Journal of Anthropological Archaeology 42 (2016) 79–87

Contents lists available at ScienceDirect

Journal of Anthropological Archaeology

journal homepage: www.elsevier.com/locate/jaa

Marginal value theorem, patch choice, and human foraging response in varying environments

Robert L. Bettinger*, Mark N. Grote

Department of Anthropology, University of California-Davis, Davis, CA 95616, United States

ARTICLE INFO

Article history:
Received 21 September 2015
Revision received 26 February 2016
Available online 11 April 2016

Keywords:
Marginal value theorem
Patch choice
Handling time
Invariance
Human foragers

ABSTRACT

The theoretical basis for understanding how human forager mobility should respond to environmental change rests on two models: patch choice and the marginal value theorem. Students of hunter–gatherers have traditionally understood the more widely favored marginal value theorem to predict that use of a given patch will be more intensive, i.e., that a greater fraction of its resources will be used, when overall (environmental) return rate decreases. We show this is true only if that patch is less affected by resource decrease than others in the environment, in the simplest case, where the number of patches available to a forager decreases without affecting the quality of the remaining patches. Then, foraging time within the patch, fraction of patch resources used, and travel time between patches will all increase. Conversely, if resources decrease across all patches uniformly, the fraction of patch resources extracted from any given patch remains constant. Within-patch foraging time may or may not decrease, but will not increase. In this case, foraging time varies independently of fraction of patch resources used and travel time. The extent to which these marginal value predictions account for hunter–gatherer mobility requires disentangling them from predictions independently generated by the patch choice model, in which as environmental quality declines, lower ranking patches are added to the foraging itinerary, decreasing travel time and either increasing or decreasing foraging time, depending on the nature of the lower ranking patches. A sample of 190 mobile hunter–gatherers suggests that a version of the patch choice model in which the patches added to the foraging itinerary are more difficult to search, and contain greater quantities of resources with higher handling times, best accounts for observed variation in foraging and travel time overall.

1. Background

Modeling human foraging adaptation has a long history (Bettinger, 1980) but quantitative modeling is recent. Among the earliest models were probably Birdsell's (1953) for aboriginal Australian populations, and Baumhoff's (1963) for aboriginal California populations. Both reasoned backward from the empirical relationship between ethnographic population and distribution of key resources (rain in Australia, salmon, deer, acorns in California). The modern approach, which reasons forward from qualities intrinsic to resources themselves (abundance, energy, handling times, etc.) to predict resource use, dates to the late 1970s (e.g., Jochim, 1976). This approach was revolutionized by the development of the contingency family of optimal foraging models, which partition foraging time into two or more components (search, foraging, travel, handling, etc.) and calculate return rates for sets of resource types (prey, patches) to determine choices that maximize rate of return.

Certainly the most influential contribution for anthropologists was by MacArthur and Pianka (1966), whose seminal article, *Optimal Use of a Patchy Environment*, described the diet breadth and patch choice models. The diet breadth model has proven vastly more useful than its more ambiguous patch choice counterpart, especially to archaeologists. The current understanding of patch use by humans rests mostly on Charnov's (1976) marginal value theorem, which envisions the rate of patch energy gain decreasing asymptotically as a function of foraging time, rather than being fixed as in MacArthur and Pianka's patch choice model. A patch can be defined as a space within which foraging occurs, separated from other patches, requiring travel from one to the next during which foraging does not occur. For hunter–gatherers, the patch can be envisioned at many scales, for example, as the foraging space, or catchment, around an individual camp, or as the spatially separate locations visited by a forager in the course of a single

---

* Corresponding author.
E-mail addresses: rlbettin@gmail.com (R.L. Bettinger), mngrote@ucdavis.edu (M.N. Grote).

http://dx.doi.org/10.1016/j.jaa.2016.03.002
0278-4165/

foraging bout. In patch choice foragers adjust to changing conditions by adding or dropping lower ranking patches from the foraging itinerary; in the marginal value theorem, they adjust by increasing or decreasing time spent foraging within patches. Unfortunately, a major generalization often drawn from the marginal value theorem – that foragers should move less often as environment worsens – rests on an incorrect, or at least incomplete, interpretation of the marginal value theorem. Our more detailed consideration developed below shows that the marginal value theorem predicts quite different responses to changes in environmental return rates depending on whether those rate changes are a function of change in patch count or within patch prey count. These and other complications limit the utility of the marginal value theorem in explaining forager resource use and mobility. While less elegant, the patch choice model provides a much better accounting of observed variation among ethnographic hunter–gatherers, and is, thus, a much better tool for archaeologists and ethnographers interested in doing the difficult job of explicating hunter–gatherer behavior past and present.

2. Marginal value theorem

The marginal value theorem (Charnov, 1976) explains optimal *within-patch foraging time* on the reasonable assumption that, because patch return rate decreases eventually to zero, it makes sense to leave a patch before its prey (i.e., plant or animal resources) are wholly exhausted if travel to other patches is possible. To maximize average return rate, a forager should leave a patch and travel to another when the return rate in the current patch drops to the overall, or environmental, return rate, i.e., the rate obtained counting both between-patch travel time and within-patch foraging time, assuming the forager leaves patches at the optimal time. Depicted graphically (Fig. 1A), time registers on the x-axis, between-patch travel time left of origin, within-patch foraging time right of origin, and acquired energy g registers on the y-axis. As foraging time increases, acquired energy increases toward an asymptote (the total energy in the patch prior to foraging, here termed *pristine patch prey count*) and patch return rate decreases to zero, representing patch exhaustion (remaining prey or patch energy = 0). The line anchored at between-patch travel time left of the origin on the x-axis and tangent to the energy gain curve has slope equal to the optimal overall/environmental return rate. Optimal within-patch foraging time (hereinafter optimal *patch residence time*) is the x-axis co-ordinate of the tangent point, its y-axis co-ordinate energy acquired within the patch before moving on. Along with foraging time we focus attention on the optimal *intensity of patch use*, defined as the fraction of total patch resources consumed at the optimal patch residence time.

Where hunter–gatherers are concerned, the conclusion most generalized from the marginal value theorem is that optimal patch residence time and intensity of patch use should vary inversely with resource abundance (e.g., Kelly, 1995: Figs. 4–14). That is, as environment improves, so should forager mobility, an idea already deeply embedded in foraging theory, Binford's (1980) forager – collector model specifically, where residential mobility varies directly with the opportunity cost of staying put, decreasing as resources grow scarcer as a consequence of declining environmental productivity. The prediction can be illustrated using a single patch energy curve to which two tangent lines are drawn (Fig. 1B); a steeper one representing a higher environmental return rate, a shallower one a lower environmental return rate. The tangent point of the lower return rate line will obviously be to the right of that for the higher return rate line, implying that lower environmental return rates result in longer patch residence times and more complete use of patch resources; the forager stays longer and leaves a smaller fraction of patch resources behind. Calcagno et al. (2014b) show that this graphical prediction holds in considerable generality: patch residence time increases as travel time increases even in heterogeneous habitats with varying travel costs.

Note, however, that Fig. 1B represents a patch that is unaffected by whatever is causing the overall environmental return rate to decline. This would happen if population growth decreased the number but not the quality of available patches, for example, or if climate change affected the quality of some, but not other, patches, or affected patches in different degrees. In any event, Fig. 1B depicts a special case, projecting optimal use of an exceptional patch, amounting to the quite sensible prediction that optimal foragers should stay longer in, and use more resources of, the places least affected by environmental deterioration. This fails to capture what specialists interested in human foraging see as surely the most important contribution of the marginal value theorem: predicting mobility change for patches whose condition mirrors that of the environment as a whole, changing in response to climate and like forces acting more or less uniformly. In this case, the overall/environmental return rate line and patch return rate curve both change, rise or fall, not just overall return rate as in Fig. 1. Some insight can be gained by making the change in overall return rate entirely a function of change in patch return rate, and the change in patch return rate entirely a function of change in pristine patch prey count. In the sections immediately below, we model the simplest case – one kind of patch with one kind of prey, varying prey abundance and handling time – to find the optimal intensity of patch use and patch residence time. This analysis was developed with human foragers in mind but generalizes to the foraging behavior of any species. Following our analysis we explore predictions from the marginal value theorem and patch choice models for patterns of settlement mobility observed across a large sample of ethnographic hunter–gatherers.

2.1. Modeling the effect of changing patch return rates

Charnov and Parker (1995) modeled acquired energy within a patch as a negative exponential function

$$g(t) = G(1 - \exp(-ct)), \qquad (1)$$

where t is foraging time, G is pristine (i.e., pre-foraging) patch energy, and c is a scaling factor for the rate of energy gain indexing difficulty of prey detection among other things. Unfortunately this treatment does not distinguish handling time from search time, which is important here, because a change in prey abundance (the variable of interest) affects search time but not handling time. This was moot for Charnov and Parker (1995), where handling was a single event terminating the use of each patch, permitting it to be treated as the functional equivalent of travel, i.e., as if there were no handling time (Charnov and Parker, 1995: Fig. 3). Normally search and handling alternate repetitively, as the forager moves from one prey to the next within the patch, preventing this gambit. Foraging that entails such handling time requires a different approach, the gain curves being different, as shown in Fig. 2, which graphs gain curves obtained from Eq. (1), which makes no separate allowance for handling time h (i.e., as though $h = 0.0$), paired with curves for the same patch incorporating handling time ($h = 0.3$), as developed below.

To explore the effect of handling we initially treat acquired energy as a step function, in which randomly encountered prey of uniform size (energy content) are taken one at a time. We assume that the time required to find and handle the $(g + 1)$th prey item, given that g items have been taken from a patch with pristine energy G, is

$$\Delta t / \Delta g = 1/c(G - g) + h, \qquad (2)$$