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Sex differences in daily activity intensity and energy expenditure and their relationship to cortisol among BaYaka foragers from the Congo Basin

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Abstract

Objectives: The pooling of energetic resources and food sharing have been widely documented among hunter-gatherer societies. Much less is known about how the energetic costs of daily activities are distributed across individuals in such groups, including between women and men. Moreover, the metabolic physiological correlates of those activities and costs are relatively understudied.

Materials and methods: Here, we tracked physical activity, energy expenditure (EE), and cortisol production among Congo Basin BaYaka foragers engaged in a variety of daily subsistence activities ($n = 37$). Given its role in energy mobilization, we measured overall daily cortisol production and short-term cortisol reactivity through saliva sampling; we measured physical activity levels and total EE via the wGT3X-bt actigraph and heart rate monitor.

Results: We found that there were no sex differences in likelihood of working in common activity locations (forest, garden, house). Across the day, women spent greater percentage time in moderate-to-vigorous physical activity (%MVPA) and had lower total EE than men. Females with higher EE (kCal/hr) produced greater cortisol throughout the day. Though not statistically significant, we also found that individuals with greater %MVPA had larger decreases in cortisol reactivity.

Discussion: BaYaka women sustained higher levels of physical activity but incurred lower energetic costs than men, even after factoring in sex differences in body composition. Our findings suggest that the distribution of physical activity demands and costs are relevant to discussions regarding how labor is divided and community energy budgets take shape in such settings.

KEYWORDS

actigraph, cortisol reactivity, hunter-gatherer, metabolism, physical activity

1 | INTRODUCTION

Life history theory posits that organisms allocate energy to the mutually exclusive categories of growth, reproduction, and maintenance, leading to trade-offs that depend on life stage (Hill & Kaplan, 1999). Hormones

produced by a variety of axes play contributing roles to these life history demands and are key mechanisms that mediate trade-offs between them (Bribiescas & Ellison, 2008; Nieuwenhuizen & Rutters, 2008; Pontzer et al., 2015). In energetically constrained settings where humans must cope with intensive physical demands, high

pathogen loads, and/or nutritional short-falls, reproductive hormone production is responsive to physiological signals of energetic status (Ellis & Boyce, 2008; Ellison, 2003; Jasienska, 2003; Muehlenbein, Hirschtick, Bonner, & Swartz, 2010; Nepomnaschy, Welch, McConnell, Strassmann, & England, 2004; Vitzthum, 2009).

For example, substantial work in female reproductive ecology has demonstrated that ovarian production of the hormones progesterone and estradiol respond to nutritional status and physical activity levels. This strategic adjustment helps calibrate women's fecundity to both longer and shorter term indices of their energetic condition thereby helping balance trade-offs between survival/maintenance and costly reproductive events (Ellison, 2003; Emery Thompson, 2013; Jasienska, Ziomkiewicz, Thune, Lipson, & Ellison, 2006; Panter-Brick, 2014; Vitzthum, 2009). Similarly, work in male reproductive ecology has demonstrated potential tradeoffs between costly investment in reproduction, often facilitated by androgenic hormones like testosterone, and investment in maintenance and survival when males are stressed energetically or by acute infection (Bribiescas, 2001; Ellison, 2003; Muehlenbein et al., 2010; Trumble, Brindle, Kupsik, & O'Connor, 2010).

Other hormones serve in proximate mechanistic roles of liberating energy (e.g., from adipose stores) and channeling energetic resources to metabolically active tissues as costs arise, such as in skeletal muscle during demanding day-to-day physical activity. The hormone cortisol (CORT) produced by the hypothalamic-pituitary-adrenal (HPA) axis, is one such hormone responsible for metabolism and energy mobilization (Sapolsky, Romero, & Munck, 2000). Two of its major functions are mobilizing physiological resources (e.g., energy release) and facilitating recovery from fight-or-flight sympathetic activation (Nelson, 2011). CORT elevates blood glucose levels by shunting amino acids and other substrates to the liver for conversion to glucose and promotes the breakdown of protein and fat stores in the body. The net result is a release of energy reserves that allow for adequate metabolic functioning (Dickerson & Kemeny, 2004; Sapolsky et al., 2000). Compared to sympathetic nervous system response, CORT is a part of the slower response to physically and psychosocially challenging conditions, with the maximum levels of the hormone peaking at 21–30 min after such stressors occur (Dickerson & Kemeny, 2004). Thus, CORT's contributing role in liberating energy stores would help provide the fuel necessary for continued physical activity following the immediate activation of the HPA axis and sympathetic nervous system in response to an acute physical or social stressor.

CORT's metabolic roles are critical for everyday energy expenditure (EE) including responding to levels of physical activity. In U.S.- and European-based lab settings, acute CORT increases substantially only in response to intensive physical activity (Brownlee, Moore, & Hackney, 2005). However, CORT's metabolic roles may be more sensitive and responsive during every day physical activity in highly active populations facing energetic constraints, such as in foraging societies (Pontzer et al., 2012). Under such ecological conditions, individuals may have a greater need to generate energy substrates "on demand" due to factors like lower circulating blood glucose compared to active

individuals in energy-replete settings like the United States (Kaplan et al., 2017). However, in the face of routine energetic and pathogenic stressors, baseline CORT coupled with acute CORT responses to intense physical activity could plausibly be constrained to limit the depletion of energetic stores and to potentially attenuate CORT's long-term negative effects on fecundity (Nepomnaschy et al., 2004). Yet, most of our knowledge on acute CORT responses to such physical demands comes from a narrow range of study designs and populations in the United States and Europe. For example, exercise physiology research specifically looking at athletes in controlled laboratory settings shows that CORT tends to go up acutely during rigorous workouts (Brownlee et al., 2005). Similarly, many studies have documented that athletes' CORT rises during sporting events, regardless of fasting status (Casto, Elliott, & Edwards, 2014; Maughan et al., 2008). Yet, the vast majority of human data related to the intersection of hormones and activity has been generated from western, educated, industrialized, rich, and democratic participants (Henrich, Heine, & Norenzayan, 2010).

While few studies which examine CORT production in subsistence settings, they show that it likely differs from that of industrialized populations. For example, forager-horticulturalists in Papua New Guinea experienced significantly lower waking CORT and their diurnal CORT slope was considerably flatter than industrialized reference populations (Urlacher, Liebert, & Konecna, 2018). The limited existing research on acute CORT reactivity demonstrates that the relationship between intensive physical activity and CORT is mixed and interpretations are somewhat hindered by research design differences. For example, among female Indigenous high-altitude residents in Nepal, the intensity of daily activities was not correlated with women's short-term CORT responses to those demands (Sarma, Gettler, Childs, & Quinn, 2018). Among Tsimane forager-horticulturalists in Bolivia, men maintained relatively elevated CORT during physically demanding hunting but only if they successfully killed an animal (Trumble, Smith, O'Connor, Kaplan, & Gurven, 2014). Among Hadza foragers of Tanzania, researchers found no relationship between daily production of CORT, as measured in urine, and overall total EE, of which physical activity costs are a component (Pontzer et al., 2015). In sum, questions remain regarding the role of CORT in responding to the often-intense daily physical demands of life in energetically constrained settings that are typical of many small-scale societies. Specifically, it is unknown whether men and women show variation in such responses, and whether socio-ecological factors, such as divisions of labor, shape these dynamics.

Models of human evolution often highlight the importance of sex-based divisions of labor in cooperative subsistence practices, sex differences in subsistence activity participation and sex-specific caloric and macronutrients returns (Gurven & Kaplan, 2006; Hill & Hurtado, 2009; Kramer, 2010; Meehan, Quinlan, & Malcom, 2013; Panter-Brick, 1992). Such models are usually based on contemporary foraging societies, where adults cooperate to pool resources: adult males and females tend to target different foods and they are shared to varying degrees. Females tend to target more reliable foods and males often target energy-dense foods that are difficult to acquire

and are shared widely outside of the household (Bird, 1999; Hawkes, O'Connell, & Blurton Jones, 2018; Hill & Hurtado, 2009; Kaplan, Hill, Lancaster, & Hurtado, 2000; Kelly, 1995; Marlowe, 2007; Wood & Marlowe, 2013). For example, in a study of 10 foraging societies, men contributed 65% of total calories and 85% of calories from energetically dense protein to the community diet on average, while women primarily contributed consistent dietary staples (Gurven & Hill, 2009; Kaplan et al., 2000). These patterns, including the sex ratio of contributions and sex-based task specialization, vary in relation to ecological factors such as latitude; sexual division in labor tends to be the most pronounced in colder climates, whereas in the tropics, where food that is gathered is more abundant, sexual division in subsistence labor tends to be comparatively reduced (Kelly, 1995; Marlowe, 2005).

Data on the variation in energetic resource acquisition, and how these resources are then shared to support highly dependent offspring, complements reproductive ecology research demonstrating the sensitivity of female reproductive physiology to energetic conditions (Ellison, 2003; Jasienska et al., 2006; Panter-Brick, 2014; Vitzthum, 2009). Specifically, reproductive ecology research shows that female reproducing bodies are highly sensitive and respond to energetic conditions; these conditions are partly shaped through behavioral strategies in how energetic resources are acquired and subsequently distributed. Though males do not have to bear the metabolic costs of menstruation, gestation, and lactation and thus have lower energy requirements for functional reproductive physiology compared to females, major differences in subsistence-specific energetic status (i.e., forager/horticulturalist vs. industrialized populations) can influence reproductive physiology at the population level (Bribiescas, 2001).

Yet, we know surprisingly little about potential individual- and sex-based differences in energetic costs of daily physical activities in such societies and, especially, male and females' short-term physiological responses to those variable demands, such as during subsistence work (Meehan et al., 2013). The energetic costs of daily activity draw resources away from other demands (e.g., maintenance-survival and reproductive functioning) and also have other accompanying physiological corollaries (e.g., production of CORT; oxidative stress) that can negatively impact reproduction, immune function, and longevity (Ellison, 2003; Emery Thompson, 2013; Jasienska, 2003; McDade, 2003; Nepomnaschy et al., 2004; Ziolkiewicz, Frumkin, Zhang, Sancilio, & Bribiescas, 2018). Thus, these are important considerations for our understanding of health and reproductive ecology in contemporary populations in energetically demanding contexts and in the evolutionary past. Also, given the vast diversity of ecologically dependent neuroendocrine responses in our species, understanding the relationship between energetic costs of daily activity and neuroendocrine systems may shed light on health and function of contemporary non-energetically stressed populations when they are faced with energetically demanding stressors stemming from changes to their environment or lifestyle.

To help address these issues, we tracked physical activity, average EE, and salivary CORT in BaYaka foragers ($n = 37$) from the Republic of Congo. Here, we measured cortisol reactivity and EE in response to short-term physical activity. We also measured EE and CORT production across the day. Similar to other Congo Basin forager societies

(Ivey, 2000; Tronick, Morelli, & Ivey, 1992; Turnbull, 1978), the BaYaka are highly egalitarian and men and women often spend a substantial portion of their day together, engaged in shared foraging activities (Hewlett, 1992; Hewlett, 1993; Lewis, 2002). Compared to other foragers, the BaYaka maintain a lower overall division of foraging labor and greater cooperation in hunting tasks (Marlowe, 2007). Food, including protein and vegetable staples, and other resources are shared widely (Boyette & Lew-Levy, 2019; Kitanishi, 1995; Marlowe, 2007). Both men and women share in political decision-making, care for offspring, and men and women often work together or alongside each other during subsistence tasks (Hewlett, 1992). With such a highly egalitarian social system, it could be posited that BaYaka physical activity demands and the associated physiological costs, such as EE (relative to body size/composition), may be relatively similar between the sexes. Consequently, we predicted that males and females would spend similar time in moderate-to-vigorous physical activity (%MVPA) and have comparable daily activity costs (EE) to each other, after adjusting for sex differences in body size and composition. We also predicted that individuals with greater %MVPA and higher total EE would exhibit greater CORT production across the day and that individuals with greater %MVPA during the hour of activity would exhibit greater acute increases in CORT during said activity.

2 | METHODS

2.1 | Study population and ethnographic context

The current study is part of a larger biocultural project on family systems among BaYaka foragers in northern Republic of the Congo (Boyette, Lew-Levy, Sarma, & Gettler, 2019; Boyette, Lew-Levy, & Gettler, 2018). Northern Congo is densely forested, with high levels of solar radiation, rainfall, and humidity, and a relatively constant mean annual temperature of 25.4°C (Kitanishi, 1995; climate-data.org, 2019). The BaYaka live a seasonally mobile lifestyle, moving between the forest and villages which they share with by farming communities. Forest activities include hunting, trapping, fishing, gathering, honey collecting, and maintaining low-input gardens producing food staples like cassava. When in the village, the BaYaka frequently collaborate with Bondongo fisher-farmers by bartering goods and services, including hunting or working in villager-owned gardens. The BaYaka community surveyed here lived in a remote village setting with limited marked integration. Overall, the population rarely suffers from food shortages, but community members frequently complained of helminth infections; compared to most individuals in industrialized populations, they have an increased pathogenic/parasitic load (Froment, 2017).

2.2 | Data collection

Participants included 37 healthy BaYaka forager adults (females = 20; pregnant females = 3). Because the BaYaka do not record age, we estimated an approximate age following methods used by Diekmann et al. (2017) and adjusted for parent-child age differences for a minimum

of 16 years. Individuals in the sample were estimated to be aged between 22 and 62 years old (males = 37.18 ± 11.58 [SD]; females = 34.15 ± 30.56). M. S. S. and V. M. collected data for this study in June and July of 2017. Village consent to conduct the research was obtained at a public meeting held during a prior field trip in 2015, and individual verbal consent was obtained from all participants during the 2017 study period. Participants were recruited among those already participating in the larger biocultural project on family systems; after hearing about what the study entailed, individuals volunteered to participate in this study. All participants had at least one child less than 18 years of age. We gave immediate compensation for research participation included rice, salt, and a bracelet, which are highly desirable commodities. Participants also received machetes and cloth at the end of the field season. The Institutional Review Board of the University of Notre Dame approved this study (IRB protocol 17-03-3687).

2.2.1 | Focal follows and activity locations

Given the heat and solar exposure, most tasks requiring intensive physical activity were performed in the mornings. Thus, M. S. S. and V. M. simultaneously conducted focal follows in the mornings with each individual (on average 3.66 hours). Most often, we followed couples with M. S. S. focusing on the female and V. M. focusing on the male, from each pair. Activities were divided into the following categories: hunting, collecting, fishing, gardening, food processing, childcare, housework, leisure, travel, and miscellaneous work (which included sharpening tools, carrying water, etc.). See Table 2 for how time was allocated, by minute, across the focal follow period.

Since location determined activity type, subsistence tasks were delineated into the locations in which they occurred—forest, garden, and house. Forest activities (40.54% of all activities) included hunting, building traps, fishing, and collecting *mbila* (palm nuts). Garden activities (43.24% of all activities) included clearing gardens, digging/planting, and harvesting parts of the manioc (cassava) plant (*boma* and *jabuka*) or banana plants. Finally, house activities (16.22% of all activities) included carrying jerry cans of water, preparing food, and home repair. For forest activities, married males and females tended to do activities as couples, working together to complete tasks in the forest itself. For many of these activities, tasks were sex specific. For example, when collecting *mbila*, males would climb up the trees and cut the *mbila* bunch down and females would locate, carry, and pick out *mbila* nuts from the greater bunch. Males and females similarly tended to work together during garden activities, though the tasks performed remained largely the same across sexes (i.e., digging, clearing brush). Of all locations, males and females tended to work alone and be the most sex differentiated in household activities. Cooking and carrying water were restricted to females though both sexes engaged in home repair.

2.2.2 | Anthropometrics

All participants were measured for height, weight, and upper arm circumference, and triceps skinfold thickness using standard techniques

(Lohman, Roche, & Martorell, 1988). Height was measured with a Seca stadiometer measured to the nearest millimeter, and weight with a digital scale measured to the precision of 1/10 of a pound. Triceps skinfold thickness was measured using Lange skinfold calipers to approximate levels of body fat as an additional marker of current health and energetic condition. Also, to compare against existing studies looking at similar parameters, we calculated fat-free mass using the Durnin and Womersley (1974) equation. All anthropometric measurements were taken during the beginning 2 weeks of the 2-month field season.

2.2.3 | Physical activity and energetic expenditure data

Physical activity levels, total EE, and heart rate were measured using the Actigraph wGT3X-bt wrist monitor and the Polar Bluetooth Heart Rate monitor (Actigraph, Pensacola, FL). We collected 12 hr of actigraphy data for each participant. Actigraph and heart rate data were processed in the ActiLife 6 software. Percentage of time spent in MVPA was calculated through the ActiLife software, and specifically refers to the time that subjects spend above a “moderate” cut point level, or 3.00–5.99 metabolic equivalent of tasks; this represents the frequency and amplitude of acceleration events over time and thus indicates a “significant” level of activity (Freedson, Melanson, & Sirard, 1998; Rothney, Schaefer, Neumann, Choi, & Chen, 2008). MVPA accounts for individual height and weight in the equation. EE was calculated using two different methods—through accelerometry and through the flex HR method. The accelerometry method is run through the ActiLife software using the Freedson equation as total active EE as the total calories (Freedson et al., 1998). The flex HR method uses the Hiilloskorpi method to predict total EE based on changes in average heart rate where HR >90 BPM is considered “heavy” activity and HR < 90 BPM is considered “light” activity (Hiilloskorpi, Pasanen, Fogelholm, & Laukkanen, 2003). This method accounts for individual bodyweight in analysis and thus, for models looking at EE we did not include bodyweight but include fat-free mass and triceps skinfolds as estimates body composition (i.e., lean and fat mass). See the supplementary information for the full formulas used in EE analysis.

2.2.4 | Salivary CORT

Salivary CORT measurements were collected via saliva samples across five time points: (a) in the early morning (6:06 a.m. \pm 7.20 min; $n = 35$), (b) pre-task (8:25 a.m. \pm 44.87 min; $n = 36$), (c) 30 min into the task (9:01 a.m. \pm 44.16 min; $n = 36$), (d) after the task (9:40 a.m. \pm 51.73 min; $n = 36$), and (e) evening (6:06 p.m. \pm 20.45 min; $n = 26$). Then, 68% of individuals gave all five samples, 24% gave four samples, and 8% gave two to three samples. Given the close proximity of individuals, participants tended to awaken, emerge from their homes, and engage with others in the community within rapid succession all

around the same time—the first sample was taken as soon as they emerged from their homes (first morning CORT = 0.27 ± 0.14 $\mu\text{g}/\text{dl}$). Wake time was obtained from Motionwatch8 actigraphs and analyzed using the CamNTech MotionWare 1.2.23 program. The difference between wake time and first morning samples was then calculated. We found that on average, the wake time was within 35.5 min of the first morning sample. The “task” was determined as the first subsistence activity of the day and samples coincided with the focal follows—“pre,” “30-min,” and “after” samples were all taken during the focal follows and kept in portable coolers with ice packs until they could be transported to the liquid nitrogen dewars. The evening samples were taken at the end of the day at sunset. The day before the sampling period for each participant, we talked to our participants to review the procedures and they chose what task they wanted to do the following day. All tasks were part of regular everyday activities and would have been done regardless if they were being sampled that day or not. Individuals were not asked to avoid routine activities such as eating or smoking tobacco prior to providing saliva. During focal follows, we recorded that 29.7% of individuals were smoking and modeled whether focal-follow smoking predicted CORT reactivity. Smoking status was not predictive of CORT reactivity during the focal follows in the full sample ($b = -3.55$, 95% CI = -43.84 , 36.74 ; $p > 0.9$), or among men only ($b = 16.14$, 95% CI = -20.66 , 52.95 ; $p > 0.3$), among whom it was more prevalent during the follows. Thus, we did not include it in the relevant analyses in the Results.

Prior to the calculation of CORT production and reactivity scores, each CORT measure was regressed on the time of the first sample and the distance of time between the first sample and that specific sample (e.g., raw preactivity CORT was regressed against the first morning sample and time between the first morning sample and preactivity sample). We then took the residual of each of those models and added the mean of the CORT variable to the residual. This procedure removed the effect of sampling time on the CORT data. Data from all five of the time points were used to calculate total CORT production across the day (i.e., waking period) using the area under the curve with respect to ground method (Pruessner, Kirschbaum, Meinlschmid, & Hellhammer, 2003). After the activity was recorded and the focal follow terminated, individuals continued the rest of the day at their own discretion. Data from time points 2 and 3 (pre-activity and 30 min, respectively) were used to calculate acute reactivity to specific morning activities. Time points 2 and 3 were used to calculate the percentage change difference (i.e., acute reactivity) in CORT after 30 min of the activity; this time frame is the window during which CORT reactivity is well documented to rapidly responding to physical and psychosocial demands (Casto et al., 2014; Dickerson & Kemeny, 2004). There was on average 36 ± 9.56 min between time points 2 and 3.

Samples were frozen and stored on site in portable liquid nitrogen dewars and were shipped to the Hormones, Health, and Human Behavior Lab at the University of Notre Dame where they were stored at -80°C . Because of logistical problems during shipment, the saliva samples went through a freeze–thaw cycle while in transit to Notre Dame. However, research suggests that given the

relative robustness of CORT to freeze–thaw cycles and short-term exposure to ambient temperatures the additional thawing should not compromise our results (Hansen & Garde, 2005; Reyna et al., 2001). Concentrations of CORT were determined using commercially available kits for enzyme immunoassay protocol developed for saliva samples (Salimetrics, Carlsbad, CA; Kit No. 1-3002). Prior to assay procedures, saliva samples were visually inspected for discoloration (such as from blood or food contamination). Samples were also vortexed and centrifuged at 3,000 rpm for 15 min to help remove particulate matter (such as from food) from the saliva. Samples were assayed in duplicate by M. S. S. Interassay coefficients of variation were 8.3 and 6.3% for high and low kit-based control samples, respectively, for CORT; the intraassay CV for CORT was 6.0%.

2.3 | Statistical analysis

We conducted all statistical analyses using Stata 14.0 (Stata Corporation). We first ran chi-square tests to compare if males and females worked in the same spaces (i.e., activity locations) and used unpaired Student's *t* tests to test for sex-based differences in other relevant study variables (Table 1). We used ordinary least squares (OLS) regression to test for sex differences in daily variation of %MVPA, EE, and CORT measures. In these models, we included estimated age and triceps skinfold thickness as an indicator of body fat as covariates. In models predicting EE, we included fat-free mass in light of prior work from a similar subsistence setting and to allow comparisons thereof (Pontzer et al., 2015). Next, we used OLS regression to test if %MVPA and EE predicted CORT AUC_g and CORT reactivity, respectively, in separate sets of models. For each CORT outcome, we ran a model with men and women's data combined and then separated by sex in order to test for differences within each sex. For models predicting CORT reactivity from physical activity, we specifically used the percentage of time spend in MVPA during the hour that the activity was in. For models predicting CORT AUC_g, we used the percentage of time in MVPA for the full 12-hr period. All individuals that did not have all five samples ($n = 12$) were dropped from the CORT AUC_g model. We evaluated significance at $p < 0.05$. However, given our relatively small sample size, we will discuss any findings where $p < 0.10$. We also conducted post hoc analyses looking at the partial correlations of %MVPA with % change in CORT, raw change in CORT, preactivity CORT, and CORT 30 min into activity.

3 | RESULTS

Males weighed more and had greater fat-free mass than females, on average, and males also had lower triceps skinfold thickness, a marker for subcutaneous body fat (all $p < 0.001$; see Table 1). We found that there were no significant differences in the locations of activity (i.e., between forest work, garden work, and housework) between

TABLE 1 Descriptive statistics for the total sample

	Full sample (m ± SD)	Male (n = 17)	Female (n = 20)	df	t
<i>Age and anthropometrics^a</i>					
Estimated age	35.49 ± 10.38	37.53 ± 11.92	33.75 ± 8.82	35	-1.11
Bodyweight (kg)	51.37 ± 6.63	55.78 ± 4.66	47.62 ± 5.73	35	-4.70**
Triceps skinfolds (mm)	9.76 ± 5.36	5.59 ± 0.91	13.30 ± 4.99	35	6.27**
FFM (kg)	41.49 ± 7.19	48.33 ± 3.62	35.68 ± 3.07	35	-11.51**
Activity location (%) ^b					0.74
Forest	40.5	47.1	35.0		
Garden	43.2	41.2	45.0		
House	16.2	11.8	20.0		
<i>Physical activity</i>					
%MVPA	34.4 ± 11.2	28.5 ± 8.7	39.4 ± 10.8	35	3.34**
Reactivity %MVPA	58.9 ± 19.6	49.5 ± 18.8	66.9 ± 16.8	35	2.97**
<i>Energy expenditure (avg kCal/hr)</i>					
EE (across the day—Hiilloskorpi)	157.63 ± 79.78	228.66 ± 55.79	97.26 ± 332.98	35	-8.88**
EE (across the day—accelerometry)	52.10 ± 18.00	69.26 ± 15.39	59.99 ± 18.74	35	-3.09**
EE (reactivity—Hiilloskorpi)	204.70 ± 105.47	287.90 ± 83.90	138.13 ± 66.65	35	-5.97**
<i>CORT</i>					
CORT AUC ^c	1.30 ± 0.46	1.38 ± 0.43	1.48 ± 0.39	23	-1.04
CORT reactivity (% change) ^d	7.2 ± 63.9	7.4 ± 58.4	7.7 ± 53.2	33	-0.03

Note: $p < .1$. * $p < .05$. ** $p < .01$.

Abbreviation: EE, energy expenditure; FFM, fat-free mass; MVPA, moderate-to-vigorous physical activity.

^aStatistical comparisons reflect Student's *t* test unless otherwise noted.

^bStatistical comparisons reflect chi-squared test.

^c $n = 25$; reported as area under the curve with respect to ground.

^d $n = 35$; reported as percentage change.

males and females (chi square, $p > 0.7$; Table 1). When adjusting for age, sex, and skinfold thickness, location of activity did not significantly predict %MVPA. However, when adjusting for age, sex, and skinfold thickness, childcare significantly predicted %MVPA (all $p > 0.5$). Despite this significant correlation, when we added childcare in the models below (Section 3.2.1), it did not meaningfully change the results, so we did not formally include them. Neither location of activity nor activity type during the focal follow significantly predicted EE when adjusting for age, sex, skinfold thickness, and fat-free mass ($p > 0.5$) (Table 2).

3.1 | Physical activity and EE

For %MVPA across the day, we found that females spent a significantly greater percentage of time in MVPA, on average 36.4%, compared to males who spent 28.5%, on average, after adjusting for triceps skinfolds ($p = 0.001$, Cohen's $d = 1.13$; Table 3). In contrast, we did not find that females' greater time spent in more physically vigorous work translated to overall higher caloric EE. Males had significantly greater average EE (mean: 253.27 kCal/hr) compared to females (mean: 84.06 kCal/hr) ($p = 0.001$, Cohen's $d = -4.28$; Table 3), including after adjustment for triceps skinfolds, and fat-free mass (Table 3).

TABLE 2 Percent of time allocated to activities during focal follows

	Full sample ^a	Male ^b	Female ^c	<i>p</i> -Value ^d
Hunting	3.6	7.9	0.0	.01
Collecting	21.0	17.9	23.6	.30
Fishing	5.7	4.1	7.0	.92
Gardening	14.0	12.6	15.1	.96
Food processing	7.9	10.7	5.5	.44
Childcare	14.9	2.2	25.7	.01
Housework	5.6	7.2	4.2	.67
Leisure	19.6	23.3	16.4	.10
Travel	32.5	37.4	28.2	.10
Saliva collection	7.8	9.8	6.0	.01
Miscellaneous work	15.4	13.9	16.8	.54

Bold values are $p < 0.05$.

^a $n = 7,098$ min.

^b $n = 3,223$ min.

^c $n = 3,875$ min.

^d*p*-Value for Wilcoxon rank-sum test.

3.2 | CORT output

Overall daily production of CORT was measured via area under the curve with respect to ground (CORT AUCg: 1.30 ± 0.46) and CORT

reactivity was measured as the percentage change in CORT between preactivity and ~30 min into activity (7.2 ± 63.9). CORT AUCg and CORT reactivity were not significantly correlated (Pearson's $r = 0.24$; $p > 0.2$). Adjusting for age and triceps skinfolds, we found that sex did not predict either overall CORT production or CORT reactivity ($p > 0.1$).

3.2.1 | CORT and %MVPA

Overall %MVPA throughout the day did not predict daily CORT production, adjusting for age and triceps skinfolds in either sex ($p > 0.1$). However, for CORT reactivity, we found that individuals with greater %MVPA showed relatively larger decreases (or more muted increases) in CORT, though the finding was not statistically significant, and the 95% confidence intervals included zero ($p = 0.14$; Table 4). In order to test for within-sex differences, we separated models by sex and found that this association was significant in males ($p < 0.05$; Table 4). To help contextualize this finding, which ran counter to our prediction, we conducted post hoc partial correlation analyses to test whether adjusting for preactivity CORT helped explain this pattern and to test for associations between %MVPA, preactivity CORT, and CORT 30 min into activity (see Suppl Table S1). Similar to findings in the previous models, we found a significant negative partial correlation

between raw change in CORT reactivity and %MVPA after adjustment for preactivity CORT ($r = -0.60$; $p < 0.05$). The magnitude of that association is similar to the partial correlation between %MVPA and percentage change in CORT ($r = -0.55$; $p < 0.05$) that mirrors Model 2 in Table 4. Neither preactivity CORT ($r = -0.002$) nor CORT 30 min into activity ($r = -0.37$) were significantly correlated with % MVPA ($p > 0.2$).

3.2.2 | CORT and EE

Predicting EE, adjusting for age, triceps skinfolds, and fat-free mass, we found that in the combined model that included men and women individuals with greater average kCal/hr across the day had greater higher daily production of CORT, though the result was not statistically significant ($p = 0.08$; Table 5). There was no significant relationship between average kCal/hr and daily production of CORT in men ($p > 0.8$). In women, those with higher average kCal/hr had significantly greater daily production of CORT ($p < 0.05$). To provide context on the effect size for this significant relationship, we compared CORT AUCg for women who were low for avg EE/hr (lowest quartile) to those who were higher for avg EE/hr (top quartile). This group comparison had a medium effect size (Cohen's $d = -0.51$). We note that when we removed the two pregnant women from the model, this relationship was no longer significant,

TABLE 3 Models testing for sex differences in %MVPA and EE

	Model 1 (%MVPA) ^a			Model 2 (EE) ^b		
	<i>b</i>	95% CI	<i>p</i>	<i>b</i>	95% CI	<i>p</i>
Male	-0.17	(-0.26, -0.07)	0.001	184.64	(110.67, 258.61)	0.001
Age	-0.001	(-0.004, 0.003)	0.72	0.56	(-0.92, 2.04)	0.44
Triceps skinfolds (mm)	-0.01	(-0.02, 0.001)	0.09	3.03	(-1.08, 7.14)	0.14
FFM (kg)	—	—	—	-2.53	(-7.12, 2.06)	0.27
Model R^2	0.306			0.725		

Abbreviations: EE, energy expenditure; FFM, fat-free mass; MVPA, moderate-to-vigorous physical activity. Bold values are $p < 0.05$.

^a $n = 37$.

^b $n = 37$.

TABLE 4 Models predicting CORT reactivity from %MVPA

	All ^a			Males ^b			Females ^c		
	<i>b</i>	95% CI	<i>p</i>	<i>b</i>	95% CI	<i>p</i>	<i>b</i>	95% CI	<i>p</i>
%MVPA	-81.28	(-190.66, 28.09)	0.14	-95.18	(-184.24, -6.13)	0.04	-74.58	(-286.58, 137.42)	0.46
Male	-54.50	(-108.78, -0.22)	0.05	—	—	—	—	—	—
Age	-0.36	(-2.28, 1.56)	0.70	0.66	(-1.03, 2.35)	0.41	-0.59	(-4.70, 3.53)	0.76
Triceps skinfolds (mm)	-4.41	(-9.28, 0.46)	0.07	16.95	(-4.48, 38.39)	0.11	-4.74	(-11.38, 1.89)	0.15
Model R^2	0.170			0.408			0.166		

Abbreviation: MVPA, moderate-to-vigorous physical activity.

Bold values are $p < 0.05$.

^a $n = 35$.

^b $n = 16$.

^c $n = 19$.

TABLE 5 Models predicting CORT AUC_g from EE

	All ^a			Males ^b			Females ^c		
	<i>b</i>	95% CI	<i>p</i>	<i>b</i>	95% CI	<i>p</i>	<i>b</i>	95% CI	<i>p</i>
EE (kCal/hr)	0.004	(−0.001, 0.01)	0.08	0.001	(−0.01, 0.01)	0.83	0.01	(0.002, 0.02)	0.02
Male	−0.86	(−2.21, 0.48)	0.19	—	—	—	—	—	—
Age	−0.002	(−0.02, 0.01)	0.80	−0.003	(−0.04, 0.03)	0.83	0.01	(−0.02, 0.04)	0.55
Triceps skinfolds (mm)	−0.01	(−0.06, 0.04)	0.67	0.04	(−0.49, 0.58)	0.85	−0.03	(−0.08, 0.02)	0.26
FFM (kg)	0.03	(−0.02, 0.09)	0.22	0.02	(−0.13, 0.16)	0.78	0.002	(−0.07, 0.08)	0.96
Model <i>R</i> ²		0.230			0.08			0.465	

Abbreviation: EE, energy expenditure; FFM, fat-free mass.

Bold values are $p < 0.05$.

^a $n = 25$.

^b $n = 11$.

^c $n = 14$.

though the pattern remained in the same direction with a modestly smaller effect size ($b = 0.006$; 95% CI = $-0.01, 0.02$; $p = 0.30$). EE did not significantly predict changes in CORT reactivity (all $p > 0.7$).

4 | DISCUSSION

Our study modeled the relationships between neuroendocrine function, physical activity intensity, and EE in BaYaka hunter-gatherers, complementing a small number of other relevant studies in small-scale societies (Meehan et al., 2013; Pontzer, 2015; Trumble et al., 2013). This study is unique in that it highlights the sex-based differences in physical activity, energetic costs, and the associated neuroendocrine corollaries, that is, CORT reactivity and production of CORT across a day in a forager population. We found that the sexes significantly differed for physical activity levels and average daily EE. Interestingly, we did not find significant sex differences for either CORT AUC_g or CORT reactivity, though we did find sex-specific patterns in the relationship between CORT AUC_g with EE and CORT reactivity to % MVPA. As we discuss in further detail below, our findings suggest that there may be important relationships between physical activity, EE, and CORT in this physically demanding and likely pathogenically stressful context.

4.1 | Sex differences in physical activity and EE

Despite being highly egalitarian, our results suggest that BaYaka women spend a greater percentage time in more intensive activity, when compared to their male counterparts. Prior work with foraging groups has shown that work patterns often vary by sex, with consequences for food acquisition, EE, and health status between the sexes (Hurtado & Hill, 1990; Kramer & Ellison, 2010; Marlowe, 2007). Despite frequent observations of sexual divisions of labor among foragers, research has shown mixed results as to whether there is any substantial or significant difference in physical activity levels between

the sexes across different populations (Gurven & Hill, 2009; Hurtado & Hill, 1990; Kaplan et al., 2000; Kramer & Ellison, 2010; Madimenos, Snodgrass, Blackwell, Liebert, & Sugiyama, 2011; Marlowe, 2007). While our data come from single focal-follows, they support the notion that BaYaka women are working harder and spending more hr in intensive subsistence activity during our 12-hr data collection periods. Given that activity intensity is calculated by accelerated motion, it is unlikely that there are any biological differences that determine sex differences in %MVPA.

Despite their increased activity level, females also had significantly lower EE (kCal/hr) than males. Their lower levels of EE were likely driven by their smaller body size, since energy usage increases per unit of body mass, as well as sex differences in body composition (Carpenter, Poehlman, O'Connell, & Goran, 1995; Kleiber, 1961; Pontzer, 2015; West, Brown, & Enquist, 1997). Yet, we observed that men still had substantially higher EE after we adjusted for skinfolds (i.e., body fat) and fat-free mass, which is strongly correlated with body weight in this sample ($r = 0.85$). Notably, our results differ from prior research among Hadza foragers in Tanzania, which found that individual differences in fat-free mass drove variation in EE, rather than sex (Pontzer et al., 2015). Our findings are generally consistent with past work showing that women have lower BMR than men, even after controlling for body composition and physical activity differences (Carpenter et al., 1995).

Given the well-documented sensitivity of female reproductive function to energetic dynamics, including energy balance and flux (Ellison, 2003; Jasienska, 2003; Jasienska & Ellison, 1998; Vitzthum, 2009), these sex differences in activity intensity versus metabolic expense merit further consideration from an adaptive perspective, especially if replicated elsewhere. In particular, even though their overall energetic costs are lower, BaYaka women seem to be expending more energy than they “need to” if work demands (activity intensity) were distributed according to broader cultural values of the group around egalitarianism and considering the lower overall division of foraging labor when compared to other foraging societies (Marlowe, 2007). Moreover, as we discuss below, only among females is EE linked to greater CORT

production across the day, which theoretically has implications for fecundity (Nepomnaschy et al., 2004). Yet, there is also male–female complementarity in our findings as well (men: higher EE, lower activity levels; women: lower EE, higher activity levels) that could be tested through adaptive frameworks at the level of pooled energy budgets *and* costs as well as divisions of labor within the community (Hill & Hurtado, 2009; Jaeggi, Hooper, Beheim, Kaplan, & Gurven, 2016; Kramer & Ellison, 2010).

These differences may also be due to variation in the types of tasks males and females engaged in. In our focal follow data, food processing and miscellaneous work predicted increased EE, though there was no significant difference between males and females in engaging in this type of work. However, these data were collected over only a couple hr. Over longer time periods, such as across the day or throughout a season, females may engage in more active and continual work that is less energetically taxing over all (e.g., foraging to collect and carry forest plants or retrieve fish). Meanwhile, males frequently focus on less consistent, but more intensive work, with short spurts of relatively demanding and energetically costly activity (e.g., sitting and waiting and then climbing to the top of a palm nut tree and chopping down a bundle of palm nuts), particularly given their larger bodies, relative to females (Hagino & Yamauchi, 2016; Hewlett, 1989; Hewlett, 1992; Meehan et al., 2013). Over the course of the day, female engagement in more continuous work that tends to be less energetically taxing could easily lead to females having a total higher percentage of time spent in MVPA. However, the intensive, yet relatively more infrequent highly energetically taxing activities done by males (i.e., hunting) may translate to higher EE and less time spent in MVPA.

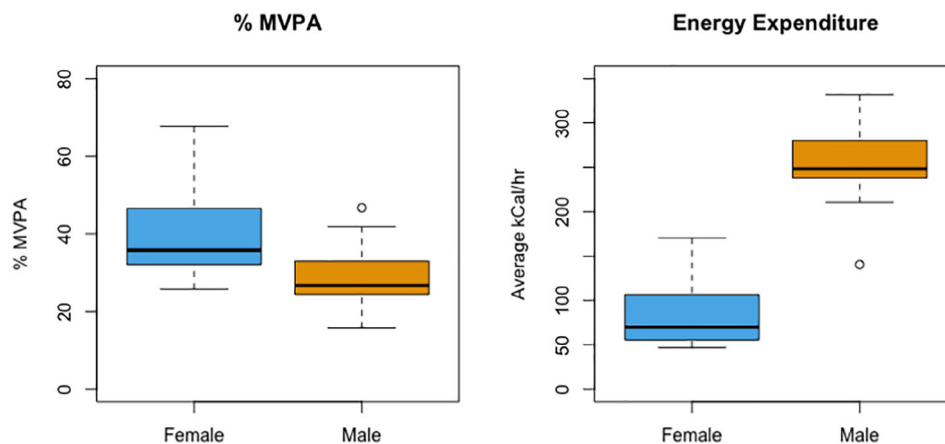
As seen in Figure 1, the range of percentage of time males and females spent in MVPA is relatively similar, with only a 10.9% average difference. This translates to approximately 1 hr across the 12-hr activity period. The magnitude of this difference is relatively similar to past work in terms of the sex distribution of forager labor (Gurven & Hill, 2009; Hurtado & Hill, 1990; Marlowe, 2007). The comparatively larger effect size for the difference between males and females in average EE is likely biologically significant, as it suggests female bodies may bear more conservative energetic costs in these settings, which

could be linked to reproduction and health outcomes. In subsistence settings, physical activity and EE are tightly linked with female reproductive output, where fertility shifts seasonally following food availability and work demands (Jasienska, 2003, 2009). The lower daily EE from everyday work among BaYaka females could thus potentially buffer against possible reproductive suppression. Further, a review of EE in endurance athletes found that females spend on average less daily EE compared to males, particularly in competitive conditions where female athletes spend on average almost half of the energy males spend (Heydenreich, Kayser, Schutz, & Melzer, 2017). Though our EE data are not directly comparable because of differences in methods, in our sample, women similarly spent half the energy men spent over a 12hr period. Compared to knowledge gained by studying athletes experiencing energetically demanding stressors over a relatively shorter timescale, an understanding of the tradeoff between activity intensity and EE in a forager lifestyle/subsistence setting, and sex differences thereof, may provide important insights into adaptive mechanisms and behavioral strategies in dealing with energetically intensive environments.

4.2 | Physical activity and CORT reactivity

Contrary to our prediction, we found that males who had greater % MVPA experienced more substantial short-term decreases in CORT during the first 30 min of daily activity (Figure 2). This pattern contrasts with research in clinical/laboratory settings as well as some field settings showing that CORT often rises in response to demanding physical activity (Brownlee et al., 2005; Casto et al., 2014; Trumble et al., 2014). While our findings potentially indicate that intensive physical activity had a dampening effect on short-term CORT production in this setting, there are a number of alternative explanations that could help to account for these observations. In our study, the activities participants engaged in during this time frame were their first household or subsistence activities of the day. Thus, for some participants, we may have captured the end of the CORT awakening response (CAR), that is, the brisk increase of CORT levels within 20–30 min after awakening to ready the body for the day, which

FIGURE 1 Box and whisker plots of sex differences in moderate-to-vigorous physical activity (%MVPA) and TEE. Females spent significantly greater %MVPA and significantly less TEE compared to males (all $p < 0.05$). See Table 2 for comparisons of % MVPA and TEE between sexes. Bars represent the interquartile range, with error bars indicating the range of % MVPA and TEE, respectively



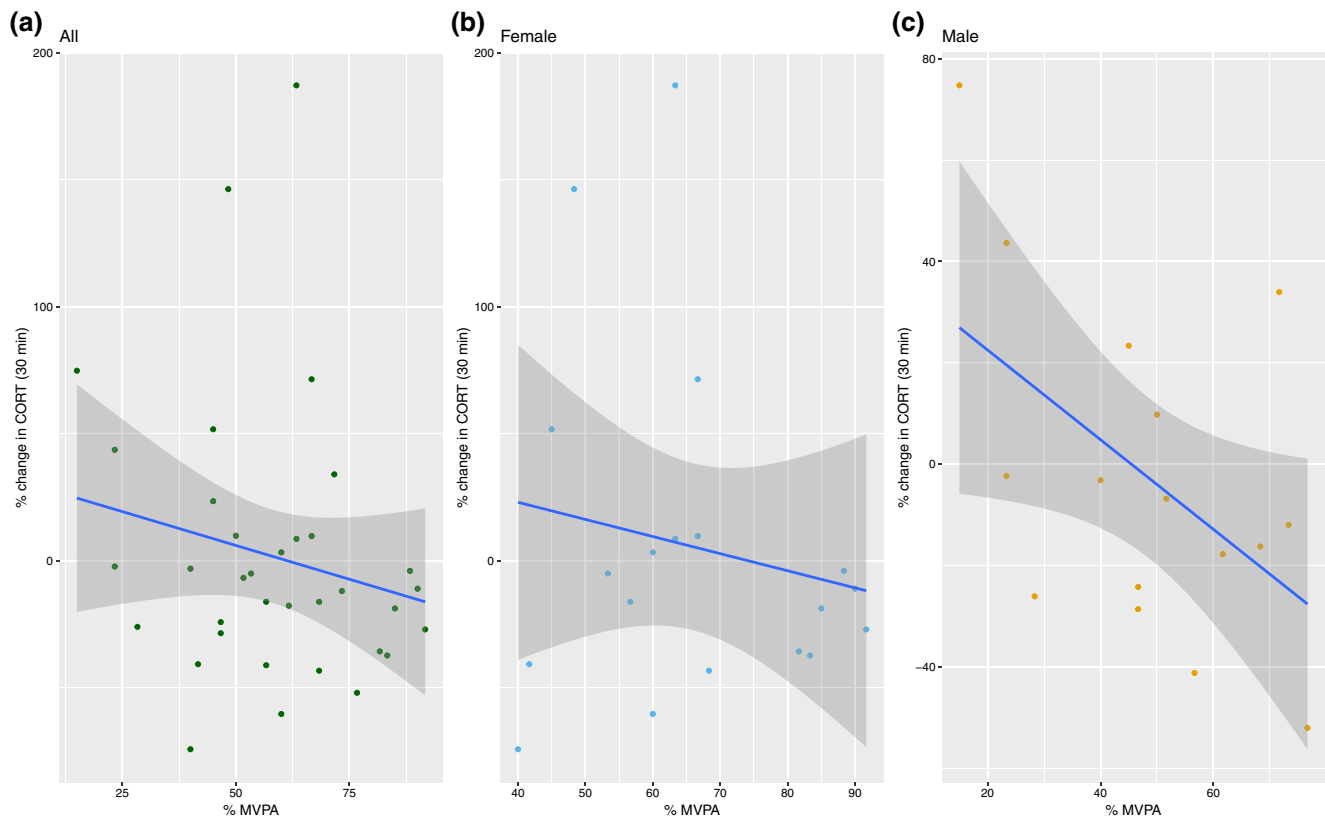


FIGURE 2 CORT reactivity according to moderate-to-vigorous physical activity (%MVPA) during subsistence task. Males that spent a greater %MVPA within the hour of activity had significantly greater decreases in CORT ($p < 0.05$); this finding was not found in females. The line represents the line of best fit and the shaded area represents 95% confidence intervals

subsequently attenuates quickly (Fries, Dettenborn, & Kirschbaum, 2009). However, given that our relevant collection times were ~3 hr after waking, it was highly unlikely that we were capturing the tail end of the CAR and renders this a highly unlikely explanation for the patterns we observed.

Additionally, it is unlikely that we captured an anticipatory reaction to the specific intensity of work. Research has demonstrated that humans can show acute anticipatory spikes in CORT in response to a number of different types of physically and psychosocially demanding conditions, such as contexts of social-evaluative threat and competition (Casto et al., 2014; Rohleder, Beulen, Chen, Wolf, & Kirschbaum, 2007). However, in our post hoc analyses we found that %MVPA was not significantly and/or meaningfully correlated to pre-activity CORT, suggesting that this CORT measure was not elevated in anticipation of subsequent intensive activity. Research in U.S. and European populations has shown that there may be a stress-reducing ameliorative effect of greater intensive physical activity on CORT reactivity in males (Gerber et al., 2014; Heaney, Carroll, & Phillips, 2014). Among BaYaka foragers, where engagement and participating in intensive subsistence related activity may have implications for men's social capital and reputations within the community (Boyette, Lew-Levy, Sarma, & Gettler, 2019; Boyette, Lew-Levy, Sarma, Miegakanda, & Gettler, 2019), participating in more intensive physical activity could lead to an anxiolytic effect. We note that

though this may be relevant to our findings, this is speculative and future research is needed to assess such an effect. While our findings were unexpected, these data hint that CORT may acutely respond differently to physical activity intensity in some field settings compared to a controlled lab environment. We hope that our findings and other relevant work (Trumble et al., 2014) help to stimulate further research on these questions in energetically and physically demanding ecologies.

4.3 | EE and overall CORT production

We found that female foragers who expended more energy across the day tended to produce more overall CORT that day (CORT AUC_G; Figure 3). This is consistent with research from the United States and Europe, showing that in athletic contexts (i.e., endurance athletes) increased EE is related to increased overall CORT production (Jürimäe, Mäestu, Jürimäe, Mangus, & Von Duvillard, 2011; Skoluda, Dettenborn, Stalder, & Kirschbaum, 2012; Tremblay, Copeland, & van Helder, 2004). Our findings are consistent with CORT's role as a metabolic signal, as it helps liberate and allocate metabolic resources during energetically costly tasks (Sapolsky et al., 2000). However, when we ran these analyses excluding pregnant women ($n = 2$), this finding was no longer statistically significant, though the relationship

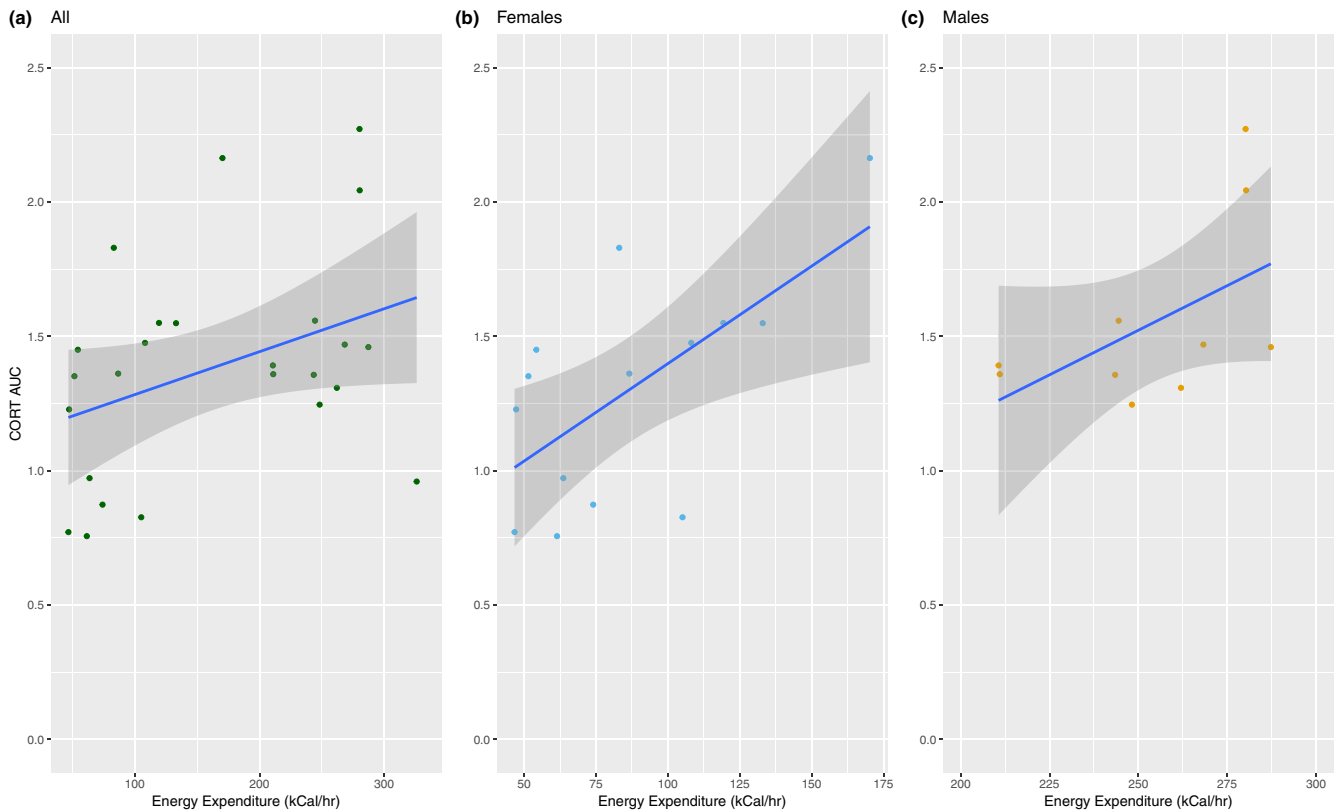


FIGURE 3 Daily CORT production (CORT AUC) according to daily energy expenditure (EE). Females that had greater EE had significantly greater production in CORT across the day (CORT AUC; $p < 0.05$); this finding was not found in males. The line represents the line of best fit and the shaded area represents 95% confidence intervals

remained in the same direction with a modestly smaller effect size. It could be that this relationship is strongest in pregnant women, though we are cautious in making such a statement given that it is based on a sample of $n = 2$, and thus suggest that more research is required. Though our total sample size was limited, we found a medium effect size for differences in CORT AUC_g between women based on whether they were expending relatively low or high levels of average EE across the day. While we cannot directly compare our CORT AUC_g values to earlier work, the magnitude of the effects in our study hint that if higher energy-expenders routinely maintained elevated levels of CORT production, it could have long-term negative implications for reproduction and health (Janicki-Deverts, Cohen, Turner, & Doyle, 2016; Kumari, Shiple, Stafford, & Kivimaki, 2011; Nepomnaschy et al., 2004). Finally, we note that it is unclear at this time why we solely observed a positive CORT AUC_g-EE correlation among females, though the lack of significant correlations across both sexes may be due to the slightly smaller sample size in men.

4.4 | Limitations

This project had several limitations that merit discussion. First, though we were able to capture 12 hr of data, we were only able to collect 1 day of data per individual, meaning the data may not be

representative of typical patterns among the BaYaka. While single, extended (e.g., 12 hr) activity periods are often used to document individual behavioral patterns in relevant research at similar sites (Assah et al., 2009; Ocobock, 2017; Sarma et al., 2018), following a greater number of individuals for several days would have provided us with more reliable data and enhanced insights on the range of activity and CORT production and fluctuation that may occur in this population. Optimally, to better characterize individuals' total CORT production throughout the day, we would have collected samples enabling us to capture the CAR measurements and possibly two or three other points during the day, repeating those measurements across multiple days (Fries et al., 2009). However, the number of saliva samples that could be taken for this study was limited because of constrained liquid nitrogen dewar space and transportation logistics, given the remote location of the community and field site. Nonetheless, by collecting data from ~25% of the adults in the group, we were able to capture a meaningful perspective on BaYaka activity during this time period.

Second, it would have been beneficial to collect more robust physical activity and EE data to augment and supplement the actigraphy findings. Options for more robust measurement of EE include a CosMed portable respiratory unit or doubly labeled water, to calibrate and validate actigraphy findings (Ocobock, 2017), which we were not able to employ here due to their cost and a lack of access to a consistent power source. In particular, past work has indicated

that actigraphy readings for %MVPA and EE may need to be calibrated specifically to the population of interest as differences in phenotype and physiological functioning may affect those data (Ocobock, 2016). The EE formulas in particular use the flex-HR method to determine heavy versus light activity; however, the formula calculations are constructed using laboratory populations. Given that subsistence populations tend to have higher physical activity levels, though not necessarily higher EE (Pontzer, 2015), compared to industrialized clinical populations, estimates calculating physical activity intensity may be largely overestimating actual activity intensity. Moreover, our readings of physical activity may be limited due to the actigraphy device having been worn on the wrist, which may potentially fail to capture the full exertion that may come with taxing activities such as climbing trees (*mbila* collection) or wading through water (fishing). While these are important methodological considerations that could plausibly underestimate %MVPA for some male-favored activities, this is not supported by our observational data of activities taking place during the focal follows. Further we think it is unlikely this would substantially alter the male–female differences we observed, as the effect size (Cohen's $d = 1.13$) for the finding was large by typical standards.

Finally, we also note that BaYaka activity discussed here is specific to life in the village. Ethnographic work confirms that for the BaYaka, including the Aka, forest camp life and village camp life differ largely due to what resources are available and how they may be obtained, with a larger emphasis on hunted and collected wild foods in the forest versus a larger dependence on agricultural foods (i.e., gardens) and meat hunted with guns in the village (Kitanishi, 1995). In the future, we hope to explore potential differences in physical activity, EE, and physiology between village and forest camps.

4.5 | Conclusion

In this study, we assessed the relationships between physical activity, EE, and CORT among BaYaka foragers. Contrary to our prediction, we found that males who engaged in more intensive activity during a subsistence task had larger short-term decreases in CORT. We also found that females with greater EE across the day had greater daytime CORT production overall, as predicted. We found biologically meaningful and significant sex differences in %MVPA as well as EE, with females spending more time in more intense physical activity but having substantially lower EE. Much prior research focusing on hunter-gatherer populations has emphasized the importance of sex-specific caloric returns. Along with other recent pertinent studies from relevant settings (Meehan et al., 2013; Pontzer et al., 2015; Trumble et al., 2013), we suggest that our results help clarify the individual and sex-specific physical activity demands and energetic and physiological costs of daily work activities by sex across individuals within the population. In particular, we hope these findings bring renewed attention to the intensity, costs, and physiological correlates of women's

activities, especially in related to sex-based subsistence roles and contributions in models of hominin evolution.

5 | HR DATA ANALYSIS

For light activity in men, the total calories (kCal/10 s) = $4.56 - (0.0265 \times \text{HR}) - (0.1506 \times \text{weight_kg}) + (0.00189 \times \text{HR} \times \text{weight_kg})$.

For heavy activity in men, the total calories (kCal/10 s) = $3.56 - (0.0138 \times \text{HR}) - (0.1358 \times \text{weight_kg}) + (0.00189 \times \text{HR} \times \text{weight_kg})$.

For light activity in women, the total calories (kCal/10 s) = $-4.70 + (0.0449 \times \text{HR}) - (0.0019 \times \text{weight_kg}) + (0.00052 \times \text{HR} \times \text{weight_kg})$.

For heavy activity in women, the total calories (kCal/10 s) = $-5.92 + (0.0577 \times \text{HR}) - (0.0167 \times \text{weight_kg}) + (0.00052 \times \text{HR} \times \text{weight_kg})$.

We report all findings as average overall kCal/hr and kCal/hr of activity.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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