

# Behavioral ecology and the future of archaeological science

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## ARTICLE INFO

### Article history:

Available online 25 February 2015

### Keywords:

Evolutionary ecology  
Optimal foraging theory  
Resource depression  
Habitat modification  
Origins of agriculture  
Colonization  
Cooperation  
Institutionalized hierarchy

## ABSTRACT

The future of archaeological science relies as much (if not more) on theoretical as on methodological developments. As with anything in biology, explaining past human behavior will require the application of evolutionary theory. As with anything in archaeology, theory is useless without clear ties to a material record. Human behavioral ecology (HBE) has become one of the central theoretical frameworks in archaeological science by providing a broad conceptual toolkit for linking principles of natural selection to operational hypotheses about variability in behavior and its material consequences. Here we review the general approach and outline cases where applying HBE models can contribute to key research issues in archaeology. These examples illustrate how foundational applications of HBE are being built upon to explain complex and diverse phenomena ranging from the origins of agriculture to the emergence of institutionalized inequality. With each case, we outline avenues where this research strategy can advance archaeological science into the future.

## 1. Introduction

Progress in archaeology relies heavily on the development of methodological tools to help extract information from a fragmentary material record. However, the future of archaeological science relies equally on theoretical developments to guide inquiry and structure the interpretation of this information. Explaining *human behavior* through its *material consequences* requires theoretical models to frame research questions and identify the data necessary to answer the questions. Human behavioral ecology (HBE) has been one of the more productive theoretical frameworks used by anthropological archaeologists to explain past human behavior (Bird and O'Connell, 2006, 2012; Broughton and Cannon, 2010; Lupo, 2007). This success derives from clear solutions to two key problems associated with explaining human behavior through its material consequences: (1) building on principals of natural selection to provide a general theory of behavior, and (2) employing models that clearly link behavior to expected material outcomes (O'Connell, 1995). Here we outline the approach and provide illustrative examples based on archaeological applications of two very simple and commonly used models: prey choice and ideal free distribution. In each section, we review foundational contributions,

discuss recent progress, and scope the boundaries of productive research where future work promises to move archaeological science forward. Starting with humble beginnings in optimal foraging models, cases illustrate how HBE has moved well beyond explanations of subsistence to explore the socioecological contexts influencing why individuals would modify their environment, begin producing food, cooperate with unrelated others, develop social institutions governing private goods, or give up some of their autonomy. By generating a strong foundation to build on, the HBE approach is beginning to bring these more difficult to understand aspects of past societies into focus. While progress is incremental, this research strategy has and will continue to explore central questions in archaeological science.

## 2. Natural selection in HBE

Nothing in biology makes sense except in light of evolution by natural selection (Dobzhansky, 1973). Following Darwin (1859), evolution by natural selection requires three necessary and sufficient conditions: phenotypic variation, inheritance of that variation, and differential survivorship and reproduction as a result of that heritable variation. Where Darwin outlined the general framework, the subsequent *modern synthesis* provided a mechanism for inheritance and a detailed approach to examine evolutionary processes moving forward (Huxley, 1942). This canonized evolutionary thinking with a focus on genes.

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While natural selection is central to HBE, genes are not the unit of study and most assume that behaviors are not the result of changes in gene frequencies. Indeed, human behavioral ecologists generally start with the premise that all individuals have equal capacity to adapt to different social and natural environments. Because quantitative traits, like behavior, are not controlled by simple genetic mechanisms, norms of reaction produce significant variability allowing phenotypically plastic traits to adjust through the lifespan in response to environmental cues; as such, behavioral variability is not genetically determined, but emerges out of the interactions between phenotypes and environments (Smith, 2011b, 2013; Winterhalder and Smith, 2000). With the phenotype as the unit of study (Smith and Winterhalder, 1992), HBE is focused on the very place where natural selection is occurring, but ignores underlying evolutionary mechanisms of inheritance. There are at least three ways to reconcile these differences between the standard evolutionary theory and behavioral ecology.

The first approach centers on an assumption of adaptive *phenotypic plasticity*. As Irons (1979, 5) states, “the most reasonable hypothesis is that behavioral differences exhibited by different populations are environmentally induced variations in the expression of basically similar genotypes (cf. Haldane, 1956), and that the ability and propensity to vary behavior in response to environmental differences is itself an adaptation.” That is, changes in behaviors are not the result of changes in genes, but in changes in gene expression that are responding to environmental stimuli. In a sense, the ability to adapt phenotypically to varied environments is the very thing that evolved through natural selection and any particular behavior is a result of this legacy of selection.

The second common maneuver is known as the *phenotypic gambit*. The strict definition of the gambit was introduced by Grafen (1984), who proposes the simplifying assumption that behaviors are controlled by the most basic genetic system (i.e., single alleles on a haploid locus). As Grafen (1984) points out, this assumption is assuredly incorrect if taken literally, but it allows work to move forward without getting distracted by placing the proximate details in a “black box”. The gambit has taken on a broader definition by many human behavioral ecologists. Smith and Winterhalder (1992, 33) suggest that “since few if any of the traits studied by evolutionary ecologists are controlled by single loci in a haploid system, the phenotypic gambit is really based on the premise that selection will favor traits with high fitness irrespective of the particulars of inheritance.” This broader meaning encompasses both the logic of the gambit and principals of phenotypic plasticity.

Finally, a third approach is currently emerging out of recent research in evolutionary biology. The proposed *extended synthesis* (Pigliucci and Müller, 2010) opens the black box to focus explicitly on the interaction between developmentally plastic phenotypes and modifiable environments, which provides two potential pathways of inheritance. The first pathway suggests that environmentally induced novel phenotypes can emerge through adaptive developmental plasticity (West Eberhard, 2005). Epigenetic feedbacks then allow this variability in environmentally induced gene expressions to be passed on to subsequent generations (Jablonka and Raz, 2009; Richards, 2006). In this scenario, individual genomes remain the same, but heritable differences in gene expression allow for phenotypic modifications in one generation to be passed to the next. The second pathway centers on the environment. Here, consider the environment in the broadest sense, including all the natural and social attributes that one generation interacts with and into which subsequent generations are born. Modifications to the environment during one generation will be inherited by the next through what some have called “ecological inheritance” (Odling Smee et al., 2003). Since the environment is responsible for driving changes in adaptive behaviors (and in gene

expression), this second pathway of inheritance may be of greater primacy (especially within archaeological applications of HBE). While the extended synthesis is presented as a revolution (Laland et al., 2014), many of these additions are simply elaborations on mechanisms well understood within standard evolutionary theory (Wray et al., 2014). Nonetheless, the approach does suggest that natural selection may sometimes operate in accordance with the HBE approximation and provides an explicit framework to consider mechanisms of inheritance that may otherwise be ignored.

Regardless of which underlying theoretical foundation one ascribes to, these approaches allow for analyses of evolution by natural selection to move forward through the investigation of adaptive phenotypic interactions with variable environments. From this point, researchers can take the final step to examine which behaviors should confer differential fitness. As with standard evolutionary theory, those strategies expected to increase an individual's likelihood of survival and reproduction should be more likely to be passed on to the next generation. While some ethnographic studies attempt to measure fitness through various reproductive proxies (e.g., Smith et al., 2003), most approaches focus on production, using optimization (e.g., resource acquisition efficiency) either as a proxy for survivorship (a necessary prerequisite to reproduction) (Smith and Winterhalder, 1992) or as evidence of how natural selection has shaped decision making.

### 2.1. Critiques of the approach

Some criticisms of the optimization approach mirror those made against the adaptationist paradigm more generally (Gould and Lewontin, 1979), suggesting that some behaviors may not be adaptive at all and assuming traits have a function *a priori* only facilitates story telling. Others take an anthropocentric tilt either arguing for human exceptionalism or asserting that human cultural adaptation operating at a group level is needed to explain behavior, including seemingly maladaptive practices (e.g., Boyd et al., 2011). However, these criticisms fail to recognize four crucial points.

First, not all behaviors need be adaptive. Through the application of the theory of evolution by natural selection, researchers are able to identify those behaviors which should, all else being equal, be constrained by ecology. In HBE, this is done through the use of formal optimality models that provide a deductive guide to empirical investigations of decisions with fitness consequences (e.g. Section 4). If a particular goal can be achieved free from constraints, then selection should not be directing the resulting behavior. Keeping a close link between model predictions and observations avoids adaptive stories about ‘spandrels’ (Maynard Smith, 1978; Williams, 1966).

Second, common HBE models do not assume that adaptation is equivalent to optimal phenotypic outcomes. That is, natural selection acting on phenotypic variability will never produce ideal behavioral outcomes in any absolute sense (Smith, 2013). Even strong selection will never produce an optimal solution due to constraints on what is possible, trade offs individuals experience relative to different goals, and changing social and physical environments which result in shifting optima. But, even weak selection should produce the best possible solution available within constraints.

Third, HBE does not suggest a singular cause for any specific behavior. Arguments to the contrary miss the point that HBE models are research tools, not essentialist rules of human behavior or descriptions of observed phenomena. What matters in operationalizing the approach are stipulated fitness related trade offs within the relational structure of given model. These are identified as functional opportunity costs that can theoretically impinge on fitness, ultimately because time and energy expenditures matter

for survival and reproduction. But how they matter is contingent on incredibly complex and dynamic social, historical, and environmental contexts. Finding the absolute “cause” (cultural, biological, historical, physiological) of behavior in such contexts is a fool’s errand: the explanation lies in processes shaping relationships between individuals and their environment. Explanation is only sought in process, focusing especially on processes likely to shape relationships that impinge on survival and reproduction (Tinbergen, 1963). This is why HBE rarely attempts to test, in any direct sense, for fitness consequences in propositions about opportunity costs: fitness is a conceptual tool, a proposition about the propensity to contribute traits to future generations (Dawkins, 1976). Models in HBE are thus simple heuristics to delineate a question and organize hypotheses about different suites of trade offs with explicitly assumed goals, decisions, currencies, and constraints.

Finally, leaving aside the challenges for group selection that Williams (1966) so lucidly articulated, deferring to ‘culture’ as an explanation of some behavior merely side steps the very phenomena requiring explanation. In most cases, behaviors ascribed to ‘culture’ are found to be explained by ecology—the interactions between individuals and their social and natural worlds—when researchers look a little bit deeper (e.g., Lamba and Mace, 2011). Within HBE, culture is simply the outcome of dynamic interactions between socially shared intent (see Tomasello et al., 2012), behavior, and the environment, not a unit of study. Cultural transmission, and the way it biases patterns of interaction, is one of an array of historical processes and proximate mechanisms (Scott Phillips et al., 2011). Culture does not buffer phenotypic variation from natural selection because culture and the way we construct our environments, is wholly natural.

Keeping these points in mind, HBE moves forward as a research strategy by examining traits thought to be under selection, recognizing optimization occurs within constraints, focusing on process, and by not losing sight of the phenomena requiring explanation. This is operationalized through formal models that allow researchers to make clear predictions about the decisions individuals are expected to make within specific contexts.

### 3. Modeling behavior

The theory of evolution by natural selection is central to behavioral ecology and its archaeological application. While other approaches in archaeology may be interested in the phylogenetic (Shennan, 2012), ontogenetic (Eerkens and Lipo, 2007) or physiological levels of explanation outlined by Tinbergen (1963), behavioral ecology is focused on explaining the adaptive function of behavior: how a particular behavior contributes to an individual’s survival and reproductive success. Human behavioral ecologists implement insights from natural selection through the use of formal optimality models. These models develop clear predictions about human behavior that can be carefully tested empirically. Ethnographic applications examine behavior across a range of conditions that can generally be divided into three categories (Winterhalder and Smith, 2000): production (e.g., Bliege Bird et al., 2009; Koster, 2008), distribution (e.g., Hawkes et al., 2010; Nolin, 2012) and reproduction (e.g., Kramer, 2011; Scelza, 2013). Here we focus on production, specifically the class of contingency models referred to as optimal foraging models (e.g., Bettinger, 2009; Charnov, 1976a, 1976b; Charnov and Orians, 1973; Emlen, 1966; MacArthur, 1972; MacArthur and Pianka, 1966).

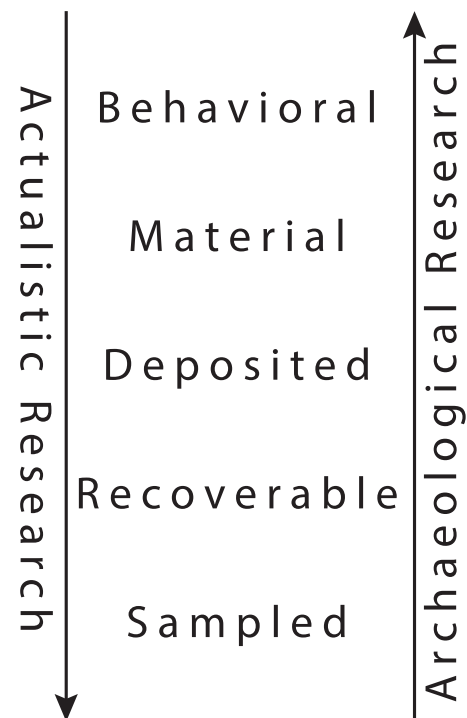
Foraging models begin by specifying a decision a forager must make when operating at a particular scale (e.g., within a patch) relative to a particular goal and currency (e.g., maximize rate of energy acquisition). Operationally, variability in goal oriented

behaviors are typically categorized into *strategy sets* (Maynard Smith, 1978) that represent contingent decisions. Individuals are expected to choose those strategies that allow them to optimally achieve the stipulated goal within a set of assumed constraints. These simplifying maneuvers are central to the success of the approach as they reduce behavior into components that trade off with each other, are observable, and potentially quantifiable. This reductionism is a key strength—not a weakness—of the approach as it allows for the scientific analysis of a problem from the interaction of its constituent parts (Bird and O’Connell, 2006).

While this approach establishes a general theory that can be used to explore the validity of explicit assumptions about human behavior, it is useless in archaeological contexts without clearly linking that behavior to patterns of material expression. Fortunately, there are fairly clear avenues to link predictions from these models to expectations about the archaeological consequences of behavior.

#### 3.1. Linking behavior to material

While anthropological archaeologists may be interested in explaining past human behavior, our empirical object of study is a mere material residue of that behavior and the complex contexts that shaped it. As such, archaeological applications of HBE require ethnographic and experimental studies to link human behavior to its material consequences. To help explain this, a useful heuristic outlined by Klein and Cruz Uribe (1984) for faunal remains can be expanded to fit the general archaeological enterprise (Fig. 1). In this framework, we begin with the behavioral assemblage which represents all of the strategies undertaken by an individual. Unfortunately, only some proportion of those strategies will produce a material assemblage. Moreover, only some subset of those



**Fig. 1.** Sequential ‘assemblages’ through which material passes as it enters the archaeological record. While archaeological science is interested in explaining the behavior of past people from a sampled archaeological collection, actualistic research is needed to understand how assemblages are biased as they transition from behavior to a sampled archaeological collection. Adapted from Klein and Cruz-Urbe (1984).

materials will be deposited in archaeological contexts. Due to post depositional processes, some of the deposited assemblage will be obscured with time. From this recoverable assemblage, our picture of behavior will be further biased by the sampling techniques deployed in archaeological field and lab work.

Fortunately, the problem of accounting for these transforms may be addressed by actualistic studies which move in the opposite direction of archaeological inquiry through ethnographic and experimental work (Fig. 1). By systematically testing predictions derived from models justified by a general theory of behavior across each assemblage, the actualistic research program is able to account for potential bias to determine what may still be visible archaeologically (O'Connell, 1995). This approach also avoids inductively bound ethnographic analogy by deriving predictions deductively from a general theory of behavior based on natural selection (O'Connell, 1995).

For a well developed example of this approach, we can turn to debates over the interpretation of fossil hominin sites in East Africa. Large bone and stone tool aggregations were initially thought to represent home bases that indicated a sexual division of labor wherein men traveled long distances to acquire large game and transported meat back to the central place in order to provision families (e.g., Isaac, 1978). O'Connell and colleagues (1988; 1990; 1992; 2002) set out to examine this hypothesis through the application of prey/patch choice and central place foraging models to Hadza foraging decisions and their material outcomes in Tanzania. Their findings identify mismatches between the modeled predictions and challenge the classic interpretation of fossil hominin sites on three fronts. First, quantitative observations examining the 'behavioral assemblage' (Fig. 1) show that large game hunting is not a reliable provisioning strategy because a) large game acquisition variance is high (Hawkes et al., 1991) and b) shared portions do not go exclusively to family members (Hawkes et al., 2001a,b). Second, analyses of field processing trade offs and the 'deposited assemblage' (Fig. 1) show that while the fine grained decisions about field butchery and transport are complex (Lupo, 2006), the overall body part representation produced by Hadza hunting is more consistent with the hypothesis that Plio Pleistocene bone aggregations represent kill or scavenge sites, not home bases (O'Connell et al., 2002). Finally, analyses of carnivore tooth and stone tool marks from a 'sampled' ethnoarchaeological assemblage suggest that hominins may have had early access to carcasses, but that research cannot distinguish between hunting and aggressive scavenging (Lupo and O'Connell, 2002). As such, the patterns observed in fossil hominin sites are not what we would expect in central places where men provisioned families, but aggregation locales such as waterholes where men and women repeatedly encountered hunting or scavenging opportunities and consumed the meat on site. These studies highlight the importance of actualistic work and the applicability of predictions derived from a general theory of behavior to situations with no possible ethnographic referent.

### 3.2. Advances in modeling

The application of HBE models to archaeological contexts has grown rapidly. Many practitioners have expanded formalizations from animal ecology to model human specific decisions. For example, pioneering researchers have adapted central place foraging models (Orians and Pearson, 1979) to examine the trade offs between field processing vs. transport (e.g., Metcalfe and Barlow, 1992), caching vs. storing food (e.g., Morgan, 2012), and front vs. back loaded processing costs (e.g., Tushingham and Bettinger, 2013). Other growing areas include the application of models to technology (Bettinger et al., 2006; Surovell, 2012;

Stevens and McElreath, 2015; Ugan et al., 2003). Because these productive areas of research are too numerous to detail here, we select two models to illustrate the utility of the approach. First we draw on the classic workhorse of HBE, the prey choice model, to highlight a number of key insights derived from its application. Then we examine emerging insights brought by the application of the ideal free distribution model. In both cases, we use recent work to illustrate the value of the HBE approach in its ability to contribute to the explanation of key research questions. We also show how the application of these foundational models has laid the groundwork to explain complex phenomena beyond foraging decisions.

## 4. Prey & patch choice models

The trade offs an organism faces in spending time to gain energy have fitness consequences. We get hungry often, and so do others that depend on us. If we consistently behave as if those trade offs do not matter, at best, adult humans have only months to live, and infants only days. Certainly we sometimes behave as if those trade offs do not matter (and when that happens it is a big deal), but it is not unreasonable to begin by assuming that we should be sensitive to the opportunity costs of food acquisition and that our capacities to evaluate energy and time trade offs are under fairly constant selective pressure. The social and physical contexts that shape those trade offs are, however, complex and dynamic. The prey choice model offers a first step in a systematic exploration of that complexity.

Assuming a forager is concerned with her or his rate of energy gain while foraging in a patch, the prey choice (or diet breadth) model asks whether she or he should pursue a particular resource on encounter, or pass it over to continue searching for a more profitable resource item. The answer depends on the forager's encounter rate ( $\lambda$ ) with the most profitable resources (Charnov, 1976b; MacArthur and Pianka, 1966). Fig. 2 illustrates this decision in a simplified three resource patch. First, resources are ranked by their post encounter profitability ( $e/h$ ), which measures the total amount of energy acquired ( $e$ ) over the total time spent handling ( $h$ ) the item after it is encountered. A forager should always take the highest ranking item ( $R_1$ ) on encounter, but should only take lower ranking items ( $R_2$  and  $R_3$ ) if doing so would increase their overall return rate ( $E/T$ ), which is measured as the total energy ( $E$ ) acquired in patch over the total time ( $T$ ) spent searching for and handling resources within the patch. As shown in Fig. 2, when the encounter rate with the higher ranking resource declines to a point where the overall return rate ( $E/T$ ) is below the post encounter return rate for the lower ranking resource ( $i \rightarrow ii$ ), a forager trying to maximize their overall return rate should start to take the lower ranking resource ( $R_2$ ) on encounter, but should still pass over the lowest ranking resource ( $R_3$ ). In this way, the model examines the dynamic interactions between resources and human decisions.

The difference between prey and patch models is one of scale. Instead of evaluating a forager's decisions while searching for prey in a patch, the patch choice model examines a forager searching for patches. In this case, it is the encounter rate with the highest ranking patch that drives decisions about whether or not an individual should enter a patch on encounter or continue searching for higher profitability patches (MacArthur and Pianka, 1966).

Predictions from prey and patch choice models have been tested ethnographically (e.g., Hawkes et al., 1982; O'Connell and Hawkes, 1981, 1984; Thomas, 2014) and ethnoarchaeologically (e.g., Bird et al., 2009; Coddling et al., 2010; Lupo and Schmitt, 2005; Thomas, 2002). While empirical findings most often confirm expectations, departures from model predictions generally drive research in interesting directions. Most departures from expectations result from differences in the constraints or goals experienced

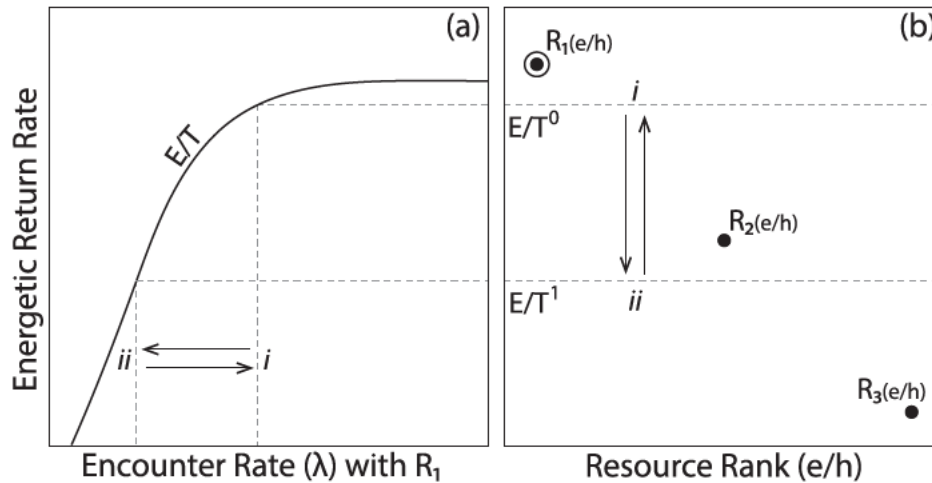


Fig. 2. Two graphical representations of the prey choice (or diet breadth) model following (a) Holt and Kimbrell (2007) and (b) Bird et al. (2009) illustrating the dynamic processes of anthropogenic resource depression ( $i \rightarrow ii$ ) and habitat modification ( $ii \rightarrow i$ ).

across individuals, which cause them to differentially evaluate specific trade offs imposed in particular contexts. These often appear to vary in patterned ways across humans by age and sex (e.g., Hawkes et al., 1995; Hawkes, 1990), highlighting the need to take these factors into account rather than modeling an androgynous ageless forager (Jochim, 1988).

For example, because children have slower walking speeds than adults, they will experience a lower encounter rate with high profitability prey items, resulting in a broader optimal prey set (Bird and Bliege Bird, 2000). In other cases, mothers may be more interested in reliably provisioning offspring than maximizing their rate of energy acquisition, leading them to target lower profitability resources that can be reliably acquired and distributed within the family (Bliege Bird, 2007; Codding et al., 2011). Men, on the other hand, may trade off energetic efficiency for the chance to acquire resources that may be shared widely in order to garner prestige through costly displays (e.g., Bliege Bird et al., 2001; Bliege Bird and Smith, 2005).

Each of these ethnographically observed departures from model predictions have led to interesting re interpretations of archaeological patterning. For example, shell middens across much of eastern Australia may reflect children's foraging decisions (e.g., Bird et al., 2002; Codding et al., 2014b), women's risk averse foraging behavior may structure settlement and mobility decisions across the Great Basin (Elston and Zeanah, 2002; Elston et al., 2014; Zeanah, 2004), and men's status seeking behaviors may be responsible for wide ranging archaeological phenomena, from men's pursuit of big game (Hildebrandt and McGuire, 2002; McGuire and Hildebrandt, 2005; O'Connell et al., 2002) to classic Mayan monumental architecture (Neiman, 1997).

Despite the interest in and progress made by such departures from model predictions, here we focus on findings related to the effects of anthropogenic impacts on the environment including resource depression, habitat modification and domestication.

#### 4.1. Resource depression

Humans, like all predators, may cause resource depression either by reducing prey populations (exploitation depression), by causing prey to behave differently near people (behavioral depression) or by causing prey to avoid areas of human habitation altogether (microhabitat depression) (Charnov et al., 1976). All of

these can have the same effect: reducing the encounter rate with the high profitability prey item (Fig. 2:  $i \rightarrow ii$ ).

Archaeological evidence for resource depression is visible with invertebrate remains even in the earliest recorded moments of behaviorally modern humans (Klein, 2008, 2009). Tested first with experimentally collected data, Klein and Steele (2013) show that Later Stone Age people in Southern Africa had a significant and negative effect on the littoral environment by changing the age structure of exploited shellfish. This pattern is repeated throughout human history, especially where coastal hunter gatherers relied heavily on the marine environment (e.g., Erlandson et al., 2008; Jerardino et al., 2008).

Depending on the life history characteristics of target prey (Whitaker, 2009) and of associated lower profitability resources (Winterhalder and Lu, 1997), vertebrate resources may be more or less susceptible to anthropogenic resource depression. Patterns of anthropogenic resource depression have been shown ethnographically (Alvard, 1993; Codding et al., 2014a), and archaeological research has provided evidence for the negative effects of human hunting on terrestrial mammals (Bayham, 1979; Broughton, 1994; Cannon, 2003), marine mammals (Hildebrandt and Jones, 1992; Jones et al., 2004) and birds (Broughton et al., 2007; Whitaker, 2010), in some cases even driving the latter to extinction (Nagaoka, 2002; Jones et al., 2008). Researchers are also beginning to model expectations of spatial variability in the abundance of high ranking resources. Bayham et al. (2012) show how resources may be highest at the social boundaries between populations which act as buffer zones for people and refugia for prey.

The implications of resource depression can be quite profound. Most notable is resource intensification (*sensu* Boserup, 1965; see Morgan, 2015), where individuals must work harder to extract more resources out of the same area of land (or sea). Because foragers are experiencing declines in their encounter rates with high ranking resources, they must shift to exploit lower ranking resources in order to maintain reasonable energetic returns in a depleted habitat. Strategies designed to cope with decreasing returns often result in a feedback loop: if lower ranking resources are generally abundant, human population densities will increase (Winterhalder and Goland, 1993) which should result in lower residential mobility (Binford, 2001) placing greater pressure on the local resources. Under these circumstances, technological innovations should shift from strategies that reduce search costs to those that reduce handling costs as foragers spend proportionally

more and more time processing lower ranked resources (Hawkes and O'Connell, 1992). Broughton et al. (2010) illustrate how the processes of resource depression and intensification can be viewed as niche construction, wherein anthropogenic impacts on the environment create novel selective pressures that alter future behavior. Patterns of depression induced resource intensification are widespread (e.g., Edwards and O'Connell, 1995; Jerardino, 2010) and the application of prey and patch choice logic have provided the tools to explain these transitions in detail. Notably, this approach has expanded our understanding of broad spectrum revolution in the Near East (Stiner, 2001) as a consequence of declining encounters with high profitability prey (Stutz et al., 2009), a pattern that may have shaped the domestication of wild plants and animals (Section 4.3).

Resource intensification may also occur as a result of factors other than anthropogenic resource depression, including climatically induced reductions high profitability prey (e.g., Broughton et al., 2008) or territorial behavior that restricts access to highly productive patches (e.g., Whitaker and Byrd, 2014). But in either case, these patterns still result from declines in the encounters with higher ranking resources. As such, it should perhaps not be a surprise that resource intensification is often followed by attempts to mitigate diminished returns through habitat modification.

#### 4.2. Habitat modification

Subsistence behaviors often result in significant modifications to the environment in ways that alter the selective pressures on future behaviors. Termed ecosystems engineering (Jones et al., 1994) or niche construction (Odling Smee et al., 2003, 2013), these modifications are often unintentional with varied co evolutionary outcomes that can even be detrimental (such as resource depression discussed above). But sometimes these modifications are intentional and benefit individuals. Despite recent statements to the contrary (e.g., Smith, 2011a), these dynamic aspects of environmental modification have always been central to archaeological applications of behavioral ecology (e.g., Bayham, 1979). Prey and patch choice models provide a way systematically investigate habitat modification within a general theory.

Within the simple prey and patch choice framework (Fig. 2), declining encounters with high profitability resources should encourage foragers to modify their environments in order to decrease search or handling time. Initial attempts to reverse patterns caused by anthropogenically or environmentally induced resource depression will likely be directed towards increasing the encounter rate with higher profitability items by reducing search costs (Fig. 2,  $ii \rightarrow i$ ). For populations well down the path of intensification who spend a greater amount of time processing low profitability resources, foragers may be more interested in reducing handling costs (Hawkes and O'Connell, 1992). Because reducing the cost of handling a particular resource may actually change its relative ranking (i.e., reducing the cost of handling  $R_2$  could raise its  $e/h$  closer to  $R_1$ , Fig. 2), habitat modification may completely restructure prey and patch choice dynamics in complex, but predictable ways. Given the compounding effects discussed above, habitat modification is unlikely to keep pace with the negative effects of resource depression, but it may introduce some novel dynamics. For example, based on predictions from patch residence time models (Charnov, 1976a), increasing patch quality should also lead foragers to stay in patches longer. If resources within modified patches become dense and predictable, this may also lead to increasing territoriality (Dyson Hudson and Smith, 1978). As such, examining habitat modification through prey and patch models may provide clear avenues to investigate complex economic and social dynamics.

While foraging populations may modify their environments in a variety of ways, including fishing weirs, antelope drives and irrigation ditches (e.g., Steward, 1937, 1938), perhaps the most significant example of habitat modification that may reduce both search and handling costs is the use of anthropogenic fire, which has a long evolutionary history in our lineage (Parker et al., 2015). Ethnographic research shows that anthropogenic fire is most frequently employed to increase short term gains by lowering search costs (Bird et al., 2005; Bliege Bird et al., 2008), but that repeated burning events may lead to long term increases in patch quality (Bliege Bird et al., 2013; Coddling et al., 2014a). As such, the effects of regularly applying fire to the landscape may have profound effects on ecosystem function, habitat heterogeneity, and vegetative succession, feeding back to shape prehistoric mobility, settlement, and socio political organization (e.g., Zeanah et al., 2015).

HBE informed archaeological investigations into the effects of anthropogenic fire are limited to date and this remains a promising avenue of study (Cuthrell et al., 2012; Lightfoot et al., 2013b,a; Scherjon et al., 2015). However, research guided by HBE has greatly increased our understanding of one of the clearest and most profound examples of habitat modification: domestication.

#### 4.3. Domestication & production

The combined effect of resource depression and habitat modification may have ultimately led to the domestication of plants and animals. While this process was probably the unintentional result of strategies aimed at increasing immediate foraging returns by reducing handling costs, the consequences are monumental. HBE has been central in furthering our understanding of this process (Gremillion and Piperno, 2009; Gremillion et al., 2014; Winterhalder and Kennett, 2006), with major synthetic works (e.g., Kennett and Winterhalder, 2006; Piperno and Pearsall, 1998) and key primary research findings (e.g., Barlow, 2002; Gremillion, 2004). However, some misunderstandings have led to a series of criticisms against the application of HBE to the study of the origins of agriculture (e.g., Smith, 2011a). The critique suggests that HBE only examines human response to changing environments while niche construction provides an alternative approach examining the effect of human behavior on environmental variability. Not only is this critique incorrect in fact, but this is little more than re branding what is already incorporated in ongoing research strategies (Smith, 2013). Niche construction is not a theory, but a common biological process. Stating that niche construction explains the origins of agriculture merely restates the question as an answer. To avoid this tautology, researchers need to rely on a general theory of behavior, such as BE, to explain why individuals would alter their environments (Gremillion et al., 2014).

Through prey and patch choice models, the HBE framework clearly delineates how the dynamic processes of resource intensification and habitat modification could lead to domestication and food production (e.g., Barlow, 2002; Kennett et al., 2006b). While ongoing research needs to continue testing these clear predictions in archaeological contexts, future work also needs to explain a number of secondary questions relating to the shift to food production. These center on the transition from an immediate to a delayed return economy (*sensu* Woodburn, 1982; Bettinger, 2006; Winterhalder and Kennett, 2009), which requires the generation of surplus, the development of food storage and the origins of novel social institutions.

Due to the delays from planting to harvest, early forays into domesticates would necessarily require foraging to subsidize individuals over the growing season. This may have been particularly true early in the process when yields from incipient domesticates

would have been minimal, providing lower returns than many foraging activities and little surplus for storage. Through this process, domestication is followed by a long period of low level food production (Smith, 2001), during which populations may switch back and forth between foraging and farming. Such patterns are common among modern hunter gatherers (e.g., Greaves and Kramer, 2014). What remains to be explained is how and why some low level food producers eventually make the transition to rely completely on domesticates.

To help address this question, Kennett et al. (2006b) use a simple variant of a predator prey model (e.g., Winterhalder et al., 1988) examining cultivator cultigen dynamics to explain the origins of maize based food production in Southern Mexico. They argue that a population cycling in and out of farming may ultimately reach a tipping point once yields from domesticates pass a certain threshold making them more attractive relative to wild resources that may be locally depressed. Also drawing on predator prey models, Bettinger et al. (2010) see similar patterns in Northern China, but argue that populations would never shift completely to food production without changes in social organization that allow for the privatization of stored foods.

By shifting to a delayed return economy, individuals will experience greater levels of risk that their efforts may not be rewarded. Due to an uncertain future potentially beset by crop failure, needy relatives and raiding parties, the benefits of low level production need to be significantly higher than wild foods (Tucker, 2006), which was not likely the case with early domesticates (Bowles, 2011). Tucker (2006) shows how this problem may be overcome by reducing future uncertainty, which could be accomplished by external factors (i.e., increased climatic stability) or internal factors (i.e., securing stored food). While both were necessary for the adoption of agriculture (Bettinger et al., 2009; Richerson et al., 2001), explaining the latter is of the utmost importance to explain full time food producers.

Key here is understanding how populations overcame novel collective action problems associated with the economic shift to stored foods. While a growing body of research focuses on the social institutions that necessarily co evolved with agricultural production systems (Bowles and Choi, 2013), it is a mistake to assume that these required some form of group selection (cf. Bowles and Choi, 2013; Richerson et al., 2001). Instead, the transition to a delayed return food production system may have co evolved with incremental shifts from public to private goods (Wiessner, 1982). Even limited resource privatization—which may be incentivized by regular environmental modification (Section 4.2)—would increase the proportion of acquired foods that producers are able to keep. As Blurton Jones (1987) modeled, this would shift the frequency dependent dynamics governing the ratio of producers to moochers, thereby increasing the proportion of producers in the population.

In such transitional contexts, individuals may find it more profitable to take lower return resources than would be predicted by the prey choice model if those resources can be kept private. Eerkens (2004, 2009) suggests that incipient forms of privatization emerge late in the prehistoric record of hunter gatherers in Owen's Valley as a result of small seed intensification, a resource that can be individually acquired, processed and stored in private. With such humble beginnings, this trend could grow into coordinated privatization through emergent leadership. These dynamics could also begin with ecological inequality resulting in differential harvesting yields for individually acquired resources and thus, differential payoffs to exclusion (or subjugation, more below in Section 5.3).

In sum, delaying returns should restructure prey and patch choice dynamics to be partially contingent on social institutions

that solve collective action problems associated with stored foods. Working out these details is a cutting edge arena of research.

## 5. Ideal distribution models

The Ideal Free Distribution (IFD) model examines where an individual should choose to live depending on the suitability of available habitats and the number of individuals already occupying those habitats (Fretwell and Lucas, 1969). The model assumes that habitats will vary in suitability, that suitability declines with increasing population density (negative density dependence) and that individuals with perfect knowledge of the environment are 'free' to move between habitats in order to maximize their access to the most suitable habitats available (Fig. 3a). With these simple assumptions, seemingly 'ideal' population distributions will result from every individual attempting to maximize habitat suitability (e.g., to maximize their rate of energy acquisition). The resulting qualitative predictions suggest that the most suitable habitat (a) should be occupied first and (b) will always have the highest population density (assuming the effect of density on suitability is constant across habitats). There are two variants to this model that also provide compelling predictions.

The first variant incorporates Allee's principal to alter the density dependence assumption so that habitat suitability initially increases with a growing population (positive density dependence). In the non human world, this is generally thought to be the result of grouping effects like shared vigilance or access to mates (Kramer et al., 2009). In the human world, this could also be due to a variety of other factors from habitat modification to economies of scale. In either case, this has the effect of delaying the point at which individuals would move to the next habitat (Fig. 3, cf.  $d_1$  and  $d_2$ ). Moreover, because of the nonlinear dynamics present under Allee's principal, individuals may choose to switch back and forth between habitats of varying suitability resulting in rapid shifts in population density (Fig. 3b,  $i$  and  $ii$ ; see Winterhalder et al., 2010).

Another variant of the IFD removes the 'free' assumption of the model (Fig. 3c). Known as the Ideal Despotic (or Dominance) Distribution model, this has the opposite effect of Allee's principal by decreasing the optimal density at which individuals should leave the more suitable habitat for the less suitable habitat (Fig. 3, cf.  $d_1$  and  $d_3$ ). While the original formulation of this despotic variant results in early departure (Fretwell and Lucas, 1969), this has been re examined focusing on the opposite question: when should a despotic switch from driving individuals out of their habitat and begin to bring individuals into their habitat under conditions of submission (Bell and Winterhalder, 2014; see also Vehrencamp, 1983). In the latter scenario, despotic distributions may reveal Allee like effects in which individuals are better off remaining longer in a high suitability habitat, even when a portion of their gains are given away to a ruling despotic.

Ideal distribution models provide predictions about dynamic interactions between demography and habitat choice that can be tested anywhere from the local to the continental scale. Here we briefly review how applications of the IFD and IDD have provided explanations of patterns of colonization, coordinated capital investments and the emergence of institutionalized hierarchy.

### 5.1. Ideal free colonization

The standard IFD provides clear predictions about settlement decisions that may be particularly useful to explain colonization events. Recently, insights from the IFD have helped explain patterning in the colonization of Australia (Allen and O'Connell, 2008; O'Connell and Allen, 2012; O'Connell et al., 2010), the Pacific coast of North America (Codding et al., 2012; Codding and

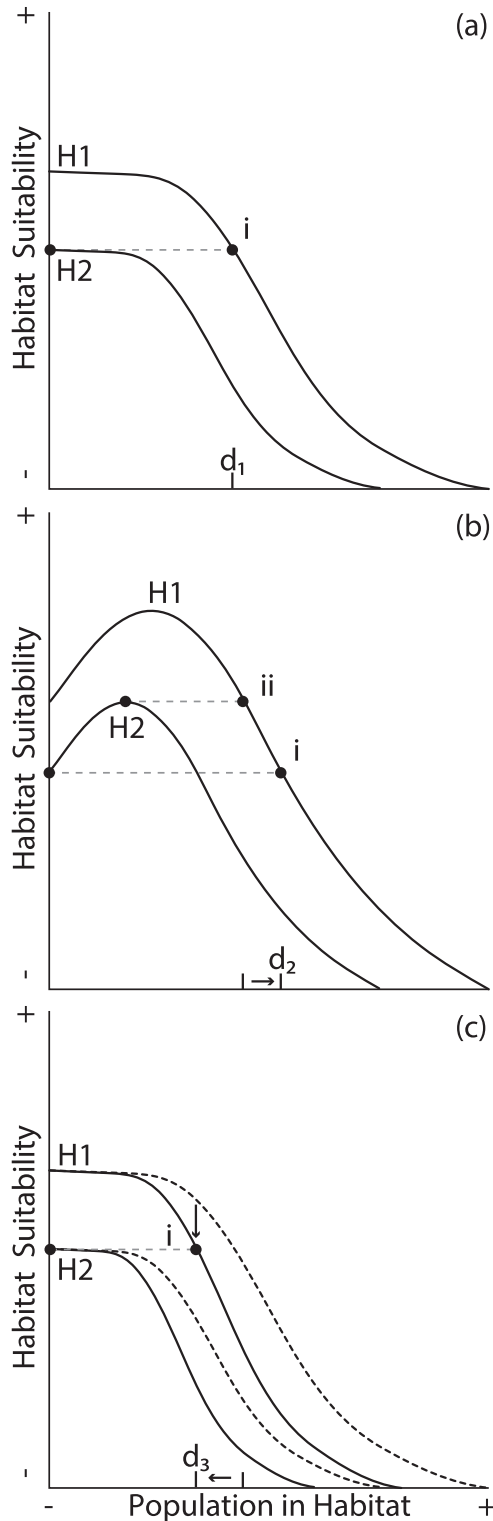


Fig. 3. Graphical representations of (a) ideal free, (b) ideal free under Allee's principal and (c) ideal despotic distribution models after Fretwell and Lucas (1969).

Jones, 2013; Fitzhugh and Kennett 2010; Jazwa et al., 2013; Kennett, 2005; Kennett et al., 2009; Winterhalder et al., 2010), Polynesian islands (Bell et al., 2015; Kennett et al., 2006a) and Caribbean islands (Giovas and Fitzpatrick, 2014). Given this rate of progress, formal applications of the IFD will likely continue to grow. Future applications have the potential to explain phenomena ranging from the migration of behaviorally modern humans out of Africa and

across the planet (Eriksson et al., 2012) to the Late Holocene movements of agricultural populations (e.g., Diamond and Bellwood, 2003; Russell et al., 2014), including European colonial expansion.

Difficulties in applying the IFD mostly center on generating a reliable proxy for habitat suitability, which unlike utility estimates in other models, must be spatially explicit for empirical evaluation. To date, researchers have relied on proxies ranging from the abundance resource specific patches (e.g., Kennett, 2005) to general estimates of environmental productivity (e.g., Codding and Jones, 2013), but no studies have adequately linked individual foraging decisions to large scale patterns in habitat suitability. To accomplish this, additional actualistic work is needed to determine if current proxies of suitability approximate aggregate estimates of in patch foraging returns (Codding and Bliege Bird, 2012). But leaving this caveat aside, the numerous positive results imply that researchers are estimating suitability well enough to approximate how prehistoric populations settled and spread through regional environments.

Beyond clear explanations of colonization events, perhaps some of the most interesting findings result from the ways in which these simple predictions can help explain seemingly complex phenomena. For example, Codding and Jones (2013) show that IFD dynamics predict the order in which ethnolinguistic groups colonized prehistoric California, the result of which produced the dense mosaic of diverse languages recorded at contact. In this case, the application of the IFD shows that apparently complex cultural phenomena (Currie and Mace, 2012) may be explained by simple dynamics linking environmental variability, demography and human decisions.

### 5.2. Positive density dependence

The addition of Allee's principal to the IFD provides the means to explore how aspects of habitat modification, capital improvements, economies of scale and the like may initially increase the utility of patches with increasing population density. This model variant can help develop expectations about where and when individuals may benefit through mutualistic interactions like cooperation.

McClure et al. (2006) suggest that intensification during Spain's Neolithic period represent Allee effects wherein farmers moved from more suitable valley bottoms to valley margins that were improved by the adoption of the plow and investments in agricultural architecture. Kennett et al. (2006a) make a similar case for the adoption of food production in Oceania. These findings suggest that capital improvements and coordinated labor may be more likely to emerge when individuals enter habitats of lower suitability, where there may be greater incentives to cooperate in order to increase subsistence yields.

Despite such progress in understanding positive density dependence, the effects of Allee's principal have remained elusive in most archaeological contexts. To further this research, future archaeological work will need to focus on the collection of fine grained quantitative data to estimate simultaneous changes in habitat suitability and demography over relatively short intervals of time. Comparative ethnographic work could also facilitate tests of Allee's principal by examining subsistence efficiency in similar environments with varied population densities and degrees of capital improvement. Additional research in this arena promises to help explain the emergence of habitual cooperation and coordinated labor across prehistoric societies.

### 5.3. Despotism and hierarchy

In almost every application of the IFD, researchers find compelling departures that suggest IDD dynamics are at play late in the prehistoric record (e.g., Codding and Jones, 2013; Giovas and



Fitzpatrick, 2014; Kennett et al., 2009). One of the best developed investigations centers on California's Northern Channel Islands, where Kennett, Winterhalder and colleagues (Kennett et al., 2009; Winterhalder et al., 2010) find that growing populations competing for access to resources in a circumscribed environment (*sensu Carneiro, 1970*) eventually find it preferable to give up some autonomy rather than move into the most marginal habitats. These results illustrate how institutionalized social hierarchies may emerge as a result of initial environmental inequality favoring the earliest colonizers who settled the highest suitability habitats—an example of how ecological inheritance can structure social developments.

Similar patterns may have occurred across Polynesia. While the initial colonization of West Polynesia seems to follow predictions from the IFD (Kennett et al., 2006a), Kennett and Winterhalder (2008) argue that the rapid expansion of populations into remote Polynesia was driven by a system of hierarchical subjugation that pushed individuals away from high suitability habitats and encouraged them to explore remote locations where they could establish their own hierarchy.

The IDD provides a nuanced approach to explain why individuals may come to subject themselves to the rule of others. But to date, the application of IDD predictions to archaeological problems is in its infancy. Continued efforts in this direction promise to explain broad patterns in social complexity, including the emergence of chiefdoms and the origins of state level societies.

## 6. Conclusion

This paper makes the case that archaeological science requires theory as much (if not more) than method to advance in the future. Because it draws predictions from a general theory of behavior guided by natural selection that can be tested in actualistic and archaeological contexts, HBE solves two of the major problems facing scientific explanations of past human behavior from its material remains. This approach directs research towards the systematic analysis of human behavior and ecology with the goal of explaining variability across the entire human experience. This is not a small task and as with any long term research strategy, progress will mostly be incremental. While many archaeological applications of HBE have been directed toward some of the most basic and easy to explain archaeological phenomena (*sensu Hawkes, 1954*), recent work has brought new insight into key research problems ranging from the origins of agriculture to the development of institutionalized hierarchy. Future work should stay the course by building on these foundations to link simple theoretical predictions about individual decisions to dynamic and complex social and environmental contexts. Ongoing applications of the approach promise to elucidate our human past by continuing to direct research towards interesting questions while providing the tools necessary to answer those questions.

## Acknowledgment

Thanks to Richard Klein for always emphasizing evolution and behavior in archaeological science. This paper benefited significantly from comments and suggestions by David Zeanah, Adie Whitaker, Polly Wiessner, Blake Vernon, Nathan Stevens, Christopher Parker, Duncan Metcalfe, Kate Magargal, Doug Kennett, Kristen Hawkes, Jack Broughton, Rebecca Bliege Bird, Adrian Bell, anonymous reviewers and especially Jim O'Connell. The authors are solely responsible for not heeding sound advice.

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