7. Bioenergetic perspectives on Neanderthal thermoregulatory and activity budgets

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Abstract

The study of adaptation in Neanderthals is confounded by equifinality – the existence of multiple adaptive pathways to the same morphological end state – manifest as an inability to discriminate between equally likely selective agents behind a given trait. The capacious chests of Neanderthals serve as one example, possibly representing an adaptation either to cold or to high activity levels. While single features may be adaptive in multiple contexts, their relative adaptive value may vary greatly between contexts. Without means of evaluating competing adaptive arguments, we have little hope of identifying the primary selective agents that operated on Neanderthal body form. Bioenergetics provides a basis for quantifying the costs and benefits of various adaptive solutions to a given environmental challenge – thus providing potential for resolving issues of equifinality. Evaluating claims of cold-adapted morphology in Neanderthals involves determining the energetic costs of adhering to Bergmann's and Allen's rules. Skin surface area (SA) is the major determinant of basal metabolic rate (BMR) in mammals, thus estimating Neanderthal SA allows an estimate of the caloric cost of their cold-adapted body form. Clinical equations exist for estimating SA from stature and mass, but these have never been tested on humans of extreme (i.e., "hyper-arctic") body form. A half-size reconstruction of a male European Neanderthal was used to test the utility of these formulae: results indicate that they can be used confidently to predict Neanderthal SA. Based on Neanderthals for whom mass and stature can be reasonably estimated, mean SA is greater than that of Inuit of comparable stature, and suggests higher BMRs in Neanderthals than reported in previous studies. The estimates derived here can be used to model Neanderthal daily energy budgets, and form the basis of evaluating the costs/benefits of hypothesized morphological and behavioral adaptations.

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Introduction

Studies of Neanderthal adaptation are increasingly adopting a bioenergetic perspective (Jelinek, 1994; Sorensen and Leonard, 2001; Steegmann et al., 2002; Aiello and Wheeler, 2003; Weaver and Steudel-Numbers, 2005), as are studies of adaptive evolution in the genus *Homo* generally (Leonard and Robertson, 1992, 1997; Aiello and Wheeler, 1995; Aiello, 1997; Aiello and Wells, 2002; Leonard and Ulijaszek, 2002). The study of the flow of energy[1] through the Neanderthal world holds the promise of a solution to some of the conundrums that exist in functional morphological or adaptive studies of these archaic humans. By evaluating adaptive mechanisms from the perspective of energy budgets – the caloric costs and benefits associated with various physical and behavioral solutions to adaptive problems – we are in a better position to identify the true selective agents at play and discard competing, less likely adaptive hypotheses.

Many attempts to explore adaptive traits in Neanderthals quickly bump up against the problem of equifinality (that there may exist many different ways to arrive at the same end state), manifest as an inability to discriminate between equally likely selective agents behind a given trait. Take, for example, the capacious chests of Neanderthals (Franciscus and Churchill, 2002; Sawyer and Maley, 2005). Were large chests an adaptation to cold (producing a somewhat more spherical body shape with a surface area/volume (SA/V) ratio more conducive to retaining heat, following Bergmann's [1847] well-known ecogeographic rule)[2] or to high activity levels (providing a greater lung capacity, thus greater ventilatory ability for sustained work output)? Were the relatively short, stout bodies of Neanderthals all about thermoregulation (again following ecogeographic rules – Bergmann's as well as the equally well-known Allen's [1877] rule),[3] or was this a body shape best suited for exerting muscular force on the environment (i.e., reflecting a musculoskeletal system with better mechanical leverage) in the accomplishment of subsistence and technological tasks (see Churchill, 1994, 1996)? Similar examples of competing adaptive hypotheses can be cited concerning Neanderthal nasal morphology, masticatory biomechanics, overall facial form, and pelvic morphology.[4]

At first blush equifinality seems less of a problem than an inconvenience. Large chests and stout bodies were probably beneficial to Neanderthals for both reasons – thermoregulation and power – and we are left only with the niggling but minor problem of being unable to determine the relative importance of the two selective agents. However, adaptive inferences can be and often are interdependent, since adaptations to one environmental problem can constrain or enhance adaptive solutions to other problems. For example, the argument that Neanderthal noses may have functioned as heat vents – that is, they were adapted to *lose heat* rather than conserve it (Trinkaus, 1987; Dean, 1988; Franciscus and Trinkaus, 1988) – depends upon the assumption of very high activity levels in Neanderthals, an assumption that in turn is based on adaptive inferences from other morphological features, like enlarged thoraces, which may in fact be adaptations to other things (such as *conserving heat*, as discussed above). Without means of evaluating such arguments, alternative adaptive hypotheses simply accrue over time with little hope of winnowing out the untenable ones.

A bioenergetic perspective provides some hope for refining our understanding of adaptive evolution in the genus *Homo*. In this paper I explore the utility of bioenergetics in research on Neanderthal adaptation by applying the approach to one aspect of their body form – their large chests. This entails first a consideration of the energetic interrelationships between ventilation, activity and