Journal of Human Evolution xxx (2018) 1–11

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

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

Erin G. Wessling [a, b, *], Hjalmar S. Kühl [a, b], Roger Mundry [c], Tobias Deschner [a], Jill D. Pruetz [d, e]

[a] Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany
[b] German Centre for Integrative Biodiversity Research (iDiv), 04103 Leipzig, Germany
[c] Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany
[d] Department of World Languages & Cultures, Iowa State University, Ames, IA 50011, USA
[e] Department of Anthropology, Texas State University, San Marcos, TX 78666, USA

ARTICLE INFO

Article history:
Received 8 September 2017
Accepted 1 March 2018
Available online xxx

Keywords:
Pan troglodytes
Cortisol
C-peptide
Creatinine
Hominin evolution

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.

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. Paleoenvironmental 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

* Corresponding author.
E-mail address: erin_wessling@eva.mpg.de (E.G. Wessling).

https://doi.org/10.1016/j.jhevol.2018.03.001
0047-2484/

Please cite this article in press as: Wessling, E.G., et al., The costs of living at the edge: Seasonal stress in wild savanna-dwelling chimpanzees, Journal of Human Evolution (2018), https://doi.org/10.1016/j.jhevol.2018.03.001

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 km^2 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-Ontl 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

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