart, in arboreal locations, and in savanna habitats.

Table I Comparison of total insect and female mosquito catches among three grouped trap distances in a study of chimpanzee sleep sites at the Toro-Semliki Wildlife Reserve, Uganda, June 2014–July 2015

	Distance 1 (1.5 m)		Distance 2 (5.2 m)		Distance 3 (8.9 m)	
	Mean ± SD	Exposure increase (%)	Mean ± SD	Exposure increase (%)	Mean ± SD	Exposure increase (%)
Total: Single	220 ± 138	98.2	200 ± 97	77.0	191 ± 141	51.6
Total: Group	111 ± 52		113 ± 52		126 ± 56	
Female mosquitoes: Single	19 ± 13	137.5	9 ± 8	80.0	8 ± 7	14.3
Female Mosquitoes: Group	8 ± 7		5 ± 5		7 ± 6	

Table II Parameter estimates as a function of distance reflecting the total change in insect load catches between the single and grouped traps in a study of chimpanzee sleep sites at the Toro-Semliki Wildlife Reserve, Uganda, June 2014–July 2015

	Estimate	Std. error	t_{obs}	*P* value
Intercept	11.9	2.6	4.6	<0.001
Distance 2 (5.2 m)	−8.8	3.3	−2.7	= 0.010
Distance 3 (8.9 m)	−12.2	3.3	−3.6	= 0.001

Discussion

We found support for the encounter-dilution hypothesis. The grouped traps factor ranked the most important in predicting overall insect exposure in statistical models that included fixed effects of habitat (gallery forest vs. savanna), trap location (arboreal or terrestrial) within the gallery forest, and associated tree species and random effects of the date (accounting for seasonal and daily variation in insect prevalence) in which the trap was set. Thus, single traps caught more insects, including female mosquitoes, than grouped traps. In addition, the distance between traps within the grouped context influenced the number of insects captured, with greater numbers of insects caught (including female mosquitoes) in traps that were spaced farther apart. These effects were strong and predictive. Relative to the single-trap condition, for example, closely grouped traps (1.5 m apart in a triangle formation) showed greater protective effects against insect exposure than traps grouped farther apart (5.2 m or 8.9 m), with a decrease in absolute insect exposure and in female mosquito exposure.

Our findings provided mixed results for the ecological hypothesis, which predicted arboreal traps would catch overall fewer insects and that traps associated with preferred tree species would catch fewer insects. Specifically, our statistical model revealed that
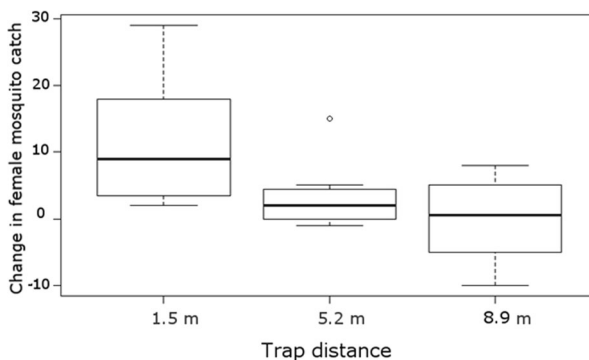

Fig. 3 A boxplot illustrating the difference of inferred mosquito exposure as a function of trap distance in a study of chimpanzee sleep sites at the Toro-Semliki Wildlife Reserve, Uganda, July 2014–May 2015. The *y*-axis, *difference in female mosquito catch*, is the total number of female mosquitoes caught in the single-trap condition subtracted from the mean number of female mosquitoes caught in the group condition. Thus, a greater value on the *y*-axis is associated with a greater overall change (reduction) in the number of female mosquitos caught in closely spaced group traps relative to the single trap. The black solid line in the box represents the median and the upper and lower bounds of the box represent the upper and lower quartiles, and the upper and lower whiskers represent scores outside the middle 50%.

Table III The effect of predictor variables on insect exposure (i.e., catch load) in a study of chimpanzee sleep sites at the Toro-Semliki Wildlife Reserve, Uganda, June 2014–July 2015

Predictor	Estimate and SE	Confidence interval	z	Importance
Traps grouped	−0.38 (0.08)	(−0.542, —0.225)	4.74	1.00
Trap location: Arboreal	0.20 (0.03)	(0.137, 0.266)	6.14	1.00
Distance between traps	0.19 (0.08)	(0.024, 0.355)	2.25	0.81
Tree species: Cynometra	−0.07 (0.03)	(−0.138, −0.010)	2.26	0.81
Habitat: Savanna	0.23 (0.11)	(0.023, 0.441)	2.17	0.78

Ground is the reference category for "location," *Pseudospondias* is the reference category for "species," *single* is the reference category for "trap context," and *gallery forest* is the reference category for "habitat." Positive coefficients indicate greater insect catches, while negative coefficients indicate lower insect catches. The total *N* for traps caught and counted in the model was 294. *Importance* is the relative variable importance as a measure of the AIC-weighted number of times the variables was included in model averaging, where the greater number of times a variable is included in the model increases overall variable importance.

trap location was the most important predictive factor, yet counter to our prediction, terrestrial traps showed less exposure to insects than arboreal traps in the gallery forest. Interestingly, these results add to a list of advantages to sleeping on the ground that have recently been discovered. In Cameroon, research found that ground nesting occurred more frequently in the dry season and in swamps during periods of greater human activity—suggestive of a strategy to avoid human hunting (Tagg *et al.* 2013, 2018). Moreover, research at Semliki found that 1) recumbent bodies are more stable sleeping on the ground than in arboreal sites, where wind gusts can disrupt and dislodge sleepers, and 2) terrestrial microclimates have greater homeostatic potential (i.e., less thermodynamic stress) than arboreal microclimates (Samson and Hunt 2012). Previous work at numerous wild chimpanzee sites supports predation as a primary driver for
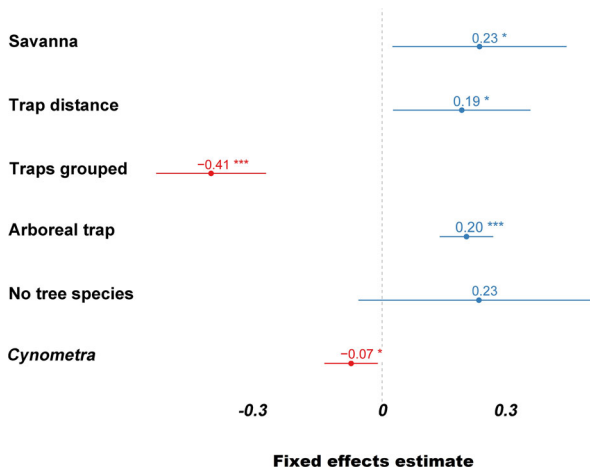

Fig. 4 A standardized fixed effects plot of arboreal (vs. terrestrial) location, trap distance (within a group), and the savanna habitat in a study of chimpanzee sleep sites at the Toro-Semliki Wildlife Reserve, Uganda, July 2014–July 2015. Overall positive predictors of insect exposure are illustrated in blue whereas negative predictors are illustrated in red. The *x*-axis indicates the position of the estimate relative to the "neutral" line (i.e., the vertical intercept that indicates no effect). Asterisks indicate levels of significance.

building sleeping platforms arboreally (Stewart and Pruetz, 2013), as approximately 95% of West African chimpanzee nighttime sleep sites are arboreal (Furuichi and Hashimoto 2000; Maughan and Stanford 2001). In East Africa, however, in the mountains of Guinea and Côte d'Ivoire terrestrial sleeping site frequencies are particularly high (Humle and Matsuzawa 2001)—as great as 35.4% (Matsuzawa and Yamakoshi 1996). These effects may explain why chimpanzees sleep terrestrially more often at sites where predation is low (Koops *et al.* 2012; Kortlandt 1992; Matsuzawa and Yamakoshi 1996; Pruetz *et al.* 2008; Stewart and Pruetz 2013). The results from this study suggest that reduction of insect exposure is an additional advantage and driver of ground sleeping.

Our analyses revealed that tree species association with traps was the second most important predictor of insect capture rate. Specifically, traps associated with tree species *Cynometra alexandri* resulted in significantly lower catch numbers than *Pseudospondias microcarpa* associated traps. Intriguingly, eastern chimpanzees at three relatively dry sites in Uganda—Ishaha (Sept, 1992), Budongo (Brownlow *et al.* 2001), and Toro-Semliki (Hunt and McGrew 2002)—show a strong preference for *C. alexandri* as a tree species with which to construct sleeping platforms. *C. alexandri* exhibits biomechanical properties that make it a firm, stable, and resilient sleeping platform, which may explain why 74.5% of the sleeping platforms recorded at Semliki have been constructed using this species despite representing only 9.6% of trees in the gallery forest (Samson and Hunt 2014). In addition, a particular biological aspect of sleeping platforms is the release of chemical compounds that repel arthropods or mask animal odor (Stewart 2011), as exemplified by orangutans who occasionally cover their sleeping platforms with branches from tree species with known mosquito-repellent properties (Largo *et al.* 2009). Although the underlying mechanisms remain unknown, previous experimental work showed that *C. alexandri* reduced potential insect exposure for night sleeping chimpanzees (Samson *et al.* 2013). Thus, our results corroborate previous research showing that chimpanzee sleeping platforms can have tree-species-specific functions that reduce pathogen exposure.

Limitations to the study were related to the resource intensive nature of setting up and processing catches from daily traps. The range of different possible combinations of conditions could not be included owing to limitations in CDC light traps and chemical lures brought into the field. Also, the chemical attractants, although standardized, have yet to be tested specifically in a chimpanzee context and thus the appropriateness of these lures to this study remains unknown. Future research should attempt to assess other factors that may be driving insect prevalence, such as setting up more single traps throughout a longitudinal study to better understand how microclimate influences the behavior of different insect vector species. In addition, future research can comparatively assess favored sleep-site tree species among all the great apes, including bedding materials used by hunter-gatherers to test for and identify physical and chemical properties that confer benefits for their use. Similarly, comparative research in great apes and hunter-gatherers could focus on the effects of group-level spatial organization on insect exposure.

Our findings have implications in the context of the tree-to-ground transition in human evolution (Coolidge and Wynn 2006), specifically regarding why early humans adopted a full-time terrestrial sleep environment. As a dry-habitat chimpanzee site, Semliki offers a mosaic of riverine forest, open woodland, and savanna grassland with

species composition, dietary demands, thermoregulatory stresses, and predation risk similar to those of early hominins (Hunt and McGrew 2002; McGrew *et al.* 1996). If early hominins innovated a variety of antipredation strategies, similar to strategies used by modern hunter-gatherers—such as fire (Wrangham and Carmody 2010), nighttime socially protected and sentinelized (i.e., where a proportion of individuals are awake while other individuals are unconscious) sleep environments (Samson *et al.* 2017), and the construction of protective structures (Worthman and Melby 2002)—then they could have taken advantage of the increased stability, reduced thermoregulatory stress, and reduced pathogen exposure of terrestrial sleep sites. Similarly, human sleep architecture is unique among primates, with humans showing the shortest sleep and highest proportion of REM sleep (Nunn and Samson 2018). Thus, sleep physiology may have evolved in response to novel conditions on the ground, selecting for more efficient sleep that is shorter and deeper (Samson and Nunn 2015). Shorter total sleep durations would have permitted longer periods of activity in which to acquire and transmit new skills, while deeper sleep may have been critical for the memory consolidation of those skills, leading to enhanced cognition in early humans (Fruth *et al.* 2018; Samson and Nunn 2015).

In summary, our study supports the encounter-dilution hypothesis in a chimpanzee dry-habitat vector-borne disease system. Specifically, the formation of groups at chimpanzee sleep sites may be influenced by a "selfish herd" behavior, in which individuals dilute their risk of insect attacks by sleeping in groups. These findings contribute to a growing body of literature that reveals the importance of evolutionary changes in sleep along the human lineage and identifies areas of future research in which to further probe these questions.

Author Contributions   DRS, KDH, and CLN conceived and designed the experiments. DRS, LAL, KG, SW, BL performed the experiments. DRS, BJW analyzed the data. DRS wrote the manuscript; other authors provided editorial advice.

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