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# Multiple Optima in Hoabinhian flaked stone artefact palaeoeconomics and palaeoecology at two archaeological sites in Northwest Thailand <sup>☆</sup>



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## ABSTRACT

High resolution analyses of flaked stone artefact technology coupled with palaeoecological reconstruction from oxygen isotope analyses of freshwater shells from two rockshelter in the highlands of Northwest Thailand are described. Previously undocumented scales of technological variation are observed in response to environmental variation across the prehistoric landscape and through time. Three models of human behavioural ecology are used to test predictions about how foragers adapted their stone artefact technology to variation in climatic conditions and proximity to stone resources. These models are found to be problematic and are modified by including multiple optima that reflect the specific ecological conditions under consideration.

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## Introduction

Despite an almost continuous tradition of archaeological research in seasonal tropical forests of mainland Southeast Asia since the 1960s, very little has been discovered about how human foragers organised their stone artefact technology under varying environmental conditions. Many studies of mainland Southeast Asian prehistoric hunter-gatherers are concerned with descriptive and definitional issues and do not encompass explanations of human behaviour or human-environment interactions (Forestier et al., 2008, 2005; Pookajorn, 1995; Treerayapiwat, 2005). That said, general statements have been made about technological change and climate change during the Pleistocene and Holocene in mainland Southeast Asia (Anderson, 1990; Gorman, 1972). Motivated by these statements, some previous work has attempted to understand human adaptation to different environments. For example, Mudar and Anderson (2007) analyse the Pleistocene fauna from Lang Rongrien in southern Thailand and interpret the assemblage as evidence of the human occupants adapting to the colonisation of a new region. Shoocongdej's (2006) work on the stone artefacts and faunal remains from the 35,000 year old sequence at Tham Lod rockshelter in northwest Thailand is similarly framed as a study of adaptive strategies in response to the availability of local re-

sources. A more explicitly theorised approach was taken by Shoocongdej (2000) who drew on general ecological principles in her analysis of the late Pleistocene record at Lang Kamnan Cave in western central Thailand. Shoocongdej describes how the assemblage indicates changes mobility strategies that reflect human adaptations to variability in seasonal resource availability.

Thanks to these pioneering studies, a foundation has been established on which theoretically robust and specialised conceptual frameworks can now be built to articulate directly between the archaeological record and environmental records. This paper builds on Shoocongdej's work at Tham Lod in an attempt to remedy this gap in knowledge by examining the relationship between human foragers and their environment using flaked stone artefacts deposited over a 35,000 year period at two sites in northwest Thailand (Fig. 1). The environmental record is examined through analysis of oxygen and isotopes from freshwater bivalves recovered during excavations at the same sites.

The case study presented here focuses on two rockshelter sites in Mae Hong Son province of northwest Thailand. Tham Lod and Ban Rai were excavated in 2001–2007 by a team of Thai archaeologists directed by Dr. Rasmi Shoocongdej of Silpakorn University. The sites are located in a very rugged location, resulting in substantial ecological variation from the base of the valleys to the tops of the ridges over relatively small horizontal distances. Tham Lod is located in a valley, close to a perennial river while Ban Rai is located high on the side of a steep valley. Although the two sites are only about 10 km apart, differences in the elevation of the two sites result in substantial differences in access to water and stone for making artefacts. This paper compares how people

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managed their stone artefact technologies at these two different locations over the late Pleistocene and early Holocene. In particular it looks at how people used stone artefact technology to manage the different levels of ecological risk that they were exposed to at the two locations, and how these changed over time. The substantial differences in the ecology and resource availability of the two sites creates a good opportunity to measure the relative importance of general climatic conditions versus small-scale variation in proximity to resources for understanding how people used stone artefact technology to mediate risk.

### Modelling prehistoric behaviour at the two sites

The most abundant cultural materials recovered from the two sites are flaked stone artefacts, so the stone artefacts were analysed to investigate how people adapted to environmental change. As a first general approximation at understanding human–environment relations at the two sites I will use behavioural ecological models derived from animal ethology. There are two critical limitations of these models in archaeological studies. First, while it is true that animals have simple heuristics with low decision loads that lead to near-optimal behaviour, humans are different because the trade-offs relating to our survival are far more complex and have much higher decision loads that can obscure the links between environmental conditions and behavioural adaptations (Sterelny, 2004). A second issue raised by Sterelny (2004) is that the incompleteness of the archaeological record and ambiguities involved in reconstructing behavioural strategies mean that models may, at best, only be tested for qualitative consistency of the predictions of the model and patterns of inferred behaviour. Despite these limitations, behavioural ecological models applied to archaeological data have produced insights about prehistoric human behaviour (Bird and O'Connell, 2006; Surovell, 2003) and it is the success of these applications that motivates this study.



Fig. 1. Map showing the general location of Tham Lod and Ban Rai.

Behavioural ecological models have divided forager decision-making into four discrete dimensions: prey choice (or diet breadth, what resource to seek); patch choice (where to seek the resource); time allocation (how long to spend seeking for each alternative); and social foraging (with whom to forage or share resources and information) (Smith, 1983). Stone artefact assemblages are typically not suitable for answering questions about prey choice because this relates specifically to what is included in a forager's diet and usually requires information about the energetic return rates of resources which are often equated to the biological species exploited. Sources of stone could be conceived of as 'prey' but they are better modelled as patches rather than prey because their location is usually static over the long term and there are no 'recommended daily intake' values for stone that correspond to fundamental human caloric and nutritional needs (Jochim, 1989). However, stone artefacts assemblages are well suited to questions about patch choice, time allocation and social organisation. These three dimensions can be investigated with the widely-used behavioural ecology models described below.

The Central Place Model is a formal expression of the relationships that can exist between the extent that a resource is used and the time spent obtaining and transporting that resource (Orians and Pearson, 1979). This model has seen extensive use by archaeologists and anthropologists working with forager groups (Beck et al., 2002; Beck, 2008; Bettinger et al., 1997; Bird, 1997; Metcalfe and Barlow, 1992). I follow Beck et al. (2002) in predicting that the further a piece of stone has been transported, the more work is extracted from that piece to justify the effort invested in transport. The payoff of the investment in time in transport is the increased return of work done by the stone. For relatively simple flaked stone artefacts where retouch of individual pieces is rare, extraction of work can be equated with assemblage-level reduction intensity. Assemblage reduction intensity refers to flaking of stone pieces to create edges to perform tasks such as cutting, scraping, sawing and chopping. More intensive reduction means more effort invested to produce these useful edges. This is similar to the field processing model, a more specific formulation of the Central Place Model. This model focuses on in-field processing or pre-processing of artefacts before they arrive at their final destination. For example assemblages with pieces that show signs of extensive cortex removal and less than expected pieces with cortex might reflect in-field detachment of unwanted material to reduce weight and increase the artefact's utility prior to transport (Clarkson, 2006).

The Patch Choice Model predicts that potential foraging locales will be exploited in order of the return rates expected from searching for and handling resources within each, adjusted for the costs of traveling (MacArthur and Pianka, 1966). The Marginal Value Theorem is a formal expression of how long a forager should remain in a patch, taking into account declining return rates over the time that foragers exploit a patch (Charnov, 1976). The key prediction of this model is that the optimal forager should leave any patch when it is depleted to the point where foraging elsewhere will yield higher returns, taking travel costs into account (Smith 1983). In brief, people are expected to choose the location and duration of patches they inhabit according to the ease of extracting resources in those patches relative to others nearby. Ethnographic data indicate that this is frequently observed amongst hunter-gatherers (Beckerman, 1983; O'Connell and Hawkes, 1981; Smith, 1991). In archaeological terms, these predictions suggest that areas or periods of higher patch yields will have evidence of more intensive human occupation as people exploit a reliable and abundant resource.

The Optimal Dispersion Model predicts optimum forager settlement patterns under different environmental conditions, assuming foragers are minimising round-trip travel costs from resource to

settlement location. As resources become more mobile and clumped, foragers are predicted to increasingly aggregate into larger groups and when resources are more stable and evenly distributed, foragers will increasingly disperse into smaller groups (Horn, 1968). In anthropological terms, the model predicts that foragers will increasingly adopt a residential settlement pattern in stable/evenly dispersed environments because small frequently-relocating settlements will always be near resources (Cashdan, 1992; Smith, 1983). On the other hand, a logistical settlement pattern is a better strategy in mobile/clumped environments, with larger settlements from which small groups of people venture out to collect resources at distant or constantly shifting patches (Binford, 1980; Harpending and Davis, 1977; Heffley, 1981). In archaeological terms, a residential settlement will show signs of a relatively low investment in economising technology because the group can easily relocate to new stone sources, while a logistical settlement will show signs of higher investment in efficiency because the group cannot easily relocate and the availability of stone sources is less predictable. Put simply, under difficult conditions people will tend to be relatively more dispersed, mobile and invest more in their stone artefact technology and under better conditions people will be relatively less mobile, more clumped and invest less in their stone technology.

Use of these models involves a trade-off between the advantages of their generality, simplicity and readily testable predictions and the disadvantage of some unrealistic assumptions of random distributions of resources and random forager search patterns (Winterhalder, 2002). My view is that the simplicity and generality of the models is advantageous because they provide a useful heuristic that gives robust and non-accidental insights into the mechanisms (i.e. systems that produce some phenomenon, behaviour or function) that influence forager behaviour in regular but not exceptionless ways (Glennan, 2010). In the following section I describe some of the specific conditions that people found themselves in during their occupation of Ban Rai and Tham Lod. I also describe the details of how I measured foragers' responses to changes in these conditions to test the predictions of the three models described above.

## Background to the two sites

### *Physical properties of the study area*

The wider area surrounding the sites is part of the southern extension of the Shan mountain ranges (Santisuk, 1988: 11), which in turn are part of a series of discontinuous limestone outcrops following the north–south alignment of mountain ranges extending from Malaysia to Myanmar (Dunkley, 1985). These uplands are a formation of hills and mountains with prominent and very steep pinnacles and ridges of limestone. The landscape that contains the two archaeological sites covers an area of about 1000 km<sup>2</sup> which is extremely rugged with 47% of the landscape area consisting of slopes over 60% (Dunkley, 1985). The Permian limestone karst that contributes these slopes rises up to 1000 m above the valley floors and accordant summits (possibly representing ancient erosion surfaces) are prominent at the top of the karst towers. Drainage in the karst systems determined the formation of extant caves (as underground streams) and rockshelters (though sinkhole evolution). Even today, drainage is mostly underground and as the landscape has evolved and eroded, numerous deep caves and cliffs have become exposed and left hanging above the valley floor. The surface flow of the few waterways in the region is also a feature of the underground drainage, with most streams ending in a drop into a limestone sinkhole. This includes the Lang River which drops into a sinkhole about 600 m from Tham Lod.

### *The distribution and quality of raw materials for stone artefact manufacture*

The distribution of non-carbonate lithologies in the study area is closely related to hydrological activity. Waterways erode through the limestone to expose non-carbonate sedimentary rocks, as well as carrying gravels from long distance upstream sources. Most streambeds in the study area are mantled by clasts from gravels to cobbles which in turn are partially covered by sandy silts. These stream deposits are composed of quartzite and metaquartzite (50%) with smaller proportions of sandstone (20%) mudstone (20%) and other sedimentary and metamorphic lithologies (10%) (Kiernan, 1991). Similarly composed deposits are also found on terraces up to 15 m above the current river levels although these are generally overlain by 0.5–1 m of sandy loam. These hillside deposits tend to be composed of sandstone and mudstone with no quartzite. They include high terrace deposits and relict cobbles probably representing lag clasts from very ancient terrace sediments that have been extensively dissected and reworked. Compared to streambed and terrace deposits, clasts in hillside deposits are very weathered and rarely intact since they are highly susceptible to erosion causing blocky disintegration. Average weathering depth of rinds on sandstone clasts in these hillside assemblages is 3.4 mm, compared to 1.1 mm for rinds on the low terraces (Kiernan, 1991).

There are two archaeological implications of this distribution of non-carbonate lithologies. First is that fine grained sedimentary raw materials such as chert and silcrete are extremely rare in the landscape of the study area, with coarser-grained raw materials such as quartzite and sandstone abundant instead. These coarser grained raw materials are less predictable and flexible in their flaking characteristics and their reduction results in a relatively restricted range of forms. The second implication is that the quality of rock declines as distance from a waterway increases. Streambed and low terrace deposits are up to 50% quartzite, while high terrace and hillside deposits tend to have high proportions of sandstone and mudstone and no quartzite. Of these three types of rock, quartzite is most desirable for making stone artefacts because the grains in quartzite are most tightly bound, making it relatively tough and able to hold a more durable working edge over a variety of edge angles and over a longer use-life, compared to mudstone and sandstone. Sandstone and mudstone, on the other hand, are sedimentary rocks with a less dense matrix that has not been compressed by heat and pressure. This lower toughness means that the morphological possibilities for durable working edges are limited to very obtuse angles and these edges have relatively short use-lives because the rock abrades relatively quickly during contact.

## Excavations and chronology

### *Tham Lod*

Tham Lod rockshelter is about 250 m away from the Lang River and about 15 m above current high water levels. It is on the edge of a relatively flat area surrounded by steep low hills and karst formations. The overhang of the rockshelter is part of a long cliff that is as a circular collapsed limestone doline about 100 m in diameter (Khaokiew, 2004). The elevation of the rockshelter is about 640 m amsl (Shoocongdej, 2006). Typical of this elevation, the surrounding vegetation is a mix of semi-evergreen forest and dry dipterocarp forest.

Excavations at Tham Lod were conducted in three areas. Time constraints limited this analysis to the deepest trench, which was located adjacent to the back wall of the shelter and covered an area of 2 × 4 m to a depth of 450 cm below the surface. The current surface of Tham Lod is not completely sheltered from rainfall and

staining on the back wall of the rockshelter suggests that water has flowed through the deposit. This water flow may explain the lightly cemented quality of the excavated sediments and the very poor organic preservation. The homogeneity of sediments at Tham Lod, probably caused by water flow from the cliff face, makes it difficult to discern depositional units. Stratigraphic data have previously been described in detail by Shoocongdej (2006) so here I just summarise the key details. Excavation units between the ground surface and unit six (about 12,000 BP) are highly likely to have been disturbed by two human burials and recent activity that has intruded modern objects into the sediments. The units below unit six, which appears to represent a roof fall event, show no signs of major disturbance, and are assumed to have a high degree of stratigraphic integrity. Dating of the sites using radiocarbon and thermoluminescence methods suggests continuous human occupation from about 40,000 BP to about 10,000 BP and steady accumulation of sediment over that period (Table 1).

### Ban Rai

In stark contrast to Tham Lod, Ban Rai is perched high up on the southern side of a steep valley. It is about 10 km from Tham Lod in the same river valley. However, the distance from the river to the site is about 200 vertical metres for Ban Rai, taking over an hour to make the difficult ascent from the river to the site. To the west of the site the river drains into a sinkhole. The site is located about 760 m amsl, 120 m higher than Tham Lod. The vegetation immediately surrounding the site is semi-evergreen, similar to Tham Lod, but with a greater bamboo component. Just upslope from the rockshelter is an ecotone where a mix of dry dipterocarp and montane forests occur. Excavations at Ban Rai covered a larger area than Tham Lod, sixteen square metres, but were less deep, ending at sterile sand at about two and a half metres below the surface. The chronology of Ban Rai is quite different to Tham Lod, with a relatively short early Holocene sequence. Human occupation at Ban Rai appears to have been continuous from about 10,000 BP and ending at about 6000 BP (Table 1).

## Methods

### Stone artefact analysis

In moving from the general behavioural ecology models described above to specific tests of their predictions with the stone

artefact assemblages it is necessary to identify a variable that has a strong influence on behavioural strategies across a broad range of contexts as well as having the quality of being reliably measured in the stone artefact assemblages (Winterhalder, 1981). There are four main hypotheses proposing a general variable that strongly influences technological strategies amongst hunter-gatherers: Oswalt's (1976) hypothesis that the nature of the food exploited is the key variable, Torrence's (1989) hypothesis that it is risk of subsistence failure, Shott's (1986) hypothesis that it is residential mobility and Shennan's (2001) hypothesis that population size is the primary variable controlling technological diversity and complexity. To identify which of these four hypotheses used to explain toolkit variation is the most general and important, Collard et al. (2005) conducted a stepwise multiple regression analysis of technological, ecological, subsistence, mobility and population data from 20 hunter-gatherer groups worldwide. Their results supported Torrence's hypothesis that risk of resource failure is the primary influence on hunter-gatherer technology. Although there are a number of different definitions of and dimensions to risk, I follow Bamforth and Bleed (1997) in defining risk as both the probability of failure and the cost of failure to meet subsistence requirements. Since the focus here is on stone artefacts, I further narrow the second part of this definition to technological risk, which refers to the risk of running out of usable tools or raw material and being unable to perform key activities (Elston and Raven, 1992: 33–34).

The work of Collard et al. (2005) suggests that risk is a sufficiently general quality relating to stone artefact technological variation. This makes risk a suitable currency for operating behavioural ecology models (Stephens, 1990; Winterhalder, 1990). For example, the Patch Choice Model predicts that individuals will stay longer in a patch when in a more profitable patch relative to other patches, as the distance between patches increases and when the environment as a whole is less productive. Staying in a patch for longer is equivalent to minimising risk by minimising exposure to other patches that probably yield less. The Central Place Model predicts that the further a forager goes the more they will return with and the more they will get out of what they bring back. This is equivalent to minimising risk by spreading it over time and space; by increasing the load with distance the forager maintains an average return rate given the travel and transport costs for all trips and smooths out variation in returns for trips of different lengths.

Efforts to directly measure risk minimisation behaviours in stone artefact assemblages have led to a variety of sophisticated

**Table 1**  
Radiocarbon ( $^{14}\text{C}$ ) and thermoluminescence (TL) age determinations for the Tham Lod and Ban Rai excavation sites. All  $^{14}\text{C}$  ages are calibrated ( $\pm 1\sigma$  error) in years before the present (BP) notation, where present is 1950 AD.

Site name/excavation unit	Dated material	Lab code	Age (yr $\pm 1\sigma$ )	Calibrated $^{14}\text{C}$ age (yr BP $\pm 1\sigma$ )
<i>Tham Lod</i>				
TL4	Organic sediment	Beta-168223	12,100 $\pm$ 60	14,070 $\pm$ 140
TL7	Organic sediment	Beta-168224	13,640 $\pm$ 80	14,764 $\pm$ 60
TL9	Calcrete	Akita-TL7	13,422 $\pm$ 541	
TL17	Charred material	Beta 194122	24,920 $\pm$ 200	29,910 $\pm$ 270
TL18	<i>Margaritanopsis laosensis</i>	Wk-20398	20,000 $\pm$ 117	23,900 $\pm$ 180
TL24	Sedimentary quartz	Akita-TL12	22,257 $\pm$ 154	
TL27	<i>Margaritanopsis laosensis</i>	Wk-20399	29,318 $\pm$ 336	34,500 $\pm$ 500
TL28	Shell (unspecified)	Beta-172226	22,190 $\pm$ 160	26,740 $\pm$ 400
TL31	Organic sediment	Akita-TL10	32,380 $\pm$ 292	
TL32	<i>Margaritanopsis laosensis</i>	Wk-20400	34,029 $\pm$ 598	39,960 $\pm$ 1050
<i>Ban Rai</i>				
BR3	<i>Margaritanopsis laosensis</i>	OZJ686	7040 $\pm$ 60	7870 $\pm$ 60
BR10	<i>Margaritanopsis laosensis</i>	OZJ687	6600 $\pm$ 70	7500 $\pm$ 50
BR12	<i>Margaritanopsis laosensis</i>	OZJ688	6850 $\pm$ 70	7700 $\pm$ 70
BR17	<i>Margaritanopsis laosensis</i>	OZJ689	7950 $\pm$ 70	8820 $\pm$ 130
BR18	Charred material	Beta-168220	7250 $\pm$ 40	8080 $\pm$ 60
BR22	Charred material	Beta-168221	8850 $\pm$ 50	9970 $\pm$ 140
BR23	Charred material	Beta-168222	8190 $\pm$ 50	9150 $\pm$ 90

and widely used approaches (Bleed, 1986; Kuhn, 1990). These approaches typically focus on the analysis of tools (Bousman, 2005; McCall, 2007), which can be defined as visually distinctive flaked stone pieces characterised by extensive retouch and having shapes and other morphological attributes that recur within and across assemblages (cf. Hiscock, 2007). For example maintainable technologies or individual provisioning strategies are identified by the proportions of certain types of tools in an assemblage (Bousman, 2005; Clarkson, 2002a; Hiscock, 2006; McCall, 2007). However, formal tools are very rare in flaked stone assemblages from mainland Southeast Asia – less than 1% of the Tham Lod and Ban Rai assemblages have measureable amounts of retouch. As a result, reduction must be analysed at an assemblage level rather than the level of the individual tool. The two assemblages analysed here are almost entirely unretouched flakes and cores so many of the methods for measuring risk minimisation behaviours on tools (e.g. Clarkson, 2002b; Eren et al., 2005; Kuhn, 1990) are of limited use in this study.

Given the rarity of tools in the assemblages from Ban Rai and Tham Lod, I have instead linked attributes of unretouched flakes to the predictions of the behavioural ecology models. The Patch Choice Model is the simplest, stating that the higher the value of the patch the longer a forager will remain there. The most basic archaeological correlate of this is simply more and larger sites with higher artefact densities in high value patches. A possible confounding factor is that technological changes unrelated to patch values are responsible for higher densities, this can be dealt with first by analysing artefact technologies (i.e. metrics and attributes such as numbers and directions of flake scars) and second by examining discard rates of other cultural materials.

Similarly, the predictions of the Central Place Model can be tested by measuring the relative degrees of pre-processing of lithic raw material prior to entering the site. The challenge here is distinguishing pre-processing from on-site processing. One approach to this is analysing core and flake ratios and metrics such as cortex percentage in assemblages recovered from archaeological sites and identifying pieces that appear to be missing from the assemblage (Holdaway et al., 2010; Reynolds, 1989). For example, if cores are present in the assemblage but certain size classes of flakes appear to be absent then it is possible that those flakes were detached from the core off-site during a pre-processing event. It is of course also possible that those flakes were made on site and carried away from the site to another location, so this is not a perfect measure of pre-processing.

In testing the predictions of the Optimal Dispersion Model, which describes the conditions under which people will adopt logistical or residential mobility patterns, I correlate these two mobility patterns with Kuhn's system of technological strategies (Clarkson, 2007: p. 24; Mackay, 2005). Clarkson describes how individual provisioning is an expected outcome from logistic mobility as people equip themselves with small, portable, versatile and multi-functional tools made from high quality raw materials as they move frequently and long distances through landscapes with little certainty about opportunities for foraging and raw material replacement. Conversely, during conditions of residential mobility people are expected to procure stone over relatively short distances (resulting in minimal pre-processing) and have a reliable supply of raw material which might be indicated by a higher proportion of cores that are relatively large and minimally processed artefacts.

To test the predictions outlined here I used assemblage-level statistics of basic flake and core attributes to indicate risk minimisation behaviours and evaluate the behavioural ecological models. The raw data used for this analysis are available online at <http://dx.doi.org/10.6084/m9.figshare.765252> (retrieved 08:24 GMT, August 22, 2013). I have previously demonstrated how some of

these basic flake variables that can be reliably measured on unretouched Southeast Asian flaked stone artefacts and how they are strongly correlated with assemblage-level reduction intensity (Marwick, 2008b, raw data and additional analyses online at <http://dx.doi.org/10.6084/m9.figshare.766200> retrieved 08:27 GMT, August 22, 2013). The five variables described in that experimental study were the presence of overhang removal, interior platform angle, the number of dorsal flake scars, the percentage of dorsal cortex and the location of dorsal cortex and these variables are also used on the assemblages described here. Detailed definitions of these variables have been presented in Marwick (2008b).

#### Palaeoecological reconstruction

Testing the predictions of these models requires data about the environment that the foragers lived in, in addition to the technological strategies they employed. Although it is common to use global climate indicators such as Oxygen Isotope Stages when interpreting temporal changes in stone artefact technology (e.g. Ambrose, 2002; McCall, 2007), these indicators give limited chronological resolution and gloss over local spatial variability. Pollen, phytolith and sediment cores in South Asia, East Asia, mainland Southeast Asia and offshore are generally aligned with global trends in showing a Pleistocene-Holocene transition from cool and dry conditions to warmer and wetter conditions, an Early to Mid Holocene precipitation maximum and a Mid to Late Holocene transition to drier conditions, usually involving stronger seasonality (Maxwell, 2001; Maxwell and Liu, 2002). However when the evidence from Thailand is examined in detail (see Marwick, 2008a: pp. 156–162), it appears that these elements are not present as uniform, synchronous signals but are characterised by high variability over time and space (Hastings and Liengsakul, 1983; Maloney, 1992, 1999; Penny, 2001; Pramojanee and Hastings, 1983; White et al., 2004).

None of the previously published proxies are near (<200 km) the archaeological sites examined here so it is difficult to determine which proxy is the most relevant for interpreting the stone artefact record. To overcome this problem, I produced a local climate proxy by analysing oxygen isotope ratios in the freshwater bivalve *Margaritanopsis laosensis* which was recovered in abundance during the excavations at Tham Lod and Ban Rai (Marwick and Gagan, 2011). This proxy gives good agreement with the overall sequence of major climatic events documented in other proxies in Thailand with the advantage of a chronological resolution that matches the stone artefact sequence. Marwick and Gagan (2011) present the data for this proxy and demonstrate that the proxy from Tham Lod and Ban Rai is in agreement with the nearest terrestrial oxygen isotope sequences with comparable ranges and resolutions, Hulu Cave and Dongge Cave in China (Wang et al., 2001; Yuan et al., 2004). To investigate the relationship between archaeological and palaeoenvironmental variables, Pearson's correlation coefficient was calculated to describe the relationship between the oxygen isotope values of the shells and the stone artefact attribute values for two sites. Bootstrap methods were used to create bootstrap distributions of coefficient values by resampling observations (displayed here in square brackets). Bootstrapping the coefficient value improves the reliability of the value under conditions when it is difficult to be sure that the assumptions of linear regression have not been violated (independence of values, independence of errors and homogeneity of variance) (Chernick, 1999; Manly, 1997). Confidence intervals for correlation statistics incorporate standard null hypothesis significance tests; if the interval includes zero then the correlation is not significant. Ninety-five percent confidence intervals for the coefficients were determined from the bootstrap distributions.

## Results of testing predictions from the two models

### Central Place Model

The Central Place Model predicts that as travel and transports costs increase then so should the amount of pre-processing of resources to optimise the delivery of useful material. In deriving predictions from this model I separated the influence of proximity of raw materials (closer resources predicts less pre-processing) and climatic conditions (drier conditions predict more pre-processing with stone procurement embedded in the pursuit of low density resources). If proximity to resources was the most influential variable then Tham Lod would have a lower frequency of pre-processing compared to Ban Rai because of Tham Lod's close proximity to the river as a source of high quality materials for making stone artefacts. On the other hand, if climate was more influential than proximity to resources, then I predicted Tham Lod would have the most extensively pre-processed assemblage because of its Pleistocene occupation, when conditions were drier and travel costs would be amplified relative to the Holocene with its higher biomass.

Pre-processing is difficult to measure on stone artefacts because stone artefacts are unlike other types of resources that have relatively distinctive low-utility or no-utility components (e.g. husks of nuts, shells of shellfish, fingers and toes of mammals) (Jochim, 1989). In stone artefact assemblages dominated by informal and unretouched pieces, it is less clear about what can be considered low-utility or no-utility components so the task becomes isolating reduction that appears to have occurred off-site. I employed two simple methods to test the predictions about pre-processing. First, the ratios of MNF to cores were calculated for each site and then for each excavation unit at each site. MNF is the minimum number of flakes, a quantification method devised by Hiscock (2002) to give a standardised measure of abundance that is minimally influenced by taphonomic processes. I expected that if stone is processed before it enters the site then the ratio will deviate from the ratio observed in a comparable experimental assemblage (described in Marwick, 2008b) which represents a closed system where no introduction or removal occurred. A lower ratio of MNF to cores would be expected in an assemblage where flakes have been detached from the cores off-site during pre-processing to increase the utility of the core as a transported mass of flakable stone. Second, the size distribution of flake scars on cores was compared to the size distribution of flakes in the assemblage. For this purpose the last five complete flake scars over 5 mm on each core were recorded. This comparison was only undertaken for the whole assemblage from each site because the number of core scars per excavation unit is too low to make reliable comparisons with the distribution of flake lengths. My expectation is that greater differences between the distributions of complete flake lengths and core scar lengths will indicate greater degrees of pre-processing because the flakes missing from the distributions have been discarded away from the site during field processing events prior to core discard.

The ratio of MNF to cores when all excavation units are considered together is higher at Ban Rai (11.0) than at Tham Lod (4.5). As an example of a closed system, the experimental assemblage described by Marwick (2008b) has a range of MNF to core ratios of 1–58, with an average of 19.9. The ratio at Ban Rai is closer to the average ratio in the experimental assemblage, suggesting that Ban Rai is characterised by less pre-processing of stone than Tham Lod. Correlations between the ratios of MNF to cores and  $\delta^{18}\text{O}$  values are low and non-significant for both sites, suggesting no influence of fine-grained climate change on this measure of pre-processing (Tham Lod:  $r = -0.181$  [–0.557, 0.194], Ban Rai:  $r = -0.007$  [–0.598, 0.582]).

Figs. 2–4 show the distribution of core scar lengths and complete flake lengths at Ban Rai, Tham Lod and the experimental assemblage. The most obvious pattern is that the difference in peak values of the flake and core scar length distributions is greater for Tham Lod compared to Ban Rai and the experimental assemblage (Table 2). Tham Lod also has a more extreme t-value for the difference in means of flake length and core scar length. These results suggest that the core reduction process at Tham Lod is probably not completely represented by the flakes there because some flakes are missing from the assemblage. One explanation for this pattern is that off-site processing may have been more frequent at Tham Lod compared to Ban Rai. A second observation is that the skew values, or size of the region between the mean and maximum values, is relatively large for the Tham Lod assemblage but on the Ban Rai and experimental assemblage it shows a smaller skew and an asymmetry in the distribution of scar lengths and flake lengths assemblage (Table 2). Permutation tests for significant differences in skewness of flake lengths at Tham Lod and Ban Rai indicate no statistically significant differences ( $p = 0.93$ ), but the asymmetries in the visualisations hint at the complex distributions of larger scar lengths as the core geometry shifts during reduction. Given that the experimental assemblage is the control data for a closed assemblage, the similarity between Ban Rai and the experimental assemblages further suggests that Ban Rai was more of a closed assemblage than Tham Lod. These two patterns support the prediction that Tham Lod would have the most extensively pre-processed assemblage because of its Pleistocene occupation, when conditions were drier and travel costs were greater than during the Holocene.

### Patch Choice Model

The predictions derived from this model are that locations and periods of higher patch yields will have evidence of more intensive human occupation as people exploit a reliable and abundant resource. Considering only the contrasting locations of the sites relative to stone and subsistence resources, it could be predicted that Tham Lod was more intensively occupied than Ban Rai because of its proximity to the river. However, given the stark difference between Holocene and Pleistocene climates in the study area, it could conversely be predicted that occupation during the wetter and warmer Holocene should be more intensive, so Ban Rai should be more intensively occupied than Tham Lod.

To test these predictions I measured the rate of artefact discard per cubic metre per 100 years at each site as a proxy for comparing habitation intensity. Analysis of stone artefact manufacturing technology at the sites revealed no major technological changes that might skew the rate of production of flakes and cores independent of the rate of stone artefact production, so in this case it is parsimonious to conclude that more artefacts over a given time period result from more frequent and intensive habitation at the site.

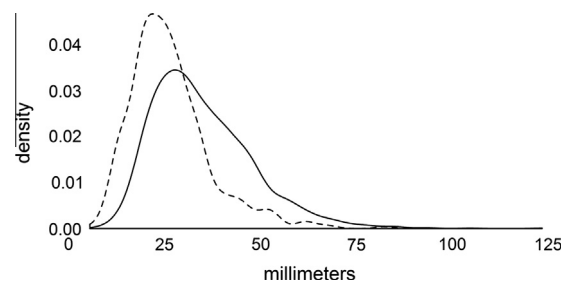


Fig. 2. Tham Lod: Probability density functions for the lengths of complete flakes and flake scars on cores (dashed line).

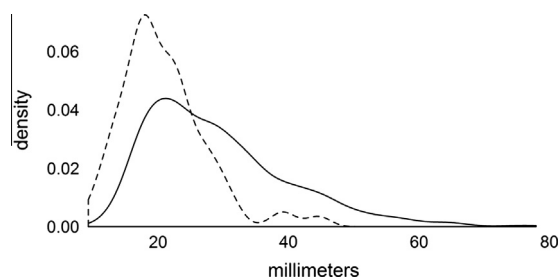


Fig. 3. Ban Rai: Probability density functions for the lengths of complete flakes and flake scars on cores (dashed line).

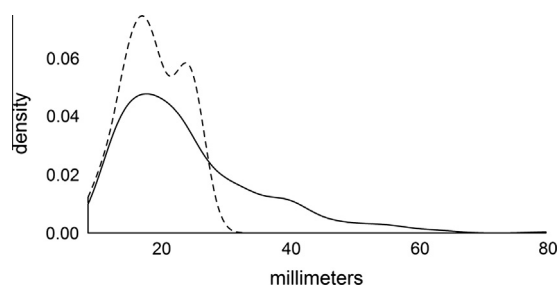


Fig. 4. Probability density functions for the lengths of complete flakes and flake scars on cores from the experimental assemblage (dashed line).

Artefact numbers were calculated for each excavation unit as minimum numbers of flakes plus the total number of cores to give a standardised measure that is minimally influenced by taphonomic processes.

The results indicate considerable variation in artefact discard between the two sites (Fig. 5). Artefact discard rates were on average ten times higher at Ban Rai compared to Tham Lod. This large difference supports the prediction that Holocene occupation will be more intensive because of increased biomass resulting from increased precipitation and warmth. The prediction that Tham Lod would have higher intensities of occupation because of its favourable location in high biomass forests and close proximity to the river is not supported. Correlations between variations in the abundance of artefacts and the oxygen isotope values at each site are weak and not statistically significant (Tham Lod:  $r = -0.205$  [ $-0.585, 0.176$ ], Ban Rai  $r = 0.099$  [ $-0.384, 0.582$ ]). The key pattern here is that the longer-term overall higher intensity of habitation at Ban Rai is likely to be because Ban Rai was occupied during the Holocene, a warmer and wetter period, relative to Tham Lod's Pleistocene occupation.

#### Optimal Dispersion Model

A model of optimal dispersion predicts optimum forager settlement patterns under different environmental conditions, assuming they are minimising round-trip travel costs from resource to settlement location. The assumptions are the same as the central place model, but the predictions here are more generally about forager mobility rather than specifically about pre-processing of stone. This increased generality suggests that predictions of the optimal

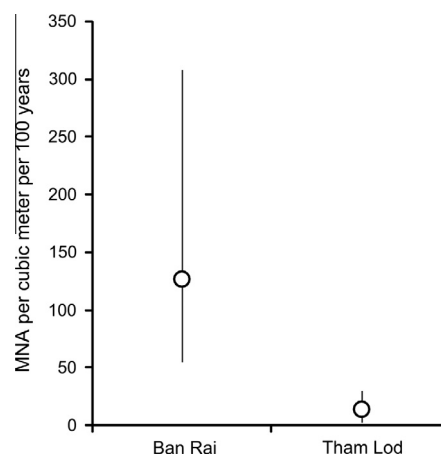


Fig. 5. Total MNA at Ban Rai and Tham Lod.

dispersion model can be more reliably tested than the central place model. The optimal dispersion model evaluated here predicts that as resources become more mobile and clumped, foragers will increasingly aggregate into larger groups practicing logistical foraging but when resources are more stable and evenly distributed, foragers will increasingly disperse into smaller groups using a residential settlement pattern. If the proximity of major resources to the two sites was the most important factor, this model predicts that occupation at Ban Rai was dominated by logistical strategies (indicated by highly reduced assemblages) compared to Tham Lod which is predicted to have been dominated by residential strategies because of its close proximity to the stream. On the other hand, if climate changes are more important than the proximity of resources, then I predict that reduction will be lower at Ban Rai because it was occupied during the Holocene when climatic conditions favoured more stable and evenly distributed environments.

To identify which site has more intensive assemblage reduction I measured five flake variables (Marwick, 2008b). Fig. 6 summarises the difference between the two sites, indicating that more intensive assemblage reduction is found at Ban Rai. Higher values for the number of dorsal flake scars, proportion of flakes with overhang removal and flakes with no cortex all indicate that cores were more extensively reduced at Ban Rai compared to Tham Lod, where the flake data suggest that cores were discarded in a less exhausted state. This indicates that foragers occupying Ban Rai tended to organise their technology around logistical strategies more than the occupants of Tham Lod who employed more residential strategies. This supports the primacy of local resource distribution over climatic conditions in explaining forager settlement patterns.

Examination of correlations of these flake variables with the oxygen isotope sequence at each site supports the claim that local resource distribution was the dominant influence on patterns of optimal dispersion. Table 3 summarises the correlation coefficients for the flake variables and  $\delta^{18}\text{O}$  values at the two sites. At Tham Lod the highest correlation between  $\delta^{18}\text{O}$  values and technological attributes is a statistically significant moderate positive correlation with overhang removal. This suggests that stone artefact technology of the occupants of Tham Lod appears to have been sensitive to climatic variation, but not in any substantial way. The simplest

Table 2  
Summary statistics for flake lengths and lengths of last five flake scars on cores. Dimensions are millimetres.

Assemblage	Flakes mean (sd)	Cores mean (sd)	t-Test result	Difference in flake and core peak values	Flakes skew	Cores skew
Tham Lod	26.2 (10.5)	34.7 (13.1)	$t(817) = -14.1, p < 0.01$	5.7	1.37	1.14
Ban Rai	20.8 (6.5)	29.2 (10.9)	$t(210) = -12.3, p < 0.01$	3.2	1.17	1.12
Experimental	18.5 (4.7)	23.9 (11.1)	$t(63) = -5.6, p < 0.01$	0.6	-0.08	1.35



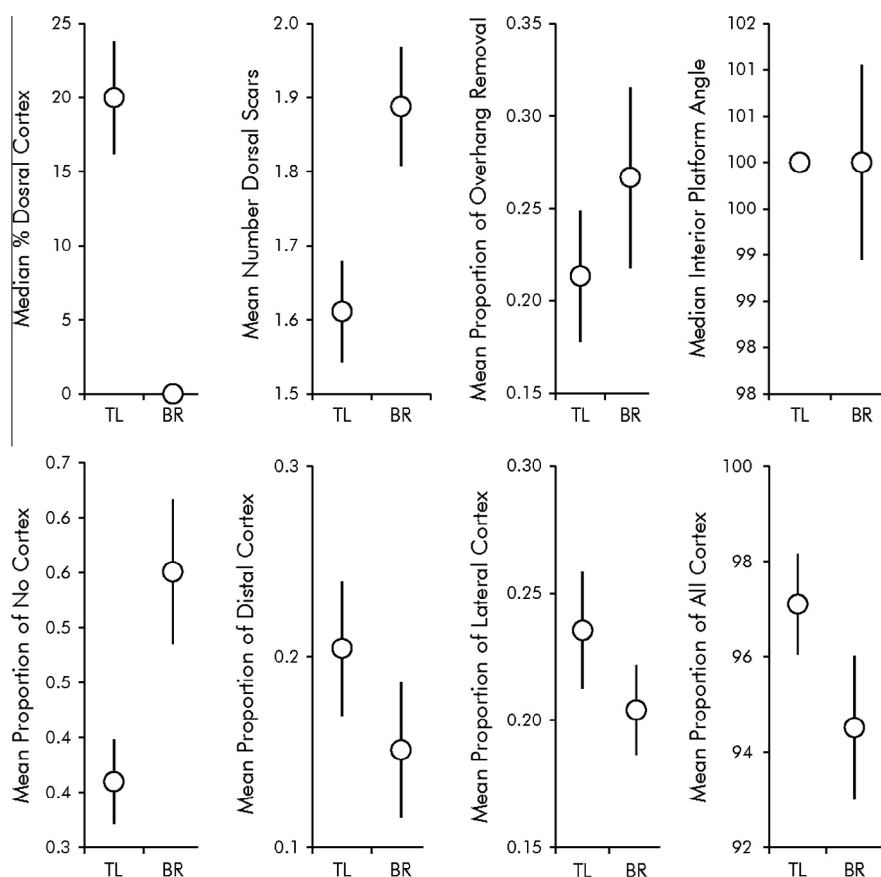


Fig. 6. Central tendencies and 95% confidence intervals for or dorsal cortex, dorsal flakes scars, overhang removal, interior platform angle and dorsal cortex distribution at Tham Lod and Ban Rai.

interpretation of these data is that foragers were largely immune from fine-grained climate changes during their occupation at this site.

In the Ban Rai assemblage correlations between technological attributes and  $\delta^{18}\text{O}$  values are similarly mostly non-significant and very low or inconsistent with models of technological sensitivity to climatic conditions employed here. For example, there is a moderate positive correlation between  $\delta^{18}\text{O}$  values and interior platform angle, suggesting that as climate varies towards more difficult conditions then reduction intensity increases. Conversely, the moderate negative correlation between  $\delta^{18}\text{O}$  values and numbers of dorsal flake scars is inconsistent with theory that predicts more intensive assemblage reduction during drier and cooler conditions.

## Discussion

Table 4 summarises the results of testing the predictions of these the models with data from Tham Lod and Ban Rai. These results are paradoxical because the predictions of the three models appear to give contradictory results for the two sites. At Tham Lod there appears to have been high frequencies of pre-processing but a residential mobility strategy and a low intensity of occupation. At Ban Rai the opposite is indicated. The problem is that the Central Place Model and the Patch Choice Model give consistent descriptions of how people managed their technology, but these are odds with the output from the Optimal Dispersion Model. The problem is not lessened by discarding the findings from the Central Place Model on the grounds that the differences in the intensity of stone reduction between the two sites (identified during testing of the Optimal Dispersion Model) may violate the

assumption that cores were exploited to equivalent degrees at the two sites. There is still the problem of why climate is the key variable influencing the Patch Choice Model and proximity to resources is the key variable for the Optimal Dispersion Model.

This inconsistency is difficult to resolve with classical behavioural ecology models. For example, Fig. 7 shows the Marginal Value Theorem schematic and while this is effective for describing the variation within each site, it is difficult to represent both sites together. If we assume that points A and B represent the range of variation at Tham Lod, then the higher values for assemblage reduction intensity at Ban Rai result in a higher intercept on the curve on the right and so the maximum level of mobility at Ban Rai should be indicated to the left of point B. On the other hand, the higher occupation intensity and lower degree of pre-processing at Ban Rai suggest that maximum mobility at Ban Rai was not higher than at Tham Lod and so should be indicated to the right of point B. This schematic has difficulty summarising the results of the three models and describing the differences between these two sites.

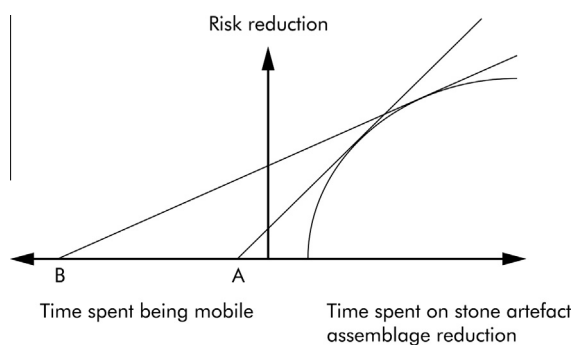
Given these inconsistencies, one possible interpretation is that behavioural ecological models are ill-suited to modelling the evidence from these sites as a single system. The reasons why the fit between archaeological data and ecological models might be poor have been widely discussed (Bird and O'Connell, 2006; Foley, 1985; Haccou and Steen, 1992; Jochim, 1989; Joseph, 2000; Laland and Brown, 2011; Martin, 1985; Metcalfe and Barlow, 1992). Four reasons are may be especially relevant here. First, these models were developed for use in situations where foraging behaviour and its outcomes are directly measurable. It might be that the archaeological manifestations of the expected interaction of variables have been altered or masked by other factors that are difficult

**Table 3**  
Correlations between technological variables and  $\delta^{18}\text{O}$  values at Tham Lod and Ban Rai. Values in square brackets are bootstrapped 95% confidence intervals.

Technological attribute	Tham Lod	Ban Rai
Overhang removal	0.435 [0.124, 0.746]	-0.124 [-0.884, 0.635]
Dorsal flake scars (#)	0.186 [-0.101, 0.473]	-0.343 [-0.888, 0.201]
Dorsal cortex (%)	-0.046 [-0.441, 0.348]	0.104 [-0.665, 0.874]
Interior platform angle (degrees)	0.122 [-0.274, 0.517]	0.320 [-0.241, 0.881]
No cortex (%)	-0.222 [-0.599, 0.155]	-0.081 [-0.687, 0.526]
Distal cortex (%)	0.184 [-0.275, 0.643]	-0.218 [-0.972, 0.536]
Crescent cortex (%)	-0.289 [-0.204, 0.782]	-0.137 [-0.682, 0.407]
All cortex (%)	-0.074 [-0.460, 0.312]	0.152 [-0.614, 0.919]

**Table 4**  
Summary of the results of testing the model's predictions.

Model	Tham Lod	Ban Rai	Most influential contextual variable
Central Place Model	High pre-processing	Lower pre-processing	Climate
Patch Choice Model	Lower intensity of occupation; low rank patch	Higher intensity of occupation; high rank patch	Climate
Optimal Dispersion Model		Less extensive stone reduction; residential strategy	More extensive stone reduction; logistical strategy
Proximity to resources			



**Fig. 7.** Classical Marginal Value Theorem model adapted for hunter-gatherers and stone artefacts.

or impossible to measure. We may simply lack access to the relevant data and the data might not be fine-grained enough to unambiguously demonstrate the predicted interactions. A second reason is that the dominant archaeological signal of prehistoric forager behaviour recorded here may have resulted from optimisation of some other behaviour, such as food resource extraction, and stone artefact activities were subordinate to this other behaviour, for

which we have no evidence from Tham Lod and Ban Rai. A third possibility is that historical factors, such as consideration of the specific interaction of costs, benefits, goals, decision variables, currencies and constraints in the study area may have led to behaviours that appear sub-optimal when evaluated by generic models, but might make more sense if we had complete knowledge of the specific historical circumstances of occupation at the two sites. A potentially powerful influence here might be cultural transmission, or social learning of technological behaviours. Suboptimal action can be a consequence of socially learned behaviours, because once the flow of culturally transmitted information is decoupled from gene flow, there is no theoretical reason to assume that the behaviour supported by culturally transmitted information will maximise biological fitness (Sterelny, 2004). Finally, our assumptions about how people were expected to organise their stone artefact technology may be wrong because the actual costs and benefits of different strategies may all be below a threshold that motivates archaeologically observable changes in behaviour. Another way to think about this is that although we can reconstruct situations where foragers might be expected to have switched strategies, in the actual experience of these situations, foragers may have found that that conditions were not sufficiently extreme to provoke the predicted technological change.

None of those reasons for the predictive failure offer much hope for resolution, they all point to the need for data that is highly unlikely to ever be available from these archaeological sites. However there is another option, namely a slight modification to the existing model in an attempt to produce an improved representation of data from the two sites described here. We can take inspiration from Wright's (1932) metaphor of the evolutionary history of an organism as a journey across a fitness landscapes with numerous adaptive peaks and low-fitness valleys. Wright's work is notable for introducing the idea of multiple optima to evolutionary biology (Whitlock et al., 1995), a concept that has received considerable empirical support (Weinreich et al., 2005), but received little attention from archaeologists (Giovas, 2013; Smith and Winterhalder, 1992: 58–59). By incorporating multiple optima into the functions that represent the past behaviours we can attempt to formalise the dynamism and complexity of the technological systems and perhaps resolve the inconsistencies noted above.

Revisiting the climate history and archaeology, we can redraw the model schematics using multiple optima in an attempt to resolve the inconsistencies apparent in schematic of the classic model. Here we present a qualitative model that has the advantages of being parsimonious and consistent with the observed data. The  $\delta^{18}\text{O}$  record indicates drier and more variable conditions during the Pleistocene which may have made locations like Ban Rai undesirable to occupy except only briefly en route to more habitable locations. Similarly, increased precipitation during the Holocene may have made Tham Lod uninhabitable because of the high density of vegetation, high humidity and inhospitable fauna such as snakes and mosquitoes. In the case of Tham Lod, this suggests that the correlation between wetness and site habitability is not a simple linear function, but has a turning point where increasing wetness ceases to increase a site's habitability and instead makes it less habitable. In the case of Ban Rai, it may have only become habitable after a certain threshold of wetness was passed, increasing the reliability availability of surface water and altering the vegetation structure so that semi-evergreen forests were more accessible from the site.

These scenarios are represented in Fig. 8. Tham Lod occupies the region between points A and B on this figure, with relatively low levels of wetness corresponding to low levels of reduction. The assemblage from Ban Rai occupies the region of the curve between points C and D on Fig. 8. The shorter distance between C and D compared to A and B on the horizontal axis reflects differences in

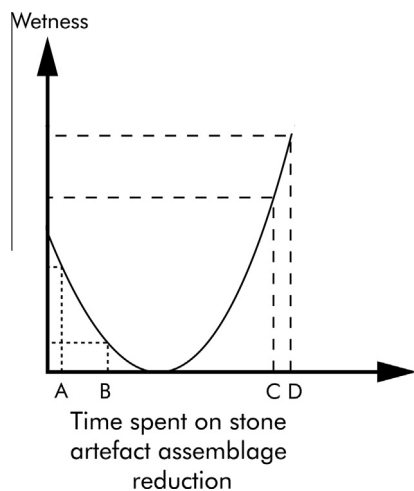


Fig. 8. Function showing probable positions of Tham Lod (A and B) and Ban Rai (C and D).

magnitude of variation in assemblage reduction intensity between the two sites. This intersection of the curve with the vertical axis is important because it indicates where no further decreases in reduction are possible (there are obvious limits on the amount useful work that can be done with unmodified cobbles). The intersection of the curve and the vertical axis represents the point where the degree of wetness is sufficiently high that further decreases in assemblage reduction are not a practical response to increasing wetness and a major reorganisation of the mobility and settlement strategy is necessary.

This may be the most parsimonious explanation for Tham Lod and Ban Rai, where the commencement of occupation at Ban Rai signalled a major shift in settlement patterns and increase in assemblage reduction was an optimal strategy for foragers during the increased wetness of the Holocene. This settlement shift is probably an outcome of innovative behaviour compelled by conditions of greater risk sensitivity. Fitzhugh (2001) proposes that as risk sensitive populations begin to experience mean yields below minimum requirements, they should switch from a risk-averse to a risk prone attitude to innovation. A risk prone attitude involves testing new technologies or strategies that might give higher pay-offs than existing ones in the new conditions. In this case, the major shift from Pleistocene to Holocene conditions was probably what caused foragers to experience mean yields below minimum requirements and trigger a brief change in risk management until the new strategy – one including Ban Rai as part of the settlement system and abandoning Tham Lod – became established.

In Fig. 9 I have redrawn the classic Marginal Value Theorem schematic to integrate the threshold turning points described above. In this modified model the relationship states that instead

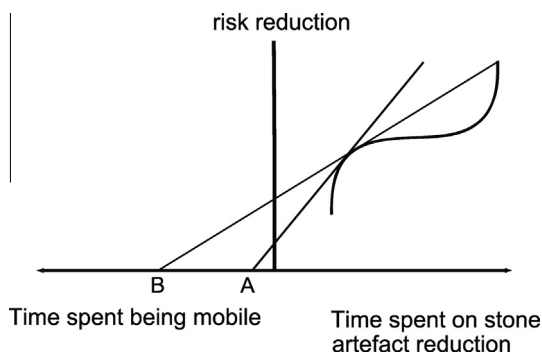


Fig. 9. Marginal Value Theorem modified to include inflection and multiple optima.

of the function ending in a horizontal asymptote, it reaches a point of inflection where increased investment in assemblage reduction leads to continuing increases in risk reduction, resembling a cubic function. For simplicity and realism, this is defined as a partial function that is not defined for values beyond certain minimum and maximum points on the horizontal axis, reflecting limitations encountered by human foragers. In this example, the point of inflection represents the shift in settlement from the low location of Tham Lod near the river to the elevated and distant location at Ban Rai. Both sites can be described as occupying the range from A to B. The introduction of a point of inflection means that when the degree of mobility is at or near point B, there are two possible optimum states. At Tham Lod the optimum chosen by the occupants is represented by the lower intercept, indicating a smaller investment of time on stone artefact reduction, corresponding to a more residential strategy. At Ban Rai the occupants chose the other optimum at the higher intercept, resulting in more time spent on assemblage reduction, corresponding with a more logistical strategy.

The advantage of the representation in Fig. 9 is that it resolves the inconsistency of signals of mobility that are not in linear proportion to time spent on assemblage reduction. In this schematic the lower mobility at Ban Rai suggested by the Central Place Model can be equated with a more highly reduced assemblage because of multiple optimal states that emerge from consideration of the specific locations of the two sites relative to stone resources and the effect that climate changes had on the habitability of these locations. The implication of this revised model is that classical models do not generalise well when constraints result in more than one optimum strategy. This is a problem that has been observed by animal ecologists, for example Kacelnik and Bateson (1996) note that risk-sensitive foraging theory makes different predictions about how animals should respond depending on the precise biological scenario, with the energy budget rule failing as a universal predictor for risk-sensitive foraging models. The poor fit of models based on energy as a currency has led Bateson (2002) to suggest that 'we may have to abandon the idea that animals evaluate alternative options using any absolute currency, but instead evaluate options comparatively'. The abandonment of an absolute currency might be an extreme suggestion, since the identification of multiple optima here means that risk reduction can still be employed as a single currency that is maximised despite switches in habitat preference.

A final observation relates to the sensitivity of technological change to climate change. Although the oxygen isotope analysis produced a palaeoclimate record with equivalent chronological resolution to the stone artefact assemblage, the generally low and non-significant correlation coefficients indicate that technological behaviours were not substantially influenced by millennial scale climate variation (the average time period represented by an excavation unit at the two sites is about 700 years). One interpretation of this result is that is that the technological strategies described here are insensitive to millennial scale climate variation and only track the lower frequency and higher magnitude events such as the shift from Pleistocene to Holocene conditions. The apparent conservatism in the technological systems examined here suggests that guided variation played a small role in the transmission of stone technological strategies between generations. When guided variation is prominent, individuals experiment with trial and error to improve the success of their technology, resulting in new technological items and wide variation in existing forms. This is an effective strategy for adapting to high-frequency environmental change where inherited technologies might lag behind current conditions (Boyd and Richerson, 1985). When the technology used by the previous generation is already well-adapted to the current conditions, then there is no advantage to investing time trying to invent new systems (and increasing exposure to the risk of the

failure of these new systems). In the literature on cultural evolution several different types of bias in cultural transmission systems have been described (Henrich and McElreath, 2003). At the two sites examined here, the process of technological transmission can be characterised as directly biased, where some technological variants are favoured over others during the process of cultural transmission. However, it could be the case that the simplicity of the technology used at these two sites is evidence of a content-based bias where people consistently chose the technology that is simplest to teach and learn as well as most robust to environmental change.

## Conclusion

In this study I have suggested how an investigation of flaked stone artefact technology can show how prehistoric people adjusted their technology according to ecological risks posed by proximity to resources and climate change. I suggest that proximity to resources and climate change were important influences on Hoabinhian technology. Finally and more generally, I suggest a revision of behavioural ecological models informed by Sewall Wright's fitness landscapes. This revision includes multiple optima that reflect the specific ecological conditions under consideration.

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