HUMAN BEHAVIORAL ECOLOGY SECTION

# Levels of Explanation in Behavioral Ecology

## Understanding Seemingly Paradoxical Behavior Along the Central Coast of Alta California

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***Abstract*** Archaeological applications of behavioral ecology apply models developed for synchronic phenomena to diachronic trends. Some problems arise out of this mismatch, one of which involves distinguishing between functional and historical levels of explanation. Historical explanations attempt to outline the diachronic emergence or evolution of some behavioral trait or strategy; in contrast, functional explanations attempt to explain the adaptive benefits an individual gains from a behavior or strategy. Here we examine the relationship between these two levels of explanation with technological and subsistence data from California's central coast, specifically focusing on explaining the function of seemingly paradoxical transitions in fishing technology that occurred during the late Holocene. By keeping these two levels of explanation separate and distinct, we highlight how archaeologists can explain the adaptive function of prehistoric human behavior that occurred within a particular historical context.

***Resumen*** Las aplicaciones arqueológicas de la ecología behaviorística aplican modelos desarrollados para fenómenos sincrónicos a tendencias diacrónicas. Algunos problemas provienen de esta falta de armonía, uno de los cuales implica distinguirse entre niveles funcionales e históricos de la explicación. Las explicaciones históricas intentan perfilar la aparición diacrónica o la evolución de algún rasgo behaviorístico o estrategia; en contraste, las explicaciones funcionales intentan explicar las ventajas adaptables que un individuo gana de un comportamiento o

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estrategia. Aquí examinamos la relación entre estos dos niveles de explicación con y datos tecnológicos y de subsistencia de la costa central de California, que expresamente nos concentra en la explicación de la función de transiciones aparentemente paradójicas en la tecnología de pesca que ocurrió durante Holocene tardío. Guardando separados y distintos estos dos niveles de la explicación, destacamos como los arqueólogos pueden explicar la función de adaptación del comportamiento humano prehistórico que ocurrió dentro de un contexto histórico particular.

**Since the 1970s, archaeological applications** of behavioral ecology have made tremendous progress in contributing to our understanding of human prehistory and behavior (see Bird and O'Connell 2006; Lupo 2007; Shennan 2008). Nonetheless, archaeologists have yet to work out all the problems associated with applying models developed for relatively high resolution, synchronic phenomena to relatively low resolution, diachronic trends. One such problem involves the relationship between historical and functional explanations. As outlined by Tinbergen (1963) and as more recently discussed by Bird and O'Connell (2006:145; see also Krebs and Davies 1993:4), functional and historical explanations are two independent levels of inquiry. Historical explanations in archaeology can be viewed as any explanation that seeks to outline the particular diachronic processes through which a behavior or strategy developed, particularly in relation to external factors whether they be ecological, demographic, technological, etc.

While often the focus of archaeological research, historical explanations are not the focus of human behavioral ecology, which attempts to explain the adaptive function of biological design in an ecological setting (Winterhalder and Smith 1992). However, archaeologists interested in explaining the function of behavior are necessarily involved in the historical level of explanation, since functional explanations require some understanding of the historical context in which behaviors occurred. In some respects, functional explanations in archaeological applications of behavioral ecology must rest on a historical explanation (or rather, a historical context), as the function of the behaviors in question may have changed through time in response to external factors explainable only within the historical level of inquiry. Thus, despite being distinct and independent levels of inquiry, functional and historical explanations in archaeology co-exist in a dynamic relationship that must be unwound if adaptive accounts of prehistoric behavior are going to achieve serious credibility. In keeping the two levels of explanation explicit, researchers may be better able to resolve ongoing debates regarding the function of specific behaviors and the particular context in which these behaviors occurred.

In this article, we examine the dynamic relationship between historical and

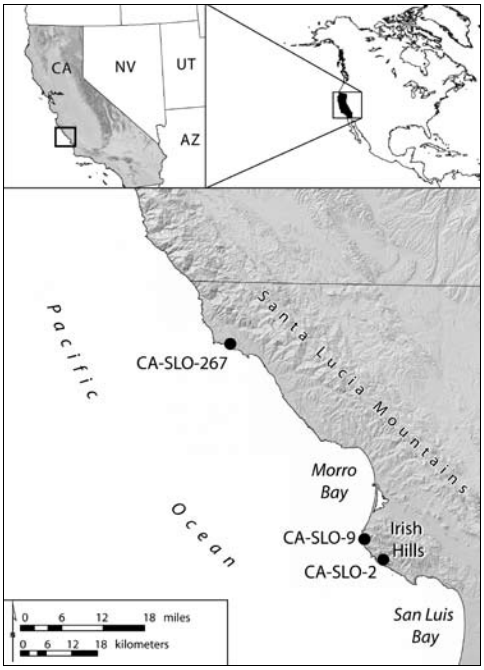


**Figure 1.** Sites mentioned in text.

functional explanations in archaeological applications of behavioral ecology. First we detail the four levels of explanation outlined by Tinbergen (1963), then we apply these concepts through an examination of the function of seemingly maladaptive changes in fishing practices along the central California coast in the late Holocene (Figure 1). Our aim is to highlight the distinction between historical and functional explanations, and in so doing, show how behavioral ecological models can provide an opportunity to revise our understanding of specific historical contexts and the adaptive function of behaviors that occurred within them.

## Levels of Explanation in Behavioral Ecology

In his watershed publication, Tinbergen (1963) redefined the study of nonhuman animal behavior by outlining four distinct levels of explanation. The first he referred to as *causal,* but may be better understood as *proximate* or *mechanistic*. A mechanistic explanation refers to the proximate physiological or chemical processes that allow some behavior to occur. The second level of analysis he called *survival value* but may also be termed *adaptive* or *functional*. Functional explanations are the primary focus of behavioral ecology (Winterhalder and Smith 1992) and, assuming some form of heredity, these explanations seek to understand the "ultimate" cause of how specific traits confer differential survivorship and reproductive success to individuals and thus lead to the prolonged presence of the trait (see Williams 1966).

The third level of explanation is *ontogenetic* or *developmental*. This level of analysis seeks to explain how a specific trait or behavior emerges within individuals as they develop through life-history. The fourth and final level of explanation is what Tinbergen (1963) referred to as *evolutionary*, or the generation of *phylogenetic* explanations that outline the evolutionary history of a trait or behavior. In archaeology, this level of explanation has also been referred to as *historical* (Bird and O'Connell 2006). Historical explanations include those that attempt to outline the diachronic emergence or evolution of some behavioral trait or strategy through time. In contrast, functional explanations attempt to explain the adaptive benefits an individual gains from such behavior.

Similar to Aristotle's *Physics* (II.3), Tinbergen's work served to outline several independent levels of inquiry that may be pursued in search of causal explanations for particular phenomena. A specific behavioral trait (or its material residue) can be explained at any level. For example, a physiological mechanism may be the proximate cause behavior x; but behavior x may also have an effect on whether an individual will survive and reproduce (Tinbergen 1963:418). Researchers may also want to know how behavior x develops in an individual's life history (ontogeny), or how it evolved in the species (phylogenetic). While an explanation is possible at each level of analysis, any two explanations do not compete with one another. The two "proximate" levels of explanation, mechanistic and ontogenetic, remain of little interest to archaeologists; however, the "ultimate" explanations, adaptive (or functional) and historical, frequently take center stage (Bird and O'Connell 2006).

Explicitly parsing these two levels of explanation in such a way can provide an avenue to answer complex questions about human behavior in the past. Below, we take this approach to explain the function of seemingly paradoxical behavior that occurred during the Middle-Late Transition period along California's central coast. Here, a comparison of fish bone assemblages and related fishing equipment at the representative Middle Period component at CA-SLO-267 (Jones and Ferneau 2002a) with the Middle-Late Transition component at CA-SLO-9 (Codding and Jones 2007; Codding et al. 2009) reveal patterns that are paradoxical in light of recent models of technological change.

## The Function of Seemingly Maladaptive Fishing Practices during the Late Holocene

Relative to other time periods in California, sites dating to the Middle-Late Transition period (MLT, ca. cal A.D. 1000-1250) show evidence for dramatic changes in material patterning (e.g., Jones et al. 1999, 2007). This time period is generally recognized as being marked by prolonged droughts (Graumlich 1993; LaMarche 1974; Stine 1994) but increased marine productivity (Kennett 2005; Kennett and Kennett 2000) caused by the Medieval Climatic Anomaly (MCA). Studies have shown that the Middle-Late Transition coincided with increased violence (Jones and Schwitalla 2008), health problems (Jones and Schwitalla 2008; Wiess 2002), widespread site abandonment (Jones and Ferneau 2002b; Jones et al. 1999, 2007), and subsistence changes (Codding and Jones 2007; Codding et al. 2010; Pilloud 2006). These transformations also appear to be associated with a "de-intensification" of fishing practices along the central coast (Codding and Jones 2006, 2007; Codding et al. 2009).

When compared with the fish bone assemblage from the well-defined Middle Period (ca. cal 600 BC to AD 1000) component at CA-SLO-267 (Jones and Ferneau 2002a), the MLT assemblage from the Coon Creek site (CA-SLO-9) differs significantly ($\chi^2$ = 426.66, $p$ = 0.0005, Table 1). This is primarily the result of significantly more large fish remains and fewer small fish remains during the MLT (see Table 1). The MLT fish bone assemblage shows that foragers began to specialize on larger fish taxa, particularly cabezon and rockfish, which make up 72.1 percent of the total NISP compared to only 38.0 percent during the Middle Period. This indicates an overall decrease in the evenness of fish species acquired resulting from a specialization on larger taxa, which is predicted by a change from indiscriminately netting fish as opposed to selectively targeting larger species with hook and line technology (see Love 1996; Pletka 2001; Salls 1988). This is also supported by a change in the frequencies of fishing related artifacts. As shown in Table 1, the Middle Period assemblage is characterized by grooved stone net weights (N = 11), an absence of notched stones, and a single shell fishhook; the opposite pattern is seen during the MLT where grooved stone net weights are absent and the assemblage is dominated by notched stones (N = 20) and circular shell fishhooks (N = 9). These overall differences are significant ($\chi^2$ = 36.65, $p$ = 0.0005).

This *historical* transition in technology and fishing strategies is seemingly paradoxical, as catching fish with hook and line technology is significantly less efficient than mass capture via nets (see Bliege Bird and Bird 1997; Smith 1991). There are two competing *functional* explanations for this sort of change in fishing practices. The first suggests that foragers were adaptively responding to changes in demographic and ecological conditions (Bettinger et al. 2006; Sosis 2000), while the second posits that these sorts of changes represent maladaptive technological loss (Henrich 2004).

## *A Simple Model of Technological Intensification*

Building on the work of Ugan et al. (2003), Bettinger et al. (2006; see also Bettinger 2009) developed a simple model of technological intensification that examines

**Table 1.** Summary of Fish Remains and Fishing Related Artifacts from CA-SLO-9 and CA-SLO-267.[a]

| | | MLT Period | | | | Middle Period | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | CA-SLO-9 | | | | CA-SLO-267 | | | |
| **Taxon** | **Common Name** | **%** | **NISP** | **Residuals**[b] | ***p***[c] | **%** | **NISP** | **Residuals**[b] | ***p***[c] |
| Embiotocidae | Surfperches | 5.8 | 44 | –2.7 | 0.0023 | 10.3 | 144 | 2.0 | 0.0244 |
| Scorpaenichthys marmoratus | Cabezon | 29.0 | 219 | 11.7 | < 0.0001 | 5.0 | 70 | –8.6 | < 0.0001 |
| *Sebastes* spp. | Rockfishes | 43.0 | 325 | 3.0 | 0.0010 | 32.9 | 459 | –2.2 | 0.0060 |
| Stichaeidae | Pricklebacks | 4.9 | 37 | –11.1 | < 0.0001 | 36.3 | 506 | 8.2 | < 0.0001 |
| | Other | 17.2 | 130 | 0.8 | 0.2174 | 15.4 | 215 | –0.6 | 0.2811 |
| | Total | 100.0 | 755 | — | — | 100.0 | 1394 | — | — |
| Large Fish Index[d] | | 72.1 | — | — | — | 37.9 | — | — | — |
| **Artifact**[e] | | | N | | | | N | | |
| Grooved stones | | | 0 | | | | 11 | | |
| Notched stones | | | 20 | | | | 0 | | |
| Circular shell fishhooks | | | 9 | | | | 1 | | |

[a] Data from Codding et al. (2009) and Jones and Ferneau (2002). The difference between the two fish bone assemblages is highly significant ($\chi^2 = 426.66$, $p = 0.0005$). NISP = Number of identified specimens.
[b] Pearson residuals resulting from a $\chi^2$ test calculated as the observed count minus the expected count all over the square root of the expected count (R Core Development Team 2010).
[c] The probability that each count differs as a result of chance alone, significant values are in bold (see Note 1).
[d] The Large Fish Index is calculated as the proportion of Rockfishes (*Sebastes* sp.) and Cabezon (*Scorpaenichthys marmoratus*) relative to the total NISP and represents the fish species thought to be caught by hook and line or spear as opposed to nets (see Love 1996; Pletka 2001; Salls 1988).
[e] The difference between these two assemblages is significant ($\chi^2 = 36.65$, $p = 0.0005$).

the relationships between the cost of manufacturing and maintaining a specific technology, the caloric return rates that such a technology provides, and the time spent foraging with that particular technology in a particular foraging activity. Their model essentially shows that technologies with higher startup and maintenance costs generally provide higher caloric returns per unit time, but whether technological intensification is worth the added cost depends on how much time a forager spends on the particular activity for which the technology is used.

The potential benefits of cooperative net fishing are further reduced by the costs of cooperation. Sosis (2000:453; see also Alvard and Nolin 2000) suggested that a cooperative fishing strategy should outweigh an individual strategy as long as the per capita benefits of cooperation are greater than the costs. Thus, given certain circumstances, it is possible for the benefits associated with individual fishing strategies with hook and line technology to outweigh a cooperative net fishing strategy depending on the costs of cooperating. These costs and benefits should, in turn, be contingent on the number of potential cooperators.

### *A Simple Model of Social Learning*

Henrich (2004) recently proposed that technological losses associated with the secession of fishing among indigenous Tasmanians was the result of maladaptive cultural loss. Assuming that individuals bias their attention towards skilled or prestigious individuals, Henrich (2004; also Boyd and Richerson 1985 [not in refs]) suggested that individuals will imitate, albeit imperfectly, skilled individuals. However, if population density is low, then there are fewer skilled individuals in the population; as a result, useful or adaptive skills and technology may be lost over generations. Thus, low population densities are a mechanism for the maintenance of inefficient behavioral traits. This maladaptive hypothesis is similar to the stance taken by some evolutionary psychologists (e.g., Buss 1999:400-403) and even some California archaeologists (e.g., McGuire and Hildebrandt 2005; McGuire et al. 2007) who presume that environmental novelty can lead to maladaptive behavioral traits.

### *Why did Foragers De-intensify Fishing Practices during the Middle-Late Transition?*

In order to understand whether this paradoxical shift in fishing practices is functional or maladaptive, analysis must first turn to the historical level of inquiry in order to test three predictions that stem from these models. First, both of the models discussed above predict that such technological changes result from declines in population densities. Therefore, if either of these models are to explain this technological transition, the data will have to provide evidence for changes in overall population densities (Henrich 2004) or at least in the number of foragers choosing to fish (Bettinger et al. 2006; Sosis 2000). Second, if this transition were maladaptive, as envisioned by Henrich (2004), the technological loss would occur over a long period of time marked by the deterioration of technical knowledge and skill; however, if this technological transition was the result of individuals attempting to maximize their energetic intake in the face of changing socio-ecological variables, it should occur relatively quickly (Smith 2000). Third, if this transition were maladaptive, it is expected by the maladaptive model to be represented by the loss of existing efficient technology and a fall back onto

**Table 2.** Size Frequencies of Red and Black Abalone from CA-SLO-9 (MLT Period) and CA-SLO-267 (Middle Period).[a]

| | Red Abalone (*Haliotis rufescens*) | | | | | | Black Abalone (*Haliotis cracherodii*) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MLT Period | | | Middle Period | | | MLT Period | | | Middle Period | | |
| Size Class (mm) | Count | Residuals[b] | p[c] | Count | Residuals[b] | p[c] | Count | Residuals[b] | p[c] | Count | Residuals[b] | p[c] |
| 0–20 | 1 | −2.4 | 0.0032 | 15 | 2.4 | 0.0185 | 0 | −1.6 | 0.0654 | 6 | 1.5 | 0.1144 |
| 20–40 | 41 | 1.2 | 0.1231 | 28 | −1.2 | 0.1230 | 11 | 0.8 | 0.2424 | 8 | −0.7 | 0.2815 |
| 40–60 | 39 | −0.3 | 0.4205 | 44 | 0.3 | 0.4053 | 19 | −1.3 | 0.0912 | 38 | 1.2 | 0.1155 |
| 60–80 | 27 | −0.7 | 0.2619 | 36 | 0.7 | 0.2549 | 11 | −1.4 | 0.0867 | 26 | 1.3 | 0.1145 |
| 80–100 | 29 | −1.1 | 0.1486 | 43 | 1.1 | 0.1528 | 26 | 0.7 | 0.2527 | 24 | −0.7 | 0.2810 |
| 100–120 | 39 | 0.7 | 0.2608 | 32 | −0.7 | 0.2736 | 22 | 1.7 | 0.0575 | 12 | −1.5 | 0.0619 |
| 120–140 | 28 | 1.1 | 0.1477 | 18 | −1.1 | 0.1500 | 6 | 1.0 | 0.2236 | 3 | −0.9 | 0.2710 |
| 140–160 | 9 | 0.0 | 0.5269 | 9 | 0.0 | 0.5687 | 2 | 0.1 | 0.5401 | 2 | −0.1 | 0.6242 |
| 160–180 | 7 | 1.2 | 0.1591 | 2 | −1.2 | 0.1644 | 1 | 0.8 | 0.3637 | 0 | −0.7 | 0.5775 |
| 180–200 | 1 | 0.0 | 0.6267 | 1 | 0.0 | 0.7300 | 0 | n/a | n/a | 0 | n/a | n/a |

[a] Data from Codding et al. (2009; see also Codding and Jones 2007; Jones and Ferneau 2002). There is a significant difference between time periods in black abalone size ($\chi^2 = 22.08$, $p = 0.0040$) and red abalone size ($\chi^2 = 24.55$, $p = 0.0010$).
[b] Pearson residuals resulting from a $\chi^2$ test calculated as the observed count minus the expected count all over the square root of the expected count (R Core Development Team 2010).
[c] The probability that each count differs as a result of chance alone; significant values are in bold (see Note 1).

preexisting, less efficient technology (Henrich 2004); the incorporation of a new technology would suggest an adaptive decision-making process envisioned by the Bettinger et al. (2006) model.

***1. Demographic Changes.*** An examination of shellfish size frequencies between multiple temporal or spatial components can provide evidence for the degree of littoral exploitation (e.g., Klein et al. 2004). A higher proportion of smaller sized shellfish suggest a more intensive exploitation of the littoral resulting from the suppression of shellfish populations; a higher proportion of larger sized shellfish suggests the opposite. A comparison of red abalone (*Haliotis rufescens*) and black abalone (*Haliotis cracherodii*) size frequencies from the Middle Period (CA-SLO-267) to the MLT (CA-SLO-9) shows that that they differ significantly (red abalone $\chi^2 = 24.55$, $p = 0.0010$; black abalone $\chi^2 = 22.08$, $p = 0.0040$). For red abalone, this is due to the significantly fewer specimens in the 0-20 mm size class at CA-SLO-9 ($p = 0.0032$) and the significantly greater number of specimens at CA-SLO-267 ($p = 0.0185$; Table 2). For black abalone, this is the result of a higher

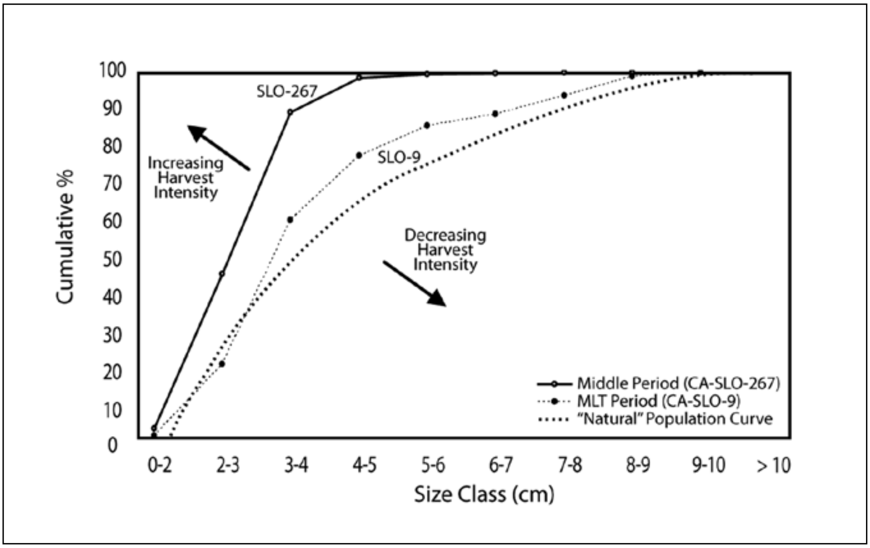


**Figure 2.** Cumulative mussel size frequencies comparing Middle Period (CA-SLO-267) and Middle-Late Transition period (CA-SLO-9) harvesting strategies relative to the "Natural" Population Curve (from Whitaker 2008).

number of large abalone (100-120 mm; $p = 0.0575$) at CA-SLO-9 (see Table 2). This same trend is apparent when comparing the cumulative California mussel (*Mytilus californianus*) size frequencies between the two time periods (see Figure 2), which shows an overall decrease in the intensity of mussel harvesting during the MLT. Overall, these diachronic trends occurring within the historical level of inquiry indicate that the MLT was marked by a decrease in the exploitation of the littoral, which suggests a lower overall density of foragers. However, since this is a prerequisite of both models, this does not clarify which model best explains this technological transition.

***2. Tempo of Change.*** Examining the timing of diachronic change should help to discriminate between the two models. Unlike the pattern envisioned by Henrich (2004), the timing of technological change during the MLT appears to have been a sudden and abrupt transition marked by rapid environmental change (Jones et al. 1999), site abandonment throughout the region (Jones and Ferneau 2002b; Jones et al. 1999, 2007) and transitions in technology visible over relatively short time periods in single locales, including the trans-Holocene record at Diablo Canyon (CA-SLO-2 [Greenwood 1972]; similar changes are also evident in Monterey County [Pohorecky 1976]). These material markers signify not a prolonged deterioration of knowledge, but rather a rapid change in technology relative to a rapid environmental shift.

***3. Maladaptive Loss vs. Adaptive Transition.*** If this pattern were maladaptive, it should be represented by the loss of preexisting efficient technology and a reliance on preexisting, less efficient technology. However, unlike the prediction derived from the maladaptive model (Henrich 2004), this event coincides with the adoption of new technology, specifically circular shell fishhooks which appear in high frequencies along the central coast for the first time during the MLT (see Codding and Jones 2007; Jones et al. 2007). These data suggest that individuals were quick to adapt to changing environmental circumstances, even adopting new technology that may have provided greater benefits in an altered environment. This could also explain the later adoption of circular shell fishhooks along the central coast that were more widespread elsewhere (Rick et al. 2002).

While this conclusion runs counter to the predictions of some models of technological change (e.g., Henrich 2004), the plastic and flexible nature of human behavior to adaptively respond to changing environments is a central tenant in human behavioral ecology (Irons 1979; Smith 2000). The data examined here suggest that linked environmental and demographic changes during the MLT altered the costs and benefits associated with cooperative fishing, resulting in higher benefits for individual hook and line fishing. Historical factors, including local demography and the tempo and type of change, provided the context to evaluate these two models of technological change. Here, a behavioral ecological model helps to elucidate poorly understood historical phenomena (i.e., the effects of the MCA on prehistoric human populations) and also suggests that some seemingly maladaptive technological changes can perhaps be more properly viewed as adaptive.

## Summary and Conclusion

Following Tinbergen (1963), the aim of this article was to highlight the distinctive roles that historical and functional explanations play in archaeological research guided by behavioral ecology. The example discussed illustrates some of the ways in which behavioral ecological models can be effectively integrated with long-term diachronic data to elucidate historical and functional aspects of human behavior. By testing predictions derived from two competing models at the historical level of inquiry, this study was able to provided a clear functional explanation for seemingly maladaptive technological transitions during the Late Holocene. Similar approaches have resolved other debates about the function of large game hunting along the central California coast (Hildebrandt et al. 2010; Jones and Codding

2010; Jones et al. 2008) and are likely to help resolve future debates over seemingly paradoxical behavior.

Human behavior, past and present, occurs within a particular context and this context must be understood as clearly as possible if adaptive accounts are going to achieve any semblance of empirical validity. By acknowledging this role of history in archaeological applications of human behavioral ecology and by making the differences between historical and functional explanations explicit, we can gain greater clarity in our interpretations and hopefully come closer to understanding and explaining variation in past human behavior.

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## Note

1. All Chi-Square ($\chi^2$) tests were performed in the R environment using a Monte Carlo simulation (with 2000 iterations) to calculate $\chi^2$ and alpha ($p$) values (R Core Development Team 2010). Tables 1 and 2 also present the results of secondary contingency table analysis that generates the significance of the contribution of each cell to the overall difference between multiple tables based on the binomial probability theorem. This function was written in R by Ian G. Robertson (Stanford University) based on a suggestion by James Allison. The same analysis can be done with the *TWO-WAY* function in Kintigh's (2009) *Tools for Quantitative Archaeology.* Greater detail of this analysis is provided elsewhere (see Codding et al. 2010).

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