

Research

Adaptation and niche construction in human prehistory: a case study from the southern Scandinavian Late Glacial

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The niche construction model postulates that human bio-social evolution is composed of three inheritance domains, genetic, cultural and ecological, linked by feedback selection. This paper argues that many kinds of archaeological data can serve as proxies for human niche construction processes, and presents a method for investigating specific niche construction hypotheses. To illustrate this method, the repeated emergence of specialized reindeer (*Rangifer tarandus*) hunting/herding economies during the Late Palaeolithic (ca 14.7–11.5 kyr BP) in southern Scandinavia is analysed from a niche construction/triple-inheritance perspective. This economic relationship resulted in the eventual domestication of *Rangifer*. The hypothesis of whether domestication was achieved as early as the Late Palaeolithic, and whether this required the use of domesticated dogs (*Canis familiaris*) as hunting, herding or transport aids, is tested via a comparative analysis using material culture-based phylogenies and ecological datasets in relation to demographic/genetic proxies. Only weak evidence for sustained niche construction behaviours by prehistoric hunter–gatherer in southern Scandinavia is found, but this study nonetheless provides interesting insights into the likely processes of dog and reindeer domestication, and into processes of adaptation in Late Glacial foragers.

Keywords: niche construction; southern Scandinavia; Late Palaeolithic; comparative method; *Canis familiaris*; *Rangifer*

1. NICHE CONSTRUCTION AND ARCHAEOLOGY

Niche construction (NC) has been defined as the evolutionary process whereby organisms modify their own and other organisms' environments in such a way that selection pressures on the current and subsequent generations are altered significantly [1]. From this point of view, adaptation can be the result of two processes: (i) environment > selection > adapted organism, or (ii) organism > NC > modified environment. The end-result of both pathways is a fit between organism and environment (adaptation), but, importantly, the process differs. This distinction was flagged-up by Lewontin [2,3] some time ago, but it is only recently that its wider implications with regards to the evolutionary trajectories in a range of species are being explored in quantitative detail (e.g. [4–9]). Odling-Smee *et al.* [10] have compiled a long list of potential niche-constructing behaviours found across most taxonomic

groups. They have also noted that humans in particular are adept niche constructors, and that many human genes may be the result of recent, culturally modified selection pressures [11]. Yet, despite considerable efforts to model human biological and cultural evolution in relation to NC (e.g. [12–23]), there are only relatively few quantitative studies of human NC [14,24]. One of the reasons for this lack may be that few disciplines have access to information on the sustained and long-term modification of ecologically relevant environmental parameters and their subsequent selective repercussions. However, 'archaeology provides unique quantitative information on population-level distributions of cultural attributes over long periods of time. This information concerns not only socially transmitted cultural traditions but also the ongoing process of niche construction' [25, p. 177]. I argue here that the tools of the comparative method, together with archaeological data, can be used to investigate hypotheses about specific prehistoric NC processes.

The NC model recognizes three domains of inheritance (cf. [26])—genetic, ecological and cultural—and archaeology can provide proxy information on all three domains. Archaeological data on craft traditions can be used to track cultural inheritance, thereby plotting the historical relationships among past communities of teachers and learners. Patterns of social information transmission among traditional societies tend to be

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One contribution of 13 to a Theme Issue 'Human niche construction'.

conservative, operating largely within family groups [27,28], often with considerable pedagogical involvement by adults [29]. This conservatism is reflected in the many well-known typological sequences, indicating high degrees of cultural inheritance stability over many generations. Phylogenetic methods are increasingly being used to describe and analyse these patterns of material culture diversity (e.g. [30–32]). The key advantage of cultural phylogenetics over traditional typological methods is that a given phylogenetic tree represents an explicit and quantitative hypothesis of how given archaeological ‘taxa’ [33] are related historically. Cultural phylogenetics thus opens the door to formal studies of adaptation using the tools of the so-called comparative method [34,35].

In addition, much archaeological data pertains directly to human modifications of the biotic and abiotic environments, both locally and transiently as well as at larger geographical and temporal scales [36,37]. Culture, it has long been argued, constitutes the human niche [38,39], and environmental archaeologists have made human niche modification and its consequences their primary concern [40]. This includes the domestication of animals and plants [41], as well as ‘domesticated landscapes’ [42, p. 323], and even ‘transported landscapes’ [43, p. 217]: landscape modifications and built environments brought about by collective human efforts as well as entire economies/ecologies taken from one place to another during dispersals. The ecological transmission of physical resources in the form of modified environments, domesticated plants and animals is particularly relevant to an archaeological application of NC theory, because traditional human economies, subsistence practices and land-use strategies can be described well with reference to ecological inheritance (e.g. [44–46]). Sterelny [47, pp. 151–152] underlines that ‘to the extent that information does flow collectively, niche construction is our best model of the generation-by-generation accumulation of skill, technology and information’ in human societies. This collective information transmission is echoed in Oswalt’s [48] distinction between weapons/instruments on the one hand, and facilities on the other. In this view, material culture that reflects personal transmission of information and use, such as projectile points, basketry or pottery (weapons/instruments), provides information on cultural inheritance in the strict sense. Material culture that reflects a collective transmission of information and use, such as tents and housing structures, fishing platforms, fortifications as well as field systems (facilities), can conceptually and analytically be framed as part of the ecological inheritance passed from generation to generation [49]. Alternatively, such features could be viewed as part of the human extended phenotype [50,51], but their selective relevance is via modified environments, particularly in subsequent generations born into a niche that already is modified in a given way [18,52]. Furthermore, facilities often have a useful life longer than a single human generation, and are continuously or periodically modified and changed. These evident ecological modifications cannot be readily related to the genotypes of those who played

no part in putting them in place. Instead, they reference the collectively held stock of ecological knowledge and its implementation: a modified environment that constitutes the ontogenetic niche for subsequent generations.

Finally, the adaptive or maladaptive effects of human NC processes should be reflected in genetic inheritance patterns of the niche-constructing populations as well as the animals and plants whose niches are affected. The increasing availability of ancient and population genetic data facilitates inferences about, and direct insights into, past demographic processes [53]. Gene frequency patterns in both modern and ancient DNA can, for instance, be used to demonstrate the evident success of early farmers and their NC behaviours involving a range of domesticated animals and plants (e.g. [54–56]). However, genetic change is merely the endpoint of what is best thought of as a continuum of processes [57–59]. Archaeologists have access to datasets that reflect the (conscious or unconscious) manipulation of the behaviour or distribution of candidate domesticates long before genetic changes take place and become widely established in the target population [59]. In addition, demographic success of the niche-constructing population itself is also reflected in a range of archaeological proxies, such as range expansion, increases in the number and/or size of sites or the number of ^{14}C dates in a given period [60,61].

In the following section, I will provide some examples of human NC that leave archaeologically visible traces. I will contrast the NC behaviours of farmers and foragers, arguing that the domestication of plants and animals [41] as well as the lasting modification or ‘domestication’ of landscapes [42,62] sets the benchmark for effective NC. I will then go on to explore in more detail a case study of prehistoric forager NC involving domesticated dogs (*Canis familiaris*) and reindeer (*Rangifer tarandus*) hunting/herding strategies in the Late Glacial of southern Scandinavia (approx. 14.7–11.5 kyr BP), where I use comparative methods to investigate the feedback relations between these two NC behaviours.

2. ARCHAEOLOGICAL SIGNATURES OF HUMAN NICHE CONSTRUCTION

A first example, the human occupation of Greenland between about AD 950 and 1500 serves to contrast the NC behaviours of farmers and foragers. Greenland was first settled by hunter–gatherer groups from North America and Siberia in several waves beginning sometime after approximately 4.5 kyr BP [63]. Around AD 950, the southern tip of Greenland was also settled by Viking (Norse) farmers from Iceland. The expanding Greenland Norse brought with them their agricultural niche package fine-tuned to Norwegian conditions, including animals and crops. They rapidly transformed local landscapes to suit their traditional niche requirements [64,65]. During milder climatic episodes—the first few hundred years of occupation—they fared sufficiently well. When the climate in the Northern Hemisphere turned colder as well as stormier during the Medieval Cold Period,

traditional crops and herding techniques began to fail [66]. Anthropogenic landscape changes such as deforestation aggravated the conditions [67,68]. The deteriorating niche quality, coupled with unfavourable climate change, isolation and an insistence on maintaining a social and economic/ecological adaptation ill-suited to High Arctic environments, culminated in the local extinction of the Greenland Norse [69]. Meanwhile, Inuit groups of the *Thule* culture thrived [63]. The impact of these groups on the landscape was subtler and took the form of various facilities (e.g. drive lines, hunting stands and marked pathways: [70–72]) placed strategically in the landscape in order to facilitate travel and the management of reindeer movements.

The fate of the Greenland Norse serves to highlight that initially successful NC can have negative adaptive consequences in the longer term [73]. Generally, however, dispersing farming populations provide good examples of extensive NC involving both landscape modifications and the domestication of plants and animals. Their genetic and linguistic legacies can be traced worldwide [74,75]. The first dispersal of farming populations to Europe in particular has been studied intensively and much data on the changing plant and animal ecologies of these pioneering groups are available [76–79]. Shennan ([25], pp. 180–181; my emphasis) further adds that the dispersal of agricultural populations into Europe ‘is a classic example of natural selection acting on people through an inherited cultural tradition, which gave a selective advantage to those who adopted it and passed it on to their children. In fact, the process involved not simply the inheritance of a tradition but also *the transmission of a new niche*, because the actual descendants of the cereal crops and animals that had originally been domesticated were being carried along as part of the dispersal’. The evolutionary success of farmers under this model is largely due to the powerful positive NC that is part and parcel of most agricultural societies [55]. Equally, however, environmental archaeological data also indicate the collapse of such early agricultural societies in some regions because farming practices destroyed the environment [80]. Continuous settlement then required further NC (e.g. slope terracing) to counteract these negative effects (e.g. [81]).

Turning again to foragers, a recent ethnographic study by Bliege Bird *et al.* ([82]; see also [83]) provides detailed insights into the kind of landscape modifications that prehistoric hunter–gatherers may also have practised, and their adaptive outcomes. They show that episodic and systematic landscape burning by Australian Aboriginals increases hunting success measured in caloric yield per unit land. The effects of this burning on the species composition of that habitat is also documented. They demonstrate how this behaviour is underwritten and maintained via a stock of knowledge transmitted from generation to generation along with the physical niche component, the territory. Indeed, it has been argued that this behaviour has considerable time-depth in Australia [84–86].

Using detailed analyses of pollen profiles, fungal spores and charcoal traces in the vicinity of prehistoric

settlement sites, it has likewise been argued that Mesolithic and Late Palaeolithic hunter–gatherers in Europe and elsewhere had similar burning practices (e.g. [87–92]), and that these had important adaptive benefits by increasing access to animals [93] and plants [94]. Increasingly, the notion of pre-Neolithic agriculture is being considered [95], and fire undoubtedly played an important role in the formation of the human niche in the long term [45,96].

It is such landscape manipulations that provide the context for the most evident process of prehistoric NC, the domestication of plants and animals [41,42]. The primary domesticate found among hunter–gatherers is the dog (*C. familiaris*). Numerous theories for why humans first began to domesticate dogs have been put forward [97,98], with many workers stressing the adaptive benefits of using dogs as hunting companions (e.g. [99,100]). The considerable extent to which dog-use enhances hunting success has recently been quantified within a behavioural ecological framework [101]. Keeping dogs also involves additional tools and trappings (tethers, leashes, pens, etc.) that together make up the constructed niche to which they are so well adapted physically, physiologically and cognitively [102–105]. From approximately 14 kyr BP onwards, the archaeological record is speckled with dog burials, signalling the symbiotic relationship and the important social as well as ecological role played by this first domesticate [98,106]. The effects of this long association between humans and dogs are evidenced by the significantly altered genetic composition, cognition, distribution and ecology of domesticated dogs, especially when compared with their now nearly extinct ancestor *Canis lupus*.

The most recent suggestions regarding the geographical origin and timing of dog domestication based on genetic data alone point to present-day southern China and argue that all extant dog breeds originated there less than approximately 16.3 kyr BP [107]. This stands in direct opposition to reports of domesticated dogs in Upper Palaeolithic contexts in Europe dating to 31.7 kyr BP [108,109] and would require an extremely rapid diffusion of this resource even if only the next-oldest European specimens were considered [99]. If, as argued above, domestication is considered as a process—and the domestication of *Canis* should be no exception in this respect [110]—then these seemingly opposing positions can be reconciled. Behavioural, morphological and genetic markers of domestication are not linked in a lock-step fashion [59]. The presence of *C. familiaris* in a range of Late Glacial archaeological sites in northern Europe [99,106,111] indicates that, at the very least, these hunter–gatherer groups were beginning to engage in symbiotic relations with wolves. Possibly, these early breeds never became fully (i.e. genetically) domesticated. Alternatively, breeds brought to Europe by dispersing farming populations later replaced these earlier lineages [112]. Either way, important questions about the process of dog domestication remain open, and southern Scandinavia constitutes a useful testing ground for investigating the emergence of this important NC behaviour.

Paralleling the first finds of *C. familiaris*, Palaeolithic foragers also began to engage in intense specialized

economic/ecological relations with reindeer. Abundant reindeer bones that comprise practically 100 per cent of all faunal remains at some Late Glacial sites in southern Scandinavia (reviewed in the next section) document the repeated emergence of such specialized economies [113]. In fact, it has been suggested that the economic specialization seen in these earliest Late Glacial pioneers indicates a move towards reindeer herd management and domestication [114–117]. Specialized reindeer herding economies are widespread in high-latitude Eurasia today, and these practices have resulted in the partial domestication of this species [118]. While the intentional breeding of reindeer is a comparatively recent phenomenon, herd management is argued to go back a very long time indeed [119–121].

Faunal remains from key archaeological sites of this period do not support the notion of comprehensive herd control [122], but domesticated and wild reindeer herds are difficult to distinguish morphologically and demographically as even managed herds roam freely much of the time. Recent genetic studies indicate multiple independent domestication events in extant *Rangifer* populations in northern Europe [123], and standard zooarchaeological techniques may therefore not be able to readily detect incipient or small-scale reindeer herd management. Reindeer hunting and reindeer herding have much in common from an ecological perspective [124]. Istomin and Dwyer [125, p. 613] describe the relationship between humans and *Rangifer* as a kind of ‘dynamic mutual adaptation’, where humans impact the behaviour and biology of wild and domesticated reindeer, while they in turn influence their human counterparts. In addition, Ingold [126] and Ventsel [127] stress the continuity between techniques and technologies of *Rangifer* hunting and herding. These technologies—drive lines and pathways, for instance—are signatures of forager NC involving reindeer, and are found in Scandinavia from at least the Early Holocene [128,129]. Ingold also notes that reindeer economies provide excellent opportunities for canine companions, and Müller-Wille *et al.* [121] point out that northern European reindeer economies not only are associated with but also require the use of dogs. In the following, I therefore explore the specific hypothesis that intense reindeer specializations akin to herd management evolved already during the Late Glacial in southern Scandinavia. I ask whether the domestication or introduction of *C. familiaris* facilitated the repeated emergence of this kind of economy, which in terms of its use of dogs and in its relationship with reindeer reflects the NC behaviours of these hunter–gatherer groups.

Odling-Smee *et al.* [10, p. 344] have suggested that such ‘signatures of past human cultural niche construction’ can be investigated using the tools of the comparative method, a powerful and well-described suite of methods for the analysis of adaptation and causal correlations in biology [35]. The comparative method requires phylogenies in order to control for the historical relatedness and attendant statistical non-independence of the units under study, known as ‘Galton’s Problem’. What such comparative analyses allow is to establish whether two given NC trait evolve in a correlated manner, where one trait, the niche-constructing trait, drives change in another trait, the

recipient trait whose fitness depends on the effects of previous NC [18]. Such correlated evolution over time establishes the feedback relations between niche modifications that are at the heart of the NC model.

Material culture phylogenies are here constructed using Bayesian phylogenetic methods and lithic projectile point data, which reflect patterns of teaching and learning in Late Palaeolithic southern Scandinavia [130,131]. Such data, in non-phylogenetic formats, have traditionally provided the backbone for the culture-history in this region [132]. Information on the presence/absence of domesticated dogs and on reindeer specialization is plotted onto these phylogenies, and the resulting pattern is queried for correlations among the selected traits. In formal terms, this paper addresses the following hypotheses:

- (H0) Dog-use and successful specialized reindeer economies evolve independently.
- (H1) Dog-use and successful specialized reindeer economies evolve in concert.

If support for H1 can be found, it can be addressed which of the traits is the primary niche-constructing and which the recipient trait:

- (H1a) Dog-use facilitate the evolution of specialized reindeer economies (dog-use = niche-constructing trait, reindeer specialization = recipient trait).
- (H1b) The adoption of specialized reindeer economies necessitate dogs (reindeer specialization = niche-constructing trait, dog-use = recipient trait).

I first briefly review southern Scandinavian Late Palaeolithic culture-history, the evidence for specialized reindeer economies and the use of domesticated dogs in this period. Then, a methodology is presented that examines the correlation between reindeer specialization and dog-use across Bayesian material culture phylogenies reflecting the major culture-historical trends of this period. The likelihood ratio (LR) test and Bayes factors (BFs) are used to assess whether these two traits are correlated. These analyses indicate that specialized reindeer hunting without dogs was probably an unstable strategy tenable only under favourable climatic conditions during the Late Glacial, and that domesticated dogs were a necessary component of successful specialized reindeer economies, as suggested by Müller-Wille *et al.* [121]. They also support the idea that domesticated dogs during this period were a costly resource that, while conferring important adaptive advantages in hunting, also required significant maintenance and training costs [133]. The periodic absence of dogs during the Late Glacial colonization of northern Europe—known also from the later human colonization of High Arctic Greenland [134]—indicates that despite the evident adaptive benefits of dog-use, they may have dropped out of the cultural repertoire on occasion. In addition to the relationship between the two NC traits under study, archaeological proxies as well as recent population genetic data indicate that a demographically viable, continuous human presence in Scandinavia was only

Table 1. The demographic and culture-historical framework for the Late Glacial resettlement of northern Europe, modified from Gamble *et al.* [137]. The event stratigraphy follows Björck *et al.* [138] and Lowe *et al.* [139]. GS, Greenland Stadial; GI, Greenland Interstadial.

event stratigraphy	GRIP ice core years of onset (BP)	chronozones	population events	techno-complexes
GS-1	Holocene 11 500	Younger Dryas	5. contraction	<i>Ahrensburgian</i> <i>Bromme</i> culture
	GI-1a 12 650	Late Allerød		
	GI-1b 12 900	Intra-Allerød Cold Phase	4. stasis and population decline	<i>Federmesser-Gruppen</i> (FMG)
	GI-1c 13 150	Early Allerød		
	GI-1d 13 900	Older Dryas	3. colonization, abandonment and re-colonization	<i>Hamburgian</i> (<i>Havelte</i> and <i>Classic</i> phases)
	GI-1e 14 500	Bølling		
GS-2	GS-2a 16 900		2. initial expansions into central Europe	Southern Scandinavia not settled
	GS-2b 19 500			
	GS-2c 21 200			
GI-2	21 800	Last Glacial Maximum	1. refugium	Southern Scandinavia not settled

possible during the later part of the Late Glacial when dogs were firmly established in the ecologically inherited repertoire of these forager groups.

3. THE SOUTHERN SCANDINAVIAN LATE PALAEOLITHIC

At the height of the Last Ice Age, southern Scandinavia was almost fully covered by ice and devoid of people. The reappearance of hunter-gatherer groups just before 14.7 kyr BP was part of the general human re-expansion from their glacial refugia. Gamble and colleagues [135–137] have provided a framework for this process incorporating insights from environmental science, population genetics and archaeology (table 1). Although southern Scandinavia became part of the human world from about 14.7 kyr BP, it remained demographically marginal until the beginning of the Holocene climatic amelioration. Population densities were low [140] and probably fluctuated in accord with environmental changes [141,142].

Traditionally, four cultures or techno-complexes are recognized in the region, arranged in chronological succession: the *Hamburgian* (divided into an earlier *Classic*, and a later *Havelte* phase), the *Federmesser-Gruppen* (FMG), the *Bromme* and *Ahrensburgian* cultures, each with a characteristic stone tool repertoire (figure 1). Numerous hypotheses regarding the process of re-colonization have been proposed. Eriksen [143, p. 169], for instance, suggests that this sequence represents ‘a continuous and largely endogenous cultural development’, while Petersen [144] argues for a discontinuous human presence. Other recent studies have also suggested that these techno-complexes may represent discrete expansion-retraction pulses [145,146], and much recent work has focused on better understanding the underlying processes of culture change. Riede [147,148] has suggested that the origin of the *Bromme* should be seen in relation to the eruption of the Laacher See volcano around

13 kyr BP and the subsequent isolation experienced by peripheral groups belonging to the FMG techno-complex. Follow-up studies have explored different forcing mechanisms responsible for the relocation of animal and human populations away from areas affected by the volcanic ash fall-out [149,150]. Economically, however, neither the FMG nor the *Bromme* are characterized by specialized reindeer hunting. In contrast, both the preceding *Hamburgian* techno-complex and the later *Ahrensburgian* cultures are seen as specialized reindeer hunters, based on faunal evidence from a range of sites [151–153]. Late Palaeolithic hunter-gatherers may also have controlled or domesticated reindeer, as discussed above, and they may have manipulated the landscape by building cairns, flag lines, hunting stands etc. in order to steer the movements of herds for their own advantage [151,154], and to facilitate travel in an otherwise relatively featureless landscape [155].

In sum, ‘northern Europe is an extraordinary laboratory for the investigation of human colonization and adaptation’ [156, p. 185]. Adaptation and range expansion are possible outcomes of NC [157]. Specialized reindeer economies emerged in the *Hamburgian* and *Ahrensburgian*, but these two cultures are separated in time by nearly 1 kyr. It is essential to take account of the historical relatedness or otherwise of these groups when discussing whether their reindeer specializations were, in fact, adaptive and whether they relate to other NC behaviours such as dog-use.

4. MATERIAL AND METHODS

As in many other regions, characteristic projectile points have provided the backbone for culture-historical reconstruction in southern Scandinavian prehistory [132]. Because of their historical sensitivity, projectile points have also been analysed, with increasing frequency, using phylogenetic methods [158]. Cultural

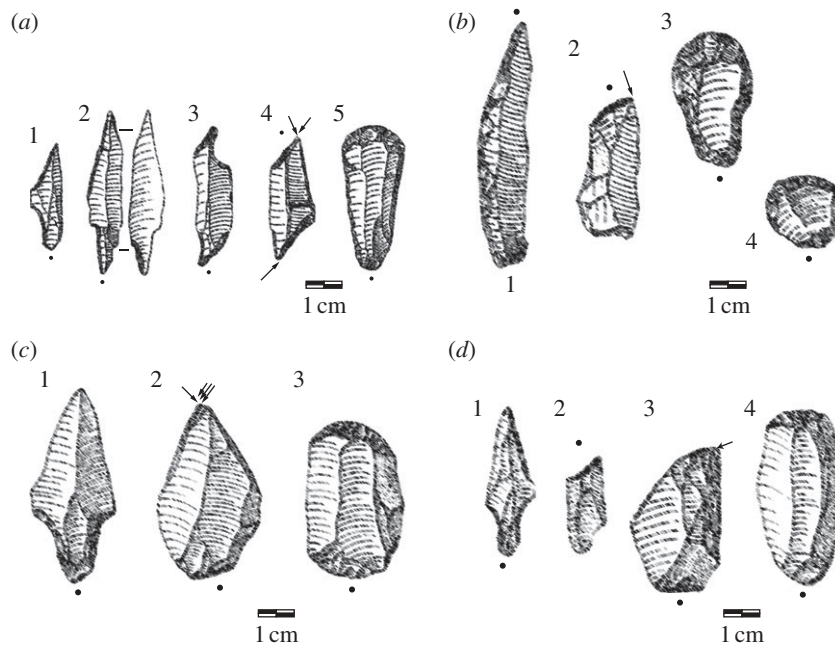


Figure 1. The formal tools of the four Late Palaeolithic techno-complexes. (a) *Hamburgian*: 1, shouldered point (*Classic* phase); 2, shouldered point (*Havelte* phase); 3, combination tool; 4, double-ended burin; 5, blade-scraper with lateral retouch. (b) *Federmesser-Gruppen*: 1, arch-backed point; 2, burin on retouch; 3, tanged scraper; 4, thumbnail scraper. (c) *Bromme*: 1, large tanged point; 2, dihedral burin; 3, end-scraper. (d) *Ahrensburgian*: 1, tanged point; 2, early microlithic (*Zonhoven*) point; 3, burin; 4, scraper. Filled dots mark the percussion end; arrows indicate burin blows. After Eriksen [132].

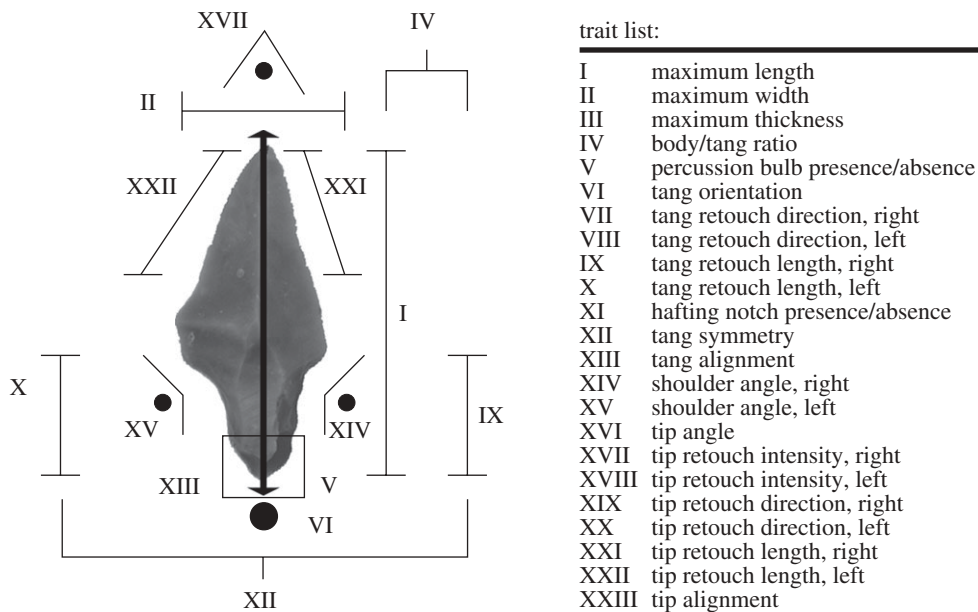


Figure 2. Measured characters. Characters used in phylogeny building are listed in table 2, and the data matrix is provided as electronic supplementary material, table S1. Photo by the author with permission from the National Museum of Denmark, Copenhagen.

phylogenetics has advantages over traditional typological approaches in that a given phylogeny constitutes a quantitative hypothesis of the historical relatedness among the chosen units of analysis [159]. Such hypotheses can then be evaluated statistically and in relation to external datasets, such as stratigraphic, geographical or radiocarbon dating information. While a phylogenetic quantification of material culture relations alone can reveal important new insights in its own right, phylogenies can also be used in

additional comparative analyses. Here, a method is presented that uses these tools to detect Late Palaeolithic hunter-gatherer NC.

(a) *Construction of archaeological taxonomic units*

The method of taxon construction largely follows that described by O'Brien *et al.* [160,161] and Darwent & O'Brien [162], although an initial analysis also used

Table 2. Attribute and attribute states used in phylogeny building.

character	character state	character	character state
I maximum length (mm)	0. ≤ 45 1. 45–68 2. > 68	VII tang retouch direction	0. opposing 1. none 2. same side
II maximum width (mm)	0. < 19 1. ≥ 19	VIII tang symmetry	0. > 2.5 1. 1.5–2.5 2. 1.0–1.4
III maximum thickness (mm)	0. < 5 1. ≥ 5	IX tip retouch	0. none 1. unilateral 2. bilateral
IV volume ^a	0. < 39 1. 39–58 2. 59–166 3. > 166	X combined tang/body ratio ^c	0. < 23 1. 23–42 2. > 42
V tang/body ratio ^b	0. unilateral retouch 1. no tang 2. < 2.0 3. ≥ 2.0	XI retouch extent ratio ^d	0. 4–18 1. 19–40 2. > 40
VI percussion bulb morphology	0. faint bulb 1. pronounced bulb 2. distinct bulb with scarring	XII tang retouch symmetry	0. ≤ 1.4 1. no tang 2. > 1.4

^aVolume = length \times width \times thickness.

^bTang/body ratio = length/shortest tang retouch.

^cLength/tang/body.

^dTotal retouch extent/(length \times width).

phylogenetic networks [163,164] to explore potential instances of blending and reticulation [159]. A total of 607 specimens were measured for a variety of characters (figure 2), which were divided into discrete character states using exploratory statistics and lithic analytical principles as guidelines [131]. Twelve of these attributes were used to construct the phylogenies presented here, and these reflect the size and shape of the projectiles as well as manufacturing methods (table 2). Each taxon comprises at least five specimens identical in their attribute compositions, thus reflecting recurrently taught and learned flint-knapping behaviour [29,131]. This approach yielded 16 taxa, of which the taxon associated with the oldest ^{14}C date was chosen as outgroup.

(b) Phylogeny construction

Bayesian Markov chain Monte Carlo (MCMC) methods are used to retrieve a sample of trees from the most likely regions of the universe of possible topologies [165]. The model of evolution used is a simple multistate model (KSTATES), where the rates of character state change are presumed to be equal, and only minimal assumptions about mode, tempo and direction of character change are introduced. The trees were rooted using the taxon associated with the oldest radiocarbon date. A total of 10 000 k iterations were run and the tree universe sampled at every 40 kth iteration to minimize autocorrelation among the trees in the final sample. The Markov chain quickly converged on the most likely tree configurations, and after a few thousand iterations, only minor fluctuations in the likelihood score of each tree are observed (figure 3). Figure 4 shows the consensus tree of the resulting tree sample

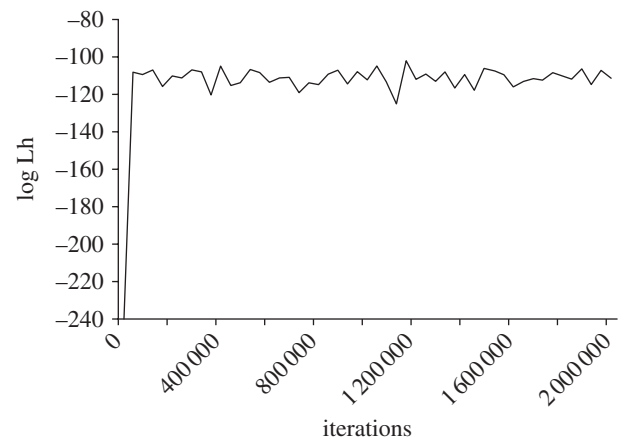


Figure 3. The Markov chains trajectory through the likelihood landscape during the first 200 k iterations.

($n = 251$). This tree differs little from those produced using other maximum-likelihood (ML) and parsimony-based approaches (F. Riede 2007, unpublished PhD thesis), and the major techno-complexes recognized by traditional typological analysis are represented in the phylogeny, albeit not all as monophyletic clades [157]. The branch lengths reflect both the chronological sequence of diversification and the degree to which these groups experienced isolation (especially the *Bromme* clade). Even rates of cultural change cannot, however, be assumed. At times, craftsmen deliberately introduce variation into the manufacturing process [171], which can rapidly increase branch length. Note that the consensus tree is not used in further analyses. Instead, the uncertainties associated with the tree-building procedure are

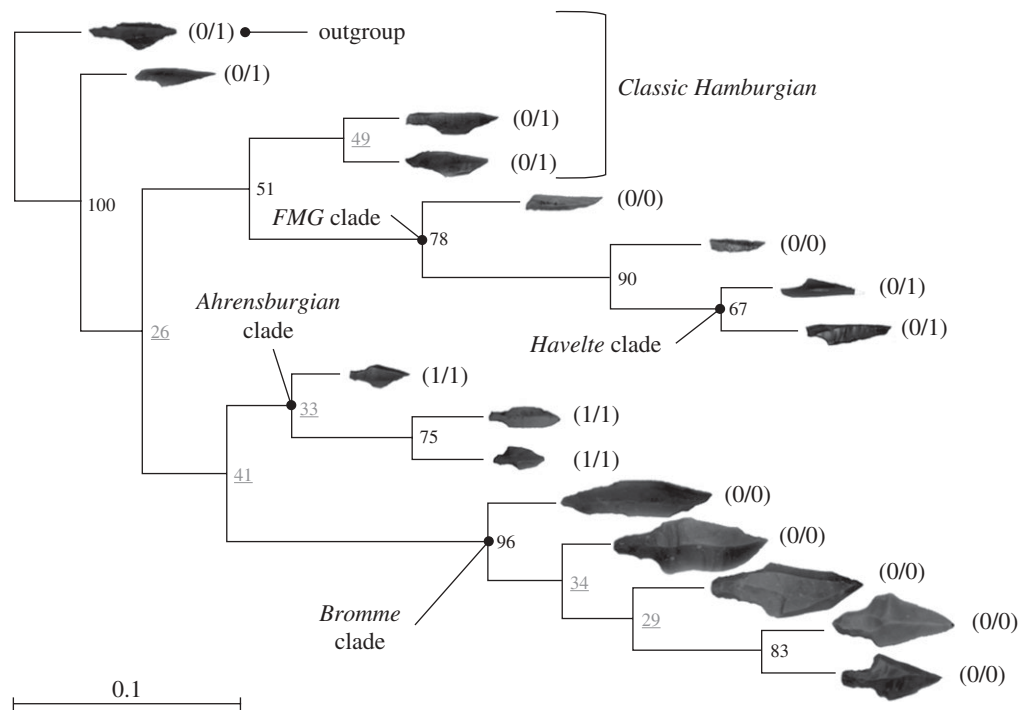


Figure 4. The consensus tree based on a sample of 251 Bayesian trees produced using the MCMC methods implemented in BAYESPHYLOGENIES [165]. Branch support values below 50 are shown in grey and reflect the inherent difficulty of accurately distinguishing the tools of some cultures from this period. The presence/absence scores for specialized dog-use/reindeer hunting are presented alongside each taxon. Information on the presence of dogs, taken from [99,106,111,166–169], is assigned to the taxa at the level of the respective cultural groupings. BAYESPHYLOGENIES is available from www.evolution.reading.ac.uk. See Walker [170] for a comprehensive bibliography of prehistoric *Canis* remains.

incorporated into subsequent analyses by querying the entire sample of 251 trees.

(c) Examining correlated trait change

Each taxon is associated with the two traits (dog-use/reindeer specialization) under investigation, scored as presence (1)/absence (0), at the level of their associated techno-complex. The ML and Bayesian algorithms implemented in BAYESTRAITS [172,173] were used to approximate trait correlations. The posterior log-likelihoods for an ML model (iterations = 1000 k; rate deviation = 80; multiple tries = 25; sample period = 20) in which the two traits evolve independently are differently distributed than those in which the two traits are assumed to evolve in concert (figure 5). The LR test, described by Pagel [172] and calculated by $2 * [\log-Lh(D) - \log-Lh(I)]$, can be used to statistically evaluate trait correlations in each tree sample. This test indicates that the mean of these likelihood (Lh) distributions is not statistically significant ($p > 0.21$, χ^2 , d.f. = 4). In the more appropriate Bayesian framework, the so-called Bayes factor can be used to assess relative support for one over the other model (see [173] for a detailed description). This analysis (parameter settings as above; burn-in = 50 k) returns a log BF ($= 2 * [\log(\text{harmonic mean}(D)) - \log(\text{harmonic mean}(I))]$) of 0.7, i.e. positive if very weak evidence in favour of the dependent model [174].

(d) Transition rate analysis

The transition rate probabilities provided as part of the output by BAYESTRAITS (table 3) give clues as to the order of correlated change, and such correlations

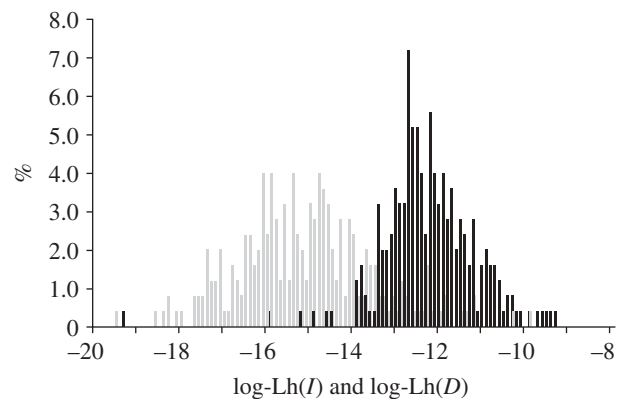


Figure 5. The distribution (in %) of log-likelihood values in the independent ($\log-Lh(I)$) (grey bars) and dependent models ($\log-Lh(D)$) (black bars).

establish which trait is the active niche-constructing trait and which the recipient trait (figure 6). In the ML-dependent model, the distributions of transition rates for each trait combination across the 251 trees show some patterning (electronic supplementary material, figure S1). The transition rates for the evolution of non-dog-using economic generalists to non-dog-using reindeer specialists are the lowest and contrast with those for the transition from dog-using generalists to dog-using specialists ($q_{12} \neq q_{34}$), indicating that it was unlikely for reindeer specialization to emerge in the absence of dogs. In addition, dog-use appears to have facilitated economic flexibility as expressed in the more frequent transitions between generalist and specialized economies in the presence

Table 3. Mean ML transition rates for the independent and dependent models.

independent model				
dog-use	0	1		
0	—	q_{01} : 13.11		
1	q_{10} : 6.22	—		
reindeer specialization	0	1		
0	—	q_{01} : 2.75		
1	q_{10} : 3.08	—		
dependent model				
dog-use/reindeer specialization	0/0	0/1	1/0	1/1
0/0	—	q_{12} : 0.07	q_{13} : 0.03	—
0/1	q_{21} : 0.43	—	—	q_{24} : 11.13
1/0	q_{31} : 1.66	—	—	q_{34} : 28.96
1/1	—	q_{42} : 19.92	q_{43} : 20.49	—

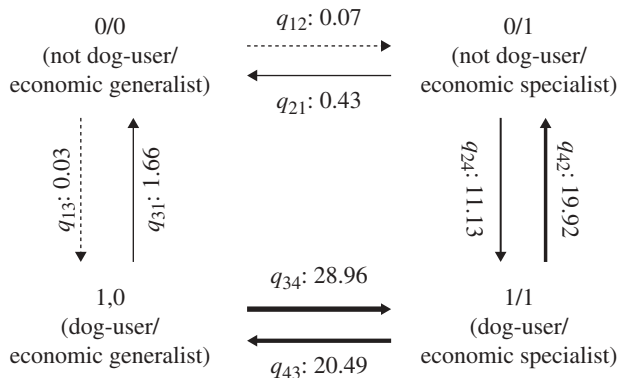


Figure 6. This flow diagram shows the mean transition rates in the dependent (ML) model. The thickness of the arrows corresponds to the transition likelihoods from one trait combination to another. BAYESTRAITS is available from www.evolution.reading.ac.uk.

of dogs (q_{43} , q_{43}), while itself being a labile trait with a relatively high likelihood of becoming lost (q_{42} , q_{31}).

5. DISCUSSION AND CONCLUSION

The foregoing analysis has found limited positive support for H1, a correlated evolution of the use of domesticated dogs as hunting/herding/transport aids and the repeated emergence of specialized reindeer economies. Both traits can be understood as a constructed niche dimension and interpreted within the NC framework. However, this support is not statistically significant. Why is the evidence for a correlated evolution of dog-use and specialized reindeer hunting not stronger, given the dependency of reindeer economies upon dogs observed today? The results of this study support the notion that prehistoric forager NC was in fact limited and intermittent, with little impact on target animals or landscapes. In this view, the fragmentary record of domesticated dogs in the northern European Late Glacial may not be the result of poor preservation, but rather of the fact that dog domestication/use was not a core part of the cultural repertoire at the time, much like in prehistoric Greenland [134]. It is possible, for instance, that early tamed or domesticated dogs did not provide significant advantages in food procurement [133]. If so, the costs of keeping these pets would regularly outweigh their benefits, particularly perhaps during

times of food crisis. It is also worth noting that the increasingly close association of humans and dogs may already at this point have resulted in the zoonotic emergence of a range of infectious diseases [175], which can be seen as a negative NC effect.

In addition, and in contrast to some recent suggestions, this study finds no support for the notion of reindeer herd management during the earliest phases (*Hamburgian*) of human presence in southern Scandinavia during the Late Glacial. The adoption of a specialized reindeer economy possibly involving a degree of herd management or incipient domestication by *Ahrensburgian* groups was contingent on the adoption of domesticated dogs. Further distinguishing between successful and unsuccessful reindeer economies may aid in interpreting these results. Both Petersen [144] and Riede [155,176] have argued that the *Hamburgian* occupation of southern Scandinavia was ultimately unsuccessful. Both mitochondrial and non-recombining Y-chromosome data in Scandinavia indicate that a demographically viable colonization of the region is linked to the *Ahrensburgian* [177–179], implying that earlier colonization attempts had been unsuccessful. The *Ahrensburgian* is accordingly associated with a range expansion as well as an increase in the number and size of settlements (e.g. [180,181]). The emergence of specialized reindeer economies together with dog-use in the *Ahrensburgian* can thus be seen as an example of positive cultural NC that enabled an efficient adaptation to the harsh GS-1 conditions.

In contrast, the appearance of *Hamburgian* hunters seems strongly correlated with a pronounced abundance of *Rangifer* during the initial stages of faunal succession, first in the southern part of Scandinavia, and then increasingly northwards [176,182]. The disappearance of the *Hamburgian* techno-complex, in this view, represents a concrete example of negative NC, i.e. the failure of an adaptive system: ‘even the most adaptable of creatures will experience limits to its tolerance space, outside of which it is unable to behave adaptively’ ([183], p. 98). In the absence of dogs, and coupled with the climatic downturn at GI-1d most probably associated with a pronounced drop in reindeer populations across the region, *Hamburgian* foragers were no longer able to uphold the cultural buffer mechanisms protecting their niche space from larger scale, independent changes in the environment. Figure 7 summarizes the NC processes investigated in this study.

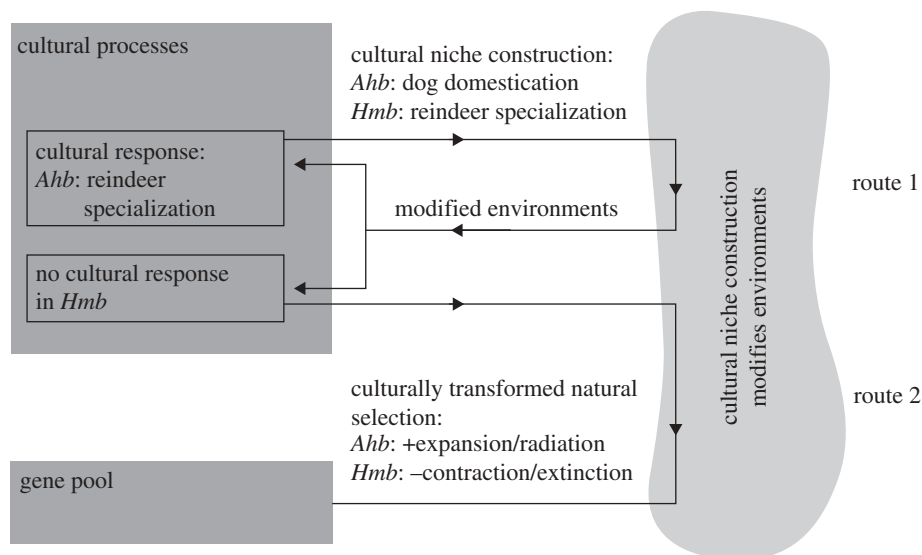


Figure 7. The correlated evolution of dog domestication and use and specialized reindeer economies during the southern Scandinavia Late Glacial provides evidence of what Odling-Smee *et al.* [10] call ‘route 1’ and ‘route 2’ NC processes. The domestication of dogs in or their introduction to southern Scandinavia during the *Ahrensburgian* (*Ahb*) led to the emergence of specialized reindeer economies, possibly involving herd management and early forms of reindeer domestication. In this case, an initial niche-constructing behaviour (dog domestication/use) drove further behavioural changes (specialized reindeer hunting/herding; route 1). The cumulative genetic effects of this NC are seen in the range expansion of *Ahrensburgian* groups and the genetic signature of this expansion in living northern European populations (route 2, positive). In contrast, the adoption of specialized reindeer economies without domesticated dogs during the earliest phase of colonization (*Hamburgian: Hmb*), while initially advantageous, ultimately led to the demise of these pioneering populations (route 2, negative). Modified from Odling-Smee *et al.* [10].

With regards to the methods used here, it should be noted that the search for correlations in analyses with few taxa is difficult [172]. Also, posterior branch support values for some clades used in this study are quite low. Larger, more robust phylogenies will increase our confidence in subsequent trait correlation analyses, yet ‘even partial phylogenetic information provides a better model of the variance in the data than completely ignoring phylogeny and assuming independence’ [34, p. 717]. A particular advantage of the time-depth provided by archaeological data is that it offers the opportunity to integrate stratigraphic and phylogenetic information, and to give directionality to both independent and dependent comparative models. Assigning particular trait states to known or reconstructed nodes would constrain comparative models, facilitating hypothesis testing. Finally, if the disappearance of the *Hamburgian* techno-complex at the GI-1d (Older Dryas) cold spell does represent a cultural ‘extinction’, then the inclusion of such ‘extinct’ taxa in the correlation analysis might distort the results of any comparative analyses [184,185]. Future work could profitably tackle these methodological issues, paralleling similar efforts in evolutionary biology [184], and by making use of some of the freely available software packages discussed by Freckleton [186].

Yet, despite the caveat of statistical non-significance, a comparative analysis of early dog domestication/use in northern Europe and the repeated emergence of specialized reindeer economies has highlighted several interesting features of this process, and a series of additional hypotheses are generated: Did the Late Glacial dogs that dispersed into northern Europe with their human partners belong to the currently dominant

lineages? If yes, current interpretations about the timing and geography of the earliest dog domestication may have to be revised. If not, then repeated but incomplete domestication events have to be considered. Ancient DNA analysis of selected Late Glacial dog remains could be used to establish the relationship between prehistoric and present dog breeds. If extinct breeds can be found, these could be used to track the expansion of human groups in Europe and to investigate the interactions between indigenous populations and later immigrants [187,188]. Likewise, the genetic analysis of Late Glacial reindeer from different periods could aid in exploring their relation to each other, and to extant wild and domestic herds. In addition, targeted archaeological fieldwork might unearth technologies more directly associated with the keeping of dogs or the herding of reindeer.

This paper has built on previous efforts to identify and track prehistoric hunter–gatherer NC signatures [189–191] by exploring a quantitative method that searches for evolutionary correlations of ecologically inherited traits across material culture phylogenies. This methodology—potentially applicable across a wide range of archaeological datasets that act as proxies for past human NC—allows a discrimination of niche-constructing and recipient traits. Given the inherent difficulties in investigating human NC experimentally, archaeological data may provide useful quantitative data on such long-term processes and their evolutionary consequences. The present analysis has not found statistically significant support for sustained NC practices by Late Glacial hunter–gatherers in southern Scandinavia, and future analysis of prehistoric NC should perhaps focus on the more

extensive environmental modifications and domestication efforts of past farming populations. In line with the arguments presented here, palaeontologists [192,193] as well as those concerned with the formation of soils [194,195] and landforms [196–199] have suggested that organisms play a demonstrable role in shaping the physical and adaptive landscapes in which they live, at scales ranging from the geological to the microscopic, from the long term to the transient. Supplementing these disciplines, prehistoric archaeology provides information on specifically human NC at specifically prehistoric timescales.

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