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Ecological variation in Later Stone Age southern African biomechanical properties



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ABSTRACT

Behavioural ecology suggests that human populations modify their behaviour, including subsistence strategy, technology, and mobility, in response to ecological variation. This paper examines if cross-sectional geometric properties (CSGPs) indicative of habitual physical behaviours, including manual activities and terrestrial mobility, vary among southern African Later Stone Age (LSA) Mediterranean Cape coast (n = 85), semiarid central interior (n = 53), and hyperarid Namib Desert (n = 17) individuals. Results will be contextualised using the dietary breadth model, which accounts for the search and handling costs associated with acquiring and processing resources. CSGPs were assessed for humeri, femora, and tibiae using periosteal moulds and 3D laser surface scans at the humerus middistal (35%) location as well as the femur and tibia midshaft (50%) locations.

Humerus strength indicators were higher among central interior and Namib Desert females. This may have occurred due to decreased resource quality and quantities in these semiarid and arid ecologies. Females in particular may have enhanced resource-processing efforts to maximise nutritional intake in sparse ecologies. Lower limb biomechanical properties indicative of strength were highest among Cape coast individuals, but it is not clear if search efforts were higher in this region, or if other factors like complex terrain imposed a biomechanical cost for individuals living in this region. Overall, local ecologies interact with subsistence strategies to impact upper limb habitual activities among LSA southern African groups.

1. Introduction

Human populations exhibit behavioural variation in response to environmental variability (Charnov, 1976; Winterhalder, 1981; West-Eberhard, 2005; Bird and O'Connell, 2006; Richards, 2006; Jablonka and Raz, 2009; Pigliucci and Müller, 2010; Mulder and Schacht, 2012; Nettle et al., 2013; Codding and Bird, 2015). Behavioural ecology predicts that human behaviours arise in response to, and interact with, local ecological conditions (Charnov, 1976; Winterhalder, 1981; Bird and O'Connell, 2006; Mulder and Schacht, 2012; Nettle et al., 2013; Codding and Bird, 2015). Furthermore, optimal foraging theory suggests that individuals trade-off between maximising nutritional intakes and minimising energetic costs to enhance individual fitness (Charnov, 1976; Winterhalder, 1981; Bird and O'Connell, 2006; Mulder and Schacht, 2012; Nettle et al., 2013; Codding and Bird, 2015).

Bioarchaeological researchers have applied behavioural ecology to examine how resource availability may impact skeletal phenotypes (Churchill and Morris, 1998; Stock and Pfeiffer, 2004; Hill et al., 2016). Long bone diaphyses respond to habitual physical behaviours undertaken during life (Jones et al., 1977; Ruff et al., 1993, 2006; Stock and Pfeiffer, 2001; Ruff, 2008; Shaw and Stock, 2009a, 2009b). Crosssectional geometric properties (CSGPs) of long bones may indicate the strength and shape properties of diaphyses, and inform on habitual physical activity patterns undertaken during life (Jones et al., 1977; Ruff et al., 1993, 2006; Stock and Pfeiffer, 2001; Ruff, 2008; Shaw and Stock, 2009a, 2009b). As such, the long bone morphology of individuals from diverse ecologies may reflect habitual behavioural variation under different environmental regimes.

Behavioural ecology and optimal foraging theory have been applied to analyses of prehistoric human behaviours using several interpretive models (Churchill and Morris, 1998; Bird and O'Connell, 2006; Codding and Bird, 2015; Hill et al., 2016). The dietary breadth model in particular allows for the generation of hypotheses regarding intergroup variation in human skeletal morphologies and inferred habitual physical activities. This model accounts for both the ecological and technological characteristics of the groups under consideration (MacArthur and Pianka, 1966; Charnov, 1976; Winterhalder, 1981; Churchill and Morris, 1998; Hill et al., 2016). Under this model, foraging is divided

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https://doi.org/10.1016/j.jasrep.2017.10.033 Received 14 July 2017; Received in revised form 10 October 2017; Accepted 22 October 2017 2352-409X/ © 2017 Elsevier Ltd. All rights reserved. into two components based on economic and energetic costs: the search costs involved with obtaining food resources, and the handling costs associated with extracting nutrition from food items (MacArthur and Pianka, 1966; Charnov, 1976; Winterhalder, 1981; Churchill and Morris, 1998). The influence of search and handling costs on habitual behaviour may be examined though analyses of the biomechanical properties of upper and lower limb CSGPs. Search costs are closely linked to terrestrial mobility as individuals traverse the landscape in search of resources. Consequently, search costs are linked to lower limb biomechanical properties. Handling costs are associated with tool technologies, and the ability of individuals to extract nutrition from food resources (MacArthur and Pianka, 1966; Charnov, 1976; Winterhalder, 1981). Consequently, handling costs are closely linked to manual activities and upper limb biomechanical properties.

Additionally, search and handling costs are expected to covary (Winterhalder, 1981; Churchill and Morris, 1998). Individuals tend to increase their search efforts in response to low resource availability or low resource quality. Consequently, when resources are found, handling efforts also increase to maximise the nutritional output of low quality or sparse resources. Alternatively, if higher resource processing efforts are undertaken, resources may be of a lower quality, which in turn would increase search efforts. This relationship emphasises the link between subsistence strategies and ecological conditions, and their impact on habitual behavioural patterns.

The southern African Later Stone Age (LSA) presents a strong context for examining physical behavioural variation in response to ecological variables (Churchill and Morris, 1998; Stock and Pfeiffer, 2001, 2004; Cameron and Pfeiffer, 2014). Southern African LSA foragers and herders represent a relatively constrained genetic population (Stynder, 2009; Tishkoff et al., 2009; Henn et al., 2011; Schlebusch et al., 2012; Irish et al., 2014; Kim et al., 2014; Barbieri et al., 2014). Ecological conditions are well documented (Acocks, 1988; Rutherford and Westfall, 1994; Mitchell, 2002; Mucina and Rutherford, 2006). There are regional and temporal differences in material culture, however the LSA is widely distributed across the region (Deacon and Deacon, 1999; Mitchell, 2002; d'Errico et al., 2012; Lombard et al., 2012). Ethnohistoric records of Khoesan populations, who represent the contemporary descendants of LSA populations, complement and further contextualise the archaeological record when interpreting past behaviours (Lee and DeVore, 1968; Draper, 1975; Marshall, 1976; Yellen and Lee, 1976; Lee, 1979; Silberbauer, 1981; Deacon and Deacon, 1999; Biesele and Barclay, 2001). As such, information from the archaeological, ecological, and ethnohistoric records may inform interpretations of past activities among LSA southern Africans.

Southern African LSA populations occupied a large geographic range throughout the Holocene and into the historic era within which three distinct ecological zones may be identified: the southernmost Cape coast, the central interior of South Africa, and the Namib Desert of Namibia (Fig. 1). The ecologies of these regions posed unique resource acquisition challenges and constraints, and provide a gradient along which the impact of resource limitations on human biology and behaviour can be tested.

The Cape coast features a Mediterranean climate. Environmental conditions are amenable, with abundant freshwater sources, a reliable plant base, and access to marine resources (Acocks, 1988; Rutherford and Westfall, 1994; Mucina and Rutherford, 2006). Cape coast LSA human skeletal remains are available from across the Holocene (10,000–200 uncalibrated bp). Individuals engaged in foraging during the majority of the Holocene, and herding was incorporated into subsistence strategies during the last 2000 years (Smith, 1998; Sadr, 1998, 2003, 2015; Mitchell, 2002; Barham and Mitchell, 2008; Sealy, 2010). However, herding does not appear to have impacted habitual physical behaviours after this transition (Cameron and Stock, in revision). As such, Cape coast LSA people engaged with a Mediterranean, resource-rich landscape.

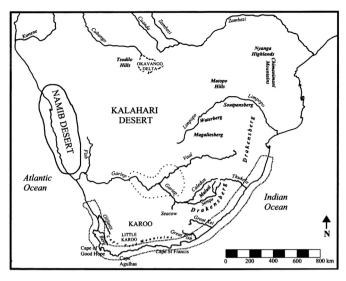


Fig. 1. Map of southern Africa with the Cape coast, central interior, and Namib Desert regions indicated. Adapted from Mitchell (2002). The stippled line indicates the Cape coast, the spaced dotted line indicates the central interior, and the solid line indicates the Namib Desert.

due to temperature extremes and unpredictable rainfall patterns (Acocks, 1988; Rutherford and Westfall, 1994; Dean and Milton, 1999; Mitchell, 2002; Mucina and Rutherford, 2006). Freshwater sources are limited to a small number of perennial rivers and waterholes, and edible plant resources are sparsely distributed (Maggs, 1971; Morris, 1992). Central interior human skeletal remains are available from the past 2000 years bp (Humphreys and Maggs, 1970; Maggs, 1971; Humphreys, 1972; Morris, 1992). Individuals engaged in a mixed herding and foraging subsistence strategy, however foraging was an essential component of subsistence activities (Maggs, 1971; Humphreys, 1972; Morris and Beaumont, 1991; Morris, 1992; Masemula, 2015). As such, central interior LSA people engaged with a semiarid landscape.

The Namib Desert is a hyperarid region where rainfall may be as little as 13 mm per year (Kinahan, 1991, 2005, 2013; Mitchell, 2002). Atlantic Ocean currents moderate temperature extremes in the Namib Desert, however vegetation is patchy and strongly dependent on fog patterns due to low rainfall (Kinahan, 1991, 2005, 2013; Dean and Milton, 1999; Mitchell, 2002). Namib Desert human skeletal remains are available from the past 1000 years bp (Kinahan, 1991, 2000). These people engaged in herding, however foraging activities were very important in this group (Kinahan, 1991, 2000). As such, the Namib Desert LSA group engaged with a sparse hyperarid landscape.

Physical behaviours have been inferred for LSA skeletons from the southern African Cape coast (Churchill and Morris, 1998; Stock and Pfeiffer, 2004). Churchill and Morris (1998), using a dietary breadth model, found no differences in musculoskeletal stress markers (MSMs) between coastal fynbos and forest LSA foragers. However, MSMs are difficult to interpret as they may represent pathological levels of physical activity (Churchill and Morris, 1998; Meyer et al., 2011; Niinimaki, 2011, 2012; Weiss et al., 2012). Stock and Pfeiffer (2004) compared CSGPs of fynbos and forest LSA foragers, and few comparisons between regions were statistically significant. There were no differences among females, however forest males had higher bilateral asymmetry and upper arm strength properties than fynbos males. This pattern may be attributed to a higher reliance on spear projectiles rather than bows and arrows due to a greater exploitation of medium- to large-sized bovids in the forest region. Cameron and Pfeiffer (2014) additionally found few significant differences in biomechanical indicators of habitual activity among forest and fynbos males and females. In these studies, the ecological similarities between these

The climate of the central interior is semiarid and prone to drought

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