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Diurnal cortisol rhythms in Tsimane' Amazonian foragers: New insights into ecological HPA axis research

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Summary Although a growing body of research has documented important pathways by which the HPA axis mediates the interface between the psychosocial world and individual health, there is a paucity of data from nonwestern populations, particularly from those populations with distinct nutritional and infectious disease ecologies. The specific objectives of this study are: (1) to document variation in diurnal cortisol rhythms among the Tsimane', a remote population in the Bolivian Amazon, (2) to explore this variation by age and by gender, and (3) to compare diurnal rhythms from this study to other population based studies of cortisol conducted in industrialized nations. Salivary cortisol samples were collected twice daily, immediately upon waking and before bed, for three consecutive days from 303 participants (age 1.6—82 years, 1564 samples) in conjunction with the Tsimane' Amazonian Panel Study (TAPS). Cortisol rhythms showed strong age effects across the developmental span, with basal levels and slopes increasing into adulthood, although individuals older than 60 years demonstrated a precipitous flattening of the diurnal slope. Cortisol profiles were elevated in adult females compared to their age-matched male counterparts, and diurnal slopes, as well as mean cortisol concentrations among the Tsimane' were the lowest reported in any population based study of HPA axis function. Although the within-population variation in cortisol profiles was consistent with the established correlates of time of day, age, and sex, the between-population comparisons revealed dramatically lower levels of HPA activity among the Tsimane'. This study provides a benchmark against which to reference cortisol levels from industrialized populations, and expands the range of documented variation in HPA axis function in a nonwestern context.

1. Introduction

A formidable body of research has identified stress as an important pathway linking the psychosocial world to individual health and well being, and many studies have focused on

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cortisol to provide a biomarker of psychoneuroendocrine activity (Adam and Kumari, 2009; Miller et al., 2009). Elevated cortisol levels have been associated with a constellation of related health outcomes, including an increased risk of central adiposity, diabetes, cardiovascular disease, hypertension, and the metabolic syndrome (Bjorntorp et al., 2000; Bjorntorp and Rosmond, 2000; Chrousos, 2000; Epel et al., 2000; Rosmond, 2005; Wallerius et al., 2003). A higher risk for depression, reduced hippocampal volume, and PTSD vulnerability also signal the burden of chronic stress on mental health, with dysregulation of the HPA negative feedback circuitry playing a central role (Burke et al., 2005; Cohen et al., 2007; Lee et al., 2002; Miller et al., 2007; McEwen and Magarinos, 2001; Sapolsky, 2001; Yehuda and Bierer, 2008). Rather than being uniformly associated with elevated cortisol, however, chronic stress may also promote hypocortisolism or adrenal exhaustion (Gunnar and Vazquez, 2001; Heim et al., 2000; Miller et al., 2007; Yehuda, 2004). In particular, stressors associated with trauma, physical threat, and those of a highly uncontrollable nature tend to elicit an elevated, flattened cortisol profile (Miller et al., 2007). Cortisol levels may also decrease over time since the onset of a stressor, further underscoring the complexities between stress and patterns of HPA activity (Miller et al., 2007).

Despite these important advances in our understanding of stress physiology, however, the vast majority of these studies have been conducted among relatively affluent, well-nourished, sedentary industrialized populations — conditions that are far from ubiquitous for most inhabitants of the world (Adam, 2006; Evans and Kim, 2007; Cohen et al., 2006; Jonetz-Mentzel and Wiedemann, 1993; Lupien et al., 2000). In contrast, there is a paucity of comparative data on HPA axis function from nonwestern populations, particularly from those whose developmental ecologies are characterized by high burdens of infectious and parasitic diseases, and marginal nutrition. Though recent studies in Botswana (Decker, 2000), Dominica (Flinn and England, 1997), Jamaica (Fernald and Grantham-McGregor, 1998), Kenya (Pike and Williams, 2006), Mexico (Fernald et al., 2009), Guatemala (Nepomnaschy et al., 2004) and Nepal (Fernald et al., 2003; Hruschka et al., 2005; Worthman and Panter-Brick, 2008), have been invaluable to our understanding of differential cortisol release in nonwestern settings, the paucity of data on the diurnal rhythm precludes population level comparisons of HPA function.

The hypothalamic—pituitary—adrenal axis (HPA) serves as a central anchor of the stress response (Sterling and Eyer, 1988). Hierarchically organized, the response is elicited in the brain upon the cognitive appraisal of a stressor, with CRH cascading from the paraventricular nucleus in the hypothalamus, which then stimulates production of ACTH from the anterior pituitary (Hellhammer et al., 2009; Miller et al., 2007). Once the circulating ACTH signal reaches the adrenal cortex, cortisol is released into the bloodstream, with negative feedback operating primarily in the hippocampus via the high density of glucocorticoid receptors (GRs), which dampen cortisol levels post-challenge (Anacker et al., 2010; Galeeva et al., 2010). Cortisol exhibits a strong diurnal pattern, with levels reaching a zenith shortly after awakening and dipping to its nadir before sleep (Dallman et al., 1993; de Kloet and Sarabdjitsingh, 2008; Kirschbaum and Hellhammer, 1994).

Its role in coordinating circadian metabolic functions coupled with its capacity for reactivity place the HPA axis at the dynamic interface mediating internal homeostasis, the local ecology, and the broader psychosocial and sociocultural environment (Romero et al., 2009; McEwen and Wingfield, 2003; Miller et al., 2009; Schulkin, 2003). By extension, the HPA axis also serves as a key mechanism of developmental plasticity, modulating competing life history domains of growth (Sloboda et al., 2009; Tsigos and Chrousos, 2002), maintenance (i.e. immune function) (Cohen et al., 2007; Cole, 2008), and reproduction (Nepomnaschy et al., 2006; Worthman and Kuzara, 2005) across a diverse array of taxa (Crespi and Denver, 2005; Power and Schulkin, 2006; Romero and Wikelski, 2010). Differential trajectories of HPA function may, over time, recalibrate thresholds for disease risk across the lifespan (Belsky et al., 2010; Chrousos, 2000; Gluckman et al., 2010; Kajantie et al., 2002; Kuzawa and Quinn, 2009; McEwen and Wingfield, 2003; Miller et al., 2002; Phillips, 2007). With the growing consensus that context matters (Boyce and Ellis, 2005), and that early life experiences can play a critical role in the developmental programming of physiological systems (de Rooij et al., 2006; Kajantie et al., 2002; Gluckman et al., 2009; Kuzawa and Quinn, 2009; McDade et al., 2010), it is especially important to utilize a comparative lens to investigate variation in HPA axis function within and between populations (Boyce and Ellis, 2005; Chisholm and Coall, 2008; Ellis et al., 2005; Worthman and Kuzara, 2005).

Beyond the utility of conducting a study of HPA axis dynamics in a nonwestern population, this is the first study to document cortisol rhythms in an indigenous hunting and foraging society, the Tsimane' of the Bolivian Amazon (Huanca, 2006; Nyberg, 2009). With a developmental milieu characterized by high levels of physical activity, marginal nutritional status, and high burdens of infectious and parasitic diseases, this remote setting provides a unique ecological context in which to explore the dynamics of HPA axis function. As with many historically marginalized indigenous populations of lowland South America, the Tsimane' are undergoing rapid lifestyle changes (Byron, 2003; Godoy et al., 2005; Godoy et al., 2006; Reyes-Garcia et al., 2003): the past 25 years have witnessed the opening of a new road and a marked increase in logging activities, providing two of the most direct ways for the Tsimane' to enter the regional market economy. Among the Tsimane' who live far from market centers hunting and foraging subsistence practices are prevalent, and overall, Tsimane' social structure remains highly autarkic, with social networks joined by lines of blood and marriage forming the prevailing conduits of social and economic exchange (Godoy et al., 2005).

Recent research has demonstrated elevated levels of infection (via the inflammatory protein CRP) (McDade et al., 2005), high parasite loads (Tanner et al., 2009), and high mortality rates among the Tsimane' (Gurven et al., 2007). Growth stunting is prevalent (Godoy et al., 2010a,b; Foster et al., 2005) and adults are also relatively lean, exhibit high levels of physical activity, and have markedly lower blood lipids and leptin levels compared to U.S. populations (Gurven et al., 2009; Sharrock et al., 2008; Vasunilashorn et al., 2010). Previous TAPS studies have revealed that greater participation in market activities is associated with higher self-reports of anger and fear, and

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have reported an association between lower wealth rank and poorer subjective health (Godoy et al., 2005; Reyes-Garcia et al., 2008; Undurraga et al., 2010). Notably, the Tsimane' do not have a direct indigenous translation for the word "stress", underscoring the utility of salivary cortisol to provide an objective measure of HPA activity in this cross cultural setting (Dressler, 1991; Nyberg, 2009).

This setting provides a compelling backdrop for the exploration of HPA axis dynamics, and permits a first glimpse into how the "typical" cortisol values derived from industrialized populations compare to those from a small-scale horticulturalist, hunting, and foraging society in the Bolivian Amazon (N = 303 individuals, 1564 samples, ages 1.6–82.2). The specific objectives of this study are: (1) to document variation in the diurnal cortisol rhythms among Tsimane', (2) to explore this variation by age and by gender, and (3) to compare diurnal rhythms from the Tsimane' to other population based studies of cortisol conducted in industrialized nations.

2. Methods

2.1. Data collection

Participants for this study were enrolled in conjunction with the Tsimane' Amazonian Panel Study (TAPS), a longitudinal study collecting data on health, quality of life, and market integration among ~1985 individuals since 2002 (Godoy et al., 2009; Leonard and Godoy, 2008). Thorough descriptions of TAPS are located at http://www.tsimane.org/index.html, and excellent ethnographic overviews of the Tsimane' are provided by Reyes-Garcia et al. (2003, 2008) and Huanca (2006).

The TAPS survey on demographics and socioeconomic factors was administered in each of the participating households during the first phase of research. An inventory of traditional and modern assets, along with income was compiled, and items were assigned current market values to assess total household wealth, used as a gross proxy of socioeconomic status in this study. During the second phase, the collection of cortisol and anthropometric data was accompanied by a brief survey on health. A dummy variable was constructed to represent whether the participant had experienced illness in the week leading up to collection, an important potential confounder of cortisol levels. The collection of salivary cortisol followed a cross-sectional wave across villages as part of the health unit, and the collection of anthropometric measurements to assess growth and nutritional status was performed on the third collection day.

In total, data from 303 individuals (175 sub adults under the age of 16, 128 adults) from five Tsimane' communities are presented in this study, and comprise a total of 1564 saliva samples. To emphasize the assessment of the person-specific basal diurnal rhythm, rather than a day-specific pattern, cortisol samples were collected twice a day over three days for a maximum of 6 samples per person. The passive drool technique was demonstrated to participants, who were given straws to help expel saliva into labeled 2 mL polypropylene vials. In an effort to capture the maximum diurnal cortisol decline, participants were asked to fill the collection vials immediately upon waking, "as soon as you open your eyes and before your feet hit the ground", and immediately before bed or "right before you close your eyes" (Adam and Kumari, 2009; Cohen et al., 2006). The nature of this collection protocol allowed for the adjustment of the morning waking and bedtime values to each individual's circadian rhythm (Adam and Gunnar, 2001). Due to logistical difficulties in this remote field setting (i.e. Tsimane' do not have time keeping devices, thus hindering adequately capturing the 30 min cortisol response to awakening), and in an effort to maximize participant compliance, this study did not collect a sample representing the cortisol awakening response (Adam, 2006; Clow et al., 2004).

Growth parameters and nutritional status were assessed using standard anthropometric techniques utilized in previous TAPS studies (Foster et al., 2005; Godoy et al., 2005; Leonard and Godoy, 2008; Tanner et al., 2009; Lohman et al., 1988). A portable stadiometer was used to measure stature (cm), and weight (to the nearest 0.1 kg) was measured with a Tanita scale. These variables were used to calculated body mass index (BMI) as (kg)/(height (m))^2.

2.2. Cortisol analysis

After the collection of saliva samples was completed in each study community, the vials were stored in the TAPS refrigeration unit in San Borja, Bolivia within seven days of initial collection. Once manually transported back to the United States, the samples were stored at −30 °C at the Northwestern University Laboratory for Human Biology Research. Subsequently, the samples were placed on dry ice and express shipped to the University of Trier, Germany. Samples were assayed in duplicate using a competitive solid phase time-resolved fluorescence immunoassay with fluorometric end-point detection (DELFIA), and exhibited a mean inter-assay coefficient of variation of 6.7%.

Salivary cortisol is relatively robust to degradation, even in tropical conditions, for at least two weeks without refrigeration (Hellhammer et al., 2009). Due to the extreme temperature fluctuations and collection time between samples, however, variables were constructed to assess potential sources of sample degradation. No significant correlations were detected between cortisol concentrations and (a) the duration (in days) between time of collection and storage in the project refrigerator in San Borja (r = 0.008, n.s.), or (b) the duration between collection time and assay completion at the University of Trier, Germany (r = 0.009, n.s.).

Cortisol values from the CARDIA study (Cohen et al., 2006) were used to illustrate population level comparisons between diurnal slopes in Fig. 3 for several reasons: the study comprises a large multi-city sample; both morning waking and bedtime cortisol values were available; and because assays were also performed using DELFIA. The comparative cortisol values presented in Table 3 were obtained from published studies of salivary cortisol if they provided data on waking, evening, all times mean, or slopes. Additional values were adapted from Jessop and Turner-Cobb (2008, p. 3). Cortisol concentrations from the Tsimane' sample and the comparative studies are reported in nmol/L.

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Table 1 Descriptive characteristics of sample and mean cortisol parameters by subgroup.

	Females <16 yrs (*N* = 91)	Males <16 yrs (*N* = 84)	Adult females (*N* = 68)	Adult males (*N* = 60)
Samples per person	5.3	4.8	5.4	5.2
Height (cm)	121.5 (19.7)*	119.2 (22.3)	152.6 (4.7)	162.9 (5.1)**
Weight (kg)	27.2 (11.4)	26.1 (11.9)	57.5 (8.5)	62.3 (8.0)**
BMI (kg/m^2)	17.5 (2.0)	17.3 (1.7)	24.7 (3.5)**	23.2 (2.4)
Morbidity (% reporting symptoms)	34.60%	37.50%*	40.20%**	28.40%

Gender differences between age-matched subadults and adults are indicated by significance *$P < 0.05$; **$P < 0.01$.

2.3. Statistical analysis

Statistical analyses were performed in Stata version 10 (Stata Corp., College Station, TX). Cortisol and BMI were log transformed to improve the normality of the distributions for the multilevel analyses. All morning waking values represent +0 h postwaking, and the bedtime values represent +16 h, and values reported for the hierarchical models are centered at +8 h post waking. Slopes values were obtained by estimating a best fit line though the multiple measures of morning and evening cortisol using hierarchical linear regression, with the coefficient for time of collection representing the diurnal rhythm (Adam and Kumari, 2009; Hruschka et al., 2005). Finally, eight pregnant women were excluded from analyses due to their dramatically elevated cortisol profiles (Obel et al., 2005).

Descriptive statistics are provided for the entire sample in Table 1, and bivariate analyses were employed to evaluate between group differences in cortisol parameters. Specifically, two-tailed t-tests were utilized to evaluate sex differences in multiple HPA parameters (AM, PM, mean, decline) in sub adults (under age 16) and adults. Finally, a series of multilevel models were used to assess variation at the within- and between-person levels, as well to assess the impact of covariates on slope and basal measures of cortisol. The use of multilevel modeling to analyze cortisol data represents a significant improvement over relying on crude averages (Adam and Gunnar, 2001; Hruschka et al., 2005; Williams, 2008), by augmenting the statistical power of these models while simultaneously adjusting for within-day correlations (Raudenbush and Bryk, 2002). In addition, this analytic strategy relaxes traditional assumptions of independence required for regression modeling, and provides a high tolerance for missing data and for unequal collection periods (Singer and Willett, 2003), issues that plague naturalistic studies of human health and pose challenges to the TAPS collection protocol in this remote field setting.

Initially, an unconditional model with no predictors was used to predict the intercept (mean midday cortisol) and to partition variance into within-person and between levels. The within person variables were added at Level 1 (covariates such as time of collection, day of collection); while the individual level covariates were entered at Level 2 (between person attributes such as age, gender, morbidity, etc.), linked by the TAPS subject identification number.

All protocol employed in this study were approved by the Institutional Review Board for human subjects research at Northwestern University. In addition, in accordance with established TAPS protocol, the Gran Consejo Tsimane', the primary Tsimane' governing body, also granted permission to the project.

3. Results

3.1. Descriptive statistics

Table 1 reports general anthropometric and health characteristics of the sample. For the 303 participants, mean morning waking levels were 5.83 nmol/L (SD 3.33) and bedtime levels were 1.94 nmol/L (SD 1.94). The all-times mean was 4.44 nmol/L (SD 4.11) and the diurnal rhythm exhibited a slope of −0.076 (SE 0.002).

While the vast majority of cortisol values in this sample were low, 1.6% of the samples had values at least 3 standard deviations greater than the population mean, similar to reports from the Whitehall II and Rotterdam Studies (Adam and Kumari, 2009; Steptoe et al., 2008). At the other extreme, less than 10% of the individuals had a slope of zero or greater, with a maximum slope of +8.89. In comparison, a recent study reported that 14% of adolescent participants in a study of racial differences in cortisol rhythms exhibited a positive slope across the day, with a maximum profile of +18.9 (DeSantis et al., 2007).

3.2. Age and sex as determinants of HPA axis activity

Although both subadult and adult females had higher morning waking and lower evening cortisol concentrations compared to age-matched males, these values did not reach statistical significance. However, the diurnal slope was significantly steeper in subadult females compared to males ($t = -2.48$, $P < 0.01$). Adult males exhibited evening cortisol levels that were on average 0.83 nmol/L lower than adult females ($t = 2.23$, $P < 0.05$), and adult females had a flatter diurnal rhythm compared to males ($t = 2.9$, $P < 0.05$). In addition, the all times mean was significantly lower among adult men ($t = 2.37$, $P < 0.05$). Thus, the gender gap widens significantly into adulthood, with adult women showing higher overall mean levels, elevated evening levels, and a flatter diurnal cortisol rhythm compared to adult males. These distinctions in cortisol profiles are illustrated in Fig. 1.

Age-related changes in morning and evening cortisol across the lifespan are illustrated in Fig. 2, which also reveals more subtle distinctions in the developmental trajectories of cortisol release between males and females. Whereas the full multilevel analysis demonstrating the impact of age on diur-

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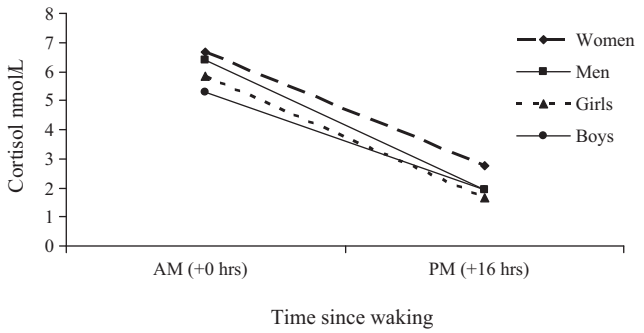

Figure 1 Diurnal rhythms vary by subgroup.

nal slopes is presented in Table 2 and interpreted in Section 3.3, here mean cortisol concentrations with standard deviations and hierarchical regression-based slope coefficients with standard errors are provided for the age groups, adjusted for gender. The interpretation of the slope coefficient is listed as a percentage decline per hour. A reasonable estimate of the early childhood pattern of HPA axis function is represented by 20 children between one and four years of age, who display low mean cortisol levels (3.8 nmol/L, SD 3.1) and a relatively shallow diurnal rhythm ($\beta = -0.05$, SE 0.01, −4.8%/h). Moderate increases in mean cortisol (4.2 nmol/L, SD 3.7) and slopes ($\beta = -0.08$, SE 0.01, −7.6%/h) occur from ages five though nine, followed by an upward shift in basal concentrations (4.7 nmol/L, SD 4.0) and diurnal rhythms ($\beta = -0.09$, SE 0.005, −8.6%/h) between the ages of 10 and 12. Compared to the early adolescent rise in HPA activity, basal levels (4.6 nmol/L, SD 3.1) and slopes ($\beta = -0.07$, SE 0.001, −6.7%/h) plateau from age 13 until age 30, followed by steady increases in average levels, exhibiting a peak in mean concentrations (5.3 nmol/L, SD 4.2 nmol/L), and a slight elevation in slopes ($\beta = -0.08$, SE 0.00, −7.6%/h) between ages 50 and 59. From 60 to 82 years, however, basal levels are somewhat reduced (4.7 nmol/L, SD 3.4), with morning cortisol decreasing and bedtime cortisol increasing markedly, resulting in a precipitous flattening of the diurnal rhythm ($\beta = -0.03$, SE 0.01, −2.9%/h).

3.3. Variance and multilevel models of diurnal HPA activity

Next, multilevel models were used to apportion variance to the within- (Level 1) and between-person components (Level 2). Before controlling for the time of day, an unconditional model reveals nearly 75% of the total variance in cortisol is within individuals, with just over 17% of the variance between persons (the intercept of Level 1, $chi^2 = 384.6$, $P = 0.000$; random effect of the intercept1/intercept 2, $chi^2 = 20.6$, $P < 0.001$). When time of collection is added to the two level model, the coefficient for the effect of time of collection on the slope is −0.076 (t-ratio −27.81, $P = 0.000$). The addition of time of collection covariate reduced the variance by 0.63 (from 1.44 in the unconditional model to 0.87 in the unconditional growth model), and therefore accounts for about 44% of the within person variance in diurnal cortisol profiles.

Three multilevel models are presented in Table 2. Model 1 presents the unconditional model, with time and day as the only time-varying Level 1 predictors, Model 2 includes the covariates age and sex, and Model 3 presents the full suite of between-person covariates with the interpretation of significant findings. To facilitate the interpretation of the fixed effects, coefficients (but not the intercept), are transformed using the following formula: ($B_{\%change} = [\exp(B_{raw})] - 1$) (Adam, 2006; Hauner et al., 2008). In Model 1, the coefficient for time of collection indicates that cortisol declines at a rate of 7% per hour from waking until bedtime. Beyond time of collection, collection day is the only other time-varying predictor, which displays a significant effect on both the intercept and slope. These findings may be, in part, the result of a large number of individuals missing the morning collection period on day 1, thus arbitrarily reducing the average concentrations, but it may also indicate the importance of factors such as mood and sleep schedule in contributing to day-to-day variation within person (Adam, 2006). Model 2 reveals the expected association with age, as each additional year of age is associated with a 0.6% increase in cortisol — an effect that becomes considerable when extrapolated across the lifespan. While the coefficient for sex does not reach statistical significance in the full hierarchical model ($P = 0.09$) presented in Model 3, the relationship is in the direction expected, with males exhibiting a 4% decrease in cortisol compared to females. The reduction in the magnitude of the relationship between sex and cortisol compared to the subgroup differences reported in the bivariate analyses may be a result of the latent effects of age that emerge in the multilevel model, which are also depicted in Fig. 2. The presence of infectious symptoms within one week of saliva collection was significantly associated with an elevated cortisol profile, while the control variables BMI and

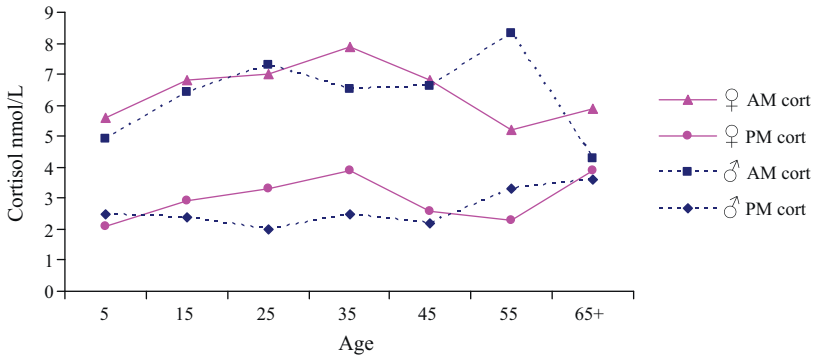

Figure 2 Patterns of HPA activity across the lifespan.

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Table 2 Multilevel models of associations between log transformed diurnal cortisol rhythms and covariates.

Fixed effect	Model 1			Model 2			Model 3			Interpretation
	Coefficient (SE)	*t*-Ratio	*P*-value	Coefficient (SE)	*t*-Ratio	*P*-value	Coefficient (SE)	*t*-Ratio	*P*-value	
Intercept (+8 h)	−1.68 (0.038)	−43	0.000	−1.88 (0.020)	−15.18	0.000	−1.9 (0.070)	−26.4	0.000	4.13 nmol/L at +8 h post waking
Time since waking (h)	−0.076 (0.002)	−27.4	0.000	−0.074 (0.003)	−24.380	0.000	−0.072 (0.003)	−27.6	0.000	−7.8% decline per hour
Day				0.058 (0.030)	1.50	0.135	0.083 (0.024)	3.49	0.000	8% increase after day 1
Age				0.007 (0.002)	3.49	0.000	0.006 (0.001)	3.45	0.001	+0.6% per year older
Sex (male = 1)				−0.075 (0.07)	−1.04	0.100	−0.045 (0.060)	−0.74	0.095	−4% if male
log BMI							0.29 (0.250)	−1.95	0.260	n.s
Morbidity							0.20 (0.075)	2.21	0.045	+23% if sick within 1 week of collection
Household wealth							0.001 (0.00)	0.75	0.460	n.s.
Random effect	Variance (SD)		Chi^2	*P*-value	Variance (SD)		Chi^2	*P*-value	Variance (SD)	Chi^2	*P*-value
Level 2 intercept	0.16 (0.41)		657.40	0.000	0.15(0.40)		662.1	0.000	0.14 (0.40)	672.9	0.000
Time slope	0.001 (0.03)		529.0	0.000	0.001 (0.03)		531.0	0.000	0.001(0.03)	531.0	0.000
Level 1	0.69 (0.03)				0.68 (0.09)				0.55 (0.74)		

household wealth were not associated with differential cortisol release. Finally, the variance components included in Table 2 are significant, underscoring the salience of using multilevel models to estimate differential trajectories in cortisol release even in the absence of a suite of time-varying covariates. Likelihood ratio tests between the three models showed improved fit and a significant reduction of the deviance between Model 1 (unconditional) and Model 2 (time, age, sex) (Δ deviance 622.3, $P < 0.001$) and between Model 2 and Model 3 (all person-level covariates) (Δ deviance 72.4, $P < 0.000$).

3.4. Population comparisons of HPA axis parameters

Fig. 3 presents a comparison between the Tsimane' diurnal profiles and the values obtained from the CARDIA study, a large US based study on SES, lifestyle factors, and cardiovascular health (Cohen et al., 2006). The comparison is dramatic: the mean cortisol values from the CARDIA study are greater than three standard deviations above the Tsimane' adult mean, and also exhibit a steeper diurnal slope compared to the Tsimane'.

To further facilitate comparisons between the Tsimane' and other populations, Table 3 provides values for multiple parameters of HPA function from other population based studies. For each parameter of HPA function collected in this study (AM, PM, slopes, overall mean), the Tsimane' have the lowest cortisol levels reported among any human population. The only study with similar values was drawn from a sample of Nepalese children age 10—14 years (Worthman and Panter-Brick, 2008), which averaged 5.97 nmol/L compared to an age-matched sample of 48 Tsimane' children with an average morning waking value of 6.0 nmol/L. Although the Nepalese morning samples were time-standardized, their collection occurred after the awakening response, and were therefore lower than had they been collected immediately upon waking (Worthman and Panter-Brick, 2008). The only other studies reporting similarly low values are from studies conducted in Botswana (Decker, 2006) and the Philippines (Kuzawa, personal communication November, 2009).

4. Discussion

This study is the first to present developmental changes in HPA trajectories across the lifespan among a small-scale hunting and foraging society in the Bolivian Amazon. Although within-population variation in cortisol profiles is consistent with the established correlates of time of day, age, and sex, between-population comparisons revealed dramatically lower levels of HPA activity among the Tsimane'. As the lowest cortisol values on record, these findings expand the documented range of population variation in diurnal HPA activity.

An absence of significant prepubertal sex differences in HPA function in this population is consistent with prior research (Kudielka et al., 2009; Kudielka and Kirschbaum, 2005; Romeo, 2005). Subtle distinctions between female and male children become amplified into adolescence and adulthood (Gunnar et al., 2009), and are similar to previous findings reporting the elevation of HPA function in adult

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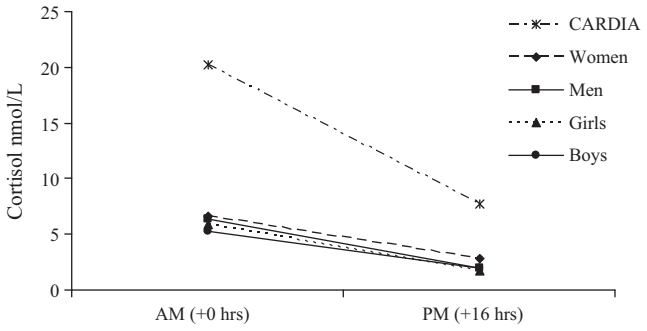

Figure 3 Comparisons between Tsimane' and US diurnal cortisol rhythms.

females (Darnall and Suarez, 2009; Hardie et al., 2002; Kudielka and Kirschbaum, 2005; Netherton et al., 2004; Rosner, 1990; Shansky et al., 2004). As evident from Fig. 2, however, there is considerable variation in diurnal rhythm within each sex throughout adulthood, and the smaller sample sizes within age categories coupled with an absence of additional lifestyle variables challenges simple interpretations of the gender gap in cortisol release.

From a developmental perspective, the flattened diurnal slopes in children under age four are consistent with the hypothesized 'hyporesponsive period' of HPA activity occurring during infancy and lasting through early childhood (Gunnar and Donzella, 2002; Lupien et al., 2009). Although measurement error or issues with compliance may contribute to some of this variation, these findings could indicate the delayed establishment of the negative feedback rhythm until the hippocampus is more fully developed, and augment the small but growing body of research on the early ontogeny of HPA function (Galeeva et al., 2010; Jessop and Turner-Cobb, 2008; Lupien et al., 2009; Rosner, 1990). Age-related increases in cortisol from puberty until middle age in both males and females are also consistent with several previous reports (Adam, 2006; Gunnar and Quevedo, 2007; Lupien et al., 2009), yet it is unclear to what extent these changes reflect adaptive shifts in the set-points of basal HPA activity that track biological development, versus the cumulative burden of stress exposures experienced over decades.

The precipitous flattening of the cortisol rhythm in individuals over age 60 is contrary to prior findings in US-based elderly populations (Ice et al., 2004; Ice, 2005), although age-related declines in other endocrine hormones have been reported among some nonwestern populations (Ellison, 2010; Ellison et al., 2002; Campbell et al., 2006). It is possible that this finding is related to senescence among the Tsimane', or alternatively, could represent a cohort-effect among individuals who did not experience the suite of rapid sociocultural and lifestyle changes that present potential stressors for younger generations. Given the high mortality rate in this population (Gurven et al., 2007), a third possibility is that selection effects contribute to the observed 'convergence' of cortisol rhythms in this age group. Without additional data to clarify its causes, the flattened slope may at the very least be considered a marker of aging in this population.

From a comparative standpoint, the low cortisol rhythms from the Tsimane' represent a departure from those documented from industrialized populations, and raise the question of whether these findings indicate pathology, or alternatively, represent naturally occurring variation in HPA function among a population with a distinct suite of sociocultural, developmental, and ecological exposures. The

Table 3 Comparative cortisol values in diverse populations.

Study	Age	*N*	Wakeup	Bedtime	Slope	Mean	Reference
Tsimane'	1.6–15.9	222	5.27	1.94	−0.07	4.16	Nyberg (this study)
Tsimane'	16–82	81	6.39	2.22	−0.08	5.00	Nyberg (this study)
Botswana	>17	64	n.a	n.a.	n.a.	5.00	Decker (2006)
Nepal	11.8	107	6.11	n.a	n.a.	n.a.	Worthman and Panter-Brick (2008)
Philippines	15–16	245	7.44	2.19	−0.10	n.a.	Kuzawa (unpublished)
Dominica	2–18	256	15.8	n.a	n.a	n.a.	Flinn and England (1997)
Romania	8.55	18	22.2	n.a	n.a	n.a.	Gunnar and Vazquez (2001)
Canada	7.9	27	18.9	n.a.	n.a.	n.a.	Gunnar and Vazquez (2001)
Chicago	13–19	257	15.6	3.61	−0.15	n.a.	Adam (2006)
US	6–7	34	19.7	n.a.	n.a.	n.a.	Bruce et al. (2002)
CARDIA US	18–30	769	20.3	7.76	−0.78	n.a.	Cohen et al. (2006)
US	5–6	28	10.0	2.22	n.a.	n.a.	DeCaro and Worthman (2008)
Chicago and LA	16–18	255	12.2	2.78	−0.55	n.a.	DeSantis et al. (2007)
US	10–12	262	8.06	n.a	n.a.	n.a.	Hardie et al. (2002)
US	7–9	68 boys	6.94–13.1	n.a.	n.a.	n.a.	Jones et al. (2006)
US	7–9	72 girls	8.06–13.9	n.a.	n.a.	n.a.	Jones et al. (2006)
US	11–17	71	11.1	n.a.	n.a.	n.a.	Klimes-Dougan et al. (2001)
US	5–14	1152	13.6	n.a.	n.a.	n.a.	Koupil et al. (2005)
US	6–10	217	13.9–25.0	n.a.	n.a.	n.a.	Lupien et al. (2000)
US	11	178	8.06	n.a.	n.a.	n.a.	Moss et al. (1999)
US	8–16	126	9.17	n.a.	n.a.	n.a.	Netherton et al. (2004)
US	10–12	1768	15.3	n.a.	n.a.	n.a.	Rosmalen et al. (2005)
US	7–15	210 boys	8.88	n.a.	n.a.	n.a.	Tornhage (2002)
US	7–15	176 girls	8.61	n.a.	n.a.	n.a.	Tornhage (2002)

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vast majority of studies on hypocortisolism have revealed associations with extreme adversity, chronic stress, abuse, major psychological trauma, or PTSD (Gunnar and Vazquez, 2001; Heim et al., 2000; Miller et al., 2007; Yehuda, 2004). Less is known about the effects of prolonged inflammatory stimulation on HPA function in a high pathogen environment, and whether this could represent another pathway to chronic adrenal exhaustion. In this scenario, it might be expected that cortisol levels (average output and slope) would decrease with age to reflect the cumulative infectious burden and emergent HPA dysregulation across the lifespan. A second hypothesis generated from the adrenal exhaustion model would predict an inability of the HPA axis to respond to acute episodes of infectious morbidity, with dysregulation of the system resulting in impairment to the HPA reactive scope. The findings from this study indicate the opposite patterns in both regards: first, age is positively associated with both cortisol output and diurnal rhythm in this population, and second, since the age- and sex-adjusted cortisol levels among individuals not experiencing acute morbidity are significantly lower compared to those reporting illness, the inhibitory capacity of the system appears to remain intact. These findings are inconsistent with HPA axis dysfunction, adrenal exhaustion, or functional resistance at a receptor level (Miller et al., 2002; Raison and Miller, 2003), but longitudinal data are necessary to further clarify the complex and reciprocal relationships between HPA activity and immune function in this setting.

A broad body of anthropological studies have reported associations between various measures of acculturation and 'westernization' experience and elevated catecholamines, blood pressure, cortisol, as well as stress induced immunosuppression (Baker et al., 1986; Dressler, 1999; Graves and Graves, 1979; James et al., 1987; McDade, 2002; McDade and Nyberg, 2010; McGarvey and Baker, 1979; Nyberg, 2009). In the absence of refined data on self-perceived stress, however, in has yet to be determined whether lower cortisol levels among the Tsimane' are reflective of a lower psychosocial burden. Moreover, while lifestyle factors and stress exposures are possible contributors to the observed differences in cortisol profiles, they likely do not account entirely for the fact that less than 2% of the Tsimane' cortisol values resemble the values reported in the CARDIA study conducted in the United States (Cohen et al., 2006). It would also be inaccurate to assert that Tsimane' lives are stress-free, as many communities are grappling with the emergence of income inequality, exploitative debt relationships with river traders, and the encroachment of logging activities (Godoy et al., 2005; Nyberg, 2009; Undurraga et al., 2010). Beyond a cursory consideration of the psychosocial contributors to differential cortisol profiles, conceptualizing how the HPA axis navigates allostasis in diverse ecologies may yield deeper insight into the broad range of factors influencing HPA axis plasticity (Bateson, 2001; Barker, 2004; Gluckman et al., 2009). Though not exhaustive, this approach would benefit from inquiry into the relative roles of early social exposures, infectious disease loads, and nutritional and energetic status as logical points of entry.

For instance, early social interactions may have important implications for the epigenetic programming of the HPA axis (Curley et al., 2009; Fish et al., 2004; Meaney, 2010; Oberlander et al., 2008; Weaver et al., 2004). Thus, behaviors such as exclusive breastfeeding, co-sleeping, and intensive alloparental care should be explored as salient factors in establishing the sensitivity of the HPA axis of Tsimane' infants and in buffering the effects of adversity during development (Champagne et al., 2003; Chen et al., 2010; Gunnar and Donzella, 2002; Levine, 2005; Lupien et al., 2009; Tronick and Reck, 2009).

Though initial efforts have been made in tracing the nuanced role of glucocorticoids in regulating inflammatory pathways (Chrousos, 1995; Dantzer et al., 2008; Elenkov et al., 2000; Glaser and Kiecolt-Glaser, 2005; Miller et al., 2002; Nadeau and Rivest, 2003; Raison and Miller, 2003; Rivest, 2003; Sorrells and Sapolsky, 2007; Vedhara et al., 2007), especially with regard to the etiology of depression, the intersection of HPA activity and immune function in a high pathogen environment has yet to be considered (Besedovsky and del Rey, 1996; Blalock, 1989; Cole, 2008). In contrast to the relatively sterile environments in most industrialized nations, Tsimane' experience high rates of infectious and parasitic diseases across the lifespan (McDade et al., 2005; McDade et al., 2008; Tanner et al., 2009). These developmental exposures may induce phenotypic variation in the immune repertoire (McDade et al., 2010), and although speculative, may also shape HPA function, which plays an integral role in dampening the inflammatory response during infection. Future investigations should thus explicitly evaluate whether lower basal cortisol levels permit up-regulation of immune function in response to frequent microbial exposures, a major threat to mortality in this population.

Finally, the metabolic actions of cortisol are numerous, and range from the mobilization of energy reserves via gluconeogenesis and lipolysis, to the intracellular modulation of ATP production (Brillon et al., 1995; Du et al., 2009; Dallman et al., 1993; Hershberger et al., 2004). Therefore, an evolved sensitivity of the HPA axis to energy status emerges as another hypothetical pathway linking diverse environmental conditions to variation in cortisol rhythms. Important international research in human reproductive ecology has documented the metabolic sensitivity of the hypothalamic–pituitary–gonadal (HPG) axis, and has illuminated how endocrine architecture is largely shaped by the environment in which it develops, and may even convey signals of ecological information across generations (Ellison et al., 1993; Kuzawa, 2005; Kuzawa and Quinn, 2009). For instance, rural nonwestern populations experiencing marginal nutrition and high levels of physical activity throughout development consistently demonstrate lower levels of reproductive steroids compared to urbanized, sedentary, industrialized populations (Ellison, 2003; Ellison and Panter-Brick, 1996; Jasienska et al., 2006; Núñez-de la Mora et al., 2007; Vitzthum, 2009). A recent study measuring leptin (Sharrock et al., 2008), an endocrine hormone released from adipocytes that signals energy status, revealed that levels among the Tsimane' are also the lowest on record, and thus provides compelling impetus for future analyses. Similar inquiry may help to determine if the low cortisol levels among the Tsimane' are influenced, in part, by homeostatic calibration of the HPA axis to energy scarcity.

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5. Conclusions

The paucity of time-varying covariates on perceived stress, mood, affect, and sleep quality preclude the evaluation of the moment-to-moment differences in cortisol in this study. Also absent are data on the menstrual cycle, birth weight, or other pre- or postnatal factors that may contribute to differential patterns of cortisol release. The cross-sectional analyses presented here provide important preliminary insight into HPA axis dynamics among the Tsimane', but additional longitudinal data will facilitate a more comprehensive understanding of individual change over time.

In sum, this is the first study to document variation in the diurnal dynamics of cortisol release among females and males across the lifespan in a remote nonwestern population. The findings of this study verify that there are distinct patterns of cortisol release associated with sex and age among the Tsimane', which may hint at the integrative role of HPA function in mediating the critical adaptive demands of developmental transitions across the lifespan. Although it is beyond the scope of this study to determine whether the lower, more conservative diurnal rhythm displayed among the Tsimane' is optimal, functionally adaptive, or 'healthier' compared to the typical rhythm exhibited in industrialized populations, continued hypothesis-driven research along the recommended lines of inquiry holds great promise in resolving this question (Ellison and Jasienska, 2007; Kuzawa and Quinn, 2009). Nevertheless, this study provides a benchmark against which to reference cortisol levels from industrialized populations, and establishes the lower bounds of variation in HPA function documented thus far.

A truly integrative approach that incorporates the energetic and developmental contingencies of HPA axis plasticity is well-positioned to elucidate how within- and between-population differences in cortisol potentiate risk for such formidable public health problems as depression, hypertension, obesity, the metabolic syndrome, and other stress-related disorders. The first step in unraveling these pathways requires a research agenda within psychoneuroendocrinology that explores the range of variation in diurnal HPA axis function across diverse populations, and grants explicit attention to the role of distinct social and ecological exposures in shaping HPA trajectories across the lifespan.

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Conflict of interest

None declared.

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