Learning Strategies and Cultural Evolution during the Palaeolithic
Replacement of Neanderthals by Modern Humans Series

Edited by

Takeru Akazawa
Research Institute, Kochi University of Technology
Kochi 782-8502, Japan
akazawa.takeru@kochi-tech.ac.jp

Ofer Bar-Yosef
Department of Anthropology, Harvard University
Cambridge, Massachusetts 02138, USA
obaryos@fas.harvard.edu

The planned series of volumes will report the results of a major research project entitled “Replacement of Neanderthals by Modern Humans: Testing Evolutionary Models of Learning”, offering new perspectives on the process of replacement and on interactions between Neanderthals and modern humans and hence on the origins of prehistoric modern cultures. The projected volumes will present the diverse achievements of research activities, originally designed to implement the project’s strategy, in the fields of archaeology, paleoanthropology, cultural anthropology, population biology, earth sciences, developmental psychology, biomechanics, and neuroscience. Comprehensive research models will be used to integrate the discipline-specific research outcomes from those various perspectives. The series, aimed mainly at providing a set of multidisciplinary perspectives united under the overarching concept of learning strategies, will include monographs and edited collections of papers focusing on specific problems related to the goals of the project, employing a variety of approaches to the analysis of the newly acquired data sets.

Editorial Board

Stanley H. Ambrose (University of Illinois at Urbana-Champaign), Kenichi Aoki (Meiji University), Emiliano Bruner (Centro National de Investigacion Sobre la Evolution Humana), Marcus W. Feldman (Stanford University), Barry S. Hewlett (Washington State University), Tasuku Kimura (University of Tokyo), Steven L. Kuhn (University of Arizona), Yoshihiro Nishiaki (University of Tokyo), Naomichi Ogihara (Keio University), Dietrich Stout (Emory University), Hiroki C. Tanabe (Nagoya University), Hideaki Terashima (Kobe Gakuin University), Minoru Yoneda (University of Tokyo)

For further volumes:
http://www.springer.com/series/11816
Alex Mesoudi • Kenichi Aoki
Editors

Learning Strategies and Cultural Evolution during the Palaeolithic

Springer
This volume is being published as part of a 5-year research project, funded by the Japan Min-
istry of Education, Culture, Science, and Technology (Monbukagakusho), on the “Replacement
of Neanderthals by Modern Humans (RNMH).” There are two basic premises of the RNMH
project. First, Neanderthals were replaced or assimilated by modern humans (Homo sapiens).
Second, the replacement or assimilation was driven by cultural differences between competing
Neanderthal and modern human groups, potentially due to some advantage(s) associated with
the culture(s) of modern humans.

The current volume focuses on how differences in the cultures of Palaeolithic or Stone
Age hominin societies might arise as a result of differences in learning strategies, social and
demographic factors, and so on. This includes the knotty inverse problem of inferring learning
strategies from actual trajectories of cultural change. With the exception of one chapter, the
replacement process itself is not addressed.

The majority of contributors to this volume are not members of the RNMH project. Nev-
nevertheless, we have invited them to submit chapters, because they are leading anthropologists,
archaeologists, biologists, and psychologists who are directly involved in the effort to decipher
hominin cultural change and cultural diversity during the Palaeolithic (see list of contributors).

In addition to the contributors, we wish to thank Jelmer Eerkens, Yasuo Ihara, Jeremy
Kendal, Steven Kuhn, Charles Perreault, Katsuhiro Sano, Jonathan Scholnick, Pontus Strim-
ling, Jamie Tehrani, Claudio Tennie, and Taro Yoshida, for valuable comments on and
constructive reviews of the chapters. Their input is gratefully acknowledged.

This volume was made possible by Monbukagakusho grant 22101004 and indirectly by the
Japanese taxpayer. We are deeply grateful for their support and interest.

Finally, we thank Ken Kimlicka and Taeko Sato of Springer, Japan for their guidance
through the intricacies of the publication process.

Durham, UK
Tokyo, Japan

Alex Mesoudi
Kenichi Aoki
## Contents

1. **Introduction to “Learning Strategies and Cultural Evolution During the Palaeolithic”**
   
   Kenichi Aoki and Alex Mesoudi

2. **Factors Limiting the Number of Independent Cultural Traits That Can Be Maintained in a Population**
   
   Laurel Fogarty, Joe Yuichiro Wakano, Marcus W. Feldman, and Kenichi Aoki

3. **The Evolution of Culturally Transmitted Teaching Behavior**
   
   Wataru Nakahashi

4. **A Population-Genetics Based Model for Explaining Apparent Cultural Continuity from the Middle to Upper Palaeolithic in Eurasia**
   
   Yutaka Kobayashi, Seiji Kadowaki, and Masaki Naganuma

5. **Mobility and Cultural Diversity in Central-Place Foragers: Implications for the Emergence of Modern Human Behavior**
   
   L.S. Premo

6. **Behavioral Modernity and the Cultural Transmission of Structured Information: The Semantic Axelrod Model**
   
   Mark E. Madsen and Carl P. Lipo

7. **Inferring Learning Strategies from Cultural Frequency Data**
   
   Anne Kandler and Adam Powell

8. **Simulating Geographical Variation in Material Culture: Were Early Modern Humans in Europe Ethnically Structured?**
   
   Mirna Kovacevic, Stephen Shennan, Marian Vanhaeren, Francesco d’Errico, and Mark G. Thomas

9. **Transmission of Cultural Variants in the North American Paleolithic**
   
   Michael J. O’Brien, Briggs Buchanan, Matthew T. Boulanger, Alex Mesoudi, Mark Collard, Metin I. Eren, R. Alexander Bentley, and R. Lee Lyman

10. **Experimental Studies of Cumulative Culture in Modern Humans: What Are the Requirements of the Ratchet?**
    
    Christine A. Caldwell

11. **Learning in the Acheulean: Experimental Insights Using Handaxe Form as a ‘Model Organism’**
    
    Stephen J. Lycett, Kerstin Schillinger, Marius Kempe, and Alex Mesoudi

**Index**

vii
Contributors

**Kenichi Aoki** Organization for the Strategic Coordination of Research and Intellectual Properties, Meiji University, Tokyo, Japan

**R. Alexander Bentley** Department of Archaeology and Anthropology, University of Bristol, Bristol, UK

**Matthew T. Boulanger** Department of Anthropology, University of Missouri, Columbia, MO, USA

**Briggs Buchanan** Department of Anthropology, University of Tulsa, Tulsa, OK, USA

**Christine A. Caldwell** Psychology, School of Natural Sciences, University of Stirling, Stirling, UK

**Mark Collard** Human Evolutionary Studies Program and Department of Archaeology, Simon Fraser University, Burnaby, Burnaby, BC, Canada

Department of Archaeology, University of Aberdeen, Aberdeen, UK

**Francesco d’Errico** CNRS (Centre National de la Recherche Scientifique), UMR (Unité Mixte de Recherche) 5199, PACEA (De la Préhistoire à l’Actuel: Culture, Environnement et Anthropologie), Université Bordeaux 1, Talence, France

Department of Archaeology, History, Cultural Studies and Religion, University of Bergen, Bergen, Norway

**Metin I. Eren** Department of Anthropology, University of Missouri, Columbia, MO, USA

**Marcus W. Feldman** Department of Biology, Stanford University, Stanford, CA, USA

**Laurel Fogarty** Department of Biology, Stanford University, Stanford, CA, USA

**Seiji Kadowaki** University Museum, Nagoya University, Nagoya, Japan

**Anne Kandler** Department of Mathematics, City University London, London, UK

**Marius Kempe** Department of Anthropology and Centre for the Coevolution of Biology and Culture, Durham University, Durham, UK

**Yutaka Kobayashi** Department of Management, Kochi University of Technology, Kami-city, Japan

**Mirna Kovacevic** CoMPLEX (Centre for Mathematics and Physics in the Life Sciences and Experimental Biology), University College London, London, UK

Research Department of Genetics, Evolution and Environment, University College London, London, UK
Contributors

Carl P. Lipo  Department of Anthropology and IIRMES, California State University at Long Beach, Long Beach, CA, USA

Stephen J. Lycett  Department of Anthropology, University at Buffalo SUNY, Buffalo, NY, USA

R. Lee Lyman  Department of Anthropology, University of Missouri, Columbia, MO, USA

Mark E. Madsen  Department of Anthropology, University of Washington, Seattle, WA, USA

Alex Mesoudi  Department of Anthropology and Centre for the Coevolution of Biology and Culture, Durham University, Durham, UK

Masaki Naganuma  Center for Ainu & Indigenous Studies, Hokkaido University, Sapporo, Japan

Wataru Nakahashi  School of Advanced Sciences, SOKENDAI (The Graduate University for Advanced Studies), Hayama, Japan

Michael J. O’Brien  Department of Anthropology, University of Missouri, Columbia, MO, USA

Adam Powell  Palaeogenetics Group, Institute of Anthropology, University of Mainz, Mainz, Germany

L.S. Premo  Department of Anthropology, Washington State University, Pullman, WA, USA

Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Kerstin Schillinger  Department of Anthropology, University of Kent, Canterbury, UK

Stephen Shennan  Institute of Archaeology, University College London, London, UK

Mark G. Thomas  Research Department of Genetics, Evolution and Environment, University College London, London, UK

Marian Vanhaeren  CNRS (Centre National de la Recherche Scientifique), UMR (Unité Mixte de Recherche) 5199, PACEA (De la Préhistoire à l’Actuel: Culture, Environement et Anthropologie), Université Bordeaux 1, Talence, France

Joe Yuichiro Wakano  School of Interdisciplinary Mathematical Sciences, Meiji University, Tokyo, Japan
Introduction to “Learning Strategies and Cultural Evolution During the Palaeolithic”

Kenichi Aoki and Alex Mesoudi

Abstract
In this introductory chapter, we first provide some background on the two major recurrent themes of the volume, i.e. learning strategies of individuals, and social and demographic characteristics of populations. This is followed by a brief summary of each chapter. Then, we conclude with some thoughts on why and how the methods and findings presented in this volume are relevant to, and might inform our understanding of, the replacement of Neanderthals by modern humans (Homo sapiens).

Keywords
Learning strategy • Demographic factors • Cultural change • Cultural diversity

This volume provides up-to-date coverage on the theory of cultural evolution as is being used by anthropologists, archaeologists, biologists, and psychologists to decipher hominin cultural change and cultural diversity during the Palaeolithic. The contributing authors are directly involved in this effort, and the material presented includes novel approaches and findings. The common theoretical framework of the volume is that cultural change constitutes a dynamic evolutionary system, which can be analyzed using tools and methods derived from the theory of biological evolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985).

Various chapters show how learning strategies in combination with social and demographic factors (e.g. population size and mobility patterns) predict cultural evolution in a world without the printing press, radio, or the internet—which is to say that cultural traits can be acquired from others only by directly observing their actions or the results of these actions. Also addressed is the inverse problem of how learning strategies may be inferred from actual trajectories of cultural change, for example as seen in the North American Palaeolithic. Mathematics and statistics, a sometimes necessary part of theory, are explained in elementary terms where they appear, with details relegated to appendices. Full citations of the relevant literature will help the reader to further pursue any topic of interest.

1.1 Learning Strategies
Before proceeding it will be useful to briefly explain what the contributing authors and the editors mean by a “learning strategy.” A learning strategy is the way in which an organism combines individual learning and social learning, either simultaneously or sequentially, and its relative dependence on each. Here, individual learning occurs when the organism depends on personal experience to gather information, e.g. by trial-and-error. Social learning refers to obtaining information from other organisms, e.g. by imitation. Biases associated with social learning in the choice of whom to copy are also an integral part of a learning strategy.
Much theoretical work has been directed toward examining the adaptiveness of various social learning biases (Boyd and Richerson 1985; Laland 2004), such as “success bias” and “prestige bias” which entail preferentially copying a successful or a prestigious individual, respectively (Henrich and Gil-White 2001; Nakahashi et al. 2012), and “conformist bias” which entails copying the majority cultural behavior of one’s group (Henrich and Boyd 1998; Wakano and Aoki 2007; Nakahashi 2007; Kendal et al. 2009; see Aoki and Feldman 2014 for a comprehensive review). “Teaching” represents a powerful adjunct to social learning, where the individual being copied (the “teacher”) modifies his/her behavior to facilitate social learning by a naïve individual (the “pupil”) (Caro and Hauser 1992). Still another aspect of learning—in particular the learning of complex technical knowledge comprising various different skills—is that cultural traits may be interdependent, some serving as prerequisites for the acquisition of others. Several chapters in this volume tackle the question of how different learning strategies might structure population-level cultural change and variation, and the even more difficult problem of how to identify these population-level signatures in the often sketchy archaeological record.

1.2 Social and Demographic Factors

Many archaeologists and anthropologists currently emphasize size and demographic factors in interpreting “sudden” and “dramatic” changes in stone tools or other cultural artefacts during the Late Pleistocene (between 130,000 and 10,000 years ago), in particular the “creative explosions” (Kuhn 2012) of the African late Middle Stone Age and the European Upper Palaeolithic (Shennan 2001; Henrich 2004; Kline and Boyd 2010; Zilhão et al. 2010; Mesoudi 2011; Clark 2011; Kuhn 2013). In fact, theoretical studies have repeatedly shown that population size can have a large effect on cultural evolutionary rate and cultural diversity (Shennan 2001; Henrich 2004; Strimling et al. 2009; Mesoudi 2011; Lehmann et al. 2011; Aoki et al. 2011; Kobayashi and Aoki 2012; Aoki 2013), as can interconnectedness of subpopulations (Powell et al. 2009; Perreault and Brantingham 2011). Transmission chain experiments conducted in the laboratory also provide some support for a link between population (or group) size and cultural complexity (Derekx et al. 2013; Muthukrishna et al. 2014; Kempe and Mesoudi 2014; but see Caldwell and Millen 2010).

However, archaeological evidence on the role of demographic factors is inconclusive or even contradictory. Two recent studies of Late Pleistocene South Africa are particularly relevant. Clark (2011) looked for signatures of population growth and/or demographic stress in an increase of diet breadth (e.g. the use of non-preferred prey animals), obtaining some support for an association with the heightened creativity of Howieson’s Poort. But, as Clark (2011) is careful to note, this association is open to an alternative interpretation, namely that rapid cultural change produced new tools, which were used to exploit novel resources. Klein and Steele (2013) (see also Klein 2008, Box 1) observed that edible shellfish remains from Middle Stone Age middens are significantly larger than those from Later Stone Age middens. If shellfish size reflects human collection intensity, then this finding suggests that the precocious appearance of modern behaviors in the Still Bay and Howieson’s Poort may not have been associated with population growth.

The claim that pre-contact Neanderthals in Spain used necklaces made of shells strung together as body ornamentation 50,000 years ago is also laden with ambiguity, in more ways than one. Zilhão et al. (2010) regards this as evidence for the cognitive equality of Neanderthals and modern humans, “support[ing] models of the emergence of behavioral modernity as caused by technological progress, demographic increase.” However, perforation may not have been anthropogenic, and shells with naturally-formed holes of appropriate size for threading may have been selectively collected. Moreover, according to Prüfer et al. (2014), Neanderthal population size in the Altai region as estimated from genetic data shows a continual decrease after one million years ago, which is not true of various current modern humans. Similarly, Mellars and French (2011) argue for small population size in pre-contact European Neanderthals (MTA) compared to the Aurignacian. By implication, both Neanderthals and modern humans achieved the same cultural level, in spite of a difference in population size. Note, however, modern human beads occur much earlier—as early as 100,000 years ago in the Levant (Vanhaeren et al. 2006)—so perhaps population size did play a role.

In addition, statistical analyses of ethnographic hunter-gatherers have failed to detect an association between population size and the number of food-getting tools (Collard et al. 2005; Read 2006). On the other hand, ethnographic food-producing societies (e.g. small-scale farmers and herders) do conform to the theoretical prediction that population size and the number of food-getting tools should be positively correlated (Kline and Boyd 2010; Collard et al. 2013). Possible explanations for these contrasting results have been suggested, including higher degrees of specialization in the latter societies.

A fundamental problem in human evolution is how to account for an apparently abrupt cultural change, without invoking a major genetic change in cognition (e.g. innovativeness), for which there is at present no strong evidence (Klein 2008). Needless to say, absence of evidence does not constitute evidence of absence, and we are obliged to keep an open mind (Akazawa et al. 2013). Richerson et al. (2009)
(see also Richerson and Boyd 2013) discuss the possibility of spontaneous transitions between stable regimes—a small population at a low cultural level and a large population at a high cultural level. Developing this idea further and based on an explicit mathematical model, Aoki (2015) shows that a saltatory cultural change can be triggered by a gradual evolutionary change in the genetic basis for innovativeness. This scenario is not inconsistent with the “neural hypothesis,” a recent version of which invokes “a neural change that promoted the extraordinary modern human ability to innovate” (Klein 2008, p. 271). However, this neural change would not be attributable to just one “fortuitous mutation” in a major gene 50,000 years ago.

1.3 Summary of the Chapters

This volume comprises ten chapters, which use a range of methods to address different aspects of cultural evolution during the Palaeolithic.

In Chap. 2, Fogarty et al. present a theoretical analysis examining the modes and pathways of social learning, and how they affect the expected number of cultural traits maintained in a population. Specifically, they compare random oblique, best-of- $K$ (an example of direct bias, which entails a preference for a particular variant of a cultural trait), success bias, and one-to-many. Given the current emphasis among archaeologists and anthropologists on demographic factors, the effect of population size is also investigated, as is the less acknowledged role of innovation.

Fogarty et al. classify cultural traits as simple or complex, depending on the ease or difficulty of acquisition by social learning and innovation. Assuming an innate upper limit to the number of cultural traits that can be imagined—a limitation that may possibly be overcome by a mechanism analogous to “embedding” in linguistics—they show that the number of simple cultural traits may saturate as population size increases, in which case a statistical association between the two variables is not predicted. At smaller population sizes, there is a major effect of the mode of social learning. By contrast, the relation between the number of complex cultural traits and population size is approximately linear and almost identical for all modes of social learning investigated. This is because most of the complex cultural traits that are maintained in the population can be accounted for by innovation alone, which raises the question of whether such traits qualify as “cultural” (Whiten et al. 1999).

In Chap. 3, Nakahashi describes and analyzes a new mathematical model for the evolution of teaching that is culturally transmitted rather than genetically determined. Teaching is here defined sensu Caro and Hauser (1992) as a knowledgeable individual (the teacher) altering its behavior in the presence of a naïve individual (the pupil), suffering a cost to do so, and thereby promoting social learning by that naïve individual. In this model, there are an infinite number of cultural traits, which are acquired by either individual learning or social learning, and where their acquisition entails a viability cost. Moreover, cultural traits are either beneficial or neutral, and only the former are assumed to contribute to fertility.

Nakahashi shows that teaching behavior can evolve culturally—i.e., teachers can invade and exist at a stable positive equilibrium—if a teacher can socially transmit more cultural traits than a non-teacher. However and surprisingly, it cannot evolve if teaching merely improves the accuracy of social learning by pupils. This latter result differs from the predictions of previous theoretical work that assume genetic determination of teaching behavior (Fogarty et al. 2011).

The next three chapters deal with structured populations. Kobayashi et al. (Chap. 4) directly address the cultural correlates of the replacement of Neanderthals (and other archaic humans) by modern humans. Their chapter begins with a detailed review of the archaeology of the Middle to Upper Palaeolithic transition in various parts of Eurasia, which suggests varying degrees of cultural continuity during/after the arrival of modern humans. In particular, China is apparently characterized by the late persistence of primitive core-and-flake industries (Norton and Jin 2009; Bar-Yosef and Wang 2012). Several Upper Palaeolithic industries in western Eurasia, e.g., the Emiran in the Levant and the Early Baradostian in the Zagros, may also exhibit recognizable elements of the preceding Middle Palaeolithic.

Kobayashi et al. describe a new model in which an invading modern human population has a demographic advantage (a higher relative growth rate), but receives unidirectional cultural influences from the indigenous archaic population. The cultural traits that the modern humans acquire from the archaics are assumed to be of a different kind from those that may be contributing to the demographic advantage of the former. Using approximate analytical methods and agent-based simulations, these authors show that biological replacement can be associated with either the rapid disappearance, the gradual disappearance, or the persistence of these autochthonous cultural traits. Gradual disappearance or persistence, i.e., cultural continuity, is predicted when a small modern human population invades a region with a relatively unfavorable physical environment. Importantly, cultural continuity is not an indicator of biological continuity.

The pattern of mobility within a geographically-structured population is recognized to be an important demographic factor in cultural evolution, through its effect on the variety of social learning opportunities (Powell et al. 2009). In addition, mobility may place a limit on the number of portable artefacts (Torrence 1983; Shott 1986). Premo (Chap. 5) gives an excellent introduction to residential mobility and logistical