CHAPTER 7

A Land of Work: Foraging Behavior and Ecology

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Work is a core theme in many of the major issues and debates in California archaeology. Work is central in understanding why the first Californians entered the region (e.g., Erlandson, this volume): how thousands of years of work following colonization resulted in the over-exploitation of particular resources (e.g., Broughton 1994), the economic intensification of work effort (e.g., Basgall 1987), shifts in the patterns of population growth (e.g., Hull, this volume), changes in the currencies that drive work (e.g., Hildebrandt and McGuire, this volume), and the emergence of social hierarchies in politically complex societies (e.g., Arnold 1992, 1993). All of these were punctuated by environmental events which alter the very foundations of work (e.g., Jones and Schwitalla, this volume).

Work is here defined as the practices through which individuals make a living; in prehistoric California, this was done through hunting and gathering. Much of the contemporary research on prehistoric work in indigenous California has been framed by human behavioral ecology (HBE). To investigate work, behavioral ecologists draw on simple formal economic models that provide general predictions about the daily decisions individuals make in the process of making a living. In archaeological contexts, these models are generally used to derive predictions that can be tested with archaeological datasets representing multiple periods of time or multiple locations in space. Of primary importance in this approach is a focus on the ecological interactions between daily subsistence decisions and environmental variability. This is because the two likely structure each other dynamically: subsistence decisions alter environments, and altered environments affect future decisions. Linking these processes to their material outcomes, archaeological applications of behavioral ecology examine the interactions between environmental variability and daily foraging decisions over the long term.
Use of these models in California has a history that extends back to the 1970s, when Beaton (1973) mentioned optimal foraging theory as a possible explanation for variation in molluscan faunal assemblages over time. This was followed by a series of papers in the 1990s that applied diet breadth (e.g., Broughton 1994, 1997, 1999; Erlandson 1991; Hildebrandt and Jones 1992; Raab 1992) and patch choice concepts (Jones 1991, 1992). The utility of these and other model theories derived from HBE is affirmed by the increase in their application in the early 2000s (e.g., Broughton et al. 2011; Cannon 2009; Codding and Jones 2007; Codding et al. 2010; Hale 2010; Jones et al. 2008; Kennett 2005; Kennett and Kennett 2000; Kennett et al. 2009; Morgan 2009; Whitaker 2008a, 2009; Winterhalder and Bettinger 2010; Winterhalder et al. 2010).

Here, we summarize and synthesize some recent behavioral ecological investigations into prehistoric work in California. First, we draw on the Ideal Free Distribution (IFD) model to examine the processes through which individuals decide where to settle to make a living. Then, we draw on the Prey Choice Model (PCM) to examine the decisions individuals make in the process of acquiring their next meal. In both cases, we highlight how these approaches have revisited and provided new insight into classic problems in California archaeology. Through these examples, we aim to show that by examining the ecology of work, archaeologists can come to understand a great deal about events in prehistory and the daily lives of individuals.

**DECISIONS OF WHERE TO LIVE AND THE IDEAL FREE DISTRIBUTION MODEL**

To understand why individuals move through space, where they settle, and what effects these decisions have on work and social interactions, archaeologists have recently drawn on the IFD model (Fretwell and Lucas 1969; e.g., Kennett et al. 2009; Winterhalder et al. 2010). The IFD examines the distribution of individuals between two or more habitats that vary in their suitability, which, like utility, is contextually defined based on the question at hand (i.e., resource availability, defensibility, access to trade routes, etc.). The model begins by assuming that individuals have perfect knowledge of the environment, are “free” to move, and, as a consequence, will “distribute” themselves “ideally” so that each individual maintains residence in a habitat that is equally suitable. The model also assumes that habitat suitability declines as a function of population density (somewhat akin to the marginal value theorem; Charnov and Orians 1973). Such negative density dependence means that the more individuals occupy a given habitat, the worse off each
The model is represented graphically in Figure 7.1A (after Fretwell and Lucas 1968; Kennett 2005). This shows an environment in which there are three habitats (H1–H3) that vary in their suitability. Based on the assumptions and predictions of the model, the first individual to enter this environment should occupy H1, as should subsequent individuals until point a, at which the suitability of H1 has declined to a point that it matches the suitability of H2. Subsequent individuals who enter the environment (either through migration or population growth) should occupy both H1 and H2 until point b, where the individual should then distribute themselves between H1, H2, and H3a.

Some very interesting archaeological predictions can be derived from this simple framework. First, the highest-ranking habitats should be occupied first, and lower-ranking habitats should only be occupied when population densities increase to a point that makes their settlement viable. Second, the highest-ranking habitat should always have a higher overall population density unless, if as figured by H3b, lower-ranking habitats decline in suitability at a slower rate than high-ranking habitats. If this is the case, initially lower-ranking habitats may end up with greater local population densities as the total population size increases. Although these predictions may seem overly simple, their relative simplicity is in fact one of their virtues in that they can easily be used to formalize hypotheses or predictions to help evaluate old, unresolved questions. Here, we discuss tests of two of these predictions with two cases from coastal California.

Figure 7.1  Graphical representations of the Ideal Free Distribution (IFD) model (after Fretwell and Lucas 1968; Kennett 2005; Winterhalder et al. 2010) and the encounter contingent prey choice model (PCM; after Holt and Kimbrell 2007).
Colonization of Inequality: Settlement on the Northern Channel Islands

Recently, Winterhalder et al. (2010; see also Kennett 2005) used the IFD to model the colonization of Santa Barbara’s Northern Channel Islands. They found that the highest-ranked habitats were occupied first and remained occupied throughout the sequence, suggesting that habitat suitability did determine where people chose to live. However, not everyone was able to live in these higher-ranked habitats. Using this same framework, Kennett and colleagues (2009) examine island population densities in the late Holocene. As population densities increased, foraging intensity increased (e.g., Erlandson, Rick, Braje et al. 2008; Kennett 2005); when these density-dependent effects are combined with punctuated climatic events evident in the record (Jones et al. 1999; Kennett 2005; Kennett and Kennett 1999), some individuals appear to have been forced into more marginal environments (i.e., habitats with low suitability) while others remained in more productive locations. Through these processes, ecological inequities in the suitability of individual’s residences may have translated to economic and social inequities. Over time, these may have stimulated the emergence of persistent unequal exchanges between individuals on the Northern Channel Islands, leading to the eventual emergence of stable social hierarchies (Arnold 1992).

Colonization of Coastal California

At larger spatial scales, this same IFD logic can be used to generate predictions about the colonization of whole continents. Specifically, it can be used to examine (1) why people should move into empty environments and (2) which habitats they should occupy within those environments.

First, if habitats do indeed decline in suitability as populations increase, unoccupied neighboring habitats with similar features should always have higher suitability than occupied ones; this should lead to the rapid dispersal of populations along unoccupied fronts (see O’Connell et al. 2010). Depending on how quickly suitability declines and the distance between highly suitable habitats, these processes should happen more or less rapidly. This can help explain coastal colonization by linking this logic with Erlandson and colleagues’ (Erlandson et al. 2007; Erlandson, Moss, and Des Lauriers 2008; this volume) identification of ecological similarities in kelp forest communities around much of the Pacific basin. Traveling along this “kelp highway” (sensu Erlandson et al. 2007) and coming ashore to forage in the rocky intertidal and onshore patches, the first Californians may have expanded rapidly, settling in new habitats as occupied habitats declined in suitability. Erlandson et al. (2007) logically conclude that this process would eventually lead to the expansion of people into South America.
Second, given some estimate of broad-scale habitat suitability, the IFD may also help explain the distribution of early sites across the state. Jones (1991) predicted that estuarine habitats may have been particularly important for the first Californians due to the availability of highly ranked resources and their high overall productivity. Revisiting this hypothesis, we examine the proportion of sites along California’s central coast that are distributed near estuaries compared with those located away from estuaries in 100-year time intervals. The results confirm the original prediction, showing that during the earliest part of the sequence, the proportion of sites located within 15 kilometers of an estuary falls between 1 and 0.5 (Figure 7.2A). But, as populations expand between 6,000 and 8,000 years ago (Figure 7.2B), highly ranked habitats around estuaries began to become overcrowded, and individuals abruptly began settling elsewhere (Figure 7.2A); at this time, the proportion of sites located within 15 kilometers of an estuary dropped from about 0.55 to 0.15, showing that individuals dispersed into inland habitats and alternative coastal locations away from estuaries (Figure 7.2A).

![Figure 7.2](image-url)  
Figure 7.2. (A) Proportion of archaeological sites occupied along California’s central coast within 15 kilometers of an estuary relative to those located elsewhere. (B) Sum number of archaeological sites occupied per 100-year interval. (C) Locations of sites in reference to the 15-kilometer buffers around estuaries. The trends are fitted with a smoothing spline.
These results suggest that most habitats along the coast declined rapidly in suitability, but that estuaries and their neighboring environs acted as oases that drew people in and maintained high population densities throughout prehistory; as such, they were likely locations of great social importance. Following Kennett et al. (2009), if social inequality is likely to develop out of inequities in habitat suitability, then estuaries and similarly suitable locales (like river mouths along the north coast of California) might have become contested and protected places as populations increased through time. Subsequent population movements and immigrations would also have a significant impact, particularly in such highly suitable habitats.

Drawing on the logical framework outlined by the IFD, we have suggested some explanations for how and why people move from one place to another. In the long term, the aggregate of these processes suggests an explanation for how an unpopulated landscape became the socially and demographically diverse California chronicled at European contact. Continued refinement of these models and their applications to questions in prehistory may further our understanding of the past by helping to explain where evidence fails to meet expectations (e.g., why wasn’t North America colonized sooner?). Different models similarly approach these decisions that occur at more fine-grained scales. Why do habitats decline in suitability, and what happens to those who remain in perpetually depleted patches? To help understand these sorts of processes, we turn to the PCM.

**Decisions of What To Do and the Prey Choice Model**

To understand the decisions people made while foraging for a living, behavioral ecologically minded California archaeologists frequently draw on qualitative predictions derived from the PCM (also referred to as the diet breadth model; see Bettinger 2009). The basic PCM is focused on understanding whether or not an individual should pursue a resource after they have come across it, or if they should ignore that resource and continue searching for other, more profitable items. To determine this, resources are ranked based on their post-encounter profitability \( (e/h) \); that is, the expected energetic return \( (e) \) for an item after it has been encountered, divided by the expected handling costs \( (h) \). There are two components to handling costs: *pursuit* and *processing*. The former includes all the activities involved in acquiring that resource after the decision has been made to pursue it. The latter includes all of the costs required to render the resource edible after acquisition (grinding, butchering, cooking, etc.). Assuming that resources are distributed homogeneously and are encountered sequentially, a resource should be pursued
on encounter only if the expected post-encounter return rate ($e/h$) is greater than the expected overall return rate ($E/T$), which is measured as the total energy acquired during a single foraging bout divided by the total time spent foraging (comprising a search shared across all resources prior to encounter and time handling each resource). In an ideal world, the highest-ranking item should always be pursued on encounter and other resources should be added sequentially as the overall return rate falls, with declines in the abundance of the highest-ranking resource.

The basic dynamics of this process are shown graphically in Figure 7.1B (after Holt and Kimbrell 2007). The line represents a forager’s overall energetic return rate ($E/T$; think, for example, the expected rate of return for a day’s labor) relative to the abundance of, and hence an individual’s encounter rate with, the highest ranking resource ($R_1$). As long as the abundance of $R_1$ remains high enough (between points $a$ and $b$), the encounter rate with that item will be high and search costs low; hence, an individual’s overall return rate will remain high enough that all other resources can be ignored on encounter. However, once the abundance of $R_1$ declines below point $b$, individual foragers should start pursuing the second-highest-ranked resource ($R_2$) on encounter because doing so will result in a higher overall return rate ($E/T$) than continuing to exclusively search for $R_1$. Thus, if individuals face declines in the abundance of the highest-ranking resource, they must either suffer extremely high search costs for the highest-ranking resources, or make the best of a bad situation and start pursuing lower-ranked resources on encounter. If individuals opt for the former, there may be some other factor at work other than maximization of the rate of caloric intake (e.g., Hildebrandt and McGuire, this volume), but if they opt for the latter, then they have chosen to intensify (sensu Boserup 1965) their daily work effort, which allows for an increase in the amount of resource acquired per unit of area (leading perhaps to population growth), but at a higher overall cost per unit of time spent working.

Because post-encounter return rates cannot be measured directly with archaeological data, researchers have come to rely on proxy measures of prey rank. As resource rank derives from variability in one or all of the three components used to calculate $e/h$ (energy, pursuit, and processing), California archaeologists have proposed (and debated) multiple proxies of prey rank based on these three measures. The first, and perhaps the least debated, focuses on the second component of handling: processing costs.

**Acorn Intensification and the Costs of Processing**

Based on the logic of the PCM, resources with extremely high processing costs are likely low ranked and should only be pursued when
higher-ranking alternatives are exhausted. Plants, and the technologies associated with processing plants, are the most obvious marker of increasing handling costs. In indigenous California, the acorn represents an iconic staple plant. But acorns require extensive processing, leaching, grinding, and cooking. Further, these cost considerations based on the PCM logic do not even include costs associated with the manufacture and maintenance of ground stone technology (for models that do, see Bettinger 2009; Bettinger et al. 2006). In general, it is highly likely that acorns were a low-ranked resource (compare with Hildebrandt 2007; Rosenthal et al. 2007), and although evidence of small-scale acorn exploitation may not represent economic intensification per se, evidence of their intensive use should mark an overall increase in work effort. This is because a heavy reliance on acorns represents not only the large-scale exploitation of a relatively lower-ranked resource, but also the transition from a more generalized to a more specialized economy (Stevens 2011).

In a classic study, Basgall (1987) used mortar and pestle technology as proxy evidence for the intensive use of acorns. A reanalysis of his results from Sonoma, Mendocino and Santa Clara counties is presented in Figure 7.3 with the addition of data from sites along the Pecho Coast in San Luis Obispo County.3 These data show that the intensive use of acorns increases significantly through time, peaking in the Late Holocene in all three locations. Increased acorn exploitation may also have resulted in (or been caused by) the intensification of landscape use in the Sierra Nevada, where the proliferation of bedrock mortars in the Late Holocene is associated with the intensified exploitation of regions that were visited only ephemerally during previous time periods (Morgan 2009; Stevens 2005). Acorns, like other plant resources, may have been high cost, but they were also reliable and could be stored. As such, this transition may have facilitated greater sedentism with a greater reliance on storage. Further, as women may have been primarily responsible for harvesting and processing acorns (as was the case ethnographically), this transition might also have meant a transition in settlement pattern biased towards women’s foraging decisions (Jackson 2004; Morgan 2008; see also Zeanah 2004).

These studies show that the intensification of acorn economies across the state seemed to have happened sometime in the late Holocene, but it is also interesting that it did not happen at the same time in the same way everywhere. As evident in Figure 7.3, acorns were perhaps not as much a staple in Mendocino or Sonoma counties as they were in Santa Clara and San Luis Obispo counties. Similarly, Hale (2010) has recently showed that although ground stone assemblage formality increases though time
in Santa Barbara and San Diego counties, assemblages in San Diego never have as many formal mortars as those in Santa Barbara. Such differences suggest that although acorn use increased in the late Holocene throughout California, the process was not uniform across the state. Such spatial variability may have to do with differences in regional population densities and/or differences in the other, higher-ranked resources exploited by native Californians.
Data on foraging return rates throughout the world typically show that animal resources are generally higher ranked than plant resources (e.g., Bird et al. 2009). But unlike plant resources, vertebrate animal resources are more likely to vary significantly in their expected energetic reward and their expected pursuit costs than in their processing costs. As the energetic reward and pursuit costs of different taxa are likely to vary significantly, establishing how exactly different animal resources vary based on these parameters has been a contentious issue. Prey size was initially thought to be the best predictor of prey rank (e.g., Bayham 1979), but this ignores the potential effects that prey mobility may have on pursuit costs (e.g., Bird et al. 2009 and references therein; see also Broughton et al. 2011). Out of these debates, a consensus seems to be emerging around the idea that the combined effects of prey body size and prey mobility are critical for predicting prey rank. As shown in Figure 7.4, we suggest that for many animal resources, prey body size can be considered as analogous to energy \( (e) \), whereas prey mobility can be analogous to handling, specifically pursuit costs \( (h) \). As such, large-slow prey should be much higher ranked than small-fast prey.

Based on these suggested rankings, researchers can estimate which of the available prey types are likely to be higher ranked, then predict how hunting patterns should vary though time based on the PCM and test these predictions with zooarchaeological analyses. Here, we

**Figure 7.4** Tradeoffs in predicted postencounter return rates \( (e/h) \) based on variability in prey body size and prey mobility for (A) terrestrially versus aquatically breeding marine mammals; (B) slow versus fast marine resources; and (C) large versus small terrestrial resources.
draw on three examples from California’s central coast, examining (1) terrestrially versus aquatically breeding marine mammals (Hildebrandt and Jones 1992; Jones et al. 2011), and (b) slow versus fast marine prey (Jones et al. 2008) and large versus small terrestrial prey (Codding et al. 2010; see also Broughton et al. 2011). As with the idealized example in Figure 7.1B, we predict that in each case shown in Figure 7.4, the higher-ranking resource (i.e., the slower-larger resource) should be pursued on encounter until its abundance declines to a point where it would be profitable to pursue the second resource on encounter.

Hildebrandt and Jones (1992) were the first to suggest that terrestrially breeding marine mammals (Otariids; Figure 7.4:A1) should be significantly higher ranked than their aquatically breeding counterparts (Figure 7.4:A2) because the former could be taken on land when at rookeries, whereas the latter could only be taken at sea with high pursuit costs. Further, because such marine mammals have relatively slow life-histories (i.e., slow reproduction and growth to maturity; Whitaker 2008a, 2008b), they should be particularly susceptible to overhunting, especially if young were taken at rookeries. As such, if hunters were exploiting rookeries, then early sites should show the highest proportion of terrestrial breeders relative to aquatic breeders, and later sites should have subsequently lower proportions. Jones et al. (2011: Table 11.1) recently revisited this hypothesis with a large dataset from the central California coast, and found that the median value per time period actually progressed in a trend opposite to the predicted direction (Figure 7.5). The only significant trend was an increase in acquisition of terrestrial breeders during the Middle Period compared with the Millingstone Period (Figure 7.5), which suggests that although terrestrially breeding marine mammals may be higher ranked compared with aquatic breeders, hunters on the central California coast rarely encountered them until the Middle Period. This suggests that foragers were not intensively exploiting rookeries, and that mainland rookeries did not exist or were extremely rare throughout most of the archaeological record.

Drawing on the distinction between slow and fast prey, Jones et al. (2008) suggested that flightless ducks (Chendytes lawi; Figure 7.4:B1) should be higher ranked compared with sea otters (Enhydra lutris; Figure 7.4:B2). If hunters in boats in nearshore environments preferentially pursued flightless ducks on encounter, leading to declines in their abundance from overhunting, then the remains of flightless ducks should decrease though time, while the remains of the more elusive sea otter should increase. An analysis of 11 temporal components from the Pecho Coast of central California supports this prediction (Figure 7.6). While the abundance of the flightless duck declined over time (Figure 7.6A), hunters began taking sea otters more and more frequently on encounter
Figure 7.5  Boxplots representing the proportion of terrestrially breeding Otariid (sea lions and fur seals) remains relative to aquatically breeding E. lutris (sea otter) remains (NISP) from 51 components along Central California (San Mateo to San Luis Obispo counties; data from Jones et al 2011). The gray portions represent 95 percent confidence intervals.

Figure 7.6  Proportion of total NISP represented by Chendytes lawi (flightless duck) and E. lutris (sea otter) remains from sites along the Pecho Coast of central California.

(Figure 7.6B) until the flightless duck became extinct around 2,000 to 3,000 years ago.

If two prey items vary in their size but not in their relative mobility, the larger of the two should be the higher-ranked prey (Figure 7.4C; Broughton et al. 2011). Some have suggested that this should result in the larger item suffering from resource depression from overhunting (Broughton 1994), although this might not be the case with deer because they have relatively fast life-histories that make them less susceptible to
overhunting than might be expected (Whitaker 2008a). Codding et al. (2010) investigated this issue on the Pecho Coast, examining the trade-offs in pursuing deer (*Odocoileus hemionus*; Figure 7.4:C1) compared with rabbits (*Syvilagus* sp.; Figure 4:C2). With the same 11 components examined here, these researchers found that unlike what Broughton (1994) suggested for the San Francisco Bay area, deer did not suffer from resource depression in this region. Instead, it appears that a robust deer population was exploited throughout the Holocene, declining only as a function of unstable climatic conditions during the Medieval Climatic Anomaly (Codding and Jones 2007; Jones et al. 1999). Whereas overexploitation might be evident with sessile resources like shellfish (Erlandson, Rick, Braje et al. 2008; see also Whitaker 2008b), not all high-ranked resources are necessarily susceptible to overhunting (Whitaker 2009). Instead, variability in the abundance of high-ranking resources may sometimes come from external factors like stochastic environmental shocks. As such, unpredictable environmental variability is just as likely to influence prehistoric work in California as are internal population dynamics. This is equally likely to be the case for the factors that shape larger-scale landscape patterns, like the IFD model and the cases discussed here.

Each of these cases illustrates a different way in which the PCM can reveal interesting aspects about work in prehistoric California. Sometimes, the predictions are met in a rather straightforward manner (Figure 7.6), but in other instances, the particulars of why the model predictions fail provide interesting insights on prehistoric work (Figure 7.5). Overall, we suggest that people are likely to preferentially target larger, slower prey; if these are particularly susceptible to overexploitation, then people will begin to pursue other items, including faster, smaller prey, or those that have higher processing costs, like plants.

**CONCLUSION**

Work is central to much of the active research in California archaeology, and many of the researchers who investigate work do so through the lens of behavioral ecology. Here, we have highlighted a series of cases that illustrate how archaeologists have used behavioral ecological models to make predictions about work in the past. The goal of such research is not to reduce the diversity of patterns evident in the record, but to explain and make sense of the variability. When combined, these models provide an overarching structure that can be used to understand variability in prehistoric work across the region. This framework helps predict where people might decide to settle, which environments are more likely to have higher population densities, and where we might expect greater
social inequities. Suitability within each environment likely depends on
the available prey and the ways in which their populations react to inten-
sive exploitation. Over time, these processes might lead to predictable
patterning in different regions.

Applied across California, such a research program might help explain
why some populations have migrated throughout the Holocene while oth-
ers may have remained in place since colonization (Johnson et al., this
volume), the location of core cultural areas, and the distribution of ethnolinguistic diversity throughout the state (Kroeber 1925). The story in each
region, habitat, and valley is likely to be different depending on the distri-
bution of resources and local population histories. But by focusing research
on these issues, we can come to understand how through thousands of
years of work, the environment encountered by the first Californians came
to be the socially constructed landscape recorded at contact.

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NOTES

1. Based on Alee’s principle, it is also possible that habitat suitability actually increases
initially as a function of increasing population density due to the benefits of aggrega-
tion, shared defense, habitat modification, etc. (Fretwell and Lucas 1968). This and
other aspects of the IFD were excluded from this discussion due to space constraints.
For extended discussions, see Fretwell and Lucas (1968), Kennett (2005), Kennett et al.
(2009), Winterhalder et al. (2010), and references therein.

2. This analysis derives from a database including sites in Santa Cruz, Monterey and San
Luis Obispo counties. Occupation histories for each site were determined using all the
calibrated radiocarbon dates available for each site. Each point in Figure 2 represents
a 100-year interval showing the proportion of sites located within 15 kilometers of a
paleo-estuary mouth (determined in geographic information systems [GIS]; see Figure
2C) relative to the total number of sites occupied during that interval. This database was
originally compiled by Angela Barrios.

3. The proportion of mortars and pestles increases significantly in each region (North
Coast: \( R^2 = 0.09, p < .0001 \); San Francisco Bay Area: \( R^2 = 0.48, p < .0001 \); Central
Coast: \( R^2 = 0.55, p < .0001 \); see Codding et al. 2010 for analytical details). The
trends are stronger in the San Francisco Bay area and the Central Coast than in the
North Coast.
4. Proportion of *C. lawi* remains decreases significantly through time ($R^2 = 0.35, p < .0001$), whereas *E. lutris* increases significantly as a function of time ($R^2 = 0.35, p < .0001$; see Codding et al. 2010 for analytical details). Total number of identified specimens (NISP) for each component and component definitions can be found in Codding et al. (2010). Data come from CA-SLO-9 (Codding and Jones 2007), CA-SLO-2 (Jones et al. 2008), and CA-SLO-585 (Jones et al. 2009).

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