

Segmented sleep in a nonelectric, small-scale agricultural society in Madagascar

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Funding information

Duke University and BASS Connections

Abstract

Objectives: We studied sleep in a rural population in Madagascar to (i) characterize sleep in an equatorial small-scale agricultural population without electricity, (ii) assess whether sleep is linked to noise levels in a dense population, and (iii) examine the effects of experimentally introduced artificial light on sleep timing.

Methods: Using actigraphy, sleep–wake patterns were analyzed for both daytime napping and nighttime wakefulness in 21 participants for a sum total of 292 days. Functional linear modeling was used to characterize 24-h time-averaged circadian patterns and to investigate the effect of experimentally introduced mobile field lights on sleep timing. We also obtained the first polysomnography (PSG) recordings of sleep in a traditional population.

Results: In every measure of sleep duration and quality, the Malagasy population experienced shorter and lower quality sleep when compared to similarly measured postindustrial values. The population slept for a total of 6.5 h per night and napped during 89% of recorded days. We observed a peak in activity after midnight for both sexes on 49% of nights, consistent with segmented sleep. Access to mobile field lights had no statistical effect on nighttime sleep timing. From PSG, we documented relatively short rapid eye movement (14%), poor sleep efficiency (66%), and high wake after sleep onset (162 min).

Conclusions: Sleep in this population is segmented, similar to the “first” sleep and “second” sleep reported in the historical record. Moreover, although average sleep duration and quality were lower than documented in Western populations, circadian rhythms were more stable across days.

1 | INTRODUCTION

Our understanding of sleep mechanisms, physiology, and chronobiology has burgeoned over the past 50 years (Campbell & Tobler, 1984; Carskadon & Dement, 2005; Heller, 2005; Mistlberger & Rusak, 2005; Zepelin, Siegel, & Tobler, 2005). However, the sample from which researchers have generated human data has primarily drawn from postindustrial populations from the United States, Europe, and Japan (Knutson, 2014). In contrast, remarkably little is known about the sleep of traditional populations that experi-

ence natural lighting (henceforth, nonelectric populations). These populations practice largely subsistence patterns including foraging, small-scale agriculture, horticultural, and pastoralist strategies, and their lives are more closely linked to natural daily and seasonal rhythms. The cross-cultural study of sleep architecture, sleep quality, sleep–wake phasing, and circadian rhythms is thus in its infancy (McKenna, Ball, & Gettler, 2007; Worthman, 2008; Worthman & Melby, 2002).

Recent advances in understanding sleep in nonelectric populations arise from increasing adoption of actigraphy, a

wrist-worn portable device that can be used in longitudinal and naturalistic sleep studies across the globe. Specifically, actigraphy has been used to assess sleep in developing countries (de la Iglesia et al., 2015; Knutson, 2014) and to characterize sleep in preindustrial societies (Yetish et al., 2015) and high-latitude populations with long photoperiods (Calogiuri & Weydahl, 2013; Paul, Love, Hawton, & Arendt, 2015). Understanding variation in human sleep patterns has important implications for global health and health disparities, given that sleep loss has been linked with impairments in mental health, immune function, glucose metabolism, inflammation, appetite regulation, cardiovascular disease, and neurobehavioral performance (Besedovsky, Lange, & Born, 2012; Bonnet, 1989; Dinges et al., 1997; Miller & Cappuccio, 2007; Natale, Plazzi, & Martoni, 2009; Simpson & Dinges, 2007; Spiegel, Knutson, Leproult, Tasali, & Van Cauter, 2005; Wright, Valdimarsdottir, Erblich, & Bovbjerg, 2007; Wyatt, Ritz-De Cecco, Czeisler, & Dijk, 1999). Importantly, these data are essential in the investigation of sleep and evolutionary mismatch, where changes in sleep ecology from our ancestral past have diverged in ways that have created new health problems for modern humans (Nunn, Samson, & Krystal, 2016).

In humans, the master circadian clock (ie, suprachiasmatic nucleus) induces alertness and entrains the timing of sleep in relation to exposure to light. Thus, whether artificial or natural, light is considered one of the most important environmental factors regulating sleep (de la Iglesia & Lee, 2014). In the past 50 years, evidence indicates a decline in the average sleep duration and quality in the United States (Czeisler, 2013), and much of this decline has been attributed to the overexposure to artificial light. Moreover, 90% of Americans use electronics, which emit short-wavelength “blue” light that can suppress melatonin (Chang, Aeschbach, Duffy, & Czeisler, 2015). In addition, de la Iglesia et al. (2015) reported evidence that a historically huntergatherer indigenous Toba/Qom community in Argentina shows shorter total sleep times and later sleep onset times after they acquired access to electricity (and artificial lighting).

High-density populations in the developing world are also associated with high levels of noise (Libert et al., 1991; Moudon, 2009; Tsai, Lin, & Chen, 2009). These noisy environments may contribute to lower sleep duration and quality and may, in turn, generate negative health outcomes, such as hypertension (Bathgate, Edinger, Wyatt, & Krystal, 2015; Gangwisch, 2014; Gangwisch, Feskanich, Malaspina, Shen, & Forman, 2013; Ibrahim & Damasceno, 2012; Kowal et al. 2012) and obesity (Goodfriend & Calhoun, 2004). Traditional populations lack environmental barriers that are common in postindustrial societies, such as insulated, temperature- and humidity-controlled buildings that blunt noise and other environmental factors that influence sleep,

including lunar phase. Thus, circadian rhythms may have greater stability in non-Western populations that have more exposure to their natural environments.

The question of sleep timing has received attention from both empirical and historical researchers interested in describing the traditional human sleep–wake pattern. In an attempt to characterize “natural” human sleep, recent studies have compared sleep in humans and nonhuman primates (Samson & Nunn, 2015) and investigated more recent effects of artificial light on postindustrial human circadian patterns (de la Iglesia & Lee, 2014). Ekirch (2001, 2006) used historical records as the basis for proposing that segmented sleep (ie, sleep divided into a “first” and “second” period) was common in both preindustrial Europe and equatorial populations (Ekirch, 2016). Similarly, early studies conducted in laboratory conditions showed that, when exposed to an experimentally short photoperiod, human sleep became unconsolidated (Wehr, 1992, 1999). Moreover, field anthropologists, working in a variety of cultures with differing subsistence strategies, often characterize nighttime activity and daytime napping as common (Worthman, 2008; Worthman & Melby, 2002).

In contrast to these suggestions of segmented (or flexible) sleep, empirical work from Yetish et al. (2015) reported that sleep patterns in three equatorial foraging societies is characterized by low-frequency napping and an absence of segmented, or bimodal sleep. Thus, the question of human sleep segmentation is an active avenue of research, and it seems likely that cultural and environmental factors modify sleep patterns through space and time. The main approach to addressing these factors is to obtain data from traditional populations without access to electricity, and with those data, to investigate the flexibility and consolidation of human sleep in relation to environmental, social, and cultural variation.

The primary aims of this study were to (1) characterize sleep in an equatorial, nonelectric, small-scale agricultural society in Madagascar, (2) compare sleep duration, quality, timing, and circadian rhythm to previously reported postindustrial values, and (3) experimentally test the effects of access to mobile field lighting on circadian activity. We obtained actigraphy data and, to our knowledge, the first polysomnography (PSG) data from a traditional human population. We used the actigraphy data to test the following hypotheses:

- Under the *postindustrial sleep degradation hypothesis*, we predict that sleep duration (total sleep time) and quality (ie, sleep efficiency and fragmentation) will be greater in the Malagasy population, as this population lacks access to the electronic and other distractions that are thought to impact sleep in Western societies. Alternatively, under the *developing economy sleep degradation hypothesis*, we predict

TABLE 1 Study sample characteristics for full sample by sex

Sleep-wake measure	Men	Women	Significance
Sleep onset	19:26 (3:21)	19:37 (3:58)	$Z = 0.49, p = 0.62$
Sleep end	05:44 (0:39)	5:26 (1:04)	$Z = 0.33, p = 0.73$
Sleep latency (h)	0.63 (1.48)	0.43 (0.47)	$Z = -0.15, p = 0.88$
Time in bed (h)	9.5 (1.8)	9.3 (1.5)	$Z = -0.83, p = 0.40$
Sleep duration (h)	6.6 (1.3)	6.5 (1.8)	$Z = -0.57, p = 0.57$
Wake after sleep onset (h)	2.1 (0.99)	2.15 (0.79)	$Z = 0.72, p = 0.47$
Sleep efficiency (%)	69.6 (13.9)	70.4 (9.7)	$Z = 0.02, p = 0.98$
Sleep fragmentation	43.6 (16.7)	38.9 (10.9)	$Z = -1.39, p = 0.17$
Cumulative night-time activity	13911 (7774)	11167 (7317)	$Z = 2.65, p < 0.01$

Data are presented as mean (standard deviation).

P values are from Mann-Whitney test for a subset of baseline (ie, nonexperiment) nights (male $n = 76$; females $n = 58$).

that sleep is impaired due to excessively noisy environments (resulting from increasing population density) and the continued use of traditional housing, which offers little noise and temperature buffering. This hypothesis predicts that sleep duration will be lower in the Malagasy population, and that noise levels will be linked to sleep-wake patterns. Additionally, dynamic environments are predicted to influence sleep architecture by reducing the relative proportion of deep-sleep stages, such as rapid eye movement (REM), where awareness of environment is at its lowest.

- In addition, under the *circadian entrainment hypothesis*, we predict that circadian rhythms will be more stable and uniform (ie, sleep-wake cycles will be less variable between individuals) across days in the Malagasy population than in a postindustrial population.
- Finally, if the *sleep segmentation hypothesis* is supported, we predict that sleep-wake patterns in the Malagasy population are segmented—as has been suggested in other populations without access to electricity—and that access to artificial field lights will consolidate sleep-wake patterns.

2 | METHODS

2.1 | Study location and participants

A sample of Malagasy adults was recruited from Mandena, Madagascar ($-14^{\circ}37'47''\text{S}$, $49^{\circ}11'11''\text{E}$) as part of a larger project designed to identify health risks in developing countries. Mandena—a high density, equatorial rural community of approximately 4000 people (within 1 km^2)—is located adjacent to the Marojejy National Park in northeastern Madagascar. This population is a small-scale agricultural society.

Rice farming is a dominant profession. Domesticated species of animals include zebu, pigs, and chickens, and individuals grow cash crops, such as vanilla and spices. The village has no infrastructure for electricity although some individuals in the village have generators or solar panels. Sleep is usually located within wooden homes, where room-sharing and co-sleeping is common.

Given there were several concomitant protocols and studies being performed during the same research period, we subset data in multiple, analysis-dependent ways. In particular, we removed incomplete data (eg, in cases of equipment malfunction or individuals removing watches for periods of time) with a remainder of 21 individuals that resulted in a total of 292 nights of complete data. For the light experiment, we compared baseline (no light) against the experiment (light access) condition, and we used the 24 h periods ($n = 124$) of data generated from these individuals in the baseline condition to compare male and female differences in sleep quotas (Table 1). Eighteen of the 21 individuals were farmers, eight of which took part in the experimental study and were removed from the NPCRA; thus, we further restricted NPCRA data to 10 individuals with longitudinal data (with an average of 12.1 consecutive nonexperimental 24 h periods). These participants had the required number of consecutive days for the analysis to be considered valid and were engaged in the agriculture process by profession.

The study was conducted between July 2 and August 20, 2015 and July 1 and August 1, 2016. Day length during this time of year ranged between 11.28 and 11.57 hours. Sunrise occurred between 06:00 and 6:20 and sunset occurred between 17:24 and 17:34. We recorded domicile type (basic = absence of cement base, bamboo walls, and thatched roof; moderate = cement base, bamboo walls, tin

roof; complex = cement base, tin walls, and roof). Additionally, household size (total number of individuals living in one house), children per household, lunar phase, and day length were recorded from the Astronomical Applications Department of United States Navy (<http://aa.usno.navy.mil/data>). Nursing status was not taken into account, which may have played a role in nighttime awakenings. We also distributed sound level meter data loggers (Noise Sentry: Convergence Instruments) to obtain dB levels within households. Each household that participated in the study had 2–3 nights of noise level data collection.

We performed a pairwise study design introducing the Coleman 400 lumens field light into an experimental *access-to-lighting* group to compare against a control *no-lighting* group. After 10 days in which baseline actigraphy data were generated for all participants (males = 5, females = 5, total $n = 10$, age range = 19–59 years), we distributed field light to five participants. After 7 days, we swapped experimental and control groups, giving the previous control group of five participants the field lights. The goal of this experiment was to compare sleep patterns between groups with and without lights, holding constant total day length and other environmental variables. Motionwatches are equipped with light sensors, which we used to verify that subjects who were given lights used them, as indicated by greater exposure to light at night than subjects without access to lights (see below).

We conducted an initial survey at the beginning of the study period with assistance from local Malagasy translators. During health screening associated with this survey, we collected data on body mass and height. All eligible subjects gave their written informed consent as outlined by the Institutional Review Board for human subjects research at Duke University. Written signed consent was obtained after verbally explaining the study and reading the consent form to the participants, in the participant's native language. Exclusion criteria included self-reported insomnia or physical disability due to injury or infirmed status that prevented the individual from engaging in occupational activity.

2.2 | Actigraphy and polysomnography

We used the Motionwatch 8 actigraph (CamNtech), with all devices configured to generate data in 1 min epochs. Participants were asked to press the event marker preceding any sleep event throughout the study, including sleep after nighttime wake bouts and before initiating daytime naps. Actigraph data were scored using CamNtech MotionWare 1.1.15 software. The software has a nap analysis function that allows for the detection of periods of inactivity that are attributable to napping or microsleeps; specifically, the software has adjustable parameters such as *nap activity threshold* and the *minimum – maximum nap length*. We used seg-

mented sleep parameters that have been validated for use in field environments using actigraphy (Samson et al. 2016) for both daytime sleep (ie, napping) and nighttime wakefulness (ie, wake-bouts). *Nap activity threshold* (50 counts) is the level at which the epoch within the specified period must be less than or equal to the entered value for the period to be scored as a nap. The *minimum nap length* (15 min) sets the minimum period of inactivity required to be scored as a nap. *Max nap length* (210 min) sets the maximum period of inactivity required to be scored as a nap. We identified a *wake-bout* as a period of 20 consecutive epochs categorized as “awake” from the beginning of sleep onset until sleep end; these settings were validated by comparing reported, event-marked events to actigraphy-scored events using the Bland–Altman technique to determine concordance (Samson et al. 2016). Results of a previous actigraphy validation study revealed that the algorithmic high-sensitivity settings are most reliable for determining sleep (Kanady, Drummond, & Mednick, 2011). Therefore, we use the high-sensitivity (ie, 20 counts) threshold setting throughout this study.

On a subset of individuals, we used the Alice PDx (Philips Respironics) mobile PSG to assess sleep and wake activity during nighttime periods. The PSG measured electroencephalography (EEG), electromyography (EMG), and electrooculography (EOG). We used the American Academy of Sleep Medicine (AASM)-recommended EEG montages (Fz-Cz, C4-M1, Oz-Cz) (Duce, Rego, Milosavljevic, & Hukins, 2014) to ensure accurate sleep staging. PSG data were obtained on nine nights from nine subjects (male = 6; female = 3; average age = 32; range = 23–42) participating in the actigraphy study.

2.3 | Statistical analyses

Statistical analyses were conducted using *R* version 3.1.3 (2016). Descriptive statistics were generated to characterize sleep in the sample population. Results, including daytime nap and nighttime wake bouts, for both men and women were presented and compared using a Wilcoxon rank sum test. The population level values generated in this study were compared using sample statistics, in unpaired, two-sample student *t*-tests against values from actigraphy studies performed in postindustrial societies (Carnethon et al., 2016; Natale et al., 2009). Ideally, such comparisons would be made with similar devices (and device-specific algorithms of sleep–wake determination) and with industrialized locations at similar latitudes, yet to our knowledge, such data do not exist. On the other hand, it has been demonstrated that reliability estimates generated from devices with algorithms based on different mathematical principles results in similar reliability (Weiss, Johnson, Berger, & Redline, 2010); in general, validation studies show more than 90% agreement when compared with PSG, the gold standard in sleep studies

(Sadeh, Hauri, Kripke, & Lavie, 1995). Importantly, total sleep times are the most reliable measure and actigraphy is particularly valid when measuring healthy normal adults (Stone & Ancoli-Israel, 2011). Therefore, we specifically chose a control group compiled at the Laboratory of Applied Chronopsychology; this dataset consisted of 282 healthy, non-flexitime/night-shift subjects (117 male, 165 female) aged 38.5 ± 14 with no complaints of sleep disturbance or daytime symptoms due to unsatisfactory sleep (Natale et al., 2009). Moreover, we also include a cross-ethnicity sample of 496 healthy, non-flexitime/night-shift subjects (198 males, 298 females) aged 47.8 ± 8.2 from Chicago, Illinois in the United States.

Additionally, Nonparametric Circadian Rhythm Analysis (NPCRA) (Van Someren et al., 1999) was performed on the baseline data generated from the study sample to characterize circadian amplitude; these values were then compared using previously established methods (Calogiuri & Weydahl, 2013; Calogiuri, Weydahl, & Carandente, 2013) against a Western, postindustrial healthy control group of adults without sleep disorder symptoms (Rock, Goodwin, Harmer, & Wulff, 2014). Activity–rest data do not typically fit well with traditional Cosinor waveform analysis; thus, NPCRA does not assume that the data fit any predefined distribution and it used full days of data over several days to determine variables associated with circadian rhythms (Van Someren et al., 1999). Furthermore, in addition to traditionally reported nighttime sleep duration *total sleep time* (TST), we also summed TST with the sleep scored during the daytime and defined this measure as *true total sleep time* (TTST). Thus, TTST is the total sum of all sleep in a 24 h period. To test if TTST significantly adds to sleep duration, we ran a paired *t*-test between TTST and TST, predicting that the former would be significantly greater than the latter. All tests performed were two-tailed with significance set at the 0.05 level.

Functional linear modeling (FLM) was used to characterize and illustrate circadian activity. This approach measures raw, time-series activity within and between samples and is more effective than summary statistics, which can mask differences across groups (Wang et al., 2011). We applied an FLM nonparametric permutation test method in the R package “actigraphy” (Shannon et al., 2015) to test the effect of mobile field lights on activity patterns in a nonelectric population. If there is no relationship between activity pattern and access to mobile field lights, random rearrangement of the group assignment should make no difference to the results. An advantage of this method is that it does not rely on distributional assumptions. The *p*-value is calculated by counting the proportion of permutation *F* values that are larger than the *F* statistics for the observed pairing. Here, we used the pointwise test (with 500 permutations) that provides a curve,

which is the proportion of all permutation *F* values at each point in the time series (Wang et al., 2011). To verify that subjects with lights were exposed to more light than when they had no access to lights, we ran a Wilcoxon test (as lux exposure of non-normally distributed).

Finally, to assess the predictors of segmented sleep, we ran linear mixed effects models for each of our three response variables (wake-bouts, napping frequency, and nap duration) using the *lme4* package (Bates, Maecher, Bolker, & Walker, 2014), with the light experiment as the main predictor. In all models, we also included sex, age, number of children, household size, daylight, moon phase, and the experimental condition as predictor variables. To control for repeated measures, we included “participant” as a random effect, and we obtained coefficients based on optimization of the log-likelihood. We used the *MuMIn* package (Bartoń, 2014) to average models with $\Delta AIC < 10$. We then made statistical inferences using a combination of standardized coefficients, *p*-values, and confidence intervals.

3 | RESULTS

Results for the Malagasy sample characterizing both men and women are presented in Table 1. In sum, we generated data for 292 days of both day and night activities. Subject ages ranged from 19 to 59 years, with 9 females (mean age: 40.3 ± 4.6 S.D. years) and 12 males (mean age: 36.8 ± 11.5 S.D. years; $p = 0.37$); farming (88%) was the primary occupation of the sample. Average household size was 5.4 ± 2.1 S.D. No one slept in a room alone. Males were characterized by greater nighttime cumulative activity (Table 1).

Results for the comparison between the Malagasy sample and postindustrial populations are presented in Table 2. By every measure, the Malagasy population was characterized by shorter sleep duration and poorer sleep quality. In addition, all of our Malagasy subjects exhibited daytime napping. On average, individuals exhibited napping behavior during 88% of the days throughout the study period (males = 1.10 ± 0.27 S.E.; females = 0.69 ± 0.29 S.E.; total nap ratio = 0.88 ± 0.19 S.E.). The average total nap duration was 55.2 ± 5.0 S.E. min. Additionally, the Malagasy population can be characterized as having a consistent postmidnight increase in wakefulness (Figures 1 and 2); the average sleep segmentation ratio (ie, the number of nights where wake-bouts >20 consecutive epochs were identified) was 0.49 ± 0.07 S.E. (males = 0.69 ± 0.30 S.E.; females = 0.36 ± 0.23 S.E.). Thus, on average, individuals exhibited wake-bout behavior during 49% of the sleep periods analyzed. Forty-three percent of respondents (9/21 individuals surveyed during the 2016 season) reported that they awoke to urinate or defecate. TTST (403.4 ± 38.6 S.E.) was significantly greater than nighttime sleep (380.4 ± 36.4 S.E.), with

TABLE 2 Sleep quantified by actigraphy compared between subjects in Mandena, Madagascar ($n = 21$) and postindustrial samples with healthy, normal shift-working subjects^a

Sleep quota	Malagasy	Italy	USA	Significance
Sleep onset	19:21 (3:38)	00:03 (1:59)	N/A	$t = 4.06, p < 0.001$
Sleep end	05:44 (0:53)	08:13 (1:19)	N/A	$t = -9.15, p < 0.001$
Time in bed (hour)	9.4 (1.6)	8.1 (1.02)	N/A	$t = 5.48, p < 0.001$
Sleep latency (hour)	0.55 (1.15)	0.16 (0.09)	N/A	$t = 5.58, p < 0.001$
Sleep duration (hour)	6.5 (1.6)	7.60 (0.96)	7.02 (1.05)	Italy: $t = -4.88, p < 0.001$ USA: $t = -2.21, p = 0.027$
Wake after sleep onset (hour)	2.1 (0.9)	0.31 (0.22)	0.71 (0.34)	Italy: $t = 2.54, p < 0.001$ USA: $t = 2.26, p < 0.001$
Sleep efficiency (%)	70.7 (12.2)	94.2 (3.1)	89.9 (4.6)	Italy: $t = 2.41, p < 0.001$ USA: $t = -1.72, p < 0.001$
Sleep fragmentation	45.9 (16.4)	N/A	20.0 (7.7)	$t = 1.44, p < 0.001$

^aAll data for comparison are drawn from Western samples, including a healthy control group (age range: 7–65, total $n = 282$) based in Bologna, Italy (Natale et al., 2009) and healthy cross-ethnicity study including averages derived from Black, Asian, Hispanic, and White subjects (age range: 35–64, total $n = 496$) from Chicago, in the United States (Carnethon et al., 2016).

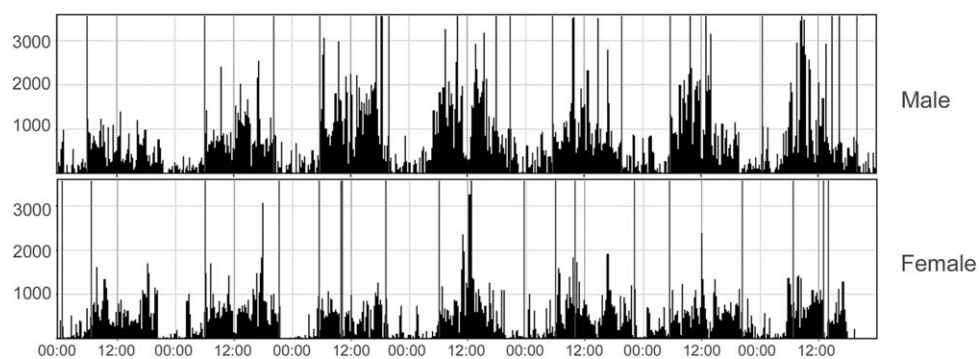
a mean difference in 23 min total sleep time ($t = -8.56$, $df = 258$, $p < 0.001$).

The NPCRA revealed stronger circadian amplitude in the Malagasy population compared to postindustrial populations, revealing less circadian fragmentation and more stability of rhythm (Table 3). Specifically, the Malagasy sample was characterized by greater interdaily stability and less interdaily variability. Notably, the M10 value for the Malagasy population was significantly greater, indicating that the average of activity values for the 10 most active consecutive hours in the 24 h cycle showed this population to be highly active compared to postindustrial populations.

The experimental group that had access to mobile field lights did not experience a phase shift in sleep–wake patterns during the nighttime sleep period. Moreover, we validated the experiment protocol by comparing the total lux sum measured after sleep onset and sleep end between the experi-

mental group ($995 \pm \text{S.E. } 149$) and the control group ($197 \pm \text{S.E. } 31$); the groups differed significantly (Wilcoxon test = $W = 2842$, $p < 0.001$), consistent with lantern use by the experimental group. We found a significant difference in circadian pattern from 11:00 to 12:00, with the light-access group experiencing a decrease in activity (Figure 3). We also discovered an association between noise level (expressed in the nightly average of maximum dB) and sleep–wake activity (Figure 4), where high dB values were related to increased activity during 03:00–04:00 and low dB values were related to decreased activity during 12:30–1:30.

After controlling for all covariates, access to lights had no effect on segmented sleep (wake after sleep onset or nap duration and frequency), yet nap frequency was increased in association to greater exposure to lunar illumination measured in proxy by lunar phase ($\beta \pm \text{SE} = 0.57 \pm 0.27$, $P = 0.04$, $\text{CI} = 0.02\text{--}1.11$) and day length ($\beta \pm \text{SE} = 0.37 \pm$

**FIGURE 1** Raw actigraphy data from a single male and female subject over 7 days

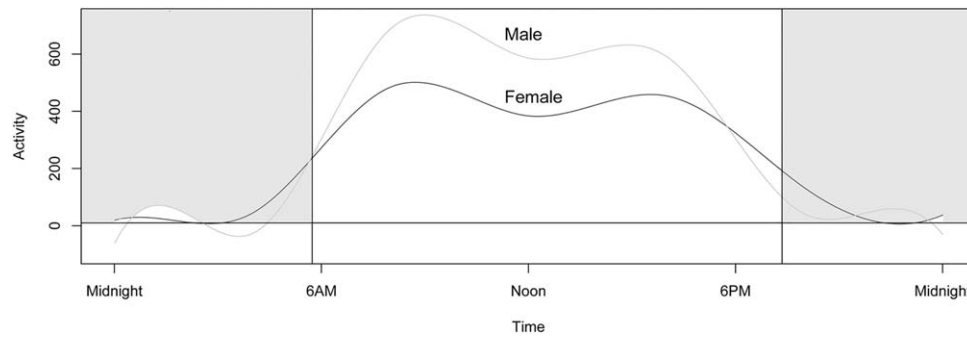


FIGURE 2 Functional linear modeling (FLM) illustrating circadian patterns among Malagasy females and males. The vertical lines are the population averages for sleep end and sleep onset based on visually assessed sleep start and end times; thus, the shaded areas are indicative of average “night-time” sleep periods. Notice the horizontal line is fixed at 20 for activity counts; we used this threshold for its high sensitivity to score awake vs. sleep (Kanady et al., 2011). Activity above the horizontal line—as assessed by the previously validated motionwatch algorithms—indicates sustained wakefulness behavior. Both females and males experienced a postmidnight increase in activity, although this was more pronounced in males

0.17, $P = 0.03$, $CI = 0.04$). Nap duration was increased in association with increased lunar phase ($\beta \pm SE, = 0.63 \pm 0.30, P = 0.04, CI = 0.05-0.71$) and day length ($\beta \pm SE = 0.38 \pm 0.17, P = 0.02, CI = 0.31-0.21$).

PSG analysis revealed low relative SWS, REM, and sleep efficiency and greater WASO as compared to Western

populations (Carskadon & Dement, 2005). The PSG group was performed mainly on Malagasy individuals living in the village, with two additional Malagasy individuals who were temporarily in the village as part of our research team. The analysis showed an average and standard deviation: time in bed (TIB) = 588.4 ± 37 min, total sleep time (TST) =

TABLE 3 Nonparametric Circadian Rhythm Analysis (NPCRA) comparing Malagasy and Rock et al. (2014) postindustrial sample

Parameter	Malagasy	Postindustrial	Significance	Definitions
Interdaily stability	0.51 (0.08)	0.44 (0.09)	$t = 2.09, p = 0.045$	Degree of resemblance between the activity patterns on individual days; ranges from 0 to 1 and may typically be about 0.6 for healthy adults
Interdaily variability	0.67 (0.16)	0.99 (0.19)	$t = -4.60, p < 0.001$	Quantifies the fragmentation of periods of rest and activity; ranges from 0 to 2 and typically is < 1 for healthy adults, with higher values indicating a more fragmented rhythm
L5	1420 (715)	1354 (583)	$t = 0.27, p = 0.78$	Average of the activity values for the 5 least active consecutive hours in the 24-h cycle
M10	33219 (11618)	21680 (4463)*	$t = 4.02, p < 0.001$	Average of the activity values for the 10 most active consecutive hours in the 24-h cycle
Relative amplitude	0.91 (0.05)	0.88 (0.05)	$t = 1.56, p = 0.13$	Calculated by dividing AMP by the sum of L5 and M10; ranges from 0 to 1, with higher values indicating higher amplitude of the rhythm
L5 onset	18:00	02:21		Onset time of the five most restful consecutive hours
M10 onset	07:18	11:19		Onset time of the 10 most active consecutive hours

For the Malagasy sample ($n = 10$), mean NPCRA analysis was 12.1 days; for the postindustrial sample ($n = 21$), the mean number of nights was 12.5. Both samples were sex balanced. We compared sample statistics using two sample t tests.

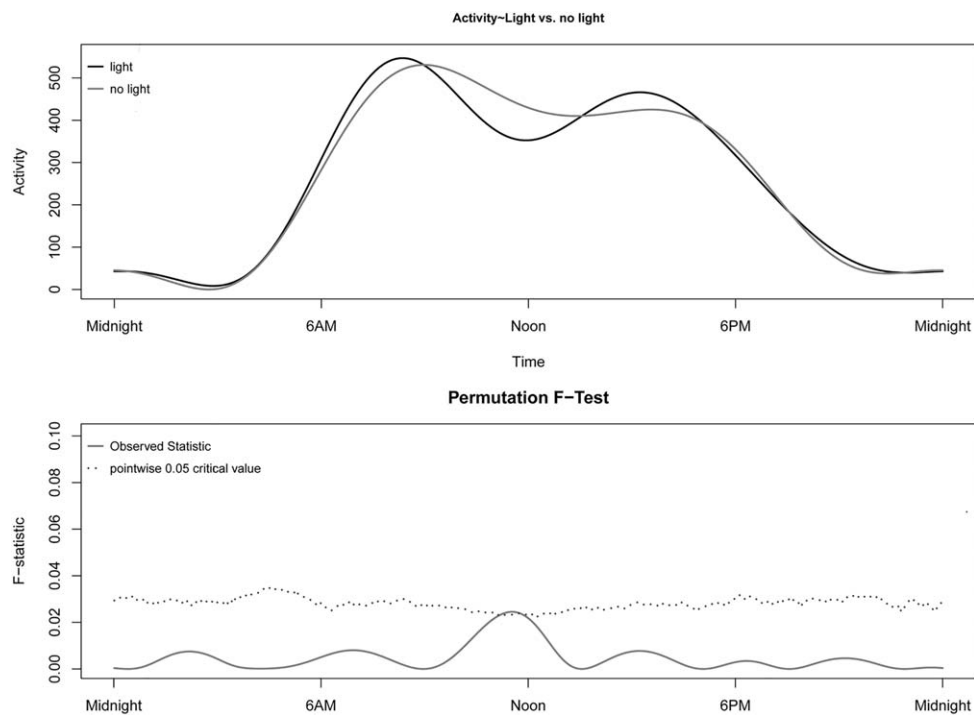


FIGURE 3 A nonparametric permutation F test comparing actigraphy data in the experimental field light group with the no-light-access control group. The pointwise critical value (dotted line) is the proportion of all permutation F values at each time point at the significance level of 0.05. When the observed F -statistic (solid line) is above the dotted line, it is concluded that the two groups have significantly different mean circadian activity patterns at those time points. For this data set, the two groups differ significantly over the time period of 11:00–12:00

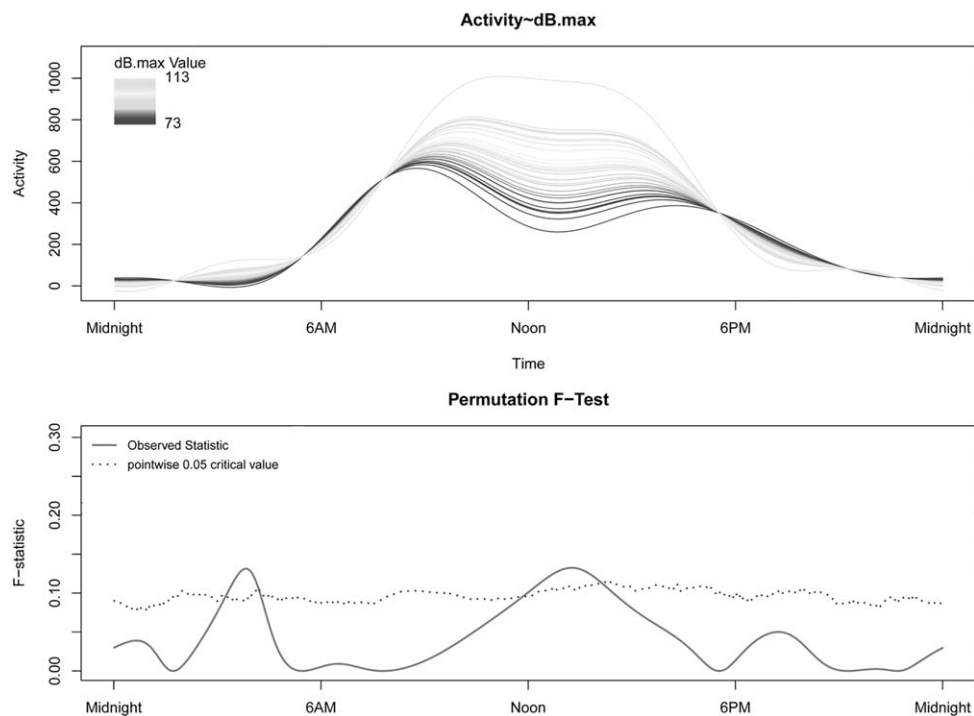


FIGURE 4 A nonparametric permutation F comparing activity and the average maximum nightly noise level ($n = 36$ nights) within each household. The pointwise critical value (dotted line) is the proportion of all permutation F values at each time point at the significance level of 0.05. When the observed F -statistic (solid line) is above the dotted line, it is concluded that the continuous measures have significantly different mean circadian activity patterns at that time point. For this data set, the greater the noise level during the night is associated with more activity between 03:00 and 04:00 and in the afternoon from 12:00 to 13:30

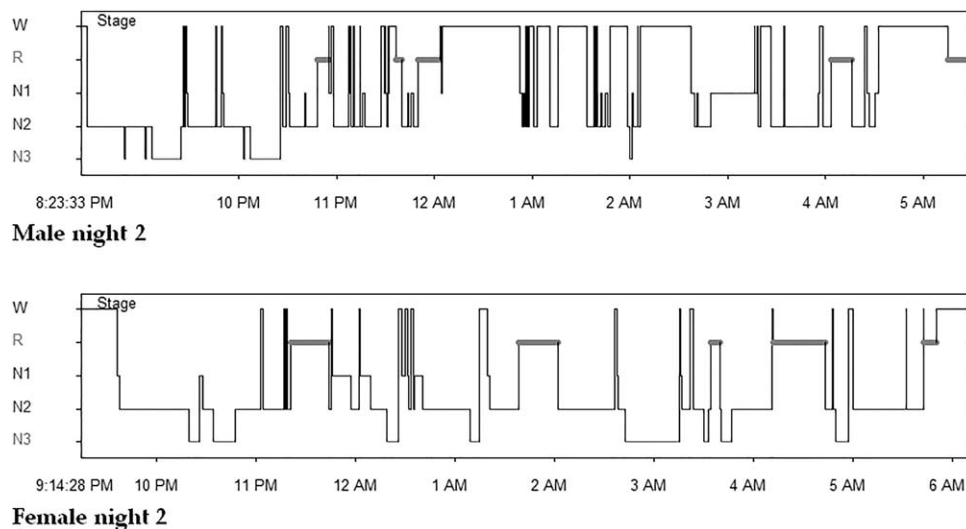


FIGURE 5 Mobile polysomnography measuring EEG, EMG, and EOG to assess sleep architecture in a nonclinical, field environment. The average sleep architecture exhibited was predominantly light NREM with relatively low proportions of SWS and REM. Note the 1 h period from 00:00 to 01:00 in a male subject, which is characteristic of a segmented sleep as a long duration wake after sleep onset episode

386 ± 78 min, stage 1 NREM (N1) = 67 ± 24.9 (19% TST), stage 2 NREM (N2) = 197 ± 65 min (50% TST), slow wave sleep (N3) = 62 ± 27 min (16% TST), REM = 52 ± 21 min (14% TST), sleep efficiency = $66\% \pm 14\%$, WASO = 162 ± 70 min, sleep latency = 38 ± 27 min, arousals = 37 ± 18 , awakenings = 14 ± 7 (see Figure 5 for examples). These results corroborate findings from actigraphy of short sleep duration and greater fragmentation among people in the village, and thus support the *developing economy sleep degradation hypothesis*.

4 | DISCUSSION

In this Malagasy rural population, we uncovered sleep patterns that differ from postindustrial populations. In particular, we discovered relatively short sleep (ie, a total sleep duration of 6.5 h), high levels of fragmentation, and stronger linkage to environmental variables (ie, a more consistent circadian rhythm). The noisy environment of this dense village may contribute to fragmented sleep. Importantly, we provide, to our knowledge, the first PSG in a traditional, nonelectric population, thus demonstrating that this is possible. Although conclusions are highly limited by the small amount of data collected, the PSG data supported many of our conclusions from actigraphy, including short and fragmented sleep. We also found evidence that this population is characterized by segmented sleep. Female and male values for sleep-wake characteristics were similar, except for greater male cumulative nighttime activity and the propensity for males to experience greater frequency of nighttime wake-bouts.

Our findings lead us to reject the postindustrial sleep degradation hypothesis, which predicts that sleep duration and quality in the Malagasy population would be improved due

to the general absence of nighttime distractions generated by television, social media, and high-quality artificial lighting. When compared to the postindustrial populations, the Malagasy had significantly lower total sleep times and sleep quality (Table 2), thus supporting predictions from the developing economy sleep degradation hypothesis. This result corroborates data showing short total sleep durations that have been documented in other developing countries (rural Haitian sleep duration = 7.0 h) (Knutson, 2014). Additionally, noise level data were linked to sleep-wake patterns, with individuals who experience greater nighttime noise exhibiting increased activity during the night. A limitation of this study is in the comparability of the postindustrial groups and the Malagasy dataset; we suggest that future, multisite studies should target demographically similar groups, using similar methods and equipment, in multiple countries.

Predictions from the circadian entrainment hypothesis were also supported. Notably, measures of the consistency of circadian rhythm, such as interdaily stability and variability (Table 3), showed the Malagasy population to have more stable rhythms. This supports the idea that changes from our ancestral sleep ecology, where physiology was in constant exposure to the environment, have had significant consequences for sleep-wake patterns, with potential downstream effects on health, thus creating opportunities for evolutionary mismatch and health disparities (Nunn et al., 2016). A limitation to this study was that the comparative, postindustrial populations used to test these predictions were derived from the literature. Future work should target large-scale research projects in industrialized populations of normal, healthy, nonshift workers in countries at latitudes matching the traditional population being compared.

Our findings also support predictions from the sleep segmentation hypothesis. Functional linear modeling of both female and male subjects directly engaged in agricultural activities show that 24 h time-averaged actigraphy sleep–wake patterns are unconsolidated, or segmented. In particular, we documented an increase in activity after midnight, which is especially pronounced in males. These data evince a pattern strikingly similar to the “first sleep” and “second sleep” pattern described by Ekirch (2006, 2016). Moreover, Malagasy participants were heavily reliant upon napping during the day, where 88% of all study days exhibited napping. This phenomenon was particularly pronounced in males, who exhibited a daily nap ratio of 1.10. Naps were also descriptively longer (mean nap time = 55.2 min) than previous reports in the post-industrial literature (mean nap time = 29.2 min) (Yoon, Kripke, Youngstedt, & Elliott, 2003). Segmented sleep ratios revealed that nighttime wake-bouts were common in the population (49% of nights), with a trend for males to experience more segmented sleep than females. Additionally, true total sleep time (the sum of daytime and nighttime sleep totals) was significantly greater when compared to nighttime sleep, indicating that daytime sleep is an important contributor to overall sleep duration throughout the circadian cycle. This result has important implications for reporting total sleep times, given daytime sleep is often under-reported in sleep studies in both Western and non-Western populations.

As for the light experiment, the nonparametric permutation *F* test (Figure 3) revealed no significant shifts in sleep–wake phasing during the average sleep period when individuals had access to lighting. Moreover, the linear mixed effects model showed that, after controlling for covariates, sleep segmentation was not influenced by access to mobile field lights. However, a significant reduction in prenoon activity occurred in the access-to-light group, which could be indicative of a sleep rebound effect to make up for lost sleep the night before. It should be noted that absence of evidence of nighttime activity may be difficult to interpret, given it may take longer than a single week for people with access to light to modify behaviors that capitalize on such access. Additionally, a caveat to working with actigraphy is that an individual can be alert and immobile, and the sleep algorithm may bias the epoch assignment toward sleep (Kanady et al., 2011); therefore, important wake behaviors that require consciousness but little activity—such as reading or meditating—could have been facilitated by nighttime access to artificial light, but scored as sleep. This also highlights that our present results illustrating prominent wake bouts in this population is a conservative estimate, given that a well-known bias in actigraphy is to score quiet wakefulness as sleep (Paquet, Kawinska, & Carrier, 2007).

Together, these results suggest that this population can be characterized as exhibiting segmented sleep, at least dur-

ing the modestly longer austral winter experienced at this latitude. Our findings concur with historical literature from preindustrial equatorial cultures suggesting the existence of segmented sleep (Ekirch, 2016). Thus, this study presents evidence contrary to the latitude segmented sleep hypothesis—namely, that segmented sleep is a feature of high latitude, annually longer photoperiods. Although this study suggests that equatorial populations can exhibit segmented sleep–wake patterns, it is essential for future research to make direct comparisons of actigraphic data across subsistence patterns and geographical latitudes globally to discover the “natural” human sleep pattern.

Intriguingly, the model did reveal the importance of lunar phase and day length light, which increased both the frequency and duration of daytime sleep. Lunar illumination has been shown to play a central role in regulating nocturnal behavior in primates (Colquhoun, 2006; Curtis, Zaramody, & Martin, 1999; Donati & Borgognini-Tarli, 2006), yet recent reviews have highlighted the lack of evidence that lunar phase effects human physiology (Foster & Roenneberg, 2008). This study presents initial evidence that humans living with few barriers to their environments are more synchronized with circadian entrainment queues, and may experience increased sleep segmentation on nights with greater lunar illumination.

In conclusion, this study provides novel findings about variation in human sleep by investigating sleep in a nonelectric, small-scale agricultural society in Madagascar. Sleep in the population is characterized as shorter and of poorer quality than similarly measured postindustrial populations, and this sleep–wake pattern was linked to environmental noise levels. Several factors likely reduced sleep times along the human lineage, such as greater predation risk on the ground and inter- and intragroup conflict, coupled with the benefits of social interaction and the acquisition and transmission of new skills and knowledge (Samson & Nunn, 2015). Thus, for humans, it may be that pressure to reduce total sleep times has been a constant, even before the advent of electricity and artificial lighting. Future studies, characterizing sleep in a greater number of traditional, nonelectric societies across latitudinal gradients, examining longer periods of access to lights, are necessary to better understand “natural” human sleep and its evolution, and to help reduce health disparities that may emerge through poor-quality sleep in developing and developed countries.

ACKNOWLEDGMENTS

We would like to thank Amanda Lee and Lane Daughtry from the Duke Sleep Clinic for assistance in scoring sleep using polysomnography. We thank Bass Connections (Global Health) at Duke University for funding support. Finally, we thank the insightful comments from the

anonymous reviewers that substantially improved the quality of the manuscript.

CONFLICT OF INTEREST

No author reports any conflict of interest.

AUTHOR CONTRIBUTIONS

Research design: Samson, Krystal, Nunn

Performed research: Samson, Manus, Fakir, Yu, Nunn

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How to cite this article: Samson DR, Manus MB, Krystal AD, Fakir E, Yu JJ, Nunn CL. Segmented sleep in a nonelectric, small-scale agricultural society in Madagascar. *Am J Hum Biol.* 2017;00:e22979. <https://doi.org/10.1002/ajhb.22979>