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CHAPTER 5

SEVEN BEHAVIORAL ECOLOGY REASONS FOR PERSISTENCE OF FORAGERS WITH CULTIVARS

Bruce Winterhalder and Douglas J. Kennett

Author's Preface

Bob was among the UC Davis faculty who recruited me from UNC-Chapel Hill in 2002. I knew his published work; reports of his personal reputation could be summarized as “gruff”. Dictionary definition. I began in Davis early in 2003, just as the Iraq War started. Many of my new colleagues in spontaneous encounters in the departmental office were outspoken in harsh condemnation of the Iraq invasion, sometimes including in their judgments the military personnel sent to pursue it. The speakers apparently were unaware of the distress this caused for staff within earshot, some of whom had children in the military and, as parents, were overwhelmed with uncertainty and dread about their children’s deployments. Bob was not one of the many; he knew the staff and he regularly dropped by quietly to ask those affected, “How’s your kid?” I didn’t know then, don’t know now, much about Bob’s politics outside of academic debates. But his empathy and the conversations he initiated with that simple question told me all I needed to know about his person. Gruff, no.

Abstract

We are not sufficiently amazed that societies engaged in foraging have survived into the present, overlapping with the rise of academic anthropology and evolutionary inquiries into our past. Agricultural societies relying nearly exclusively on domesticated animals and plants have been only partially successful in supplanting populations engaged in foraging for non-domesticates, even in contexts where foragers had access to domesticated cultivars for thousands of years. We advance seven behavioral ecology reasons that foragers endure, that the

transition from food gathering to food production either was not initiated, was initiated and resulted in a stable mixed-economy, or was initiated and then reversed. They include: 1) structural impediments to a full commitment to farming, like mobility; 2) comparable relative profitability of individual tasks associated with foraging and cultivation ensuring that they mix without dramatic impacts on the foraging economy; 3) fluctuating marginal reversals of selection; 4) population ecology constraints on foraging intensification; 5) barter and trade; 6) discounting of delayed return subsistence activities; and, 7) challenges to successful agricultural risk management. Prehistoric societies that fully and irreversibly made the evolutionary transition to horticulture/agriculture were either unaffected by such impediments or happened upon or devised solutions to them. Our hypotheses illustrate concepts such as opportunity costs, marginal advantage, discounting and risk, basic to the theoretical analysis of any evolutionary transformation.

Introduction

Over the last three or four generations of scholarship ideas on the origins of agriculture have changed dramatically. Childe (1965) argued that terminal Pleistocene droughts concentrated humans, plants and animals together in oases where propinquity highlighted the natural advantages of food production. Agriculture was adopted easily and quickly, with momentous results, a *Neolithic Revolution*. This view was up-ended by the challenge of the 1965 *Man the Hunter* conference (Lee and DeVore 1968) and Sahlins’ follow-up book, *Stone Age Economics*, in which he argued that hunter-gatherers were the “original affluent society” (1972a). With foraging characterized in such salubrious terms, what was seen as an auspicious invention, a sudden and beneficial leap for a receptive humanity, was now viewed as a slower and unhappy eviction from a hunter-gatherer paradise of Zen economics. Against its disadvantages (Diamond 1987), humans were pushed into agriculture by powerful causal forces such as overpopulation or elite exploitation (Cohen 1977; Hayden 1990). Analysis by Bowles (2011) confirms that hunting and gathering generally was more productive than early cereal cultivation.

Subsequent work on domestication and agricultural origins has moved through models based in ecosystem ecology and production scheduling (Flannery 1968), to diverse socio-ecological models that cite climate change,

population growth and movement, technological innovation, social factors such as feasting and elite-induced production of a surplus, or some combination of these factors as causal elements (reviews in Barker 2006; Bellwood 2005; Smith 1998; Svizzero 2016; Zeder 2006). More recently, foraging theory and human behavioral ecology have addressed this problem with socio-economic models (Gremillion et al. 2014; Hawkes and O’Connell 1992; Piperno and Pearsall 1998; Winterhalder and Goland 1997). We ourselves write from this perspective (Kennett 2005; Kennett and Winterhalder 2006; Smith and Winterhalder 1992a), favoring investigation of mechanisms over a focus on particular causal agents. For instance, the diet breadth model expresses relationships among resource encounter rates, relative profitability, and the type and variety of resources to be harvested. As a result, it can generate predictions from one or more of a wide variety of causal inputs affecting these variables, from climate change, to population growth, to extraction of surplus.

Through the almost ninety years since Childe’s first writing, our explanatory models have proliferated in number and diversity. The origins of agriculture, initially perceived as quick revolutionary invention, now appear to have been a gradual, perhaps piecemeal, even intermittent transition (Fuller et al. 2014; Larson et al. 2014). The newest empirical wrinkle is that even a word like “transition” may mislead, as it too readily insinuates teleology into the problem, implying an unstable intermediate period within on-going directional change, a passage with a destination. New archaeological evidence and improved AMS ¹⁴C dating now indicate that in some independent centers of agriculture (e.g., Near East, Mesoamerica, Eastern North America; see Smith 2001) cultivars figured as fairly regular but *low predominance* items in the economies of foragers for thousands of years before they became, at least in some cases, staples and eventually domesticates in fully horticultural or agricultural systems of food production.

The pattern has been christened “low level food production” in a summary of the evidence by Smith (2001; current review in Svizzero 2018). Low-level food production refers to societies that derive less than 30-50% of their caloric intake from cultivars or domesticates with the balance coming from hunting and gathering of wild foods. It is a diverse and well-populated space, apparently

stable and of significant duration (e.g., for the Mexican case see Smith 2001: 25). Smith’s review highlights:

...the most obvious and intriguing set of questions centering on resource management involve how different human groups combined nonintensive and intensive strategies of exploitation of some wild species with active management of others, as well as the small-scale storage and planting of domesticated seed stock and the herding of domesticated animals, below the threshold of agriculture? [Smith 2001:35]

The long duration (see Fuller 2007) of low-level food production is not easily attributed to constraints on the pace at which human selection might result in plant domesticates, at least in some key cases. Under ideal conditions, 20-30 wheat generations of feasible selection intensities is sufficient to change a wild type population to a recognizable domesticate (Hillman and Davies 1992). Models of optimal harvesting behavior likewise suggest that domestication could have been rapid (Svizzero 2018). Even if artificial selection for wheat and other cereal domesticates was significantly slower in practice, taking on the order of 500 or 1,000 years (Fuller 2007; Tanno and Willcox 2006) or longer with maize (Kennett et al. 2017; Ramos-Madrigo et al. 2016; Vallebuena-Estrada et al. 2016), processes of genetic change have the potential to be fairly rapid relative to the establishment of dependence on agricultural production.

Likewise, global environmental conditions auspicious for agriculture were quickly established at the end of the Pleistocene (Piperno 2017; Richerson et al. 2001), millennia before agriculture itself took hold in many cases. The rapid early Holocene shift to warmer and wetter conditions, high productivity, CO₂-rich environments, and relatively stable climate set in place an environment auspicious for cultivation and plant domestication. Potentially rapid rates of genetic selection and of early Holocene environmental change favorable to agriculture elevate the potential importance of examining socio-economic arguments for the persistence of low-level food production and of foragers themselves.

Habitual language fails us here. Used to characterize low-level food production, words like “delay,” or “interim” inappropriately suggest a holding back of the inevitable. The term “protracted” (sources in Svizzero 2018) carries

like connotations. It now also seems misleading to speak of a “transition,” meaning a temporary period of readjustment, an “intermediate stage.” Even *low-level food production* is suspect. The diminutive invites the response: “Come on folks! We know what’s coming. Ratchet it up and let’s be done with it!” Instead, the evidence appears to require that we acknowledge that alongside, not “interposed between,” foragers and food producers are persistent alternative economies in which people practice elements of hunting, gathering and cultivation in relatively stable but novel combinations. Foraging mixed with use of cultivars is not an interlude but a successful form of subsistence production in its own right. It is different from ethnographically documented horticulture in its significantly lesser degree of dependence on cultivars or animal management, and its use of species not fully domesticated. For instance, Amazonian horticultural societies typically get 70-80% of their calories from cultivated crops (Speth and Scott 1989: 74); hunting in horticultural societies in highland New Guinea (Rosman and Rubel 1989: 36) carries important ritual meaning but contributes little economically. For this mixed but largely hunting-based economy we prefer the term Foragers with Cultivars (or, FwCs). The question is, how do we understand FwCs?

This is the context for our discussion: *even when nascent full-scale food production in the form of horticulture or agriculture is available through human management of cultivars, its emergence as a dominant form of economy is not foretold or imminent.* This raises three questions:

1. What socio-ecological circumstances and evolutionary processes lead to regular use of cultivars?
2. What keeps the two components of a mixed, food gathering/food production economy in a persistent relationship, given the standard view that agriculture is much more readily, perhaps even unavoidably and quickly, intensified? And,
3. What, in some unknown percentage of cases, finally kicks a mixed economy toward dominance by agriculture or, in the reverse scenario, toward a foraging economy that once again lacks cultivars or domesticates

FwCs also raise a broader issue: How and with what tools are we to understand an economy and form of prehistoric

society that largely lie beyond the reach of ethnographic analogy (Wobst 1978)? We argue that human behavioral ecology, broadly construed and backed with comparative multi-species analysis (Winterhalder 2001), is essential to this task.

The Persistence of FwCs

We focus here on the second of the questions posed above: Why is it that a revolution fails to materialize—in at least some foraging economies once they adopt cultivars? Especially, why would foraging endure and food production fail to intensify, as has been a standard view? We pose seven socio-economic reasons for the empirical observation of FwCs persistence, discussing each of them briefly. Our seven reasons join seven offered by Richerson et al. (2001) and the nine case studies of contemporary hunter-gatherer societies in (Codding and Kramer 2016; see Discussion).

Reason #1: Many foraging economies are dependent on structural adaptations – residential movement, tight scheduling, food-sharing, limited property rights, etc. – that are incompatible with the full intensification of food production.

We focus on mobility as an example. Sahlins’ (1972a) vividly argued that by wanting little and easily procuring more than enough, hunter-gatherers live a life unaffected by scarcity. Their limited wants are the result of a simple ecological condition: keeping production on advantageous terms requires mobility and this limits foragers to a portable inventory of material goods. Geographically fixed resources like field plots, or weighty or bulky equipment or items of material wealth are not an attraction; people who have to carry their belongings are reluctant to accumulate many of them. Adopting Sahlins’ view, foragers know their advantage and are prescient enough to reject the false seductions of agriculture, with its sedentism, demanding work requirements and unreliable yields, and spatially fixed or weighty elements of infrastructure.

For many -- but not all (see Arnold et al. 2016) -- hunter-gatherer societies, mobility impedes a simple forager to full time farmer transition. Mobility is necessary to counter localized depletion of resources and spatial variability in their occurrence. Sahlins says of foragers (Sahlins 1972a: 33, italics original), “. . .the economy is seriously afflicted

by the *imminence of diminishing returns*. . . Thus the first and decisive contingency of hunting-gathering: it requires movement to maintain production on advantageous terms.” This observation is usefully recast in terms of constrained optimization and the formal foraging theory model known as the marginal value theorem (Charnov 1976). Foragers move among environmental patches as diminishing returns from their immediate surroundings (Charnov et al. 1976) makes relocation attractive. Nothing prevents us from conceptualizing an opportunity to cultivate as one among other patches visited by mobile foragers. We need only recognize that cultivation need not imply sedentism, the continuous presence of the cultivator or his or her participation in all elements of the growth cycle, weighty implements that cannot be left behind, or harvests significantly more bulky or encumbering than those gained from uncultivated resources.

Why is this important? Mobility is one of several structural constraints that often come with foraging. Sahlins’ observations on diminishing returns, matched to formal models predicting when those will occur, open up a wide-ranging realm of analytical opportunities (Gremillion et al. 2014; Winterhalder and Kennett 2006). Among them are increased theoretical and comparative confidence in claims about mobility and the degree to which it constrains engagement in fully developed forms of agriculture. But that does not eliminate the possibility of cultivation as a variation on the adaptive use of environmental patchiness by mobile foragers.

Reason #2: *Whatever their profitability or relative resource ranking, cultivars characterized by low-yield will be absorbed into the foraging economy with a minimal impact on hunting and gathering, producing a persistent, mixed form of subsistence.*

Our second reason for the persistence of FwCs, or indeed the reversion from cultivation back to foraging (e.g., ^{Fremont}Freeman, Barlow 2002), draws from the distinction in foraging theory between the relative ranking or profitability of a resource and its yield or productivity (Winterhalder and Goland 1993, 1997). Rank refers to the net return rate, expressed, for instance, in kcal/hr, associated with the pursuit, capture or collection, handling and processing of a resource, once encountered or located. Rank is used to order resources for purposes of their evaluation in the diet breadth model (Schoener 1974). Yield is the amount of the resource available to

be harvested and its ability to regenerate, a function both of density and reproductive capacity (Winterhalder et al. 1988). Resource rank and productivity can vary independently with three potential outcomes to the incorporation of a cultivar into a hunter-gatherer economy (Figure 1, inferences based on Winterhalder et al. 1988, 1999).

Low rank, low yield. Envision foragers reaching far enough down the ranked list of potential resources to pick up a low profitability cultivar. Broad spectrum foraging (see Stiner 2001) is an example. Cultivars are a small part of the diet, have little effect on human population density and thus induce minimal additional depletion of more highly ranked, non-cultivated resources. The cultivar has only a small effect on subsistence risk. Low cultivar yield is a sufficient explanation for FwC persistence even if cultivar rank responds positively to selection for increased profitability, without significant changes of productivity, moving it toward the category *high rank, low yield*.

Low rank/high yield. Hunter-gatherer diet breadth for whatever reason expands in this case to include a low rank but high yield resource. This high yield cultivar will assume prominence in the diet, in terms, say, of total kcals consumed;

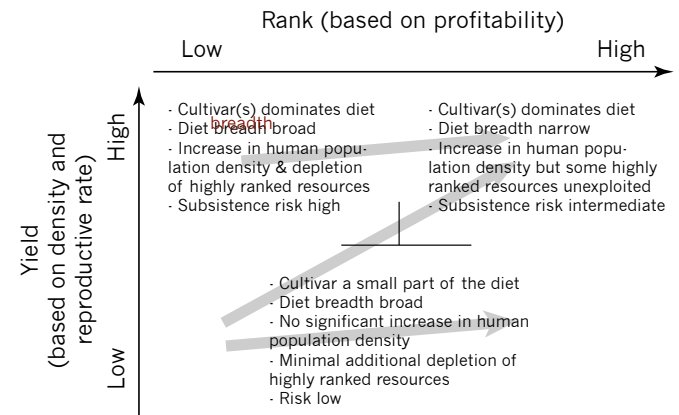


Figure 1: Inferences about subsistence, population and risk arising from profitability ranking and yield properties of potential domesticates.

its productivity, not its profitability, dominates its impact. It will not cause the diet to contract but it will promote forager population growth. With increased forager density comes over-exploitation and depletion of more highly ranked resources, which always will be pursued when encountered. As high-ranking non-cultivars diminish in density or are locally extirpated, risk increases significantly and subsistence efficiency and welfare decline. This possibility will not explain persistent FwCs; rather, it is consistent with pressures for fuller domestication of the cultivar.

High rank/high yield. In this case, diet breadth narrows and, as the cultivar is both profitable and productive, it becomes a major component of the diet. Because it has a high rank and is encountered frequently – meaning in this context that it occupies considerable collecting and handling time -- it will push other previously harvested resources out of the diet. Population density expands, but previously harvested species are available as fall back foods should cultivation fail or be subject to shortfalls. Risk is intermediate. Domesticates that behave as in this scenario will not promote persistent, low level food production.

Cultivar rank and yield have quite different consequences for subsistence dynamics and consequently for socio-economic evolution.

Reason #3: *The trade-offs guiding subsistence choices and thus trends toward greater dependence on foraging or food production from cultivars, occur at the margin. Because of this, fluctuating environments and population dynamics can keep foraging and cultivating in a shifting balance with one another for long periods. Similarly, resource appraisal governed by short-term opportunity costs may direct populations to unconventional mixes of foraging and engagement with selected elements of a full agricultural cycle.*

The decision to incorporate a low-ranking cultivar into the diet is a choice *at the margin*. As a consequence, cultivar engagement is susceptible to repeated reversals due to the fluctuating instabilities of natural environments and the repeating cycles of predator prey dynamics. Both may guarantee long periods of too'ing and fro'ing at the subsistence margin. FwCs may be a

result of these dynamics (Barlow 2002, 2006). There are density-independent and density-dependent forms of this situation.

Density-independent selection reversals may have been common. Referring to the desert west of the United States, Upham (1994: 139-140) speaks of a *shifting continuum* from nomad hunter-gatherers to sedentary agriculturalists, with dependence on one repeatedly out-balancing the other due to reversals of fortune:

“It is likely that there was a shifting continuum around the margins of nuclear areas as individual families of villagers were forced to return to nomadism because of local crop failures or environmental disasters, and as different groups of nomads were unable to continue their foraging activities because of circumscription by agriculturalists. . . sedentism was not viewed as an irreversible settlement choice.”

In an analogous dynamic, recent research on the evolution of hunter-gatherer subsistence and settlement emphasizes shifts and reversals at the margin of the forager/collector continuum (e.g., Habu and Fitzhugh 2002: 6). The Jomon of Japan (Habu 2002) and the Thule of northern Canada (Savelle 2002) develop into collectors but faced with a changing environment return to foraging.

Figure 2 shows Kohler and Van West's (1996) time-series estimate of maize productivity in the American Southwest based on a synthesis of geo-hydrological,

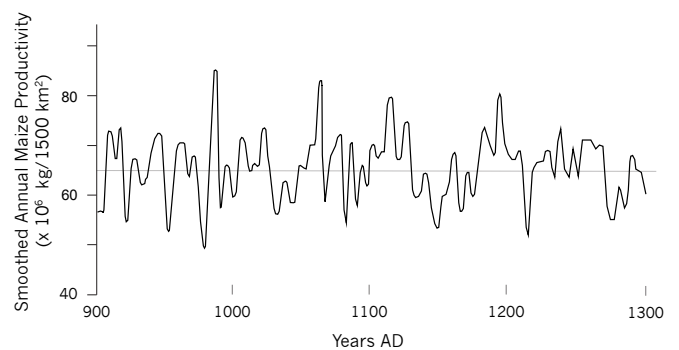


Figure 2: Variation in estimated annual maize productivity in the US southwest for the period AD 901 - 1300 (redrawn from Kohler and Van West 1996).

paleoclimatic and dendrochronological evidence. If the marginal profitability at which maize cultivation would enter the diet lies within the range of these fluctuations, then each peak of maize productivity tugs the human population toward greater investment in cultivation, each trough tugs them toward hunting and gathering. Engagement with both kinds of production remain in the economy, perhaps for lengthy periods. Evolutionary biologists better able to watch evolution in real time note this back-and-forth quality, as environmental fluctuations tug natural selection and phenotypes first in one direction and then the reverse (Weiner 1994).

The *density-dependent* form of this relationship is evident in population ecology simulations of hunters and their resources (Winterhalder et al. 1988). In the simulated time series shown in Figure 3 human population grows and the density of targeted species declines, along with net acquisition rate. Eventually foraging efficiency drops to the point at which the marginal human growth rate is zero and the system stabilizes. Along the way there is the phenomenon of *switching*, rapid reversals in the

acceptance or avoidance of items ranked at the subsistence margin.

The process works as follows. It takes only an incremental drop in the marginal efficiency of foraging to bring a new, lower-ranking resource into the diet. Pursuit and handling of the new resource consumes a significant part of the time devoted to foraging and it contributes a portion of the food required. As a consequence, higher ranked resources suddenly are less heavily exploited. With relaxed harvesting, they begin to rebound in numbers. They soon are encountered with sufficient frequency that foraging only for the highest ranked resources again is optimal and the newly added resource drops from the diet. The pattern then repeats. In terms specific to FwCs, if a population that is depleting gathered or hunted resources shifts some part of their subsistence effort and food consumption to cultivars, then reduced exploitation of highly ranked wild foods will cause those species to recover in density. This reverses the desirability of bothering with the low-profitability cultivar, initiating a move back toward greater dependence on hunting and gathering. Repetition of this cycle can keep both subsistence practices and associated diets in the subsistence repertoire for long periods of time.

Density-independent and density dependent processes might prolong a mixed economy independently or by acting together. Temporal gaps in the practice of cultivation would interrupt or slow selection pressures on cultivars and, if prolonged, might induce repeated set-backs to the accumulation of traits favorable to domestication. Multi-year gaps in cultivation may have caused diminished seed viability. The local population ecology of early cultivation likely was dynamic and episodic. This view is consistent with a polycentric view of the origins of agriculture, entailing multiple, local domestication events in a region (Willcox 2005). Based on surviving genomes, Fuller (2007: 6, 13) notes a “minimum of seven domestications of wheat and barley in the Near Eastern Fertile Crescent region. . .[and] . . .at least three, and perhaps five, distinct centres of plant domestication in India. . .”

In periods of subsistence stress differentially affecting cultivars, FwCs may have (re)turned exclusively to the reliable and familiar tasks of hunting and gathering, their declining density and dispersion threatening maintenance of essential knowledge and food cultivation practices. Henrich’s account of how the Tasmanians lost fish-

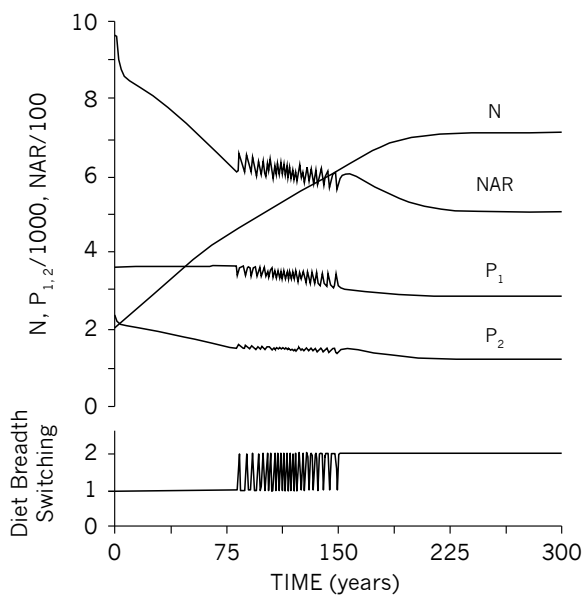


Figure 3: Simulated population ecology dynamics of a forager and two resource species. N = scaled human population; NAR = net acquisition rate; P1 and P2 = scaled densities of two resource or prey types (redrawn from Winterhalder et al. 1988).

ing and other complex technologies is instructive here (Henrich 2004). Isolated from mainland Australia beginning around 3000 cal BP, Tasmanians suffered a striking atrophy of their subsistence tool kit. Henrich cites dozens of items of puzzling loss in the late Holocene: cold weather clothing, bone tools, fishing gear including traps, nets, hooks and spears, sewn bark canoes and string bags. The sense is one of maladaptive deterioration in the toolkit of a small, isolated society. Henrich's simulations of social learning dynamics suggest that isolated, low density societies find it more difficult to overcome the imperfections of social learning, making it harder to generate and maintain complex adaptations.

Read (2006; cf. Henrich 2006) challenges some of Henrich's evidence on the Tasmanians and develops an alternative explanation for adaptive loss, one that distinguishes between knowledge and maintenance of motor tasks that require learning and differentiate individuals by skill level. Read's proposed mechanism is not as population sensitive as Henrich's, but it also might help us to understand the difficulties of generating and preserving novel, complex adaptations when populations decline.

We of course look backward through history and prehistory, our vision drawn to the lineages of those societies that fully made the transition to agriculture and managed to persist after doing so, usually at high population density and with high archaeological visibility. We do not so readily see the stumbles and turnabouts that are the predictable consequences of evolutionary processes faced with environmental fluctuations, dynamic population processes, and conditions challenging the maintenance of accumulated cultural information, or in the case of seed stock, genetic information.

The concept of *opportunity cost* is closely related to marginal valuation. Trade-offs in behavioral ecology models are relative; choice of an activity is compared to the opportunity foregone in electing it. Barlow's (2006) analysis of cultivar use among the Fremont is an excellent illustration, offering further insight into FwCs.

The Fremont existed from AD 600 to 1,400, generally in the region centered on the contemporary state of Utah. They lived among neighbors, some of whom practiced foraging, others farming. Fremont sites share many characteristics of adjacent Southwestern agriculturalists – the suite of maize, beans and squash, for instance. But

they also persist in hunting and gathering: “. . .diversity is a hallmark of the Fremont. Occupants continued to rely on hunting and the collection of wild plants throughout the Fremont period, with archaeological evidence supporting an unusual degree of variation between assemblages in the relative importance of agricultural crops” (Barlow 2006: 92).

Taking note of this situation, Barlow (2006) closely analyzes the trade-offs between foraging and farming. Her critical innovation is recognition that early cultivation is a sequence of activities, each of which competes with the opportunity costs of hunting and gathering *at the time and season it is performed*. For instance, it may make sense to plant a crop of maize, then leave to resume a hunting and gathering round that later includes a return pass-by for a harvest if the crop has been successful. It may not make economic sense to put a lot of effort into cultivation options at other points in the agricultural development cycle, e.g., weeding, guarding, etc., each of which must offer a better benefit-cost ratio than the foraging options *at the time*.

In the Southwest, the highest maize return rates of 1,300 to 1,700 kcal/hr were associated with a low-intensity plant and harvest strategy that returns about 3 bushels per acre. These return rates roughly match collection rates for pine nuts (*Pinus monophylla*) and bulrush seeds (*Scirpus*), 1,200 to 1,700 kcal/hr. The upshot is a long period in which the Fremont engaged in some cultivation alongside foraging, led by fluctuating opportunity costs to recombine in novel arrangements specific elements of subsistence practices that we tend to place exclusively within one or the other of these two categories. “*Farming investments should only have intensified when higher-ranked foraging opportunities diminished, and Fremont farmers should have decreased farming effort during the times and in the locations where higher-ranked foraging opportunities were abundant*” (Barlow 2006: 97, italics original).

Barlow's observations suggest that persistent FwCs are more likely if the plants available and susceptible to cultivation have return rates that more-or-less match the low-ranking foraging opportunities being undertaken, but also fall below the return rates and yields associated with higher-ranking foraging opportunities and thus fail to supplant them. For instance, although California has a Mediterranean environment, California prehistory is notable for not having evidence of domesticates or a

transition to farming. Blumler (1992) suggests that this is because California lacked large-seeded grass analogs to the wheat and barley of the Middle East, thus cultivars with the potential to compete with and perhaps displace high-ranking hunting and gathering tasks.

***Reason #4:** Logistic population ecology constraints on intensification of foraging will limit agricultural intensification if both foraging and agriculture are essential to the economy.*

Predator-prey simulations (Winterhalder et al. 1988) show that as forager density increases, exploitation pressure grows on highly ranked and sought-after resources. High ranked prey decline in density coincident with a fall in overall foraging efficiency, bringing a series of lower-ranked resources into the best-choice diet (Figure 2), a pattern of resource depression widely observed in late Pleistocene and Holocene archaeological sequences (Broughton 2002; Butler 2000; Kennett et al. 2006; Nagaoka 2005). Resource depression provides one mechanism for sustained contact with lower-ranking plant species that became cultivars and eventually domesticates (Piperno and Pearsall 1998). It also signals a more difficult economy, as declining return rates take their toll on population welfare.

Less frequently noted are possible effects on resource yield (Winterhalder 1993). If foragers respond to declining return rates by investing more time in foraging, then equilibrium yield and with it equilibrium forager population density will first rise and then fall (Figure 2 in Winterhalder et al. 1988). This introduces a form of economic impedance in the foraging economy: beyond a certain point, the harder foragers press on their non-cultivated resources the lower the yield of those species. Yield falters. Setting aside some special cases, ^{in coastal contexts} e.g., the Chumash, Calusa, or Pacific Northwest Coast societies, ~~in coastal contexts~~ foraging economies do not readily or sustainably intensify.

Consider a FwCs society that remains dependent on hunting and gathering while also cultivating a low-rank but high yield cultivar (Figure 1), a case we earlier identified as one unlikely to feature a long period of FwCs. Population growth spurred by the successful experimental use of cultivars could push human density into the range at which wild resources are over exploited. If foraging and cultivation are coupled such that neither is viable on

its own, the negative consequences of heightened pursuit of non-domesticates will constrain the intensification of agriculture. Continued dependence on foraging, perhaps because it is the only food source during certain seasons or because it supplies essential nutrients not found in the cultivars, will impede the shift to high levels of dependence on food production. With this type of obligate coupling, even a high yielding domesticate might not induce the abandonment of foraging in a system of mixed economic practices.

***Reason #5:** Groups more dependent on production via cultivars may have been linked through barter and trade to groups more dependent on foraging, exchange among them ensuring that both secure a mixed economy at the level of consumption.*

Barter and trade likely were much more common in prehistory than has been recognized (Dempis and Winterhalder 2018). Reinforcing Barlow's (2006) observations on the Fremont, exchange offers further options for prehistoric economies unlike those we have traditionally associated with either of foragers or agriculturalists, economies that recombine particular economic practices in novel but stable configurations based in consumption rather than production.

Ethnographic observations that the Mbuti and related groups of African tropical forest hunter-gatherers were dependent on trade with local agriculturalists provoked a major ecological anthropology debate centered on the question, "Have hunter-gatherers ever lived in tropical rain forest independently of agriculture?" (title from Headland and Bailey 1991, introducing a collection of papers on the issue). For our purposes, the answer is less important than the documentation on both sides of the issue acknowledging the depth and persistence of the trade-based interactions between foragers and farmers in tropical forest settings.

In a related example, Svizzero (2015a) analyzes why complex Mesolithic hunter-gatherers living along the northern margins of Europe, the Ertebølle, adopt agricultural practices from cultures in the interior of Europe only after a period of contact and trade lasting 1,500 years (5,400 to 3,900 BC). This millennium and a half of interaction offered abundant opportunity for the Ertebølle to adopt farming, but they only did so at its conclusion. Svizzero rejects explanations based in cultural and demic diffu-

sion, offering instead an economic argument. Ertebølle hunter-gatherers traded raw material commodities such as seal fat, furs and honey for manufactured goods such as ceramics, axes and ornaments produced by agriculturalists. Svizzero argues that the terms of trade would favor the manufacturing side of the relationship, which slowly worsened for the extractive economy of foragers, until they were constrained to adopt farming (for a second, similar case see Svizzero 2015b). Yield constraints on non-domesticated resources (see reason #4) are a specific example of the disadvantages of hunter-gatherers in a trade relationship with societies able to manage yields of cultivars.

Svizzero (2016) also presents the hypothesis that cultivation may have been initiated as a baiting tactic to attract game, thus to facilitate continued hunting and gathering. He notes that archaeological evidence from the Near East and the domestication of caprines is consistent with this view. This idea represents another manner in which specific practices of foraging and farming could compose complementary and interdependent elements of subsistence in a mixed economy.

Reason #6: *Short-term investment in the sequential suite of activities required for temperate zone agriculture has to compete at discounted rates with the opportunity cost of foraging.*

This explanation for the persistence of FwCs is related to the distinction between *immediate* and *delayed return* foraging economies (Woodburn 1982), used by Woodburn and others (e.g., Testart 1982) to examine food storage and the development of inequality in hunter-gatherer societies. Delayed returns have a present value subject to discounting. Present value is reduced because of the loss of use during the wait and the possibility that the reward will be diminished or even disappear before it is gained. It is the discounted, present value of a newly planted crop that competes against the opportunity costs of foraging at the time of planting, to the disadvantage of agriculture. Seeds in the ground, plants maturing in a field, stored grain, all have to be discounted due to the hazards of hail or drought, spoilage, vermin, the depredations of herbivores, and possibly theft, all of which reduce their present value.

Tucker has developed an anthropological application of discounting in his studies of the Mikea of south

central Madagascar (Tucker 2006). Mikea identity as foragers began in the 17th century when they fled to the Mikea forest and took up hunting and gathering to escape onerous tribute obligations imposed on them by Andrevola Kingdoms (Yount et al. 2001). They remained foragers to avoid slavery, regional political insecurity and ultimately taxation and resettlement by the French in the 19th century. They are a reminder that farmers facing socio-environmental pressures can become hunter-gatherers. Today they have an economy shaped by economic diversification, regional conflict and self-imposed isolation. Typically, Mikea combine hunting and gathering for small game, tubers and honey with low-investment, extensive maize and manioc horticulture, along with trade and craft production. Tucker has examined their choice to pursue a highly diverse portfolio of activities that place foraging alongside cultivation and marketing.

Mikea are said by their neighbors to be desultory farmers. While this probably is a good reputation to have if taxes on production are a burden, Tucker proposes a dynamic analysis focused on trade-offs between *hatsake* (swidden corn cultivation) and *ovy* (tuber) foraging. Well fed by their immediate return foraging, Mikea work at planting their fields. But every day planting depletes short-term food supplies and leads to hunger. Hunger elevates the subjective discount rate of the harvest, which after all may be months away, reducing its present value and compelling the Mikea to return to foraging. After several days of hunting and gathering, well-fed and holding a couple of days of food supplies, the discount rate applied to agriculture declines and Mikea make the switch back to agricultural work. Neither source of subsistence can get the upper hand because they alternate with fluctuations in the endogenous discount rate, as a function of hunger. “Mikea cultivate because the rewards are high compared to foraging, but they refrain from intensification because immediate needs limit their capacity for future investment” (Tucker 2006: 24). We suspect that Mikea subsistence tactics would be immediately recognizable to a time-traveling visitor from the Fremont.

Discounting reminds us that the opportunity costs of continuing to forage are not the potential returns of cultivars, but those potentials adjusted for what may be a long delay and uncertain prospects of a fulsome harvest. Combining Tucker’s insights with those of Barlow, we

would want to discount agricultural production by its component activities.

Reason #7: Growing dependence on food production heightens subsistence vulnerability, keeping foraging attractive until societies were able to work through the formidable task of re-organizing their risk-mitigating institutions to accommodate agricultural production.

Hunter-gatherers have evolved sophisticated risk-buffering capacities based in face-to-face intra-group exchange, mobility, social institutions guaranteeing reciprocal access, and reserves of fallback or starvation foods (Jaeggi and Gurven 2013; Smith 1988; Wiessner 1982; Winterhalder 1990). Intra-band food sharing by foragers is a well-documented adaptation to subsistence (Gurven et al. 2004; Peterson 1993; Winterhalder et al. 1999). Our models for achieving similar risk-buffering in temperate zone agriculture (Halstead and O’Shea 1989) are less developed, but appear to entail significantly different scales of space and time as well as broader social institutions (Winterhalder 1990). Examples are the dispersal of plots in the open field system of the English Midlands (McCloskey 1976) or the state-level processing and storage of freeze-dried potatoes by the Incas (Murra 1984).

Although we know little about this -- indeed little about the probability distribution of pre-industrial agricultural yields themselves (Lee et al. 2006) -- it may have been quite a difficult evolutionary task to reconfigure socio-economic institutions from the day-to-day, inter-family, risk-sensitive adaptations of band societies, small, face-to-face groups of low density and high mobility, to the institutions required for inter-annual risk buffering within agricultural communities of much higher density, greater sedentism, delayed return production and fewer fallback options (Winterhalder 1990). As an example, inter-annual foods storage might seem an ideal means of buffering subsistence shortfalls due to crop failures, but dynamic analysis reveals it has some serious liabilities (Winterhalder et al. 2015).

We do know that the period during which cultivars became dominant components of the diet was difficult for human health and welfare. Bioarchaeological study of bone and enamel pathologies indicate lower quality diets and more frequent and more severe periods of food shortfalls in communities newly dependent on cultivars

(Cohen and Armelagos 1984; Larsen 1995). There must have been repeated instances of trial-and-error failure in development of new institutions for handling subsistence risk in this novel setting. *FwC* economies may be the result of an inability to forego the security of foraging during the period in which risk management of agriculture is still being perfected.

Discussion

The persistence of hunter-gatherers into the present is remarkable. A standard explanation is that the foragers who survived did so because their environments were too marginal to invite their displacement by agriculturalists or pastoralists. However, there is nothing marginal about California, where prehistoric food production using domesticates did not develop, or particularly attractive about environments in the US southeast, where it did. Further, the net primary productivity of habitats occupied by ethnographic foragers is statistically indistinguishable from those occupied by agriculturalists (Porter and Marlowe 2007), contrary to the argument for marginal zone survival of foragers. That explanation also is suspect because it deprives the foraging economy of any adaptive virtues that might compete with those of food production, save the ability to persevere in places that no one else wants.

By contrast, we believe foragers have persisted because their economies have enduring advantages (see Codding and Kramer 2016). The Mikea, who in ethnohistoric time are relatively new to this means of production (Yount et al. 2001), remind us that foraging can compete even when fully developed agriculture is an option.

In 1982 Hunn and Williams (1982:6) published bar graphs showing the relative frequency of ethnographically recorded societies with varied degrees of dependence (0-5%, 6-15%, etc.) on gathering, hunting, fishing, herding and agriculture. The sample of 200 comes from Murdock’s (1967), *Ethnographic Atlas*. The distribution for agriculture is bi-modal, with peaks at 0-5% and 45-55%; societies with 5-35% dependence on agriculture are disproportionately rare. Hunn and Williams suggest this bifurcated distribution is evidence that societies transitional between foraging and food production are unstable. In their view, the transition from hunting-gathering to agriculture is “a dynamic process leading – in most of the earth’s environments – to a rapid (in the

time frame of human evolutionary history) and radical transformation in modes of production” (p. 5). The Hunn and Williams graphic is reprinted in Zvelebil (1996) and Smith (2001), both of whom question the inference. We do as well. Hunter-gatherer societies with low levels of food production may be rare in the contemporary ethnographic world where they must compete with fully developed agriculturalists. But no ecological logic requires they be similarly rare during the (pre)historic period in which societies were experimenting with various degrees and forms of cultivation, perhaps in the form of mobile foraging among patches (see reason #1).

Referring to the evolution of agricultural systems of production, Richerson et al. (2001: 403, Table 2) described a set of “[p]rocesses that may retard the rate of cultural evolution and create local optima that halt evolution for prolonged periods.” Like ours, their list of factors favoring mixed economies contains seven entries: (1) small-scale geographic regions may limit opportunities for innovations and their diffusion; (2) minor climate changes may defeat agriculture in marginal environments; (3) pre-adapted plants may be rare; (4) density-dependent increases in infectious diseases may limit population growth of groups switching to food production, impeding intensification; (5) complex technologies like food processing and storage may evolve slowly; (6) complex social institutions also may evolve slowly; and (7) ideological evolution may operate at odds with adaptive processes. Richerson et al. (2001:404) speak of these factors as “historical contingency against the steady, convergent adaptive pressure toward ever more intense production systems.” They thus adopt a language of adaptive intensification and inevitability that we have tried to avoid in offering reasons that adaptive pressures, as well as historical contingencies, may act against agricultural production intensification.

Of the Richerson et al. (2001) proposals clearly different from ours, #1, #2 and #3 draw attention to regional environmental constraints. Sources of suitable cultigens may be rare and their diffusion inhibited by geography. Disease may have limited population, thus intensification (#4), or the maintenance of information (Henrich 2004) or seed stocks required for use of cultivars, as we note above. Proposal #7 draws attention to the possibility that cultural evolutionary processes affecting ideology may diverge from and inhibit those guiding the economic features of subsistence evolution. We say little about such constraints. Proposals #5 and #6 cite difficulties

of evolving complex technological and institutional adaptations and are similar to our narrower focus on like problems with the development of institutions for mitigating agricultural risk. The Richerson et al.(2001) list is consistent with their emphasis on climate and cultural evolution; ours more consistent with the interactive socio-economic mechanisms of human behavioral ecology.

In arguing for the inevitability of intensification once salubrious Holocene environmental conditions were in place, Richerson et al. (2001: 402) allow that the process might proceed at different paces in different locations, but they argue that reversals are rare. If they mean that once densely settled agricultural societies create an environment of intensive production, odds are against a return to foraging, we would agree. If they mean that selection pressures affecting FwCs early in the history of agricultural origins were persistently in one direction, we disagree. We argue the situation likely was much more dynamic, reversals of directional subsistence trends common.

It will take more and much better evidence to sort through the relative merits of these proposals. It also will take recognition of the divergent but interacting temporal scales associated with the evolutionary ecology processes that we and Richerson et al. are highlighting. Human foraging decisions operate in short-term, ecological time; environments fluctuate seasonally and annually; the dynamics of population ecology occur over multi-generational time; and, evolutionary processes like natural or cultural selection generally take place on temporal scales that are yet longer. Researchers and the analyses they present typically specialize on one of these scales, treating others as relative constants or freezing them through equilibrium or *ceteris paribus* assumptions. This is normal, but it is worth remembering the advantages of methods that disaggregate these scales so that it will be possible eventually to understand their interdependencies. A full discussion would take us afield, but we must acknowledge a referee for raising this important point.

We have suggested seven possibilities for the persistence of FwCs, each of which draws on the concepts and models of behavioral ecology. For economy of presentation, we have not summarized the underlying theoretical justifications (Smith and Winterhalder 1992b; Winterhalder and Smith 1992) for our perspective, nor

have we described in detail the core foraging models. Those ably are covered elsewhere (Bettinger 2009). We acknowledge that few of our seven possibilities have been examined in detail with archaeological or ethnographic evidence, or tested through simulation models or other means; our effort primarily is heuristic. We close with four general observations.

First, this kind of exercise is important even for prehistorians not interested specifically in the origins of agriculture. Consider Martin Wobst's mischievous title from *American Antiquity* (1978), "The archaeo-ethnology of hunter-gatherers or the tyranny of the ethnographic record in archaeology," and the general question: What conceptual tools might help us to recognize and explain novel economic forms like FwCs, forms that are absent, unrecognized or certainly under-appreciated in ethnographic research? If behavioral ecology helps us to think productively about this case without ethnographic guidance, we may recognize and find entry to others. Barlow's (2006) treatment of agriculture as a suite of potentially separable activities, each set against the opportunity costs of foraging options, is an encouraging example.

Second, we believe Sahlins' (1972b) injunction to avoid formalist (neo-classical) economic concepts in favor of "Zen" economics is misguided. What we need is a disciplined means of deciding which of the basic concepts of neo-classical economics transcend the context of contemporary market economies. Guidance on this most basic of theoretical questions can come only from evolutionary theory informed by comparative studies across species and societies, that is, from empirical work. While elements of Sahlins' caution were merited -- some aspects of modern economic theory do not belong in the past -- his argument has been over-generalized to an unfortunate degree.

Among those concepts we believe useful for evolutionary anthropology analysis are opportunity costs, marginal analysis, risk-sensitivity and discounting (Winterhalder and Kennett 2009). Each helps us to assess trade-offs fundamental to successful subsistence behavioral adaptation in any species. Making such distinctions is important because these concepts and the greatest variety of empirical cases we can glean from the comparative record of subsistence systems in social species (Winterhalder 2001) together offer another means

of envisioning socio-economic arrangements not evident from ethnographic analogy.

Svizzero (2018) notes that debates about rate of domestication (protracted vs. rapid) typically have focused on factors exogenous to human behavior, the availability of auspicious genetic mutations or rates of climate change being examples. Adopting the perspective of human behavioral ecology, he argues that a focus on human choice, driven by the economics of harvesting and processing, points toward a scenario of rapid selection for the genetic changes that produce domesticates. We argue for application of the same theoretical framework, but shift away from the process of genetic domestication as such. Our focus on trade-offs entailed in choices between various subsistence tasks associated with foraging or cultivation and farming leads us to consider mechanisms that would *impede* full adoption of those domesticates, however rapidly they became available. We do not expect Svizzero's or our use of human behavioral ecology will quickly settle issues of pathways and timing, but we do believe that moving them within a common theoretical framework makes solutions more accessible.

Third, it may have been only a few instances from the many societies likely to have experimented with prehistoric cultivation, but in some cases foragers and FwCs *did not* persist. Rather, they evolved full or nearly full dependence on agriculture. If we have correctly interpreted potential impediments to this result, then in these cases the impediments either were different from our analysis, absent or they were successfully overcompensated. Our seven reasons raise many possibilities, from cases that happened to engage low rank but high yield cultivars, to lessening discount rates on activities associated with food production, to adaptive realization of economies of scale in risk reduction.

Finally, we end by emphasizing the intellectual transition from agricultural origins as a revolution, which coupled cultivation, domestication, intensification and agriculture, to a processual transition of mixed subsistence practices in novel combinations. FwCs allow us to envision stable forms of subsistence that uncouple cultivation, domestication and the emergence of full-scale economic dependence on food production. FwCs combine subsistence practices in ways largely unfamiliar to us from ethnography, combinations only awkwardly captured in our standard categories. We require new

ways of studying them and one of the most promising of those is behavioral ecology theory (Bird and O'Connell 2006; Codding and Bird 2015; O'Connell 1995).

Conclusion

Now encompassed within national states and broadly commodified market economies, foragers continue to exist in small numbers across the globe, sometimes in spite of significant economic, political or more directly coercive pressures to assimilate to other economic practices. Based on a summary of nine ethnographic cases, each described in detail in their edited volume, Codding and Kramer (2016) divide the reasons for the contemporary endurance of foragers into those that are economic and those that are social. The economic rationales center on the observation that continued hunting and gathering, facilitated by selective use of contemporary technologies, represents in many cases the best local option for securing a livelihood. The social rationales focus on reluctance to give up valorized practices such as band collaboration and food sharing, gender role equity, and maintenance of social networks, low status differentiation and ritual activities. Foraging societies no longer are evolving as foragers in a world of foragers, but are making production and consumption decisions exposed to the contemporary possibilities of pastoralism, horticulture, agriculture, wage employment and entrepreneurial activities. With proper attention to that enormous difference of context, they may provide us further clues about the mechanisms that lead to novel forms of economy, recombined from elements not respecting our traditional academic categories.

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We hope that the usual suspects deserving appreciation in this spot will forgive us a simple declaration that we continue to be inspired by the presence in our personal and academic lives of our colleague, Robert Bettinger.

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