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The costs of living at the edge: Seasonal stress in wild savanna-dwelling chimpanzees

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ABSTRACT

Adaptations associated with shifting from a predominately forested habitat to a more open environment are considered a crucial step in hominin evolution. Understanding how chimpanzees, one of our closest-living relatives, are exposed to the selection pressures associated with living in a relatively sparse, hot, and dry environment can inform us about the relative importance of potential environmental stressors involved in adaptations to drier environments. We investigated the extent to which chimpanzees living in an extreme savanna habitat experience seasonal variability in either energy balance or thermoregulation (dehydration and heat exposure), as well as whether these potential environmental constraints are taxing to chimpanzee individuals. Specifically, we tested the hypothesis that savanna environments impose seasonally-relevant costs to chimpanzees. To this end, we collected 368 urine samples from one community of chimpanzees at Fongoli, Senegal, and measured c-peptide, creatinine, and cortisol as measures of physiological responses to environmental food, water, and heat constraints, respectively. We then evaluated the influence of climatic and phenological factors on these indicators. Results illustrated significant seasonal variation in all biomarkers, which corresponded to relevant ecological correlates. Furthermore, creatinine but not c-peptide correlated with cortisol levels, suggesting that chimpanzees in this environment endure periods of heat and dehydration stress, but are able to avoid stressful levels of negative energy balance. Using savanna chimpanzees as a referential model, our research lends support to the notion that thermoregulatory challenges were a significant factor in hominin evolution, and suggests these challenges may have overshadowed the challenges of maintaining adequate energetic balance during the expansion of the hominin range from wetter to drier environments.

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1. Introduction

Adaptations associated with shifting from a predominately forested habitat to a more open environment have been frequently proposed to have played a key role in hominin evolution. Paleo-environmental evidence suggests that climate change during the Plio-Pleistocene led to increased aridity and a biome change from forest to woodland-savanna mosaics (Vrba, 1985; Cerling, 1992; Reed, 1997; Wynn, 2004; Fernández and Vrba, 2006; Bobe and

Leakey, 2009; Levin et al., 2011), and that several hominin lineages occupied these habitats to some degree following that change (Reed, 1997; Bobe and Behrensmeyer, 2004; White et al., 2009; Copeland et al., 2011). Most hominin-bearing localities indicate woody canopy cover of less than 40% at the time of inhabitation (Cerling et al., 2011), suggesting that open savanna or savanna-woodland habitats played a pivotal role in “the hominin ecological niche” (Quinn et al., 2013:66). Corresponding changes associated with increased aridification and a decrease in woody cover likely led to a shift in the availability of food resources (Bromage and Schrenk, 1995), and increased exposure to warmer temperatures (Passey et al., 2010). Many changes in hominin physiology are thought to be directly associated with thermoregulatory

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advantages derived as a result of significant thermoregulatory selective pressures, although reconstructing the relative strength of physiological stress they endured in such an environment has proven to be challenging. Notably, bipedalism, hair loss, and increased sweating capacity are considered some of the greatest changes in the hominin lineage tied to these pressures (Wheeler, 1984, 1991, 1992a). Yet the role of thermoregulatory adaptations in human evolution is inferred from the evidences of the adaptations themselves and not demonstrations that these selection pressures were significant to individuals lacking these adaptations.

Understanding the physiological constraints experienced by one of our closest living relatives occupying a hot, open environment can help us to better understand the relative importance of various factors involved in human evolutionary adaptations to drier environments. Specifically, by understanding the basic physiological principles involved when a closely related species encounters thermoregulatory or other environmental challenges, we stand to gain a better understanding of the circumstances under which strategies for countering these challenges could evolve. Most *Pan* populations studied inhabit wet, predominately forested habitats (Boesch and Boesch-Achermann, 2000; Morgan and Sanz, 2006; Furuichi and Thompson, 2007; Head et al., 2011), which fail to mimic the conditions under which key aspects of hominin evolution are thought to have occurred. The Fongoli chimpanzee (*Pan troglodytes verus*) population, however, endures the hottest and one of the driest conditions within the entire range of the species (McGrew et al., 1981; Pruetz, 2007). Historically, rainfall at Fongoli averages only 945 mm annually, while temperatures average 28.3 °C but reach as high as 45.9 °C, averaging over 2 °C higher than the next hottest chimpanzee long-term research site, Taï (Côte d'Ivoire), where temperatures only reach as high as 36 °C (E.G.W., unpublished data). Likely due to high dry season temperatures, chimpanzees at Fongoli appear to depend heavily upon drinking from free-standing water sources (Pruetz and Bertolani, 2009), which likewise become scarce during the long dry season; at this time water is available from only one or two locations within the entirety of their >85 km² home range (Skinner and Pruetz, 2012). Fongoli therefore represents ideal conditions for studying seasonal environmental constraints associated with living in an open, savanna-woodland environment in one of our closest living relatives, as significant intra-annual environmental fluctuations at Fongoli provide the background upon which direct individual responses to environmental extremes can be measured. At present, Fongoli represents both a theoretical and realized limit, in that its placement at the northern edge of the current West African chimpanzee distribution likewise represents the actual edge of climatic and ecological extremes that chimpanzees currently endure across the continent.

Research on the Fongoli chimpanzees offers significant support to the hypotheses (McGrew et al., 1981; Kortlandt, 1983; Pruetz and Bertolani, 2009) that chimpanzees at the range limit endure seasonal stresses associated with heat, food, and water. Therefore, the asynchrony of seasonal peaks in the aforementioned factors makes Fongoli well suited for studying environmental constraints. Extreme temperatures at Fongoli likely lead to efforts to avoid heat stress, which also affects energy-budgeting and restricts movement during certain periods of the day (McGrew et al., 1981; Pruetz and Bertolani, 2009). Additionally, the purported benefits of cave use at Fongoli (Pruetz, 2007), an infrequent ($n = 17$, this study) but important thermoregulatory behavior typically performed during the dry season, as well as the frequent observation of pool use (Pruetz and Bertolani, 2009) in a species typically regarded as hydrophobic (Angus, 1971), supports the assumption that strategies to cope with heat exposure play a significant role in savanna chimpanzee behavioral ecology (McGrew et al., 1981). Such behaviors

have never been reported for chimpanzees in other localities, with the exception of cave use in the nearby Falémé Region (Boyer-Ont and Pruetz, 2014). In general, to date, research devoted to thermoregulation is scarce in chimpanzees (Takemoto, 2004; Pruetz, 2007; Kosheleff and Anderson, 2009; Koops et al., 2012; Samson and Hunt, 2012), or primates in general outside the context of hibernation and torpor (Brain and Mitchell, 1999; Hill et al., 2004; Hill, 2006; Hanya et al., 2007; Campos and Fedigan, 2009; Mitchell et al., 2009; Nyakudya et al., 2012; Gestich et al., 2014; Lubbe et al., 2014; Wark et al., 2014; Thompson et al., 2014, 2017).

Restricted water availability intensifies stress associated with thermoregulation in primates (Mitchell et al., 2009) and dehydration is the most frequently proposed stressor to savanna chimpanzees (Pruetz and Bertolani, 2009; Skinner and Pruetz, 2012)—the latter even having been postulated to be one of the main determinants of the ecological limit of the chimpanzee geographical range (McGrew et al., 1981; Kortlandt, 1983). Maintaining a large home range (Pruetz and Bertolani, 2009), a heavy reliance on nutrient-rich alternative food sources like termites (Bogart and Pruetz, 2011), and even tool-assisted hunting (Pruetz and Bertolani, 2007; Pruetz et al., 2015) have been suggested as coping mechanisms employed by Fongoli chimpanzees for dealing with a presumably food-scarce environment that likewise varies considerably in food availability within the year.

Despite considerable observational evidence that chimpanzees employ stress-avoidance behaviors in a hot and open savanna-woodland mosaic habitat, the physiological effects of these purported stressors have not been quantified. If behavioral mechanisms are employed as stress reducing strategies to ease the impact of a challenging environment, these likely also come at a cost to energy or time that could be spent on other functions, such as social or nutritional maintenance (Dunbar et al., 2009). While Fongoli chimpanzees do appear to adjust their activity budget to minimize energy expenditure when thermoregulatory costs are high (Pruetz and Bertolani, 2009), these mechanisms too are limited by time needed for other requirements. Previous attempts to quantify these stresses (Skinner and Pruetz, 2012) suggested the late dry season (when temperatures are hot and dry, but fruits are abundant) to be particularly limiting, but this work has subsequently been attributed to methodological error (Kierdorf et al., 2015) and therefore remains inconclusive. We therefore examined whether ecological conditions in the savanna-woodland environment imposed physiological constraints on chimpanzees and, if so, how and to what extent these constraints were realized. Quantification of these effects in one of our closest living relatives has great potential to inform us of physiological mechanisms necessary for an organism for adapting to hotter, drier environments.

Specifically, we expected these constraints to be realized in the forms of dehydration, nutritional, and thermoregulatory challenges, as has been posited previously (McGrew et al., 1981; Kortlandt, 1983; Pruetz and Bertolani, 2009). If chimpanzees are affected by the highly seasonal environment at Fongoli, we expected that internal responses to environmental fluctuations should likewise be seasonal and linked to relevant environmental factors. However, to evaluate the importance and realized impact of these fluctuations, we evaluated the relationship between variation in biomarker levels indicative of respective environmental pressures and variation in cortisol levels. Here we tested the hypothesis that savanna environments impose seasonally-relevant costs to chimpanzees. Specifically, we examined (a) whether Fongoli chimpanzees demonstrated seasonal variation in heat exposure, dehydration levels, and food availability; (b) whether particular environmental variables could be linked to seasonal variation in physiological condition; and (c) whether these physiological markers of responses to climatic conditions and food scarcity were

linked to physiological deviation from homeostasis, as indicated by cortisol.

We therefore measured creatinine, a breakdown product of muscle metabolism traditionally used as a control for urinary concentration in hormone studies, as an estimate of an individual's hydration status (Viberti et al., 1982), whereby higher levels of creatinine indicate an individual to be less hydrated. To measure energy balance, we used the insulin by-product c-peptide, as it has been demonstrated to accurately reflect the physiological response to experimental or natural dietary restrictions (Emery Thompson, 2017), whereby increases in c-peptide levels indicate better energetic status. Lastly, we used cortisol as a measure of general physiological stress, with higher cortisol levels indicating a higher degree of hypothalamic–pituitary–adrenal (HPA)-axis activation in response to a stressor, and by controlling for other potential stressors, we evaluated residual cortisol variation as an indicator of potential thermoregulatory challenges. Cortisol has been successfully applied as a non-invasive marker of stress across a number of settings (Beehner and Bergman, 2017), including thermoregulatory challenges in primates (Beehner and Bergman, 2017) and other vertebrates (Christison and Johnson, 1972; El-Halawani et al., 1973; Edens and Siegel, 1975; Harikai et al., 2003). By linking seasonal variation of these indicators to observable ecological and climatic patterns, we investigated physiological constraints for apes living in a savanna-mosaic habitat and the relative importance of various potential selective pressures associated with adapting to such environments.

2. Methods

This research was conducted between January 2013 and January 2014 at the Fongoli Savanna Chimpanzee Project (FSCP) field site in south-eastern Senegal (12°40' N, 12°13' W), on a group of 32 wild chimpanzees. Fongoli is characterized by marked seasonality in temperature and precipitation with a wet (June–September) and a dry (November–April) season (Pruetz and Bertolani, 2009). We conducted all-day focal animal sampling (Altmann, 1974) on 12 male individuals for 2564.8 total observation hours. All occurrence data were collected on heat and dehydration avoidance behaviors typically observed at Fongoli, like drinking from free-standing pools, pool use (Pruetz and Bertolani, 2009), and cave use (Pruetz, 2007) by the focal individual, and were determined as number of visits/focal observation time on the day prior to sample collection to account for variation in the duration of focal animal follows. We considered each behavioral observation of pool use, cave use, or drinking independent, and regarded them as separate instances of the aforementioned behavior.

2.1. Environmental data collection

Temperature and humidity data were collected at 10 min intervals at the FSCP camp using an automatic data logger (Onset Hobo Temp/RH Data Logger) supported by daily min–max thermohygrometer data—see [Supplementary Online Material \(SOM\) S1](#) for details. Daily minima, maxima, averages, and ranges were calculated for both temperature and humidity. Daily mean temperature and humidity were used to calculate daily mean heat index using the methods employed by the National Oceanic and Atmospheric Administration (NOAA, 2014). We obtained data on photoperiod from the U.S. Naval Observatory Online Repository (USNO, 2015). Rainfall data were collected daily using a rain gauge located at FSCP basecamp. The depths of four water sources frequently visited by the Fongoli chimpanzees were measured monthly to create an index of water availability ([SOM Equation S1](#)).

We created three measures of food availability (FAI_{total} , FAI_{fruit} , FAI_{ripe}) based on phenological data collected monthly on 887 trees along a 3.4 km by 20 m transect (see [SOM S1](#) for details). We recorded the percent abundance of new and mature leaves, flowers, and ripe and unripe fruit production in the crown for each tree over 10 cm and *Saba senegalensis* lianas over 5 cm diameter at breast height (DBH), assigning a score between zero and four corresponding to an estimated percentage of crown coverage for each item (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%). FAI_{total} was based on all plant-based food items eaten by chimpanzees at Fongoli, FAI_{fruit} was based on only ripe and unripe fruit items, and FAI_{ripe} was based solely on ripe fruit. These indices therefore provided a relative measure of monthly food availability for species and plant parts consumed by chimpanzees.

2.2. Behavioral data collection

Periods when a female is in estrus have been shown to be a particularly stressful time for both males (Surbeck et al., 2012a,b, 2015; Georgiev et al., 2014) and females (Muller et al., 2007; Emery Thompson et al., 2010). During these periods, male–male aggression increases (Goodall, 1986; Emery Thompson and Wrangham, 2008) and parties are larger (Pepper et al., 1999; Boesch and Boesch-Achermann, 2000; Hashimoto et al., 2001). We therefore used the number of estrous females seen over the course of a focal follow as a partial proxy for potential perceived social stress, and controlled for this variable in the cortisol model. We controlled for potential effects of dominance status in all models using David Scores (Gammell et al., 2003) derived from pant-grunt observations ($n = 532$) among same sex dyads (1 = lowest, 20 = alpha). Females were assigned ranks below males, and individuals (two pairs) tied in score were assigned identical ranks. As chimpanzees are known to vary their party sizes as a means of mitigating potential food resource competition (Chapman et al., 1995; Anderson et al., 2002) and this measure is known to correlate with c-peptide levels in bonobos (Surbeck et al., 2015), we controlled for average party size observed for the focal individual on the day prior to each sample in the c-peptide model. Party size measurements differed among observers at Fongoli; parties were measured as all individual chimpanzees observed over the course of a day, or summarized to daily means based on all visible individuals every 15 min collected during focal follows. These two measurements correlated poorly ($r^2 = 0.33$). Therefore, to account for the discrepancy in method used we also included the observer and their interaction with party size into the model. In all models we used observations of injuries and diarrhea to control for their potential effects on physiological condition (see [SOM S1](#) for details).

2.3. Urine sample collection and analysis

We collected urine samples of identified individuals below night nests and during morning voids (until 1200 h) from seven adult females and 13 adult males over the study period ($n = 368$, mean \pm SD = 18.4 ± 8.6 samples/individual, range = 2–33 samples/individual). Adults were defined as individuals over 12 years of age, as this has been suggested to represent the age at which individuals reach reproductive maturity (Wroblewski et al., 2009). Specific gravity (SG) was measured using a refractometer (TEC, Ober-Ramstadt, Germany), and creatinine was measured via colorimetric reaction with picric acid (Bahr et al., 2000) for all samples ($n = 368$). We successfully analyzed 353 samples for c-peptide levels using a commercially available immunoassay kit (DIAsource, C-Pep-EASIA KAP0401; see [SOM S1](#) for details). C-peptide values were corrected by creatinine and are expressed in ng/mg creatinine, with the exception of their use in the cortisol model, when

they were corrected by SG and are expressed in ng/ml SG (to avoid confounding c-peptide and creatinine). Samples were re-run and/or diluted if their measured values did not fall into the linear range of the assay or if duplicate measures differed by more than 10%. Intra- and inter-assay coefficients of variation of low and high value quality controls were 2.7% and 6.7% ($n = 4$) and 5.0% and 4.8% ($n = 16$), respectively.

We successfully extracted 363 samples for cortisol (see SOM S1) following Hauser et al. (2008). However, we corrected cortisol levels of chimpanzee urine samples from Fongoli using deuterated testosterone, because a coelution at the retention time of the traditional internal standard for cortisol, prednisolone, prevented us from using this standard. Urinary cortisol levels were measured using liquid chromatography-tandem mass spectrometry using an adaptation of Hauser et al.'s (2008) method (see SOM S1), and are expressed in ng/ml SG. All research was non-invasive and was approved by the Government of Senegal and the Direction des Eaux et Forêts et Chasses.

2.4. Statistical analysis

We used linear mixed models (LMM) using a Gaussian error function (Baayen, 2008) fitted separately for each response (c-peptide, creatinine, cortisol) with a generic seasonal term (sine and cosine of Julian date; Stolwijk et al., 1999) as a test predictor, to determine whether these physiological indicators varied seasonally. This seasonal term assumes a single annual cycle with regular periodicity, an assumption we felt fitting given the natural annual cycle observed for the majority of environmental variables considered. All models were fitted in R (version 3.3.1; R Core Team, 2016) using the function lmer of the R package 'lme4' (version 1.1–12; Bates et al., 2015). To control for any potential diurnal effects on the indicators of interest, we controlled for time of day when the sample was voided. As a control for potential degradation of physiological indicators due to in-field processing times, we also accounted for the time lag from sample void until it was frozen in liquid nitrogen (range = 0.51–6.77 h), although processing effects are not expected to cause degradation of the physiological indicators of interest at this time scale (Higham et al., 2011). In each model, we controlled for variables which might influence hormone levels (as described above, see SOM S1). Additionally, in the cortisol model we included the values of creatinine and c-peptide as additional test predictors. For ease of comprehension, each response was transformed on a square root scale and all quantitative control predictors were z-transformed for comparability of estimates, with the exception of sine and cosine of Julian date, and pool and cave use. Furthermore, we included individual and date as random effects and random slopes as required (Schielzeth and Forstmeier, 2009; Barr et al., 2013; see SOM S1 for details). We compared the fit of the full models using a likelihood ratio test with those of a respective null model lacking only the test predictors of season but identical to the respective full model in all other terms (Forstmeier and Schielzeth, 2011; see SOM S1). Marginal effect sizes (proportion explained by all fixed effects) and conditional effect sizes (proportion explained by all fixed and random effects) for each model were estimated using the package 'MuMIn' (Nakagawa and Schielzeth, 2013; Bartoń, 2017).

To identify the strength of various climatic and ecological variables in explaining the seasonal variation of the aforementioned physiological responses, we used multimodel inference (MMI) (Burnham and Anderson, 2002) by replacing the generic seasonal term in each model with a combination of all potentially relevant climatic variables and a consistent set of control predictors and a maximal random slopes structure (Schielzeth and Forstmeier, 2009; Barr et al., 2013; see SOM S1). Prior to MMI, climatic data

were condensed into two representative climatic factors to reduce redundancy among these highly correlated variables. For this we first conducted a principal components analysis to identify the number of components with an eigenvalue of at least one which revealed two principal components (after removal of rainfall which appeared uncorrelated with the other predictors). Next, we conducted a factor analysis with varimax rotation. The loadings of the variables on the factor revealed that the first factor was positively correlated with indicators of wetness (e.g., water availability index) and negatively with heat (e.g., maximum daily temperature), while the second factor was most correlated with measures of potential perceived heat (e.g., daily mean heat index) and minimum temperature (Table 1). These two factors, their interaction, rainfall, and the three food availability indices (Fig. 1) composed the full model from which we created a set of 81 models (including two null models). The set of models we fitted for a given physiological biomarker (creatinine, c-peptide, or cortisol) comprised all possible subsets of environmental predictors of the full model (see SOM S1). All models comprised the original control predictors that had been included in the initial model together with the generic seasonal term, as well as the random effects within both individual and date included into the full model (i.e., the fitted models were LMMs). We then compared the sum of weights for each climatic and ecological variable derived from the AICc (Burnham and Anderson, 2002) values of the models containing them to an expected weight for each predictor. This weight was calculated given the predictors' occurrence in the model set and the models' relative degrees of freedom, assuming all models performed equally well in order to identify the relative explanatory strength of each predictor.

3. Results

All environmental variables (temperature, humidity, heat index, rainfall, and food and water availability indices) significantly varied seasonally within the year (SOM Fig. S1 and Tables S1–S2). Temperatures and rainfall varied considerably, whereby maximum daily temperature averaged 37.7 °C (but ranged from 27 to 48 °C) and monthly water availability was lowest (13%) in June and January and highest (83%) in September and October. September was the scarcest month for all food availability indices, and the decline was especially marked for ripe fruit.

We observed significant seasonal variation of creatinine levels (Fig. 2a, Table 2; full and null model comparison: $\chi^2 = 20.803$, $df = 2$, $p < 0.001$, marginal $r^2 = 0.211$, conditional $r^2 = 0.568$), which

Table 1

Results of the factor analysis of the environmental variables. Loadings of the original environmental variables on the two resulting factors (largest absolute loading per covariate indicated in bold), the eigenvalues of each factor and the percentage of the total variance explained by each factor.

Environmental variable	Factor 1	Factor 2
Temperature (minimum)	0.081	0.937
Heat index (mean)	–0.081	0.760
Temperature (mean)	–0.530	0.786
Relative humidity (range)	–0.305	–0.799
Photoperiod duration	0.271	0.770
Cumulative rain	0.339	–0.738
Water availability index	0.699	0.162
Relative humidity (maximum)	0.898	–0.309
Relative humidity (minimum)	0.963	0.214
Relative humidity (mean)	0.977	–0.065
Temperature (maximum)	–0.940	0.165
Temperature (range)	–0.782	–0.585
Eigenvalues	5.247	4.391
Variance explained	0.437	0.366

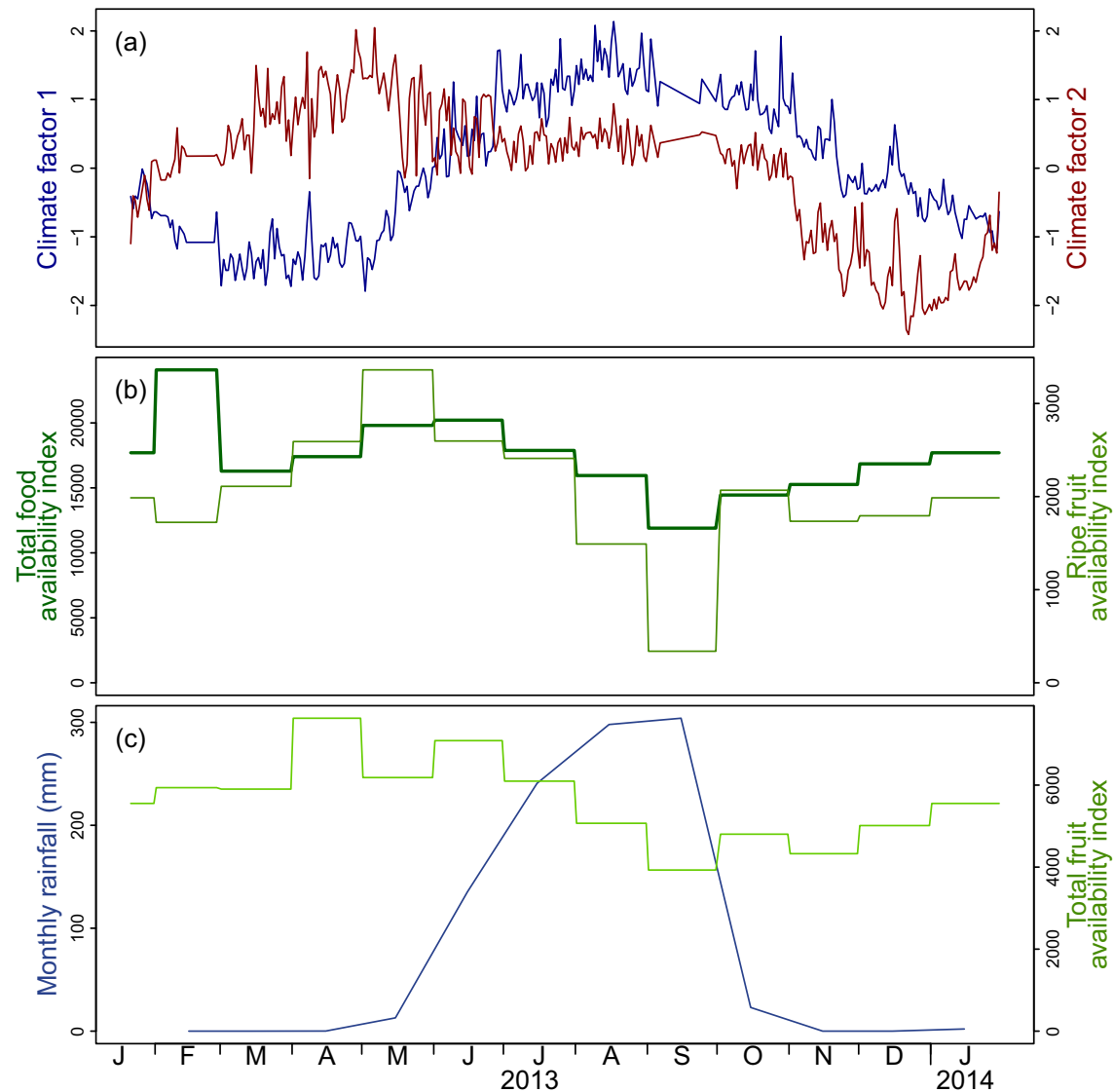


Figure 1. Variation over one annual cycle (January 2013–January 2014) of a) climatic factors 1 (blue, left axis) and 2 (red, right axis), derived from the factor analysis; b) total food (dark green, left axis) and ripe fruit availability (light green, right axis) indices; and c) monthly rainfall (blue, left axis) and total fruit availability index (green, right axis).

peaked towards the end of the dry season (March), whereas they were lowest towards the end of the wet season, in October (monthly means range = 0.52–1.98 mg/ml). For creatinine, MMI resulted in a 95% best model confidence set comprising 31 of a total of 80 models that converged (SOM Table S4), into which neither null model was included. Specifically, both Factor 1 (representing dryness as well as maximum temperature) and Factor 2 (perceived heat) appeared particularly important (sum of weights ≥ 0.95), with full model estimates indicating that creatinine peaked when temperature was highest and water availability was lowest. Furthermore, all food availability indices received some support (Table 3).

Although used as a control variable for urinary concentration in our study, urinary specific gravity indicated that Fongoli chimpanzees likely experience extensive periods of dehydration. Specific gravity averaged 1.0225 when controlling for potential sex, individual, or date biases in the dataset, with 56.4% ($n = 206$) of measured samples indicating SG levels higher than 1.020, a threshold commonly used to indicate dehydration in human subjects (e.g., National Wrestling Rules Committee, 1988). The majority

of samples from seven months exceeded this threshold ($\geq 50\%$: December to June, September), with almost all samples from the late dry season (February to April) exceeding this threshold.

Urinary c-peptide values showed significant seasonal variation (Fig. 2b, Table 4; $\chi^2 = 23.090$, $df = 2$, $p < 0.001$, marginal $r^2 = 0.161$, conditional $r^2 = 0.235$). Of 81 models that converged (SOM Table S5), we obtained a 95% best model confidence set including 48 models, which included the null model with the generic seasonal term. All predictors but ripe fruit availability received support from the MMI, but total food availability outperformed all others (Table 3), whereby c-peptide increased with increasing total food availability.

Lastly, there was a significant overall impact of c-peptide, creatinine, and season on chimpanzee urinary cortisol values (Table 5; $\chi^2 = 61.045$, $df = 4$, $p < 0.001$, marginal $r^2 = 0.210$, conditional $r^2 = 0.469$). More specifically, increases in creatinine increased cortisol levels (Fig. 3b, Table 5), whereas c-peptide values did not appear to explain variation in cortisol levels (Fig. 3a). Additionally, when controlling for the effects of c-peptide and creatinine on cortisol levels, cortisol levels showed significant

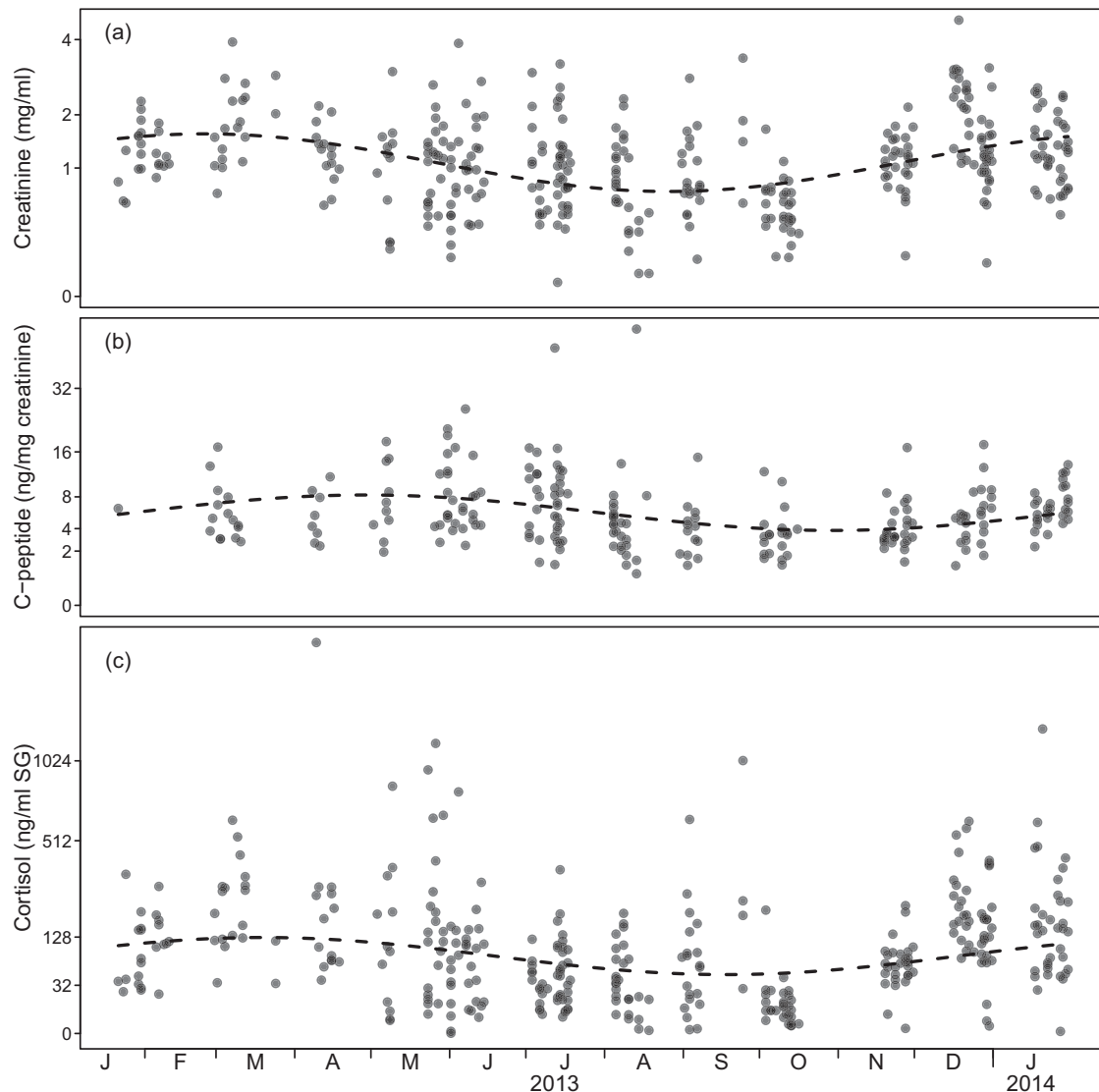


Figure 2. Seasonal variation of biomarkers of dehydration, energy balance, and heat exposure. Shown are creatinine (a; $n = 248$ samples), c-peptide (b; $n = 241$ samples), and cortisol levels (c; $n = 232$ samples) over one annual cycle. Lines depict the fitted models. All biomarkers were transformed to a square root scale.

seasonal variation over the year (Fig. 2c; $\chi^2 = 22.717$, $df = 2$, $p < 0.001$), with highest average values in the late dry season (April) and lowest values in the transitory month of October (monthly range = 17.99–295.04 ng/ml SG). MMI provided a 95% best model confidence set comprising 26 models, out of a total of 76 models that converged (SOM Table S6). The generic seasonal term ranked first and was included in the best model set. Furthermore, climatic Factor 1, representing mainly dryness and maximum temperature, was the only variable to have Akaike weights larger than expected, corresponding to a negative relationship with cortisol levels (SOM Table S3), where cortisol levels were higher when temperatures were high and water was least available.

4. Discussion

In line with our predictions, we found seasonal variation in all three indicators of physiological effects at Fongoli, which was best explained by the expected ecological correlates for each physiological indicator. While we observed seasonal variation in c-peptide

values (an indicator of energy balance), which was best explained by food availability, periods of food scarcity did not translate into increased cortisol levels. What did prove taxing was the climatic impact of the dry season when temperatures were hottest and the habitat was driest, as Fongoli chimpanzees appeared to suffer from dehydration and heat stress during this time. Our observations can be summarized in four main points.

First, chimpanzees at Fongoli showed significant seasonal variation in energy balance, which corresponded strongly with overall food availability. As previous work has shown seasonal patterns of c-peptide in wild primates, including chimpanzees (Emery Thompson, 2017), it is therefore expected that, in such an extremely seasonal environment as Fongoli, seasonal effects are also observed even when behavioral measures, like varying traveling subgroup size, are considered. Although chimpanzees are generally regarded as ripe fruit specialists, preferring these over other dietary items (Wrangham, 1977; Goodall, 1986; Wrangham et al., 1991; Tutin et al., 1997; Boesch and Boesch-Achermann, 2000; Morgan and Sanz, 2006; Pruett, 2006; Head et al., 2011;

Table 2

Effect of season (represented by sine and cosine of Julian date) on urinary creatinine levels (square root transformed; $n = 268$). Statistically significant results ($p \leq 0.05$) appear in bold.

Term	Estimate \pm SE	χ^2 ^a	p
(Intercept)	0.990 \pm 0.068	—	—
Test predictors			
Sine (Julian date) ^b	0.179 \pm 0.046	20.803	<0.001
Cosine (Julian date) ^b	0.134 \pm 0.037		
Control predictors			
Rank ^c	−0.014 \pm 0.025	—	—
Time of day (hours) ^d	0.007 \pm 0.037	—	—
Processing time (hours) ^e	−0.051 \pm 0.033	—	—
Sex ^f	0.107 \pm 0.065	—	—
Health (Injury) ^g	−0.117 \pm 0.102	—	—
Health (Diarrhea) ^g	0.034 \pm 0.175	—	—
Drinking visits ^h	−0.388 \pm 0.413	—	—

^a Degrees of freedom are 2.

^b Sine and cosine of Julian date together represent a seasonal term and are therefore not treated separately.

^c z-transformed, mean \pm SD at the original scale: 12.418 \pm 5.057 (range 1–20, with 20 representing the highest social rank).

^d z-transformed, mean \pm SD at the original scale: 7.985 \pm 1.415.

^e z-transformed, mean \pm SD at the original scale: 3.324 \pm 1.438.

^f Estimates refer to the comparison with the reference category: female.

^g Estimates refer to the comparison with the reference category: healthy.

^h Per hour focal follow.

Piel et al., 2017), ripe fruit availability performed poorly in explaining c-peptide variation. In contrast, the strength of total food availability in explaining energy balance in Fongoli chimpanzees highlights the importance of non-ripe fruit food items for the chimpanzee diet here and subsequently the energy balance of these individuals (Pruetz, 2006). Multiple lines of evidence from Fongoli, including our own findings, illustrate a heavier reliance on non-ripe fruit items (Pruetz, 2006; Bogart and Pruetz, 2011; Lindshield et al., 2017) than is observed at other sites (Wrangham, 1977; Goodall, 1986; Wrangham et al., 1991; Tutin et al., 1997; Boesch and Boesch-Achermann, 2000; Morgan and Sanz, 2006; Head et al., 2011; Piel et al., 2017).

Second, chimpanzees at Fongoli showed significant seasonal variation in creatinine levels corresponding to seasonal variation in temperature and water availability. Creatinine levels peaked during the late dry season when temperatures were highest and water availability was lowest, suggesting that chimpanzees at Fongoli experience physiological effects of water scarcity, for which they were not able to adequately compensate behaviorally. These results were further supported by the high proportion of samples in which SG exceeded the standard dehydration threshold (1.02) for humans, suggesting that if similar thresholds for chimpanzees exist, Fongoli chimpanzees were commonly dehydrated at the end of the dry season. Such a pattern was observed despite Fongoli chimpanzees employing compensatory behaviors like drinking, which likewise has been observed to follow seasonal creatinine patterns (E.G.W.,

Table 4

Effect of season (represented by sine and cosine of Julian date) on urinary c-peptide levels (square root transformed; $n = 241$). Statistically significant results ($p \leq 0.05$) appear in bold.

Term	Estimate \pm SE	χ^2 ^a	p
(Intercept)	2.196 \pm 0.301	—	—
Test predictors			
Sine (Julian date) ^b	0.409 \pm 0.088	23.090	<0.001
Cosine (Julian date) ^b	−0.215 \pm 0.079		
Control predictors			
Rank ^c	0.009 \pm 0.081	—	—
Time of day (hours) ^d	−0.019 \pm 0.072	—	—
Processing time (hours) ^e	−0.002 \pm 0.088	—	—
Sex ^f	−0.207 \pm 0.201	—	—
Health (Injury) ^g	0.930 \pm 0.314	—	—
Health (Diarrhea) ^g	0.569 \pm 0.478	—	—
Party size ^f	0.264 \pm 0.148	—	—
Observer ⁱ	0.491 \pm 0.277	—	—
Party size ^j \times Observer	−0.046 \pm 0.243	—	—

^a Degrees of freedom are 2.

^b Sine and cosine of Julian date together represent a seasonal term and are therefore not treated separately.

^c z-transformed, mean \pm SD at the original scale: 12.418 \pm 5.057 (range 1–20, with 20 representing the highest social rank).

^d z-transformed, mean \pm SD at the original scale: 7.985 \pm 1.415.

^e z-transformed, mean \pm SD at the original scale: 3.324 \pm 1.438.

^f z-transformed, mean \pm SD at the original scale: 12.635 \pm 8.967.

^g Estimates refer to the comparison with the reference category: female.

^h Estimates refer to the comparison with the reference category: healthy.

ⁱ Estimates refer to the comparison with the reference category: method (total individuals observed).

^j Party size was measured using two methods.

unpublished data), and occurs more frequently during this period when water is most scarce but necessity is highest.

As expected, higher temperatures and dry conditions, as well as high night-time temperatures and heat index, were correlated with higher creatinine levels. In addition, all three food availability indices, particularly both fruit availability indices, were significantly associated with creatinine levels. As an individual's water intake comes from both preformed and freestanding sources, it is possible that preformed water in Fongoli diet fruit items contribute seasonally varying amounts of water to chimpanzees' water intake levels. Chimpanzee hydration levels likely varied in part due to variation in particularly wet foods representing a larger part of the diet during periods of reduced water intake from freestanding sources. It may be possible that chimpanzees inhabiting drier environments employ specific strategies to capitalize on available preformed water in food items when hydration needs are highest. Further investigation of seasonal variation in water content and temporally varying food preferences might therefore help to clarify the role of food as a water source and additional characteristics considered in food item selection. Ultimately, the risk of dehydration is also considered relevant to hominin evolution as $\delta^{18}\text{O}$ stable isotope evidence suggests several hominins were obligate drinkers

Table 3

Summary of multi-model inference results for creatinine, c-peptide, and cortisol with potential environmental variables. Results include the size of the 95% best model confidence set (size of total model set included in parentheses), as well as the performance (model rank) of the two null models. Expected weights for each environmental predictor are indicated in *italics*, and sum of Akaike weights (based on AICc) per environmental variable that are indicated in **bold** represent weights larger than their expected values given the model set. Full model results including individual estimates are indicated in **SOM Tables S4–S6**.

Sum of weights	Confidence set (# models converged)	Null model ranks ^a	Factor 1	Factor 2	Factor 1: Factor 2	Ripe fruit index	Total food index	Total fruit index	Rainfall
Expected	—	—	<i>0.42</i>	<i>0.42</i>	<i>0.08</i>	<i>0.37</i>	<i>0.37</i>	<i>0.37</i>	<i>0.37</i>
Creatinine	31 (80)	65, 49	0.99	0.95	0.58	0.65	0.43	0.66	0.40
C-peptide	48 (81)	79, 7	0.45	0.44	0.27	0.24	0.78	0.44	0.48
Cortisol	26 (76)	53, 1	0.63	0.20	0.04	0.18	0.18	0.14	0.23

^a Null model ranks are provided for models including only the intercept, and a generic seasonal term (sin and cosine of date), respectively; best model: rank 1.

Table 5

Effect of season (represented by sine and cosine of Julian date), creatinine, and c-peptide levels on urinary cortisol levels (square root transformed; $n = 232$). Statistically significant results ($p \leq 0.05$) appear in bold.

Term	Estimate \pm SE	χ^2_{2a}	p
(Intercept)	8.051 \pm 0.849	—	—
Test predictors			
Sine (Julian date)^b	2.112 \pm 0.412	22.717	<0.001
Cosine (Julian date)^b	0.530 \pm 0.357		
Creatinine^c	3.612 \pm 0.404	37.402	<0.001
C-peptide ^d	0.087 \pm 0.260	0.109	0.741
Control predictors			
Rank ^e	−0.892 \pm 0.408	—	—
Time of day ^f	0.379 \pm 0.359	—	—
Processing time ^g	−0.152 \pm 0.311	—	—
Number in estrus ^h	0.048 \pm 0.310	—	—
Sex ⁱ	2.055 \pm 0.999	—	—
Health (Injury) ^j	1.038 \pm 1.096	—	—
Health (Diarrhea) ^j	3.717 \pm 1.756	—	—
Pool use ^k	−4.750 \pm 2.500	—	—
Cave use ^k	5.264 \pm 6.740	—	—

^a Degrees of freedom are 2 (season) and 1 (creatinine and c-peptide).

^b Sine and cosine of Julian date together represent a seasonal term and are therefore not treated separately.

^c z-transformed, mean \pm SD at the original scale: 1.213 \pm 0.766.

^d z-transformed, mean \pm SD at the original scale: 7.644 \pm 5.371.

^e z-transformed, mean \pm SD at the original scale: 12.418 \pm 5.057 (range 1–20, with 20 representing the highest social rank).

^f z-transformed, mean \pm SD at the original scale: 7.985 \pm 1.415.

^g z-transformed, mean \pm SD at the original scale: 3.324 \pm 1.438.

^h z-transformed, mean \pm SD at the original scale: 1.395 \pm 1.263.

ⁱ Estimates refer to the comparison with the reference category: female.

^j Estimates refer to the comparison with the reference category: healthy.

^k Per hour focal follow.

(Grine et al., 2012), and were unlikely to obtain sufficient water sources from preformed water in foods.

Third, environmental temperature had a clear impact on urinary cortisol levels in Fongoli chimpanzees, even after controlling for measures of dehydration (creatinine) and energetic status (c-peptide). Hence, hot temperatures represented a stressor, independent from and in addition to the potential impact of water and food shortage. This seasonal effect was likewise observed even when controlling for potential social stressors or behavioral mechanisms (pool and cave use) presumably aimed at reducing potential thermoregulatory stress. Thermoregulatory challenges have already been observed to elicit glucocorticoid level increases across a number of animal taxa (Christison and Johnson, 1972; El-Halawani et al., 1973; Edens and Siegel, 1975; Harikai et al., 2003; Beehner and Bergman, 2017). The observation of cortisol values positively correlating with environmental temperature while

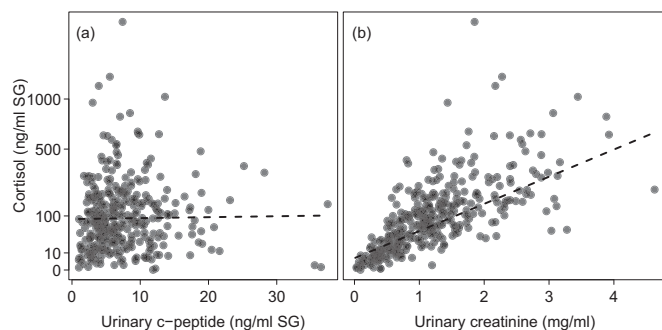


Figure 3. Effects of urinary c-peptide (a) and creatinine levels (b) on urinary cortisol concentration ($n = 232$ samples). Urinary cortisol levels are displayed on a square root scale.

controlling for both pool and cave use suggests that these behavioral mechanisms are insufficient to fully buffer against the damaging effects of an extreme climate. In light of the observed heat stress, the question remains as to how effective these behavioral strategies are in reducing the assumed stress, although initial evidence in the form of behavioral control estimates relative to environmental predictor estimates in the full models suggests these behaviors do offer some respite from environmental, specifically thermoregulatory, stress.

Finally, Fongoli chimpanzees exhibited patterns of heat and dehydration stress, but not of nutritional stress. While controlling for season and behavioral compensatory mechanisms, as well as other potential confounders, creatinine values positively correlated with cortisol values, whereas no apparent relationship existed between cortisol and c-peptide values. The relationship between cortisol and creatinine suggests chimpanzees became dehydrated enough during the dry season to elicit an increase in cortisol levels. Physiological variation in hydration status was visible in Fongoli chimpanzees and potential dangers of water restriction are dramatic. Therefore, maintaining adequate hydration in a savanna environment is likely a strong selective pressure for chimpanzees in a savanna-mosaic habitat.

Conversely, the absence of a correlation between c-peptide and cortisol values suggests that Fongoli chimpanzees experienced variation in energy balance due to the variation in the amount of food available to them, but they did not appear to suffer considerably during leaner periods. Several studies have revealed glucocorticoids to vary according to variation in food availability in primates (Beehner and Bergman, 2017) and other mammals (Kitaysky et al., 2007), which poses the question as to why we did not find such a relationship. A likely explanation is that variation in energy balance in Fongoli chimpanzees simply did not reach a point at which individuals experience stress. Fongoli chimpanzees rely on important staple food items like termites (Bogart and Pruett, 2011), exudates and cambium from *Pterocarpus*, and pith of young trees during periods of low food availability. These items have a high nutritional value (Lindshield, 2014), suggesting that switching to these food items, when more preferable food items like ripe fruit are not available, allows chimpanzees to avoid severe nutritional deficits. Beehner and McCann (2008) drew similar conclusions when they also failed to find an effect of seasonal changes of glucocorticoids, which led them to suggest that geladas were able to sufficiently exploit fallback foods.

However, the indication that thermoregulatory and hydration challenges were significant environmental stressors to chimpanzee individuals at Fongoli supports previous conclusions that the late dry season is a difficult time for survival in this habitat (Skinner and Pruett, 2012). Likewise, the fact that Fongoli chimpanzees experienced both dehydration and thermal challenges during seasonal periods that partially overlap suggests that the effects of heat and hydration challenges in Fongoli chimpanzees are likely confounded by physiological mechanisms for coping with both environmental constraints simultaneously. Temperature regulation depends on an individual's ability to dissipate heat (such as via sweating or exhalation), and advantages gained from battling thermoregulatory challenges, in turn, can contribute to dehydration. Substantial research has shown that responses to thermal stressors are magnified when coupled with water restriction, and that exercise in these conditions worsens the effect further (Sawka and Pandolf, 1990). Therefore, as heat and dehydration pressures occur in parallel, there is likely a synergy between the two effects, with each worsening the effect of the other.

Moreover, counter strategies to heat exposure and dehydration are likely compromised by additional needs like maintenance of

nutritional or social requirements. While Fongoli chimpanzees sit in the shade, in pools, and in caves to minimize thermal stress (Pruetz, 2007; Pruetz and Bertolani, 2009), they must budget their time with other needs in order to balance the costs of becoming dehydrated, reduced food intake, or even socializing. Supporting this, Pruetz and Bertolani (2009) demonstrated that Fongoli chimps modify their activity budget to avoid activity during the hottest times of the day, especially so during the hottest times of the year when such active behaviors are most costly and maintaining access to water and food necessitates exposure to and activity in hot, exposed areas. Fongoli chimpanzees could alternatively eat or drink during the night-time when temperatures are cooler (as has been observed, especially during the dry season; Pruetz and Bertolani, 2009), but this may also be accompanied by other costs like increased risk of predation (Dunbar et al., 2009; Lindshield et al., 2017).

5. Conclusions

Our work provides physiological evidence of the relative importance of three potential selective pressures involved in living in savanna habitat for one of the closest living relatives of humans. At the species level, it contributes to our understanding of the strength of these environmental constraints on chimpanzee distribution at the biogeographical range limits, and refutes the assumption that chimpanzees are able to remain thermoneutral throughout their range (David-Barrett and Dunbar, 2016). More broadly, our research provides insights into how early hominins, particularly those that had not yet undergone significant hair-loss, might have coped physiologically with thermoregulatory challenges of more open savanna or savanna-woodland environments. It likewise lends support to the assumption that thermoregulatory challenges likely posed a significant factor in hominin evolution (Wheeler, 1984, 1991, 1992b; Ruxton and Wilkinson, 2011a,b), and suggests that these challenges may have overshadowed the challenges of maintaining adequate energetic balance in this type of environment (Speakman and Król, 2010). Therefore, it lends support to the notion that mechanisms allowing individuals to cope with thermoregulatory pressures conferred an evolutionary advantage during the expansion of hominins from wetter, more forested habitats to drier savanna environments. Clarification as to how such seasonal variation differs in other chimpanzee populations, as well as to whether seasonal increases in cortisol materializes into specific fitness disadvantages will further illuminate the evolutionary relevance of dehydration and thermoregulatory stress. Moreover, further investigations as to how individuals cope with these stressors via various behavioral mechanisms or via time budgeting will inform us about the role that these strategies play in mitigating costs associated with a difficult environment.

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Supplementary Online Material

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References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–266.
- Anderson, D.P., Nordheim, E.V., Boesch, C., Moermond, T., 2002. Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. In: Boesch, C., Hohmann, G., Marchant, L. (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp. 90–101.
- Angus, S., 1971. Water-contact behavior of chimpanzees. *Folia Primatologica* 14, 51–58.
- Baayen, R.H., 2008. *Analyzing Linguistic Data: A Practical Introduction to Statistics Using R*. Cambridge University Press, Cambridge.
- Bahr, N.I., Palme, R., Mohle, U., Hodges, J.K., Heistermann, M., 2000. Comparative aspects of the metabolism and excretion of cortisol in three individual nonhuman primates. *General and Comparative Endocrinology* 117, 427–438.
- Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language* 68, 255–278.
- Bartón, K., 2017. MuMIn: Multi-Model Inference. R package version 1.40.0.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67, 1–48.
- Beehner, J.C., Bergman, T.J., 2017. The next step for stress research in primates: To identify relationships between glucocorticoid secretion and fitness. *Hormones and Behavior* 91, 68–83.
- Beehner, J.C., McCann, C., 2008. Seasonal and altitudinal effects on glucocorticoid metabolites in a wild primate (*Theropithecus gelada*). *Physiology and Behavior* 95, 508–514.
- Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207, 399–420.
- Bobe, R., Leakey, M.G., 2009. Ecology of Plio-Pleistocene mammals in the Omo–Turkana Basin and the emergence of *Homo*. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), *The First Humans—Origin and Early Evolution of the Genus Homo*. Springer, New York, pp. 173–184.
- Boesch, C., Boesch-Achermann, H., 2000. *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford University Press, Oxford.
- Bogart, S.L., Pruetz, J.D., 2011. Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology* 145, 11–20.
- Boyer-Onti, K.M., Pruetz, J.D., 2014. Giving the forest eyes: The benefits of using camera traps to study unhabituated chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *International Journal of Primatology* 35, 881–894.
- Brain, C., Mitchell, D., 1999. Body temperature changes in free-ranging baboons (*Papio hamadryas ursinus*) in the Namib Desert, Namibia. *International Journal of Primatology* 20, 585–598.
- Bromage, T.G., Schrenk, F., 1995. Biogeographic and climatic basis for a narrative of early hominid evolution. *Journal of Human Evolution* 28, 109–114.
- Burnham, K., Anderson, D., 2002. *Model Selection and Multimodel Inference*, 2nd ed. Springer, Berlin.
- Campos, F.A., Fedigan, L.M., 2009. Behavioral adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. *American Journal of Physical Anthropology* 138, 101–111.
- Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 97, 241–247.
- Cerling, T.E., Mbua, E., Kirera, F.M., Manthi, F.K., Grine, F.E., Leakey, M.G., Sponheimer, M., Uno, K.T., 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences USA* 108, 9337–9341.
- Chapman, C.A., Chapman, L.J., Wrangham, R., 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36, 59–70.
- Christison, G., Johnson, H., 1972. Cortisol turnover in heat-stressed cows. *Journal of Animal Science* 35, 1005–1010.
- Copeland, S.R., Sponheimer, M., de Ruiter, D.J., Lee-Thorp, J.A., Codron, D., le Roux, P.J., Grimes, V., Richards, M.P., 2011. Strontium isotope evidence for landscape use by early hominins. *Nature* 474, 76–78.
- David-Barrett, T., Dunbar, R.I., 2016. Bipedality and hair loss in human evolution revisited: The impact of altitude and activity scheduling. *Journal of Human Evolution* 94, 72–82.
- Dunbar, R.I., Korstjens, A.H., Lehmann, J., 2009. Time as an ecological constraint. *Biological Reviews* 84, 413–429.
- Edens, F.W., Siegel, H.S., 1975. Adrenal responses in high and low ACTH response lines of chickens during acute heat stress. *General and Comparative Endocrinology* 25, 64–73.
- El-Halawani, M., Waibel, P., Good, A., 1973. Effects of temperature stress on catecholamines and corticosterone of male turkeys. *American Journal of Physiology* 224, 384–388.

- Emery Thompson, M., 2017. Energetics of feeding, social behavior, and life history in non-human primates. *Hormones and Behavior* 91, 84–96.
- Emery Thompson, M., Wrangham, R.W., 2008. Male mating interest varies with female fecundity in *Pan troglodytes schweinfurthii* of Kanyawara, Kibale National Park. *International Journal of Primatology* 29, 885–905.
- Emery Thompson, M., Muller, M.N., Kahlenberg, S.M., Wrangham, R.W., 2010. Dynamics of social and energetic stress in wild female chimpanzees. *Hormones and Behavior* 58, 440–449.
- Fernández, M.H., Vrba, E.S., 2006. Plio-Pleistocene climatic change in the Turkana Basin (East Africa): evidence from large mammal faunas. *Journal of Human Evolution* 50, 595–626.
- Forstmeier, W., Schielzeth, H., 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology* 65, 47–55.
- Furuichi, T., Thompson, J., 2007. The Bonobos: Behavior, Ecology, and Conservation. Springer Science & Business Media, Berlin.
- Gammell, M.P., de Vries, H., Jennings, D.J., Carlin, C.M., Hayden, T.J., 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Animal Behaviour* 66, 601–605.
- Georgiev, A.V., Russell, A.F., Emery Thompson, M., Otali, E., Muller, M.N., Wrangham, R.W., 2014. The foraging costs of mating effort in male chimpanzees (*Pan troglodytes schweinfurthii*). *International Journal of Primatology* 35, 725–745.
- Gestich, C.C., Caselli, C.B., Setz, E.Z., 2014. Behavioural thermoregulation in a small Neotropical primate. *Ethology* 120, 331–339.
- Goodall, J., 1986. The Chimpanzees of Gombe: Patterns of Behavior. The Belknap Press of Harvard University Press, Cambridge.
- Grine, F.E., Sponheimer, M., Ungar, P.S., Lee-Thorp, J., Teaford, M.F., 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. *American Journal of Physical Anthropology* 148, 285–317.
- Hanya, G., Kiyono, M., Hayaishi, S., 2007. Behavioral thermoregulation of wild Japanese macaques: comparisons between two subpopulations. *American Journal of Primatology* 69, 802–815.
- Harikai, N., Tomogane, K., Miyamoto, M., Shimada, K., Onodera, S., Tashiro, S., 2003. Dynamic responses to acute heat stress between 34°C and 38.5°C, and characteristics of heat stress response in mice. *Biological and Pharmaceutical Bulletin* 26, 701–708.
- Hashimoto, C., Furuichi, T., Tashiro, Y., 2001. What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. *International Journal of Primatology* 22, 947–959.
- Hauser, B., Deschner, T., Boesch, C., 2008. Development of a liquid chromatography-tandem mass spectrometry method for the determination of 23 endogenous steroids in small quantities of primate urine. *Journal of Chromatography B, Analytical Technologies in the Biomedical Life Sciences* 862, 100–112.
- Head, J.S., Boesch, C., Makaga, L., Robbins, M.M., 2011. Sympatric chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: Dietary composition, seasonality, and intersite comparisons. *International Journal of Primatology* 32, 755–775.
- Higham, J.P., Girard-Buttoz, C., Engelhardt, A., Heistermann, M., 2011. Urinary C-peptide of insulin as a non-invasive marker of nutritional status: some practicalities. *PLoS One* 6, e22398.
- Hill, R., Weingrill, T., Barrett, L., Henzi, S.P., 2004. Indices of environmental temperatures for primates in open habitats. *Primates* 45, 7–13.
- Hill, R.A., 2006. Thermal constraints on activity scheduling and habitat choice in baboons. *American Journal of Physical Anthropology* 129, 242–249.
- Kierdorf, H., Witzel, C., Kierdorf, U., Skinner, M.M., Skinner, M.F., 2015. "Missing perikymata"—fact or fiction? A study on chimpanzee (*Pan troglodytes verus*) canines. *American Journal of Physical Anthropology* 157, 276–283.
- Kitaysky, A.S., Piatt, J.F., Wingfield, J.C., 2007. Stress hormones link food availability and population processes in seabirds. *Marine Ecology Progress Series* 352, 245–258.
- Koops, K., McGrew, W.C., de Vries, H., Matsuzawa, T., 2012. Nest-building by chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: Anti-predation, thermoregulation, and antivector hypotheses. *International Journal of Primatology* 33, 356–380.
- Kortlandt, A., 1983. Marginal habitats of chimpanzees. *Journal of Human Evolution* 12, 231–278.
- Koshelev, V.P., Anderson, C.N., 2009. Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American Journal of Physical Anthropology* 139, 172–181.
- Levin, N.E., Brown, F.H., Behrensmeyer, A.K., Bobe, R., Cerling, T.E., 2011. Paleosol carbonates from the Omo Group: Isotopic records of local and regional environmental change in East Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 307, 75–89.
- Lindshield, S., Danielson, B.J., Rothman, J.M., Pruett, J.D., 2017. Feeding in fear? How adult male western chimpanzees (*Pan troglodytes verus*) adjust to predation and savanna habitat pressures. *American Journal of Physical Anthropology* 163, 480–496.
- Lindshield, S.M., 2014. Multilevel analysis of the foraging decisions of western chimpanzees (*Pan troglodytes verus*) and resource scarcity in a savanna environment at Fongoli, Senegal. Ph.D. Dissertation, Iowa State University.
- Lubbe, A., Hetem, R.S., McFarland, R., Barrett, L., Henzi, P.S., Mitchell, D., Meyer, L.C., Maloney, S.K., Fuller, A., 2014. Thermoregulatory plasticity in free-ranging vervet monkeys, *Chlorocebus pygerythrus*. *Journal of Comparative Physiology B* 184, 799–809.
- McGrew, W.C., Baldwin, P.J., Tutin, C.E., 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, West Africa. *Journal of Human Evolution* 10, 227–244.
- Mitchell, D., Fuller, A., Maloney, S.K., 2009. Homeothermy and primate bipedalism: is water shortage or solar radiation the main threat to baboon (*Papio hamadryas*) homeothermy? *Journal of Human Evolution* 56, 439–446.
- Morgan, D., Sanz, C., 2006. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goulougo Triangle, Republic of Congo. In: Hohmann, G., Robbins, M., Boesch, C. (Eds.), *Feeding Ecology in Apes and Other Primates*. Cambridge University Press, Cambridge, pp. 97–122.
- Muller, M.N., Kahlenberg, S.M., Thompson, M.E., Wrangham, R.W., 2007. Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society London B* 274, 1009–1014.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4, 133–142.
- National Wrestling Rules Committee, 1988. 1998–1999 Wrestling Weight Certification Program. NCAA, Indianapolis.
- N.O.A.A., 2014. The Heat Index Equation. http://www.wpc.ncep.noaa.gov/html/heatindex_equation.shtml. (Accessed 24 December 2017).
- Nyakudya, T.T., Fuller, A., Meyer, L.C., Maloney, S.K., Mitchell, D., 2012. Body temperature and physical activity correlates of the menstrual cycle in chacma baboons (*Papio hamadryas ursinus*). *American Journal of Primatology* 74, 1143–1153.
- Passey, B.H., Levin, N.E., Cerling, T.E., Brown, F.H., Eiler, J.M., 2010. High-temperature environments of human evolution in East Africa based on bond ordering in paleosol carbonates. *Proceedings of the National Academy of Sciences USA* 107, 11245–11249.
- Pepper, J.W., Mitani, J.C., Watts, D.P., 1999. General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology* 20, 613–632.
- Piel, A.K., Strampelli, P., Greathead, E., Hernandez-Aguilar, A., Moore, J., Stewart, F.A., 2017. The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa valley, western Tanzania. *Journal of Human Evolution* 112, 57–69.
- Pruetz, J., Bertolani, P., 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology* 17, 412–417.
- Pruetz, J., Bertolani, P., 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savannah-mosaic environment: Implications for hominin adaptations to open habitats. *PaleoAnthropology* 2009, 252–262.
- Pruetz, J.D., 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Hohmann, G., Robbins, M., Boesch, C. (Eds.), *Feeding Ecology in Apes and Other Primates*. Cambridge University Press, Cambridge, pp. 161–182.
- Pruetz, J.D., 2007. Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behavior. *Primates* 48, 316–319.
- Pruetz, J.D., Bertolani, P., Boyer Ontl, K., Lindshield, S., Shelley, M., Wessling, E., 2015. New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Sénégal. *Royal Society Open Science* 2, 140507.
- Quinn, R.L., Lepre, C.J., Feibel, C.S., Wright, J.D., Mortlock, R.A., Harmand, S., Brugal, J.P., Roche, H., 2013. Pedogenic carbonate stable isotopic evidence for wooded habitat preference of early Pleistocene tool makers in the Turkana Basin. *Journal of Human Evolution* 65, 65–78.
- R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* 32, 289–322.
- Ruxton, G.D., Wilkinson, D.M., 2011a. Avoidance of overheating and selection for both hair loss and bipedality in hominins. *Proceedings of the National Academy of Sciences USA* 108, 20965–20969.
- Ruxton, G.D., Wilkinson, D.M., 2011b. Thermoregulation and endurance running in extinct hominins: Wheeler's models revisited. *Journal of Human Evolution* 61, 169–175.
- Samson, D.R., Hunt, K.D., 2012. A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. *American Journal of Primatology* 74, 811–818.
- Sawka, M.N., Pandolf, K.B., 1990. Effects of body water loss on physiological function and exercise performance. In: Lamb, D.R., Gisolfi, C.V. (Eds.), *Perspectives in Exercise Science and Sports Medicine: Fluid Homeostasis During Exercise*. Benchmark Press, Indianapolis, pp. 1–38.
- Schielzeth, H., Forstmeier, W., 2009. Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology* 20, 416–420.
- Skinner, M.F., Pruett, J.D., 2012. Reconstruction of periodicity of repetitive linear enamel hypoplasia from perikymata counts on imbricational enamel among dry-adapted chimpanzees (*Pan troglodytes verus*) from Fongoli, Senegal. *American Journal of Physical Anthropology* 149, 468–482.
- Speakman, J.R., Król, E., 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology* 79, 726–746.

- Stolwijk, A., Straatman, H., Zielhuis, G., 1999. Studying seasonality by using sine and cosine functions in regression analysis. *Journal of Epidemiology and Community Health* 53, 235–238.
- Surbeck, M., Deschner, T., Schubert, G., Weltring, A., Hohmann, G., 2012a. Mate competition, testosterone and intersexual relationships in bonobos, *Pan paniscus*. *Animal Behaviour* 83, 659–669.
- Surbeck, M., Deschner, T., Weltring, A., Hohmann, G., 2012b. Social correlates of variation in urinary cortisol in wild male bonobos (*Pan paniscus*). *Hormones and Behavior* 62, 27–35.
- Surbeck, M., Deschner, T., Behringer, V., Hohmann, G., 2015. Urinary C-peptide levels in male bonobos (*Pan paniscus*) are related to party size and rank but not to mate competition. *Hormones and Behavior* 71, 22–30.
- Takemoto, H., 2004. Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *American Journal of Physical Anthropology* 124, 81–92.
- Thompson, C.L., Williams, S.H., Glander, K.E., Teaford, M.F., Vinyard, C.J., 2014. Body temperature and thermal environment in a generalized arboreal anthropoid, wild mantled howling monkeys (*Alouatta palliata*). *American Journal of Physical Anthropology* 154, 1–10.
- Thompson, C.L., Powell, B.L., Williams, S.H., Hanya, G., Glander, K.E., Vinyard, C.J., 2017. Thyroid hormone fluctuations indicate a thermoregulatory function in both a tropical (*Alouatta palliata*) and seasonally cold-habitat (*Macaca fuscata*) primate. *American Journal of Primatology* 79, e22714.
- Tutin, C.E., Ham, R.M., White, L.J., Harrison, M.J., 1997. The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42, 1–24.
- U.S.N.O., 2015. Rise, set, transit, twilight data services. <http://aa.usno.navy.mil/data/>. (Accessed 24 December 2017).
- Viberti, G., Mogensen, C., Keen, H., Jacobsen, F., Jarrett, R., Christensen, C., 1982. Urinary excretion of albumin in normal man: the effect of water loading. *Scandinavian Journal of Clinical and Laboratory Investigation* 42, 147–151.
- Vrba, E.S., 1985. Ecological and adaptive changes associated with early hominid evolution. In: Delson, E. (Ed.), *Ancestors: The Hard Evidence*. Alan. R. Liss, New York, pp. 63–71.
- Wark, J.D., Kuhar, C.W., Lukas, K.E., 2014. Behavioral thermoregulation in a group of zoo-housed colobus monkeys (*Colobus guereza*). *Zoo Biology* 33, 257–266.
- Wheeler, P.E., 1984. The evolution of bipedality and loss of functional body hair in hominids. *Journal of Human Evolution* 13, 91–98.
- Wheeler, P.E., 1991. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. *Journal of Human Evolution* 21, 107–115.
- Wheeler, P.E., 1992a. The influence of the loss of functional body hair on the water budgets of early hominids. *Journal of Human Evolution* 23, 379–388.
- Wheeler, P.E., 1992b. The thermoregulatory advantages of large body size for hominids foraging in savannah environments. *Journal of Human Evolution* 23, 351–362.
- White, T.D., Ambrose, S.H., Suwa, G., Su, D.F., DeGusta, D., Bernor, R.L., Boissarie, J.-R., Brunet, M., Delson, E., Frost, S., 2009. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. *Science* 326, 67–93.
- Wrangham, R.W., 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock, T.H. (Ed.), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*. Academic Press, London, pp. 504–538.
- Wrangham, R.W., Conklin, N., Chapman, C., Hunt, K., Milton, K., Rogers, E., Whiten, A., Barton, R., 1991. The significance of fibrous foods for Kibale Forest chimpanzees. *Philosophical Transactions of the Royal Society B* 334, 171–178.
- Wroblewski, E.E., Murray, C.M., Keele, B.F., Schumacher-Stankey, J.C., Hahn, B.H., Pusey, A.E., 2009. Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour* 77, 873–885.
- Wynn, J.G., 2004. Influence of Plio-Pleistocene aridification on human evolution: Evidence from paleosols of the Turkana Basin, Kenya. *American Journal of Physical Anthropology* 123, 106–118.