J Archaeol Method Theory (2010) 17:323–355
DOI 10.1007/s10816-010-9093-9

A Niche Construction Perspective on the Middle–Upper Paleolithic Transition in Italy

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Abstract This paper presents an overview of the Middle–Upper Paleolithic transition in Italy in light of recent research on the Uluzzian technocomplex and on the paleoecological context of the transition. Drawing on the realization that human niche construction can be documented in the pre-agricultural archaeological record, niche construction theory is used as a conceptual framework to tie together facets of the behavioral, biological, and ecological dimensions of the transition interval into formal models of their interaction over time and in diverse contexts. Ultimately, this effort shows how foragers of the transitional interval in the Italian peninsula were active agents in shaping their evolutionary history, with consequences of some adaptive systems being felt only much later and directing the forces responsible for the ultimate disappearance of the Mousterian and Uluzzian technocomplexes in favor of the proto-Aurignacian industry, the exact nature of which clearly appears to vary on a regional level.

Keywords Niche construction theory · Italy · Middle–Upper Paleolithic transition · Neanderthals · *Homo sapiens* · Lithic technology · Mobility strategies · Subsistence strategies

This paper builds on recent archaeological research that has used niche construction theory (NCT) to derive novel insights about prehistoric human adaptations and ecological legacies. It begins by presenting a discussion of one of the central question in anthropological archaeology—that of the disappearance of Neanderthals and Middle Paleolithic industries during the Middle–Upper Paleolithic transition to lay the groundwork on the potential interpretive benefits a niche construction perspective can bring to archaeological research focused on transitional intervals in

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prehistory. This is followed by a discussion of what niche construction is and how it can be implemented in archaeological scholarship, explicitly addressing the necessary datasets to do so convincingly. This is followed by an in-depth study of the Middle–Upper Paleolithic transition in the Italian peninsula that uses niche construction theory as a conceptual framework to generate new models of how that process unfolded in that region of the Old World.

Prime Movers and Irreconcilable Differences

The Middle–Upper Paleolithic transition refers to the interval ca. 50–30 ky BP, the period that saw the Neanderthal disappear from the Eurasian fossil record, and the successive appearance of *Homo sapiens*. That time period also sees the plethora of Mousterian industries that had dominated the archaeological record disappear, to be replaced by a variety of regional Aurignacian facies and of so-called transitional industries that show some, if occasionally tenuous affinities to both technocomplexes in addition to their own, regionally specific characters. Given this coincidence, the processes of Neanderthal disappearance and of the development of Upper Paleolithic industries are often seen as intrinsically linked, with modern humans playing a determinant role in both. In a very real sense, then, studies of the dynamics of the transition interval have and continue to focus on biocultural explanations to a much greater extent than almost any other anthropological question.

In spite of this, much current research on the Middle–Upper Paleolithic transition continues to seek prime movers to make sense of this critical interval in our species' history. Because this transition involves both biological and behavioral dimensions, however, it has proved nearly impossible to formulate coherent explanatory models that account for the process' multifaceted paleoanthropological manifestations. For one thing, most general models of the transition have been formulated at a continental scale, while it is becoming increasingly clear that regional perspectives offer more appropriate levels of resolution to understand the process (Hovers 2009; Olszewski 2009; Riel-Salvatore 2009). This paper explores a second factor contributing to this problem, namely the fact that the majority of researchers have tended to emphasize behavior or biology as the key aspect of the debate, generally considering the other as essentially epiphenomenal to the first. In practice, this amounts to ranking different classes of evidence on distinct levels of empirical and methodological relevance; since the transition broadly coincides with the replacement of Neanderthals by early *H. sapiens*, the archaeological record is often the principal casualty of this two-tiered approach to paleoanthropology (Marks 2003).

A strong case can be made, however, for decoupling the various dimensions researchers involved in "transition studies" engage with (Ames and Riel-Salvatore n.d., unpublished manuscript). For instance, stone tools do not inform researchers about the biology of their maker—at least not directly. They are separated from biology by the intermediary buffer of behavior (i.e., how it was used, potentially in fitness-enhancing ways). Only once this conceptual gap has been adequately bridged can conclusions about links between the morphological and behavioral records be proposed.

Efforts to eschew the tug-of-war between biology and culture as the principal driving force of the transition have emphasized the importance of ecological factors as an alternative avenue of investigation in the process of the transition (e.g., Carrión *et al.* 2008; d'Errico and Sanchez-Goñi 2003; Fedele *et al.* 2003, 2008; Finlayson 2004; van Andel *et al.* 2003). Too often, however, this has resulted mainly in suggesting new potential prime movers to explain the process (e.g., global climate change, catastrophic volcanic eruptions) rather than explicitly integrating these new data with the biological and behavioral records, thus perpetuating a multitiered approach to the data implicated in the transition. In spite of this, it is now abundantly clear that paleoecology contributes some fundamental information to the study of the range of forces at play during this period.

A Human Biocultural Revolution?

That said, many recent studies drawing on other bodies of archaeological and anthropological data are contributing to a more refined understanding of the processes that underpin the formation of the archaeological record of the transition interval. For instance, Tostevin's (2007) research on reconstructing acculturation pathways during the transition usefully draws from ethnohistory (e.g., White 1991), while O'Connell's (2006) recent and thoughtful discussion about potential mechanisms of outcompetition of Neanderthals by *H. sapiens* is informed by literature on the Holocene archaeological record of several continents where such interactions have been documented.

By analogy mainly to the Neolithic Revolution, others have suggested that the Middle–Upper Paleolithic transition is best understood, discussed, and analyzed in revolutionary terms (Gilman 1984; Bar-Yosef 1998, 2002; Mellars 1989; Mellars *et al.* 2007). Because the Neolithic Revolution encompasses behavioral, biological, and ecological dimensions, this framework theoretically could be a useful manner to structure observations and inferences pertaining to the Middle–Upper Paleolithic transition (Bar-Yosef 1998; Harrold 2007). However, Childe (1934) originally labeled as "revolutionary" the processes leading to domestication economies and to urbanism by analogy to what had defined the Industrial Revolution, namely dramatic increases in human population size resulting from a fundamental reorganization of the means of productions (Greene 1999). By extension, therefore, for the "Upper Paleolithic Revolution" to be a useful heuristic in addition to a catchy turn of phrase, the transition interval needs to be unambiguously associated with archaeological evidence of significant demographic growth.

So far, however, available data about population size over the transition interval remain ambiguous. Some reconstructions propose an upward kink in population coinciding with the very beginning of the transition interval (e.g., Biraben 2003), while others suggest that important population growth postdates that time by as much as 20,000 years (e.g., Clark 1999). Studies of assemblage frequencies also provide contradictory interpretations, with some arguing that Early Upper Paleolithic site densities were low and almost indistinguishable from Middle Paleolithic ones (e.g., van Andel *et al.* 2003) and others arguing that that early *H. sapiens* display notably higher site (and by extension, population) densities (e.g., Bocquet-Appel and

Demars 2000). Given recent demonstrations of the important influence of taphonomic bias on apparent patterns of diachronic site frequencies (Surovell and Brantingham 2007), these divergent views are perhaps not surprising.

Similarly, while human-accumulated faunal assemblages have been argued to indicate population growth pulses beginning with the transition interval (Stiner *et al.* 1999, 2000), the demographic expansion implied by this evidence is only conspicuously evident in the later phases of the Upper Paleolithic (Stiner and Kuhn 2006: Figs. 3 and 4). Perhaps not coincidentally, large mammal remains at some transition-age sites suggest that Early Upper Paleolithic (EUP) populations likely experienced repeated crashes following a form of "boom-bust" cycle vectored by fluctuations in prey abundance (Morin 2008), a pattern that contrasts sharply with the expectations of sustained population growth over the transition interval.

In sum, the available demographic data for the transition interval indicate that, at present, it can only tenuously be considered revolutionary by analogy to the Neolithic and Urban Revolutions (McBrearty 2007; McBrearty and Brooks 2000). This is unfortunate, especially because, as detailed above, the transition to food production economy encompassed behavioral, biological, and environmental dimensions, much like the Middle–Upper Paleolithic transition. That said, however, other aspects of the process of the transition from foraging to agriculture can help shed light on given aspects of the transition interval, and new theoretical developments indicate how to do so most productively.

Neanderthal Niche Construction

In recent years, renewed theorizing of the transition to agriculture has profitably been informed by NCT, itself a relatively new development in evolutionary biology (Oodling-Smee *et al.* 2003). From this perspective, the emergence of food production economies has been argued to correspond to moments when human activities began to leave especially conspicuous traces of both willful and unintentional human impacts on their environment, in addition to far-ranging changes in health and subsistence practices. Indeed, Smith (2007a) recently described *H. sapiens* as the "ultimate niche engineers", arguing that a focus on human niche constructing behavior allows researchers interested in the emergence of domestication economies to weave together multiscale observations (e.g., individual domesticated species *vs.* causal mechanisms of domestication) into coherent evolutionary scenarios.

While Smith emphasizes the ecological dimension of human niche construction, in actuality, NCT builds on more traditional evolutionary theory by suggesting that evolution is shaped by the recursive interaction of behavior, biology, and ecology (Oodling-Smee *et al.* 1996, 2003; Laland *et al.* 2000; Laland and O'Brien 2010). Organisms that modify their ecosystem to maximize fitness can also spur and/or instate new ecological conditions that may in turn impact the fitness of other species that occupy the same ecosystem. Thus, NCT highlights the dynamic, often unstable interplay between these three domains of inheritance as the principal evolutionary pathway that directs the evolutionary history of a species and its wider ecosystemic context. It also underscores that the ecological legacies of organisms should not *de* *facto* be construed as negative, but rather seen as introducing stochasticity in the dynamics of the ecosystems that they inhabit, as short-term advantageous modifications that can have both positive and negative consequences in the longer run, for them as well as other denizens of a given environmental setting.

Given the conspicuous amount and diversity of archaeological material and the extent of human-induced landscape modification generally associated with a sedentary, agricultural lifeway, it not surprising that most prior archaeological treatments of NCT have focused on the record of the development of food-producing societies (e.g., Bleed 2006; Smith 2007a, b). It is nonetheless clear that human niche construction has much greater time depth, as suggested by potential evidence of human-induced landscape burning in southern Africa some 55,000 years ago (Smith 2007a; cf. Laland *et al.* 2001), and that an agricultural economy is clearly not a prerequisite for humans to leave archaeologically visible traces of niche construction (Riede 2005), a somewhat different observation than noting that hunter–gatherers modify their environment in ways they see as advantageous. Indeed, since arguably noncultural animals like ants and beavers are often invoked as examples of niche-constructing organisms, it would be surprising—indeed shocking—if human foragers and their hominin ancestors *had not* engaged in some form of prehistoric niche construction. The question, then, is one of identifying niche constructing behavior in the archaeological record of pre-agricultural hunter–gatherer populations.

As the papers in this volume demonstrate, NCT can profitably guide archaeological research by broadening the range of evidence usually considered by archaeologists and providing a novel perspective on how to integrate them. NCT also offers a means to relate human evolution writ large to the wider natural world and, by extension, the opportunity to reappraise the evolutionary histories of other hominins and contextualize them in relation to that of our own species. For instance, Smith's (2007a) reference to niche construction by early modern human foragers can be expanded to better understand the evolutionary fate of Neanderthals, a regional population of hominins that first appeared between 300 and 250 kya along the northwest shore of the Mediterranean before spreading as far east as Siberia and as far north as southern England (Serangeli and Bolus 2008; Hublin 2009). Beyond their distinctive morphology—itself often argued to represent a suite of biological adaptations to their environments (Holliday 1997; Steegman *et al.* 2002; cf. Finlayson 2004)—Neanderthals are also characterized by new manners of engaging with their environment and by a suite of new behaviors that demarcate them from their predecessors.

For instance, the various Mousterian industries associated with Neanderthals (see Howell 1998) mark a shift away from the hand axes and flake assemblages of the preceding Acheulean and thus new ways of managing the mineral resources that were essential component of their technological repertoire (Debénath and Dibble 1994; Boëda 1994; Monnier 2006). Neanderthals are also associated with the first consistent evidence of artificial habitation structures (Jaubert and Delagnes 2007; Chu 2009) and of regular, systematic fire use in Eurasia (Mellars 1996), both of which enabled them to colonize areas previously devoid of human occupants (White 2006). Fire use is especially important since its association with other prehistoric foragers show that it often results in unintentional but large-scale burning with far-ranging that can have long-term ecological effects (Pyne 1998; Bliege Bird *et al.* 2008).

Neanderthals were also the first hominins to practice the "selective harvesting of prime adult ungulate prey" (Stiner 2002: 22), a significant departure from earlier prey procurement because it is sustainable in the long-term only for omnivorous animals at the top of their regional food chain (Bocherens and Drucker 2006). This sustainability was not always given, however, as indicated by ungulate exploitation patterns at Kebara Cave (Israel) that show that Neanderthals occasionally over-exploited some ungulate populations (Speth and Clark 2006). In addition, Neanderthals were the first Eurasian hominins to exploit small game (Villa and Lenoir 2009) and perhaps even some marine resources (Erlandson 2001; Stringer *et al.* 2008). It is also clear that they made extensive use of the plant resources available to them, as demonstrated by direct evidence in the form of the plant starches and phytoliths trapped in dental calculi (Henry and Piperno 2008), as well as indirectly by the presence of remains of various species of edible plant in Middle Paleolithic sites (Henry *et al.* 2004). Ecological surveys also strongly suggest that Neanderthals would have been able to procure a wide range of roots, seeds, and nuts throughout their ranges (Hardy 2009).

Lastly, Neanderthals were among the first hominins to adjust their mobility strategies and technology in response to shifts in local conditions, including seasonality and large-scale ecological change. This is attested by the fact that Neanderthals were the first hominins to settle Eurasian highlands as well as the markedly seasonal environments of central and eastern Europe (Hopkinson 2007). Likewise, in Jordan, seasonal transhumance has been argued to characterize Neanderthal settlement patterns (Henry 1995), while other studies have shown that they responded to large-scale climatic shifts by switching between predominantly residential to predominantly logistical land-use strategies (Barton 1998; Riel-Salvatore and Barton 2004, 2007; Riel-Salvatore *et al.* 2008).

New technologies and original ways of organizing them as part of distinct mobility strategies are what permitted the breadth and diversity of Neanderthal socioecosystemic adaptations manifest in their regional archaeological record (Hovers and Kuhn 2005). A range of new flake-production systems, notably prepared-core technology, allowed Neanderthals to effectively adapt to the ecological constraints of their widening world by alternating between technological strategies that provisioned individuals or provisioned places, to use Kuhn's (1992, 1995) terminology. On the landscape, this was reflected by an alternance between residential and logistical land-use strategies in response to fluctuating conditions (Barton 1998; Riel-Salvatore and Barton 2007). Residential mobility implies the frequent relocation of base camps in response to depletion of immediately available resources. In contrast, logistical mobility implies the more long-term occupation of a base camp provisioned with needed resources through forays at distant points on the landscape targeted at specific resources (Bamforth 1986; Kelly 1983, 1992; Nelson 1991; Shott 1996; Riel-Salvatore and Barton 2004). Such mobility patterns also resulted in at least occasional transfers of lithic resources over distance of several hundred kilometers (e.g., Slimak and Giraud 2007), an unprecedented pattern in the archaeological record (Féblot-Augustins 1997). This is also attested by the first documented instances of "landscape lithification" (*sensu* Webb 1993), whereby foragers effectively scatter usable lithic raw material over a landscape originally devoid of it, as a result both of their repeated exploitation of that landscape (through discard) and of its anticipated use in the future (through stockpiling; e.g., Martinez and Mackie 2003).

Returning to the central theme of this paper, the great time depth of human foragers leaving archaeologically visible traces of the interaction between their behavior, biology, and ecology provides a new way to approach the interaction of these three spheres of inheritance in the past to illuminate the evolutionary mechanisms of episodes of change in the archaeological record. In light of the extensive range of niche constructing behaviors displayed by Neanderthals (Table 1), NCT also provides a robust conceptual framework to integrate their evolutionary history with that of *H. sapiens* (cf. Laland *et al.* 2008). It is therefore worthwhile to examine how this fresh perspective can lead to a more holistic analysis of multidimensional human evolutionary processes and especially the Middle–Upper Paleolithic transition.

Past Human Niche Construction in Theory and Practice

Niche construction is the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches and to a degree tailor their own and others' selective environments (Oodling-Smee *et al.* 2003; Laland and Sterelny 2006). It "expands" traditional evolutionary theory by incorporating ecological inheritance as an important vector of reproductive fitness, alongside culture and biology (Fig. 1). From an archaeological standpoint, niche construction describes long-term adaptive human behavior that leaves a material signature. This adaptive signature can also be accompanied by the equivalent of selectively neutral variation accruing in drift-like fashion, so that not all aspects of the archaeological record of a given period can necessarily be understood from an NCT perspective. Pragmatically, prehistoric human niche construction can be equated with facets of human behavior that are subject to positive selection due to their fitness-enhancing potential and that have left an archaeological record laden

Table 1 Neanderthal Niche Constructing Behaviors

Selective hunting of prime-aged ungulates
Supplementing diet with systematic procurement of small sessile animals
Occupation of new biomes (mountains)
Seasonal exploitation of altitudinal gradients
Provisioning places in lithic raw materials
Flexible mobility patterns
Controlled use of fire
Short-range projectile weaponry
Occasional long-distance raw material transfers
Gathering of vegetal resources, for various uses (food, bedding)

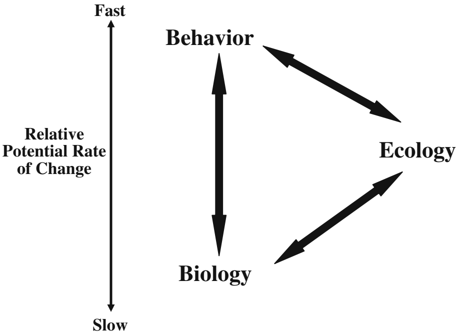

Fig. 1 Simplified rendering of NCT and the relationship between behavior, biology, and ecology

with ecological implications. Explicitly identifying these three dimensions is therefore key to profitably using NCT as a conceptual framework in archaeological research.

Like all evolutionary theory, NCT depends on diachronic data to track the outcomes of various evolutionary trajectories. Archaeology is defined by a fundamental concern for and an abundance of accumulated diachronic information about human behavior over time, much of which can therefore be used to inform reconstructions of the evolutionary history of human and groups of humans in both the recent and "deep" past (Laland and O'Brien 2010). This diachronic component is thus also central to archaeological studies of human (better, hominin) NCT. As Fig. 1 indicates, however, the rate of change within each domain of inheritance varies significantly, with change in behavior being on the whole potentially more rapid than that ecological change, which in turn tends to be faster than biological change. This is a result of the time needed for adaptively advantageous behaviors to become "fixed" within a population before its full biological impact can be felt. Interestingly, behavior that is not adaptive in the long-term can nonetheless have medium-term ecological consequences that can, down the line, result in unintended biological effects (e.g., a net fitness decrease as a result of drought provoked by suboptimal farming practices, even if these are abandoned within less than a human generation).

Dual inheritance theory (DIT) as detailed by Boyd and Richerson (1985) and Richerson and Boyd (2005) provides a precedent for an NCT-like approach to human evolutionary processes that most archaeologists are familiar with, albeit a somewhat simpler one. Conceptually, transmission follows similar pathways in DIT and NCT: culture and biology—and in NCT ecology—serve as distinct but ultimately related inheritance systems that each can accrue variation that can impact an organism's fitness (cf. Winterhalder and Smith 2000). In effect, from an archaeological standpoint, NCT can be understood as the integration of DIT with the concept of *ecaptation*, defined as "the process by which an organism intentionally alters its environment for the purpose of increasing its fitness to the organism's perceived needs" (Hommon 2005: 20), with the caveat that such alterations can also have a determinant impact on the fitness of other species. This subtlety is rendered particularly elegantly in Bleed's (2006) discussion of the bidirectional influence that prehistoric humans experienced in their long-term relationships with other gregarious mammals, namely reindeers and dogs.

Archaeological research informed by NCT thus clearly cannot simply consist in documenting how and how much humans modified their ecosystems in the past. That humans have a long history of impacting their environments is already well appreciated by the discipline as a whole (Redman 1999; van der Leeuw and Redman 2002). Rather, the success of an NCT perspective is dependent on the analyst's ability to accurately assess the influence of various degrees and forms of environmental embeddedness in shaping the evolutionary history of given hominin groups.

Archaeology offers a unique window on past human–environment interactions and on how they engaged with the constructed socioecosystems resulting from the purposeful activities of past populations. This has stimulated a renewed interest in human ecology that transcends simple determinism. It has also prompted interest in questions about the scales of observation and analysis used by researchers as they attempt to integrate environmental data of variable resolution with a more-or-less coarse-grained archaeological record where individual decisions, human life histories, and evolutionary trajectories are blurred by assemblage accumulation and site formation processes (Layton 2008).

By giving humans an active role in shaping their selective environment, NCT offers a powerful conceptual toolkit to incorporate human environmental legacies in explanatory models of cultural and biological evolution in ways that eschew ecological determinism. Much like nonlinear models applied to archaeological questions (Beekman and Baden 2005), NCT therefore does not constitute a predictive approach *per se* (cf. Peeples and Anderies 2008), although the conclusions reached as a result can certainly serve as test hypotheses for future research (see below). For prehistoric research, then, NCT offers a theoretical framework that is both *flexible* and *empirically inclusive*. Its flexibility is reflected by the variety of transmissions routes derived from the potential interaction of the three inheritance systems (Oodling-Smee *et al.* 2003: 338; Fig. 9.1) and the fact that these routes can further be nuanced by emphasizing the asymmetric influence of given systems under changing conditions. This asymmetry is manifested when changes in one system have a disproportionate impact on the subsequent importance of another inheritance domain over the course of the evolutionary history of an organism or group of organisms, a side effect of the rate at which variation can accrue within each domain of inheritance. The empirical inclusiveness of NCT, on the other hand, is reflected by the fact that the explanatory models it generates actively discourage the identification of single prime movers in favor of recursive relationships between inheritance systems whose contribution can fluctuate over time and across shifting sets of selective pressures. NCT thus permits the repatriation of archaeological data into credible and explicitly theoretically grounded evolutionary inquiry.

For paleoanthropological research, which deals with a record that is, by its very nature, often discontinuous and fragmentary, NCT also permits the investigation of the interaction between two inheritance systems when evidence for the third may be missing from the record. For instance, many Paleolithic assemblages are not associated with any human remains; they almost always comprise lithic and faunal material, along with paleoenvironmental proxies (e.g., pollen, charcoal, microfauna). Even when human remains are found, these can be so rare and/or so fragmentary as to preclude meaningful conclusions about hominin biology. In such situations, an NCT perspective nonetheless permits a formal investigation into the changing relationship between the cultural and ecological dimensions of the record, with the possibility of relating the resulting conclusions to what biological dimensions can be observed in, inferred from, or assumed about the fossil and/or genetic records. In addition, biological data provided by human remains dating to the periods that bracket a period of interest can often suggest something about the selective forces at play during the intervening evolutionary process. This in turn permits informed speculation about evolutionary feedback loops likely to have been selected for during that interval. NCT therefore encourages development of multidimensional, context-dependent explanatory models of specific segments of our species' evolution.

The Middle–Upper Paleolithic Transition in Italy as Human Niche Construction

These characteristics of NCT make an especially appropriate framework to help disentangle the intensely regional character of the Middle–Upper Paleolithic transition, as reflected by the wide range of "transitional" industries and of geographically discrete facies of the Aurignacian (Djindjian *et al.* 2003; Clark and Riel-Salvatore 2005; Bar-Yosef and Zilhão 2006). Here, an example drawn from the Italian transitional record is provided to help illustrate how this may be the case.

The Italian peninsula is a naturally circumscribed region that is nonetheless ecologically and topographically heterogeneous. In Italy, the transition interval follows the Middle Paleolithic (ca. 130–45,000 BP) and was a comparatively long-lasting interval (Riel-Salvatore 2007; Holt *et al.*, unpublished manuscript; Higham *et al.* 2009) associated with at least three distinct "cultural entities": the Late Mousterian, the Uluzzian, and the proto-Aurignacian (Bietti 1997; Kuhn and Bietti 2000; Ronchitelli *et al.* 2009).

The Late Mousterian is a generally flake-based lithic technological system documented all over the peninsula and associated mainly with the procurement of large ungulates, although some evidence of shellfish collection and small game hunting is also known (e.g., Stiner 1994; Fiore *et al.* 2004). The Late Mousterian is highly polymorphic, with a trend toward higher frequencies of notches and denticulates in many assemblages (Palma di Cesnola 1996), although much regional typotechnological variability is nevertheless evident in the archaeological record (Kuhn 2005).

The proto-Aurignacian is an EUP industry that first appears in northern Italy where it differs markedly from the Late Mousterian (Palma di Cesnola 1993). It is characterized by a bladelet-based technological system in which the principal retouched components are marginally backed bladelets, by some organic technology and by personal ornaments consisting mainly of pierced marine shells, as well as various coloring materials, especially ochre (Negrino 2002; Kuhn 2002). The subsistence patterns associated with this industry comprises the exploitation of large ungulates, as well as a consistent, but variable, association with a range of small game including shellfish, hares, and various bird species (Stiner *et al.* 2000).

In contrast, the Uluzzian is a technological system based largely on bipolar blank production resulting in high frequencies of splintered pieces (*pièces esquillées*; Riel-Salvatore 2009). Its typological inventory comprises both Middle and Upper Paleolithic tools, including backed crescent-shaped microliths taken as the industry's type fossil in spite of their overall low frequency (Palma di Cesnola 1989, 1993). Uluzzian subsistence practices appear to have focused largely on large mammals, with suggestive evidence that some small game may also have been targeted (Riel-Salvatore 2007, 2009; Ronchitelli *et al.* 2009; cf. Cassoli and Tagliacozzo 1997). Like the proto-Aurignacian, this EUP industry is also associated with organic technology, shell ornaments, and coloring materials, including ochre and limonite. Unlike the other two industries under consideration in this study, the Uluzzian's distribution in stratigraphic contexts is limited to southern Italy (Bietti and Negrino 2007; Riel-Salvatore 2009; Riel-Salvatore and Negrino 2009). Claims for an Uluzzian presence in northeastern Italy at Grotta di Fumane (Peresani 2008) so far are missing the detailed typotechnological information needed to evaluate them and that assemblage is therefore excluded from consideration here. Very promising ongoing analyses of this material (Peresani *et al.* 2009), however, suggest that it should soon be possible to directly compare the Fumane assemblages to the Uluzzian ones from southern Italy.

While the authorship of the Late Mousterian can be securely attributed to Neanderthals (Alhaique *et al.* 2000), that of the proto-Aurignacian and Uluzzian is debated due to a paucity of associated diagnostic human remains. By analogy to contemporary bladelet assemblages in Europe, the Italian proto-Aurignacian is usually assumed to have been manufactured by *H. sapiens* (Broglio 2005; Mellars 2006; Teyssandier 2008), while the Uluzzian is generally likened to transitional industries such as the Châtelperronian, that are argued to have been the handiwork of Neanderthals (Gambassini 1997; Mussi 2001; Palma di Cesnola 2004). The Italian transition interval is potentially quite lengthy (up to 10–12,000 radiocarbon years), comprises a diverse set of technological traditions, is associated with detailed associated paleoecological records, and is bracketed by periods associated with a great deal of human paleontological data (Riel-Salvatore 2007). It therefore provides a rich empirical dataset on which to found reconstruction of hominin evolutionary trajectories at a regional scale and to investigate diachronic patterns of recursive interaction between behavior, biology over the course of this process.

For ease of discussion, each of the three inheritance systems (Fig. 1) will be discussed separately before their NCT-based integration is presented. The ecological and chronological information available for the transition interval provides a useful backdrop for the rest of the discussion. Figure 2 summarizes the chronological information drawn from dated assemblages falling within the transition interval presented in calendar years (Riel-Salvatore 2007: 55–114), juxtaposed with global trends of climate variability drawn from the GISP2 ice core (Meese *et al.* 1997). As shown by van Andel (2003), the trends recorded in the Greenland ice cores broadly correspond to oscillations in the frequency of arboreal pollen in lake cores from Valle di Castiglione (Follieri *et al.* 1988) and Lago Grande di Monticchio

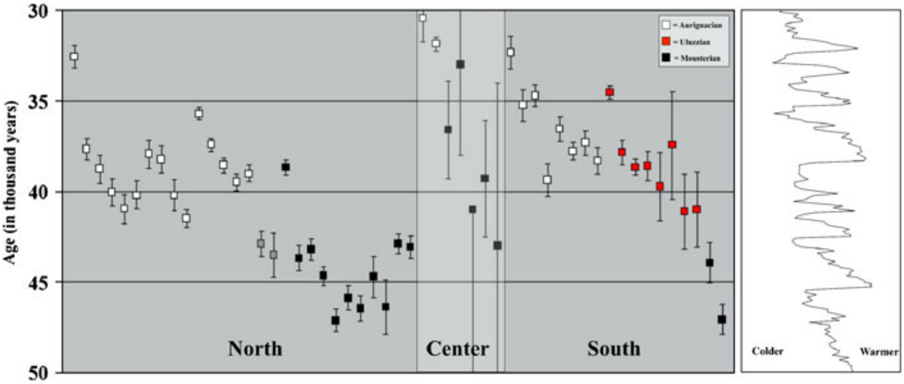

Fig. 2 Chronological and paleoclimatic data for the transition interval in Italy, with regions indicate at the *bottom* (data from Riel-Salvatore 2007). Climate curve (*right*) drawn from GISP2 Ice Core data (Meese *et al.* 1997), measuring δ^{18}O levels

(Allen *et al.* 2000), making it an adequate proxy of climatic change trends for the peninsula as a whole over the transition interval.

Figure 2 indicates several trends. First, within the range of error, Uluzzian and proto-Aurignacian assemblages first appear roughly contemporaneously in the southern and northern thirds of the peninsula, respectively. Second, the Late Mousterian is the only industry documented in the center of the peninsula when the EUP complexes appear to the north and south. Admittedly, the transitional chronology for central Italy is based mainly on ESR and U/Th age determinations that come with much larger error ranges than the radiocarbon dates from the rest of the peninsula; this, however, is an issue of with the dating methods and not with the age determinations themselves. While the dates included in Fig. 2 come from sites located west of the Apennines, no diagnostic proto-Aurignacian or Uluzzian assemblages are known from east-central Italy, while some undated Late Mousterian ones are documented in that region (Arzarello *et al.* 2004; Peretto and Minelli 2006), and unpublished radiocarbon dates place them at between 40 and 33,000 radiocarbon years BP (Peretto *et al.* 2009). This reinforces the impression that a comparatively recently dated Late Mousterian can reasonably be generalized to central Italy as a whole (Riel-Salvatore 2007, 2009). Third, no specific instance of climate change appears to coincide with the appearance of EUP technocomplexes in Italy, although overall climate change clearly was fast-paced and dramatic during that phase of the Late Pleistocene (Finlayson 2004; Finlayson and Carrión 2007).

These observations suggest that the Uluzzian and the proto-Aurignacian emerged roughly contemporaneously at opposite ends of the peninsula at a time when they appear to have been separated by a "Late Mousterian buffer" of sorts. If correct, this reconstruction contradicts the acculturation model that sees the Uluzzian emerging as a result of a direct Aurignacian influence on groups using Mousterian industries (Riel-Salvatore 2007, 2009). There is also an important ecological dimension to this reconstruction: While Italy is often described as a Pleistocene biogeographical refugium for Mediterranean faunal and floral communities in periods of climatic downturn (e.g., Tzedakis *et al.* 2004), it is only *central* Italy that served as a dependable refugium for those biotic communities (Blondel and Aronson 1999). The perduration of the Mousterian thus is correlated with stable, predictable ecological conditions in central Italy. In a like manner, the new EUP technocomplexes are first documented in those parts of the peninsula marked by greater ecological instability and pronounced paleoenvironmental change during the transition interval (Riel-Salvatore 2007). Such correlations are certainly not *de facto* proof of causation, but any credible explanation of the dynamics of the transition in Italy needs to account for them.

The scant fossil evidence is available for the transition interval in the Italian peninsula associates the Late Mousterian with Neanderthals, while the proto-Aurignacian and Uluzzian are only associated with isolated deciduous human teeth. For this reason, scenarios implying some degree of biological determinism are best avoided in favor of other data that permit some observations about human populations before and after the transition interval. It has also recently been shown that Neanderthals contributed a small amount of genetic material to populations of contemporary non-African modern humans (Green *et al.* 2010), indicating that from a strictly biological standpoint, the two populations were not completely distinct. This reinforces the perspective that attributing technocomplexes to given hominin populations does little to clarify how the morphology of toolmakers alone influenced the process of the transition.

While the evidence for population growth at the outset of the transition interval is equivocal at best, continental-scale data on hominin mortality profiles before and after the transition interval do, however, indicate a significant shift in mortality patterns following the transition. Figure 3 summarizes age-at-death data from known Mousterian (ca. 100–40 kya) and Gravettian (ca. 30–20 kya) burials (Riel-Salvatore and Clark 2001: Tables 1 and 2). These data indicate that Middle Paleolithic hominins buried considerably more juveniles than Gravettian-age populations, which suggests that, other things being equal, more children died in the Middle than in the Upper Paleolithic. An alternative interpretation of these trends is that they reflect changes in the conception of personhood in the Gravettian, with only children older than 4 years of age being considered full members of society and susceptible to being interred with the regards conferred to older individuals (Zilhão 2005; Zilhão and Trinkaus 2002). More prosaic explanations may, however, more parsimoniously explain this pattern, and they must be discounted before such social interpretations can be considered. In other words, reduced childhood mortality needs to be

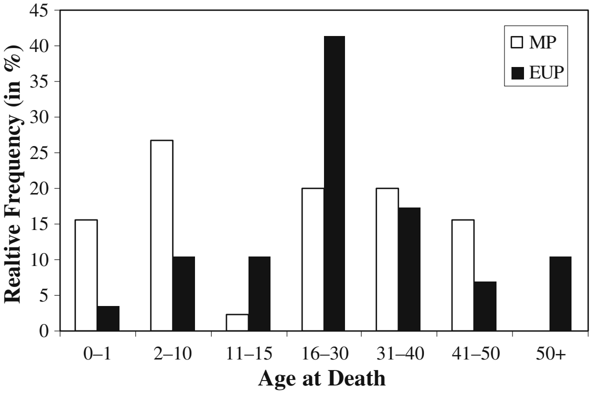

Fig. 3 Mortality profiles for Mousterian (*white*) and Gravettian (*black*) populations

effectively factored out in order to accept this social explanation. In this respect, it bears emphasizing that the Gravettian is undoubtedly associated with a broader subsistence base than earlier periods (Pearson 2008; Richards and Trinkaus 2009), as well as with evidence for the systematic exploitation of plant foods and their preparations as fallback foods (Aranguren *et al.* 2008). This is in addition to studies that show that *all* Upper Paleolithic humans (i.e., including remains from nonburial contexts) reached old age much more frequently than Middle Paleolithic hominins (Caspari and Lee 2004, 2006). These various lines of evidence strongly suggest that changes in subsistence practices resulting in decreased childhood mortality rates are by far the most likely explanation for the different age-at-death trends for the Mousterian and the Gravettian.

Infant mortality therefore seems to have decreased notably over the transition interval, and given the time frames involved, the selective forces driving this shift are more likely to have been behavioral and/or ecological rather than biological in nature (Fig. 1). One behavioral explanation might be the emergence of a formalized sexual division of labor at that time, as reflected archaeologically by evidence for the systematic exploitation of previously low-ranked small game (Kuhn and Stiner 2001, 2006). The new technologies associated with the EUP have been argued to reflect the onus put on procuring these resources (Bright *et al.* 2002; Ugan *et al.* 2003). A clear causal link between these technologies—which appear to mainly indicate greater reliance on projectile weaponry—and the procurement of fast-moving small game remains to be demonstrated, however, especially since using projectile weaponry to capture small game would have been, quite literally, overkill (Riel-Salvatore 2007: 128–129). In fact, ethnographic evidence suggests that the most effective ways to derive high returns from leporid hunting is to use nets, snares, driving and clubbing, hand capture, and opportunistic spearing, in decreasing order of effectiveness (e.g., Hockett and Haws 2002; Lupo and Schmitt 2002).

A shift in diet is certainly a plausible mechanism to explain changes in patterns of hominin life history, especially given nutritional ecology studies that show that small game is not necessarily low-ranked and therefore not directly indicative of a switch to last-resort subsistence practices (Bicho and Haws 2008; Hockett and Haws 2003, 2005). Furthermore, ethnographically based models strongly suggest that sexual division of labor is unlikely to have emerged under sub/tropical conditions and that it is thus unlikely to have been associated with modern humans dispersing from Africa into Eurasia just prior to the Middle–Upper Paleolithic transition (Marlowe 2007).

Whatever the case may be, the systematic exploitation of small game, especially fleet-footed species, unquestionably represents a departure from the subsistence strategies associated with Mousterian technology for most of its duration in Italy. Incorporating such resources in the diet during the transition interval likely provided a nutritional boost that could have increased the returns of foraging activities as well as stabilized these return rates in those areas where small game was especially abundant. This, in turn, may have resulted in both a decrease in child mortality and an increase in average life expectancy (cf. Caspari and Lee 2006). An expansion of subsistence strategies to include small game may therefore had a doubly positive impact on population growth by increasing the number of individuals to reach reproductive age and by lengthening life expectancy. A side effect of this two-pronged stimulus in population growth might also have been a reorganization of some of the social structures in place at the time to formally accommodate greater amounts of “grandmothering” by older individuals and children within the social structure (Hawkes *et al.* 1998).

This synthesis provides the overall evolutionary backdrop against which the Middle–Upper Paleolithic transition must be understood and into which an NCT model of this process can be anchored. From a behavioral standpoint, the cultural–historical data already attest that this inheritance system accrued some significant change over the transition interval. What remains to be established, however, is just how much of that change was selective as opposed to neutral in nature. In a way, this crucial distinction echoes the “form *vs.* function” debate over the interpretation of what is the principal vector of variability in the morphology of lithic implements (Binford 1973; Binford and Binford 1966, 1969; Binford and Sabloff 1982; Bordes 1969, 1973, 1981; Bordes and de Sonneville-Bordes 1970). With the benefit of time, it has become clear that there is no “one or the other” answer to this debate, but rather that there is a need to develop frameworks that allow us to recognize style in lithic technology and distinguish it, when and if possible, from the functional constraints that limit the range of stone tool morphologies suited to given tasks (Jelinek 1976; Sackett 1982; Barton 1997).

In practical terms, then, the behavioral inheritance system as manifest archaeologically can be argued to comprise “formal” and “behavioral” dimensions; the boundary between the two can be porous (Barton 1997). In the context of this discussion, the formal aspect refers to what toolkits “looked like”, that is, the stylistic decisions that go into shaping lithic technology. This can be understood mainly as what analysts isolate through technotypological study. It embodies aspects of the archaeological record that tend to be more selectively neutral and therefore change over time following drift-like, generally stochastic processes. In contrast, the behavioral dimension of lithic technology reflects the manner in which people actually put these toolkits to use procuring and processing the resources essential to their survival, in accordance with the precepts of “behavioral archaeology” (Schiffer 1972, 1976; Skibo and Schiffer 2008). Because it is directly tied to biological fitness, the selective pressures on this dimension are likely to be more positive in nature, with variation in toolkit structure that enhances fitness being subject to active selection (Riel-Salvatore and Barton 2004). Thus, it is important to highlight how these two sides of technology jointly shape artifact morphology since change in one is not necessarily linked to or commensurate to change in the other.

The cultural–historical data for the transition interval in Italy (i.e., the emergence of new technocomplexes) indicate that formal change was intimately associated with the beginning of the transition interval, though why this is the case remains unclear. In fact, because the difference between the formal and the behavioral is rarely made explicit in most transition research, change in one tends to be conflated with change in the other, as exemplified by scenarios that assume that the formal differences between the Aurignacian and the Mousterian *must* have behavioral meaning since they seemingly coincide with the disappearance of the latter one (Mellars 2005).

However, formal interassemblage differences do not necessarily mean that the behavioral strategies that they represent necessarily differed, at all or in degree, as has been shown in recent behavioral studies of the transition interval (Riel-Salvatore and Barton 2004; Riel-Salvatore *et al.* 2008). In fact, some of the common wisdom assumptions about the advantages of blade technology over flake technology (in terms of greater utility, etc.) have recently been shown to not be supported by empirical evaluations (Eren *et al.* 2008), making considerations of the behavioral dimensions of lithic assemblages all the more relevant.

Humanity in Transition: Culture, Biology, and Ecology

Combining archaeological, demographic, and ecological data underscore a series of intriguing patterns associated with the transition in Italy (Fig. 4, for a map of the sites discussed in the text). On a formal level, for instance, one "culture" (the Mousterian) is succeeded by three others (Late Mousterian, Uluzzian, proto-Aurignacian), which in turn are generally seen as being eventually supplanted by a single one, the Aurignacian *sensu lato*. This shift was undoubtedly a multimillennial process, although some debates persist about its overall pace (e.g., Fedele *et al.* 2008, Giaccio *et al.* 2009). Chronologically, the transition interval in Italy can be divided into three phases (Fig. 2):

1. The appearance of EUP industries (Uluzzian, proto-Aurignacian) alongside the Mousterian (ca. 42–41,000 BP)
2. The gradual expansion of the Uluzzian and proto-Aurignacian at the expense of the Late Mousterian in central Italy (ca. 41–37,500 BP)
3. The disappearance of Late Mousterian and Uluzzian assemblages from the record and Aurignacian-like assemblages are found all over the peninsula (after 37,500 BP)

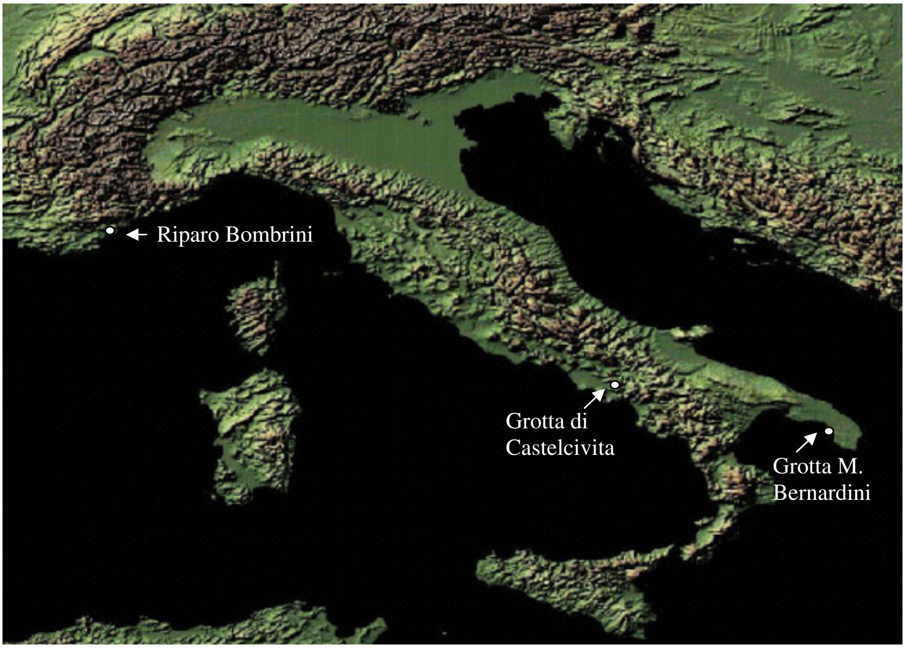

Fig. 4 Map of the Italy indicating the location of the sites discussed in the text

Phase 1 seems to unfold during a series of severe and closely spaced climatic oscillations (Finlayson and Carrión 2007). It is unlikely, however, that climate change *per se* would trigger cultural change of the magnitude seen during the transition interval, especially since these changes in ecological conditions would have taken several generations to be felt fully by forager populations. Rather, as I have argued elsewhere, behavioral ecological models suggest that new technological systems are most likely to be developed and adopted under conditions of resource unpredictability and of low overall residential mobility (Riel-Salvatore 2007, 2009; Barton and Riel-Salvatore 2010; see also Kelly 1995). As concerns the stability of the resource base, centennial-scale climate change would have mainly required adjustments of human subsistence strategies. Rather, the *scale of variability* in climatic conditions is more likely to prompt changes in subsistence strategies and their associated technological systems. The more unpredictable the climatic context (i.e., variable in both rate and magnitude), the more likely foragers are to invest in developing new technologies designed to attenuate the long-term risks to survival (Bamforth and Bleed 1997; Kelly 1995; Binford 2001).

Finlayson (2004) has singled out the beginning of the EUP as correlated with some of the most frequent and dramatic episodes of Late Pleistocene climate change, a factor he sees as determinant in the emergence of Aurignacian and “transitional” industries across Eurasia (Finlayson and Carrión 2007). This moment corresponds to phase 1 of the present study, which was associated with high variability in environmental conditions and by extension with increasing unpredictability in resource procurement. Whether or not phase 1 was also associated with lower degrees of residential mobility can be investigated through the behavioral dimension of the archaeological record using a range of methods. One, dubbed the whole assemblage behavioral index (WABI), explicitly permits the reconstruction of the prevalent mobility strategies represented by even formally distinct lithic assemblages (Riel-Salvatore 2007; Riel-Salvatore and Barton 2004, 2007; Riel-Salvatore *et al.* 2008; cf. Barton 1998; Villaverde *et al.* 1998). By positing that an assemblage’s retouch frequency and lithic volumetric density are inversely related, the WABI identifies a continuum of mobility linking residential and logistical mobility (*sensu* Binford 1980, 1982). Large assemblages associated with overall low degrees of retouch have been shown to reflect predominantly logistical land-use strategies whereby a home base is occupied for long periods of time and task groups are sent to a range of “satellite sites”; this strategy effectively bring resources to people (Binford 1980; Kuhn 1992, 1995). In contrast, low-density assemblages associated with high retouch frequencies reflect residential mobility strategies whereby the home base is moved more often, whenever the returns of the resource base found in the site’s immediate vicinity dips below a certain threshold of energy returns; it can be conceived of as a strategy that brings the people to the resources (Binford 1980; Kuhn 1992, 1995).

By focusing on assemblage-scale variability in lithic collections that are best understood as palimpsests of repeated human occupations—as opposed to single instances of occupation—the WABI also provides an interpretation of long-term variability appropriate for assemblages that accumulated over hundreds or thousands of years (Kuhn 2004; Riel-Salvatore and Barton 2004; Riel-Salvatore *et al.* 2008). Since some of the variability in prehistoric land-use strategies documented by the

WABI and conceptually similar approaches appears related to ecological conditions (e.g., Marks and Friedel 1977; Meignen *et al.* 2006) and to the effective abundance of lithic resources at given localities (Sandgathe 2006), this method highlights how hominins actively adjusted their behavior to best exploit the ecosystems in which they lived (Riel-Salvatore and Barton 2007; Riel-Salvatore *et al.* 2008).

Figure 5 presents the WABI pattern from the site of Grotta Mario Bernardini, a karstic cave located close to the Ionian Coast of the Salento peninsula in southern Italy that has yielded a long sequence of Mousterian and Uluzzian deposits (Borzatti von Löwenstern 1970, 1971). At this site, the earliest Uluzzian (level A IV) is associated with that industry's most logistical land-use strategy and differs markedly from the clearly residential mobility modality of the Late Mousterian. The earliest Uluzzian deposits of nearby Grotta del Cavallo and of Grotta di Castelcivita, near modern-day Naples, also clearly associate the beginning phases of that industry with logistical mobility (Riel-Salvatore 2007). The middle Uluzzian assemblage at Mario Bernardini (level A III) indicates a return to the general Mousterian pattern of residential mobility, while the terminal Uluzzian (level A I–II) indicates a "hyper mobile" strategy that has no analogs in the Mousterian and may reflect a new manner of navigating the EUP landscape or, alternatively, use of the site as a logistical task site (see discussion in Riel-Salvatore and Barton 2004, 2007). Again, similar trends are evidenced in the later phases of the Uluzzian sequences at Cavallo and Castelcivita.

Figure 6 presents the WABI pattern from the transitional sequence of the site of Riparo Bombrini, a collapsed rockshelter located in coastal Liguria, near the modern-day border with France. Seven Late Mousterian and two proto-Aurignacian assemblages were found at the site (Holt *et al.*, unpublished manuscript; Riel-Salvatore 2007). The pattern here distinguishes the Middle and Early Upper Paleolithic mobility strategies more dramatically than was the case in southern Italy. Overall, the Mousterian appears less residentially mobile than the proto-Aurignacian, a datum corroborated by each period's raw material exploitation patterns: Mousterian lithotype exploitation is almost exclusively local, with the odd implement coming from single sources located up to 150–200 km away (Riel-Salvatore 2007; Holt *et al.*, unpublished manuscript). In contrast, proto-Aurignacian lithic procurement is nonlocal to a much greater extent, with several exotic sources

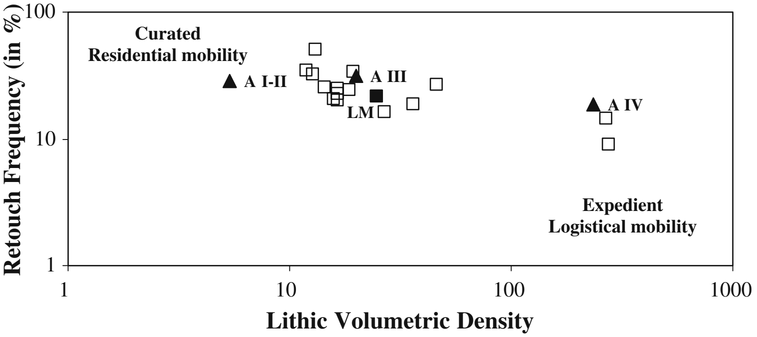

Fig. 5 WABI patterns for Grotta Mario Bernardini. *White squares* Mousterian, *black squares* Late Mousterian, *black triangles* Uluzzian

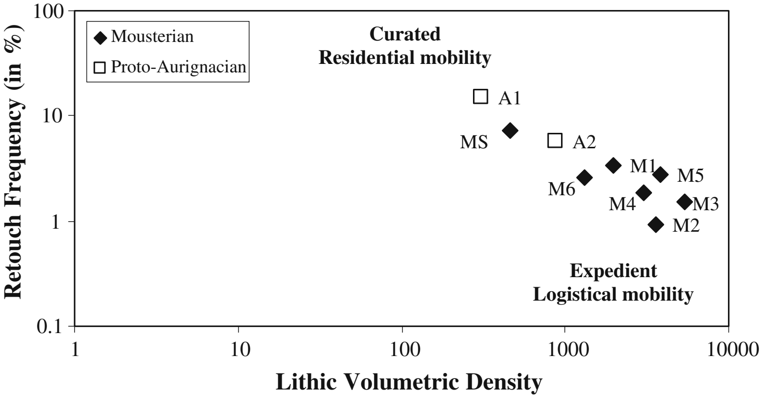

Fig. 6 WABI patterns for Riparo Bombrini

located both east and west of the site being exploited concurrently, resulting in a procurement network stretching over at least 400 km (Negrino 2002; Negrino and Starnini 2003; Riel-Salvatore and Negrino 2009).

While the Mousterian and proto-Aurignacian at Bombrini appear distinct in terms of how their makers navigated their landscape and exploited its resources, internal dynamics are evident in both industries (Riel-Salvatore 2007). The Mousterian, for instance, evidences three clusters of assemblages, only one of which (comprising assemblages M2–M5) corresponds to a true logistical strategy. A second cluster (M1 and M6) indicates a more residential mobility pattern, while a single assemblage (MS—the most recent Mousterian assemblage at the site) indicates that the site might have been used by Neanderthals as a task site or as part of a "hyper mobile" strategy akin to that documented in the most recent Uluzzian assemblages from the Salento. Similarly to the Late Mousterian, the proto-Aurignacian appears organized along a mobility continuum of its own, with the earliest assemblage (A2) reflecting a more logistical organization while the more recent assemblage (A1) attests to a more residential mobility strategy. In this, the EUP of northern Italy appears to mirror at least some aspects of the dynamics that characterize the EUP in meridional Italy.

The situation in Central Italy also evidences changes in mobility during the transition interval. Late Mousterian assemblages there that are coeval with the EUP in northern and southern Italy (e.g., Grotta Breuil, Grotta di Sant'Agostino) indicate "an overall increase in the duration of individual site occupation events and concomitantly lower levels of residential mobility, responses to changes in the terrestrial habitat brought on by declining sea levels" (Kuhn 2005: 116). This is in contrast to earlier Mousterian assemblages in the region that indicate a greater reliance on residential mobility (Stiner 1994; Kuhn 1995).

These data indicate that throughout the peninsula, phase 1 was characterized by an increased reliance on logistical mobility. Phase 2, in contrast, is associated with a return to more residential mobility strategies in the north and south of the country and a continued dependence on logistical mobility in central Italy. While logistical mobility is characteristic of forager adaptations in more seasonal and/or unpredictable environments and reflects lower numbers of yearly residential moves, it is also associated with larger overall annual ranges being exploited to provision home bases with needed resources (Kelly 1995). This leads to an apparent paradox in that residential mobility and a higher number of annual moves result in smaller effective ranges for the foragers that adopt it. This is compounded by the fact that logistical mobility is more often associated with and embedded within what Whallon (2006) terms nonutilitarian forms of mobility (i.e., network and information mobility) aimed at gathering information about neighboring regions and to strengthen alliances with nonlocal groups that can be depended on in times of subsistence-related duress. This would also increase the overall degree of territorial coverage associated with logistical mobility.

Discussion: Building Conceptual Bridges Across EUP Inheritance Systems

The data pertaining to the different phases of the transition interval in Italy can now be integrated into a holistic model of the variable interaction between the components of the "triple inheritance system" of NCT in northern, central, and southern Italy. During phase 1, central Italy was a Mediterranean refugium that, in spite of minor fluctuations resulting from successive Dansgaard–Oeschger events, maintained relatively stable resource predictability. At that time, Late Mousterian foragers living there adopted more logistical mobility strategies that contrast with the residential mobility strategies that had dominated in the region to that point. This behavioral shift may well have been related to demographic packing in this part of the peninsula during the transition interval. van Andel *et al.* (2003), Davies and Gollop (2003), and Finlayson (2004) argue that, in climatically unstable periods, both modern humans and Neanderthals contracted their ranges southward (cf. Hublin and Roebroeks 2009). This claim is based on studies of radiocarbon-dated sites that indicate demographic packing in the Italian peninsula in such periods (van Andel *et al.* 2003), and within Italy, there would have been a secondary concentration of population in more ecologically stable regions, i.e., central Italy. Climatic instability immediately prior to and over the course of the transition would have therefore increased overall population density in southern Europe, including in Italy where the Mediterranean contributed to maintaining overall more mesic and temperate conditions (Finlayson 2004: 16, 68).

In contrast, northern and southern Italy saw significant changes in their biotic communities during the transition interval (Blondel and Aronson 1999). At the beginning of the transition, southern Italy became characterized by much more open, steppic environments, as indicated both by palynological studies (e.g., Allen *et al.* 2000) and the composition of zooarchaeological assemblages, especially in the Salento (Riel-Salvatore 2007: Table 3.2). In contrast, the northernmost third of the peninsula shifted toward an ecological mosaic of more open terrain and pockets of vestigial Mediterranean woodlands (Ravazzi and Pini 2009; Stiner 2005), an ecological context also attested to by zooarchaeological and palynological studies (Holt *et al.* 2006, unpublished manuscript; Kuhn and Stiner 1998). These paleoenvironmental shifts at both ends of the peninsulas stand as likely stimuli for foragers in those regions to develop behavioral adaptations designed to maximize the potential returns from the fluctuating resource bases caused by unstable ecological conditions.

Phase 1 can therefore be conceptualized as dominated by an inheritance route defined by the recursive interaction between stochastic ecological change (i.e., increasing ecological variability) and behavioral change. In those parts of the peninsula characterized by shifting environmental settings, the “formal” (i.e., typotechnological) component of the behavioral inheritance system was also marked by dramatic shifts. In contrast, in all regions, the “behavioral” component of the cultural inheritance system shifted in a common direction, albeit for different reasons depending on the area. In the north and south, the adoption of logistical mobility appears to have been partly a strategy to allow for the development of new technological systems and to exploit a broader range of subsistence resources. In central Italy, the shift toward more logistical strategies may have been linked partly to slight changes in ecological conditions (i.e., lower sea levels) but appears to have been principally a response to demographic packing in the region. In all cases, however, phase 1 was associated with an expansion of the diet breadth resulting from prolonged occupations of base camps and more intensive exploitation of their immediate catchment ranges, as reflected by the incorporation of small game in the diet.

One of the consequences of this first-order set of inheritance dynamics appears to have been net population growth in northern and southern Italy during phase 2, as reflected by the increased regional distribution of Uluzzian and proto-Aurignacian sites at that time (Palma di Cesnola 2004). It could be argued that these patterns of site distribution are, in part, an artifact of the prevalent mobility strategies (residential *vs.* logistical) that result in different amounts of sites and site visibility at a landscape, but the sparse available data do not at present allow an independent evaluation of this possibility. Additionally, the case for population increase is also supported by the stress evident in some small game communities as a result of sustained human exploitation (Stiner *et al.* 1999; 2000). Northern Italy sees an increase in the breadth and processing costs of exploited small game species, with a shift toward faster-moving species such as hares and birds (Stiner and Kuhn 2006). In southern Italy, the faunal record suggests that hares were incorporated in the subsistence base in the later phases of the Uluzzian of the Salento (Palma di Cesnola 1966, 1967; Borzatti von Löwenstern 1970) and that birds became proportionally more frequent than fish in the small game inventory of Castelcivita over the course of the Uluzzian (Cassoli and Tagliacozzo 1997; Riel-Salvatore 2007: Table 4.1, Fig. 4.1).

Thus, the legacy on phase 2 of the culturally dominated inheritance route of phase 1 appears to have been both biological (i.e., population growth) and ecological (i.e., stressed small game communities). This inheritance route, along with the fact that phase 2 sees a returns to less variable ecological conditions (Fig. 2), in turn, leads to a further shift in the behavioral dimension of the cultural inheritance system, with proto-Aurignacian and Uluzzian foragers reverting to mainly residential mobility strategies (Figs. 5 and 6). What data are available for central Italy during phase 2 suggest that there was no shift in either facet of the cultural inheritance system, that is, that people continued making Late Mousterian assemblages, organizing themselves logistically, and exploiting small quantities of shellfish to complement the large ungulates that were the basis of their diets. This implies a large degree of cultural, biological, and ecological stability in that region.

Phase 3 saw Late Mousterian and Uluzzian assemblages disappear from the record while proto-Aurignacian assemblages became common in central and southern Italy. While behavioral data such as that provided by the WABI for the earlier phases are not available for phase 3, it is nonetheless possible to propose a likely NCT inheritance system for this period that can serve as a testable hypothesis for future studies. The presence of proto-Aurignacian-like assemblages over the whole peninsula at that time suggests that the implicated inheritance routes were related, at a minimum, to population growth and to patterns of ecological optimization, as had been the case in the previous two phases.

The last phase of the transition interval corresponds to a warmer period (including Dansgaard–Oeschger event 8) that saw the peninsula recolonized by Mediterranean biomes (Blondel and Aronson 1999), the expansion of which would have brought foragers using proto-Aurignacian and Mousterian technology in direct competition in north-central Italy. The former were pre-adapted specifically to efficiently extracting resources from discontinuous patches of Mediterranean ecosystems, and their success at doing so is reflected in both their comparatively high population densities and their ability to extract higher nutritional yields from Mediterranean biomes. This ecological and demographic disparity would have set the stage for a potentially very rapid adoption in central Italy of proto-Aurignacian cultural conventions, with concomitant very rapid genetic takeover, as suggested by some modeling work (Zubrow 1989).

In southern Italy, which was still largely a steppic environment during phase 3, albeit an increasingly wooded one (Allen *et al.* 1999, 2000), the Uluzzian cultural inheritance system could have still been the subject of strong positive selection. However, the demographic advantage of populations making proto-Aurignacian assemblages over Uluzzian populations (i.e., a shift in the biological inheritance system of southern Italy) could have created an interface for the integration of some of the elements of inheritance systems of both that were most liable to positive selection. In other words, the need to balance between the selective cultural features of the Uluzzian and the selective pressures of the biological dimensions of the proto-Aurignacian over an uneven ecological backdrop that still exerted strong selection on the Uluzzian system would have generated a form of niche constructed “middle ground” (*sensu* White 1991). This would have been an original cultural inheritance system that could have combined features of both proto-Aurignacian and Uluzzian technologies while being neither.

This perspective is alone in being able to accommodate the fact that no Aurignacian-like assemblages are currently known south of Campania rather than postulating a scenario of competitive exclusion of the Uluzzian by the proto-Aurignacian. It also opens up new avenues of research into the social processes that may have led to such an integration, especially as they may have been vectored by shifting mobility strategies that may have facilitated the transmission of various behavioral components from one group to the other (e.g., Tostevin 2007). This scenario helps reconcile of the observations that some patently Uluzzian elements (e.g., high frequencies of splintered pieces) are found in all southern “proto-Aurignacian” assemblages, all of which also have distinctly non-Aurignacian features relative to their northern counterparts. A good example of the latter one is represented by the significantly lower frequencies of retouched bladelets in southern proto-Aurignacian assemblages (Table 2). This “middle ground” perspective thus helps make sense of a broader range of data than most alternative views that postulate Uluzzian acculturation through hazy social pathways (e.g., Mussi 2001).

Table 2 Retouched Bladelet Frequencies in Northern and Southern Italian Proto-Aurignacian Assemblages

	Retouched bladelet frequency (%)	Cluster	Cluster average
Mochi	57.3	North	66.45
Bombrini A1	66.8	North	
Bombrini A2	77.3	North	
Fumane A3 + A2	80.3	North	
Fumane A1 + A1T	77.2	North	
Fumane D6	53.0	North	
Fumane D6 + D3	62.3	North	
Fumane D3	57.4	North	
Castelcivita PA-C	44.9	South	25.1
Castelcivita PA-D	21.9	South	
Paglicci 24 B	18.2	South	
Paglicci 24 A4-2	34.7	South	
Paglicci 24 A1-0	46.5	South	
La Cala	1.1	South	
Serino	8.1	South	

Conclusions

This study has shown that the Middle–Upper Paleolithic transition in the Italian peninsula was associated with a breadth of empirical data that demonstrate the intertwined nature of changes in human behavior, biology, and/or ecology. Most of the data discussed here are not new, but since they have usually been approached as monolithic prime movers in the search for a general explanation of what "caused" the transition, their integration using a NCT framework provides new, compelling insights into the mechanics of the transition process in that part of the Old World. This perspective articulates an explicit concern with the changing importance of these given factors over time, their potential interrelatedness (Laland and Sterelny 2006), and the notion that the impact of changes in one system of inheritance may not be felt immediately (e.g., Laland and Brown 2006). NCT provides a robust conceptual framework to relate these eclectic datasets, and it permits the development of models that are both context specific and grounded in a broader body of evolutionary theory (Oodling-Smee *et al.* 2003).

Over the course of the transition interval in Italy, behavioral changes as disparate as demographic packing, population growth, increased longevity and childhood survivorship, increased diet breadth, incipient human environmental impacts, shifting mobility strategies, and technotypological changes have all been shown to represent distinct manifestations of human niche construction that are nonetheless fundamentally interrelated at varying scales. While building on recent work that underscores the importance of climate and paleoecology to the transition process (e.g., d'Errico and Sanchez-Goñi 2003), this study emphasizes that the environment alone does not provide a sufficient explanation for it. The advantage of NCT in this context is to show that the importance of each of these changes was dependent on the situational variables within which they manifested themselves and how these diverse trends can be integrated into an explicit series of nested evolutionary inheritance systems that feedback on one another. This underlines the importance of approaching the transition interval at a regional scale and in multiple locally defined sequential time slices (Riel-Salvatore 2009). In this, although it is firmly rooted in contemporary evolutionary theory, NCT serves as a welcome deterrent from an undue reliance on one-size-fits-all models that try to explain the transition synthetically as a purely continental process driven by one or at most a few general forces (Hovers 2009).

Perhaps most importantly, an NCT perspective on the transition presents all hominin populations implicated in this process as active agents that proactively shaped their evolutionary trajectories. This is in contrast to many models that present some or all of the hominin populations involved (especially Neanderthals) as passive Pleistocene bystanders able only to react to the pressures exerted upon them by external forces. If NCT's only contribution is ultimately to infuse interpretive models of the transition and of the evolutionary fate of Neanderthals and early Eurasian *H. sapiens* with this realization, its relevance will have been richly underscored.

Some readers may feel that the issues of the evolutionary fate of Neanderthals in Italy and of their links to the Uluzzian have not been sufficiently addressed in the preceding pages. This, in a way, is one of the points of this paper, namely that a

Table 3 List of Some Potential Proxy Measures to Reconstruct Dimensions of Late Pleistocene Hominin Behavior, Biology, and Ecology

Behavior	Ecology	Biology
Mobility	Climate change	Population density
% retouch	Ice cores—^{18}O shifts	Demographic models
% formal cores	Lake cores—% tree pollen shifts	Site density
% of nonlocal lithotypes	Climate unpredictability	Site size
Range size	C.V. of ice/lake core data	Gene flow
Distance of material transfers	Resource depression	Hybridization models
Isotope studies	Species richness of faunal assemblages	Adaptive mutation models
Intensity of intergroup contact	% of calories provided by small game	Selection for gracility
Frequency of personal ornaments/coloring	Resource redistribution	% shifts in postcranial robusticity
Shift in subsistence	% allochthonous materials within given artifact assemblages	Local archaic contribution
Proportional representation of new hunting tool types		Prevalence of Neanderthal-derived features
		Importance of archaic genetic introgression
		Offspring survivorship
		% of population reaching reproductive age

productive discussion of the paleoanthropological record can take place even in the absence of fossils on the basis of which to unambiguously attribute authorship of given industries or of given shifts in the archaeological record. I have tried to demonstrate how explicit expectations can be generated on the basis of the available data without having to depend on preconceptions derived from assumptions about authorship. The validity of the recursive evolutionary relationships proposed above can easily be assessed by new data, fossil or otherwise, as indeed should be the case of any evolutionary explanatory model.

An NCT perspective also permits the generation of likely models for those periods of the record for which evidence is scant or missing altogether. In the case of this paper, it is clear that the domains of the triple inheritance system proposed for phase 3 are more speculative than those of phases 1 and 2, or than those of the periods following the transition interval. However, because the periods that bracket phase 3 are associated with multiple sets of reliable empirical data on which to found the specific models of inheritance likely to have operated during that interval, this speculation is constrained by the hard data drawn from the record before and after it. This stands in contrast to approaches to the transition interval that depict it as though it was a stand-alone period of prehistory detached from both the legacies of past human actions and from its consequences for later human evolution.

This study has highlighted a number of potential axes of behavioral, biological, and ecological variability that could be targeted in future investigations of the complex and dynamic evolutionary inheritance systems of the transitional interval in other regions. Some of these lines of evidence are summarized in Table 3 and include several of the proxies used in the present analysis. By helping focus future research on specific facets of the record as well as on what are likely to be important potential links between them, NCT offers a promising conceptual avenue toward a richer, more contextualized, and ultimately probably more realistic understanding of the Middle–Upper Paleolithic transition than has been the case in recent synthetic analyses of this time period. As such, NCT can and does contribute significantly to our understanding of the transition and to our capacity to present its internal dynamics in terms of variables that must be linked to earlier and later periods of prehistory, a crucial component of any effort seeking to link this specific period of our recent evolutionary past to the broader history of human evolution.

Acknowledgments Thank you to Kevin Laland and Mike O'Brien for stimulating comments on a preliminary version of this paper presented at the 2008 SAA meetings. Thanks especially to Lydia Pyne for introducing me to NCT, for co-organizing the symposium on which this volume is based, and for her patience during the editing process. Cathy Cameron, Jim Skibo, Fabio Negrino, Enza Spinapolice, and an anonymous reviewer all gave pointed feedback that helped tighten the arguments presented in this paper, although any errors of fact or omission are mine alone. Support during this research was provided by a Postdoctoral Fellowship of the Social Sciences and Humanities Research Council of Canada.

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