

# Chapter 16

## Demography, Environment, and Human Behavior



Cedric Puleston and Bruce Winterhalder

### Introduction

Archaeology's broad engagement with the long-term evolution of human subsistence systems and social forms hinges upon poorly understood relationships among environment, demography, production, and society. Specific examples are conveniently phrased as questions. How long will it take for a colonizing human population to fill a previously unoccupied habitat and what factors determine this duration? At what point in its growth trajectory will a natural fertility population's economic status and its demographic health be greatest, and how does that compare to its situation near equilibrium, when it has stopped growing? At what phase of growth would it make the most sense for a commanding oligarchy to invest a subject population's output into the construction of monumental architecture, and would it be wiser to extract tribute in the form of goods or as labor? Does the presence of food storage structures indicate a population better buffered against variability in food supply and thus famine? How should we assess which theory provides the better explanation of human (pre)history: the demographic pessimism of Malthus or the technological optimism of Boserup? Put somewhat differently, what is the relationship among population, economic intensification, and economic surplus? These questions and more like them routinely engage archaeologists.

Here we consider such questions from the perspective of demography and population ecology. The questions pivot on births and deaths and their linkages via human behavior to environment, technology, and labor. Because they involve complex, dynamic interactions, the effects of these linkages—and answers to the questions like those posed just above—can be difficult to predict from intuition alone. Although the political economists Malthus, Ricardo, and others were pursuing such issues in the eighteenth century, as have others since, we will argue in this chapter that they remain potent. They endure despite scientific progress because of their importance. Most importantly, current analytical modeling tools provide new and promising insight into these old problems.

These tools come from the fields of demography and ecology. Demography is the study of population processes in which the rates of birth and death interact to describe how one generation gives rise to another. Demography is closely bound up with environment and modes of life: how people acquire food and material goods, pay tribute and taxes, construct homes and communities, find partners and raise children, age, and die. The relationships often are reciprocal; environment, production, and society affecting rates of birth and death narrowly and evolutionary change more

---

C. Puleston (✉) · B. Winterhalder  
Department of Anthropology (Evolutionary Wing), University of California, Davis, Davis, CA, USA  
e-mail: [puleston@ucdavis.edu](mailto:puleston@ucdavis.edu); [bwinterhalder@ucdavis.edu](mailto:bwinterhalder@ucdavis.edu)

broadly. To varying degree, each of these factors leaves imprints via human behavior on the archaeological record. Having information about the ecology and demography of population allows us to mobilize analytical models (Winterhalder 2002) capable of making predictions about the behavior of individuals and the systems in which they reside. We can then evaluate the predictions against the empirical record gained by archaeologists.

We use models, unconsciously or consciously, whenever we formulate research questions, choose methods, or analyze and interpret results; archaeologists do so as well (Kohler and van der Leeuw 2007, p. 4). Whether explicitly acknowledged or not, we impose a model whenever we try to explain the impact of natural, sexual, and cultural selection (Brown and Richerson 2014) on economic organization and intensification, surplus, social evolution, or the formation and persistence or disappearance of societies. Our approach attempts to make such models as explicit as possible. In doing so we make the claim that demography is of little use to evolutionary archaeology unless it is treated in the context of population ecology, with populations understood to be dynamic and interdependent with their environment. Secondarily, this is a claim about the necessity to archaeological research of explicit analytical models.

We begin in Section “[Demography, Population, and Environment Since Malthus](#)” with a brief summary of the major steps from Malthus to contemporary approaches. In Section “[Modeling Demography and Work in Environmental Context](#),” we describe the state of the art for modeling the linkages between demography and human behavior, focusing on one promising and well-vetted approach. Section “[Space-Limited Insights and Their Archaeological Significance](#)” is divided into subsections addressing the applications of this approach to questions with archaeological implications. In Section “[From Simulation Models to Evolutionary Archaeology](#),” we describe several recent cases in which archaeologists have integrated these methods into their own work, and in Section “[Concluding Thoughts](#),” we summarize.

## Demography, Population, and Environment Since Malthus

The demographic arguments of Robert Thomas Malthus (2003 [1798]) are well known, largely for three reasons: they were presented as semiquantitative model, they were embedded in a wealth of data, and the relationship portrayed between geometric potential for population growth and arithmetic development of agricultural production—and the misery this mismatch foretold for the poor—was consequential for social policy. But Malthus recognized that the problems he was addressing were about much more than demography. His argument included an economic element focused on the growing dominance in Europe of markets for labor and food. As population grew, a larger workforce competing for limited jobs would depress wages, while at the same time, growing demand for food in limited supply would push up its price. Although less explicitly modeled, this economic dynamic was as unrelentingly hard on human welfare as the demographic one.

Malthus sometimes is criticized for neglecting ecology, particularly the agroecological base of subsistence. Indeed his early and most widely known writings say little about the role of environment. Nonetheless, Malthus’ later diaries of his travels through continental Europe, Scandinavia, and the British Isles show him to be an engaged and acute observer of weather, seasonality, soils, crops, agricultural techniques and yields, and the welfare of the laboring populations engaged in subsistence production. The biographer Mayhew describes these records as Malthus’ environmental economics (Mayhew 2014, p. 103–127). Here too Malthus was seeking dynamic understanding, a model by which to work, as he and the economist David Ricardo popularized the concept of the declining marginal returns to agriculture. They were among the first to emphasize that, as production increased, lands of lower and lower suitability came under cultivation and average output consequently declined, substantiating his conviction that agricultural yields could not keep pace with population potential.

The dynamics of a system like the one Malthus described often are fit to a logistic equation, in which the growth rate of the population is a function of how close it is to its carrying capacity. Carrying capacity is defined as the maximum number of individuals that can be sustained in an environment under a particular form of production, often denoted by the letter  $K$ . Expressed as an intuition in Malthus, the relationship was formalized by Pierre François Verhulst in 1838 and is often put in the form

$$\frac{dN}{dt} = rN_t \left(1 - \frac{N_t}{K}\right),$$

in which  $N_t$  is the population size at time  $t$  and  $r$  is the maximum rate of growth. In prose, the rate of change in the growth of a population of size  $N$  with respect to time ( $dN/dt$ ) is a function of its maximum rate of growth ( $r$ ) times its size ( $N_t$ ) discounted toward zero by proximity to its carrying capacity,  $K$ . This saturating function yields an S-shaped population trajectory. While it can be quite useful in the study of chemical reactions and bacterial growth, it is less useful in the study of complex social organisms with the potential to manipulate fertility and modify their environments, like humans.

The logistic has another serious shortcoming: it is entirely phenomenological. By this we mean that it may capture the *pattern* of increase typically for simple populations in laboratory conditions, but it provides little insight into the *mechanisms* that underlie density-dependent growth. That's because key terms like  $r$  and  $K$  are meaningful only to the degree that they can be translated into observable variables like births, deaths, and the efficiency and sustainability of subsistence production. Without such translation it is difficult to test and interpret the logistic model.

Work in the 1920s by mathematicians Alfred Lotka and Vito Volterra on commercial fisheries was a major advance on the logistic. Instead of fixed values for  $r$  and  $K$ , they developed models that envisioned each as a variable: the predator or consuming population grew or declined at a rate depending on the density of its prey; the prey, in turn, grew or declined depending on the intensity of its exploitation. Their models and those that followed generate much more complex and potentially realistic interactions, including population booms and crashes, stable cycles, time lags, and differing degrees of persistence and stability. Readers will find an excellent account of these early models in Hutchinson (1978).

Hunter-gatherers are predators on populations of terrestrial game, fowl, fishes, and plants. Their subsistence effectiveness depends on the selective harvesting of the animal and vegetable foods they encounter. Building on Lotka and Volterra, Winterhalder and students (1988; see also Freeman and Anderies 2012; Szulga 2012) modeled a forager population that grew or declined in size as a function of its foraging efficiency. The human foragers in the analysis are linked via an optimal diet selection model to an environment of animal and plant populations with densities that increase or decrease as a function of whether or not they are exploited upon encounter. The model builds toward greater ecological realism by incorporating biological situated variables such as prey density and kilocalorie value and the time required for pursuit and harvesting of resource species. It allows prediction of how diet is affected by changes in consumption needs, climate, or other impacts on prey density or technological developments affecting harvesting efficiency. Implications for conservation biology and sustainability (Winterhalder and Lu 1997) and domestication (Winterhalder and Goland 1997) follow.

With the advent of cultivation and agriculture, humans began extensively to modify their landscape and to undertake direct reproductive and population management of the resources critical to their economy. In an agricultural scenario, the fixed carrying capacity envisioned by Verhulst or the predator-prey dynamics of Lotka and Volterra are no longer suitable. Mathematical biologist Joel Cohen (1995) cataloged long-standing attempts to estimate the Earth's carrying capacity, coming to the conclusion that we are no closer to consensus today than in Malthus' time, for sound reasons. Human carrying capacity is a conditional and changing property, a function of environment, technology, economy, labor, and consumption, all of which vary over time and space. Similar problems plague archaeological attempts to set prehistoric carrying capacities at regional or local

scales (Glassow 1978). Even Malthus allowed for slow, linear changes in food availability, fostered by technological developments but handicapped by the declining marginal productivity of the wastelands being opened up to cultivation.

Attention to behavioral and technological innovations that increase food supply is at the core of work by the development economist Ester Boserup (1965). Boserup often is cited as the antidote to the dismal vision of Malthus, of a world dominated by overpopulation and unavoidable hunger. In her 1965 book, *The Conditions of Agricultural Growth*, Boserup focused on relationships between labor, production techniques, and agroecological yields. Low-density populations are well served by extensive systems of shifting cultivation; systems generally are characterized by high yields to labor but low yields per unit of land due to long fallows. Boserup argued that as population density increases, fallow is progressively shortened or even eliminated. This increases the workload of the farmers who must seek higher yields from the same or perhaps even declining amounts of land. The extra human labor goes into soil amendments and the mulching, weeding, and like efforts required as a substitute for the natural regenerative capacity of the system under less intense or less frequent use.

Contrary to Malthus, Boserup describes a model of agricultural intensification in which yield per unit area increases through innovations prompted by increasing human population density. At low densities, farmers can avoid extra work through fallowing, with its extensive demands on land; however, as density increases, they take the option of employing technological innovations and harder work to coax more food from the increasingly limited land available. Boserup's examples emphasize fallow-based intensification, but the analysis is more generally applicable to other forms of technology substitution.

Although it has been remarkably productive (e.g., Morgan 2014), Boserup's model has limitations. It is developed in informal conceptual terms, and some of its elements are, like those of Verhulst, phenomenological and thus difficult to ground in empirical observation. For instance, the Boserup model assumes but does not explain population growth, and it does not describe the mechanisms by which increasing population density spurs intensification or innovation. Supporting evidence has been mixed (compare Kristinsson and Júlíusson 2016; Pacheco-Cobos et al. 2015), although to be fair, no more mixed than that for the Malthusian approach. Nonetheless, Boserup is critical because her analysis gives redress to factors neglected in Malthus, especially to the potential for innovations that escape the confining arithmetic increase that Malthus allowed for agricultural productivity. As a consequence, her approach better fits to historical evidence in which changing methods, such as shortening or lengthening fallow, allow yields to match population, whether it is growing or declining in density.

In 1998 demographic anthropologist James Wood (1998; see also Lee 1986) proposed a model that linked demography and preindustrial economics, to some degree synthesizing Malthus and Boserup. Wood focused on the marginal agricultural productivity of labor, the yield in food per unit of labor for the last worker added to the system. If resources required to produce food are limited, as a population increases in size, ultimately its marginal productivity must fall. The number of mouths to feed increases but each new pair of hands provides less and less additional food. Eventually the system approaches a stable equilibrium defined by the density-dependent effects of "well-being" on rates of fertility and survival. Wood (1998, p. 110) concluded that "left to itself, a preindustrial system of production will tend toward a state in which the average individual is in just good enough condition to replace himself or herself demographically."

By means of this brief historical summary—written from an explicitly "presentist" point of view (Stocking 1968)—we mean to observe that writers since the late eighteenth century have recognized the importance of understanding the causal mechanisms linking environment, demography, production, and society. There is intellectual continuity to this research tradition, from Malthus to present; there also are recent and important changes: (a) we are moving from loosely conceptualized models stated in prose to more formal mathematical conceptualization, susceptible to more disciplined analysis; (b) we have improved our ability to represent the mutual interactions among multiple

variables; and (c) we today are more attentive to the possibility that both Malthus and Boserup may be correct, the importance of their respective insights varying with the time and situation, incumbent upon us to appraise.

## Modeling Demography and Work in Environmental Context

We divide recent developments in the modeling of ancient populations into two categories: (1) agent-based and (2) analytical models. Agent-based models are based in computer simulation; analytical models are equation-based and may or may not entail simulation. We describe each category briefly.

Agent-based models, exemplified by the work of archaeologist Timothy Kohler, track simulated individuals who follow a set of behavioral rules and interact in a virtual environment. The Village Eco-dynamics Project (reviewed in Kohler et al. 2012) uses agent-based models to study the Pueblo people of the American Southwest, creating rules regarding demography, maize agriculture, trade, social organization, and site abandonment in an ecologically realistic environment that suffers droughts and floods and in which animal populations responded to hunting pressure. The modeling efforts provide insight into population trends and the settlement patterns observed in the archaeological record; they also have been applied to questions regarding the emergence of social stratification and cooperation. Kohler and colleagues argue that modeling is an important supplement to traditional archaeological methods:

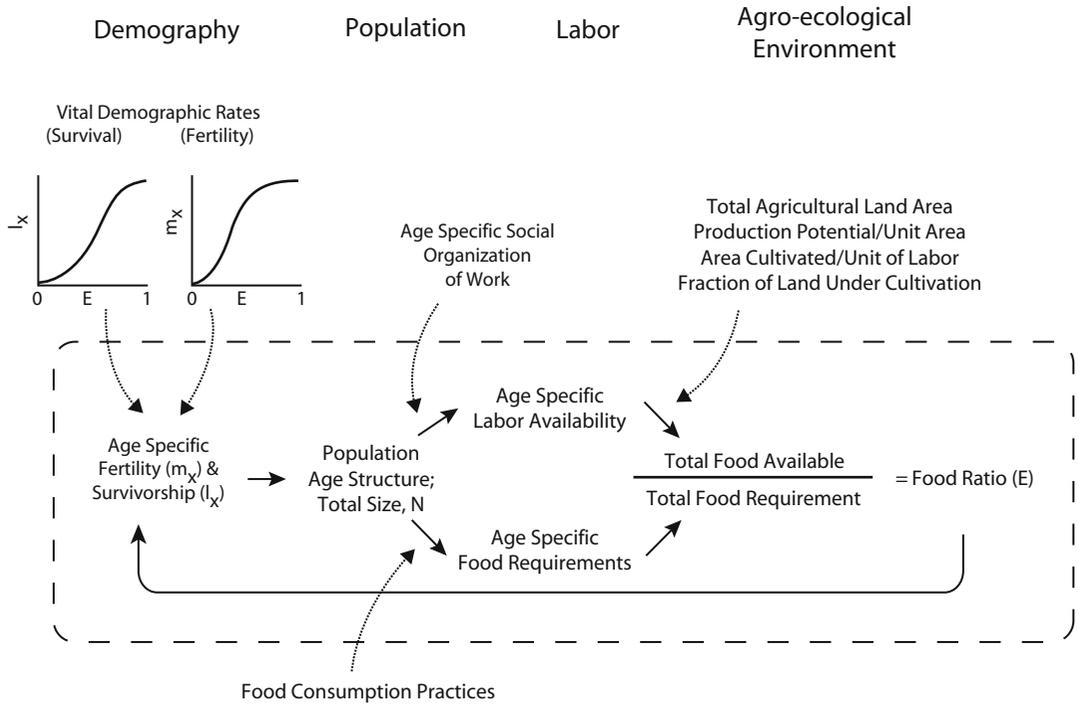
[A]s modellers we begin with processes and use computation to reveal the patterns that emerge through time and space. Working in this way . . . resolves many of the problems associated with intuition and ethnographic analogy, important as these strategies may remain (Kohler et al. 2012, p. 40).

In another example, Tkachenko et al. (2017) develop an agent-based model parameterized to hunter-gatherers and applied to an analysis of the migration from Beringia into the Americas. Lake (2014) reviews the use of agent-based models in archaeology.

Analytical population models typically begin by defining the population's growth rate as a function of one or more environmental variables, for instance, the dynamics of a renewable resource or changes in climate. This equation-based approach can yield mathematical solutions or approximations amenable to determination of key properties like equilibrium conditions and their stability, a major advantage. For instance, the economists Brander and Taylor (1998) model the rise and fall of Easter Island's population in response to the human rate of forest destruction, an exercise that inspired a generation of responses. Roman et al. (2017) formulate a model of the Classic Maya in which the population may allocate labor resources among swidden, rain-fed intensive agriculture, and monument construction. Each of these three occupations is tracked separately. The authors conclude that drought most likely played only a minor role in the depopulation of Maya urban centers. Purely analytical approaches tend to focus on techniques that may be difficult for the mathematically uninitiated to parse. Nonetheless, significant progress in analytical models that speak to archaeological questions have come from the fields of economics, population biology, and theoretical ecology (e.g., Anderies 2000; Kögel and Prskawetz 2001; review in Nagase and Uehara 2011).

Inspired by intellectual traditions emerging from Malthus and Boserup, and building on Wood (1998), theoretical population biologist Shripad Tuljapurkar and members of his lab at Stanford have created an explicit analytical model of the basic relationships between human demography, population, work, and agroecological environment (Lee and Tuljapurkar 2008; Puleston and Tuljapurkar 2008; Lee et al. 2009; our Fig. 16.1). We follow this analytical research tradition, based in mathematical solutions, approximations, and simulation, for the remainder of the chapter.

Tuljapurkar's "food-limited demography" approach refines Wood's concept of well-being with a more concrete mathematical relationship, the "food ratio," or  $E$ .  $E$  is defined as the kilocalories



**Fig. 16.1** The space-limited population ecology model. Core components of the model and their causal connections (solid arrows) are shown within the dashed line rectangle. Demographic, biosocial, and agroecological factors determining the form and parameter values assigned to those core components are shown around the circumference, with dotted arrows indicating their point of action. We provide a step-by-step description of one iteration through the core components in the text; a more complete description of the mathematical and programming details can be found in Puleston et al. (2014) and references therein

available to individuals in a population as a fraction of the kilocalories required to keep their fertility and survival at levels undiminished by hunger. If the food ratio is 1, then there is exactly enough food to avoid the demographic effects of kilocalorie shortfalls. If  $E < 1$ , then the population growth rate is diminished due to corresponding decreases in fertility and increasing mortality. If  $E > 1$ , the population has food kilocalories in excess of need, but the excess does not affect vital rates; births and deaths and thus the growth rate are unaffected. The model relies on specific functions parameterized from studies of famine to delineate the effect of hunger ( $E < 1$ ) on vital rates (Box 16.1).

**Box 16.1: A Model of Food- and Space-Limited Population Growth**

Population dynamics hinge on the balance of food production and consumption. Production is calculated from a function tracking the fraction of available land in actual cultivation (called  $F$ , unitless and ranging from 0 to 1), which is multiplied by the product of total arable land ( $A_m$ , in ha) and the yield ( $Y$ , in kcal/ha/day).  $F$  is usually expressed as a saturating exponential function of the form

$$F = 1 - e^{-\frac{HkN\phi}{A_m}}$$

(continued)

**Box 16.1** (continued)

where  $H$  is the number of hours an individual of the most productive working age devotes to agriculture and  $k$  is the conversion from worker-hours to area cultivated (ha/worker-hour). Note that this expression of  $H$  is in terms of working-aged individuals, regardless of sex or other designation. If there is a division of labor, then  $H$  would be multiplied by the fraction of individuals engaged in agriculture.  $N$  is the total agricultural population size. The variable  $\phi$  is the average age-weighted labor contribution, relative to the most productive age class. It is also weighted by the age structure of the population to provide a measure similar to the dependency ratio but reflecting a producer ratio instead. It can be expressed as the dot product of the vector of relative worker productivity by age ( $\phi$ , ranging from 0 to 1) and the population structure vector ( $\mathbf{u}$ , whose elements sum to 1):  $\phi = \langle \phi, \mathbf{u} \rangle$ . The product  $N\phi$  represents the number of equivalent high-quality workers in the population, and the ratio in the exponent within  $F$  represents the maximum area the population could farm with the labor available to it, as a fraction of the total arable area. These elements allow the calculation of total production, in kcal/day:

$$\text{Production} = Y A_m F.$$

The amount of food necessary to avoid hunger and maximize fertility and survival also depends on the age structure of the population:

$$\text{Baseline consumption} = J N \rho,$$

where  $J$  is the calories required to feed the most energetic age class without diminishing vital rates and  $\rho$  is the age- and structure-weighted relative need. Similar to  $\phi$ , but representing the caloric needs of a typical individual in the population,  $\rho = \langle \rho, \mathbf{u} \rangle$ , where  $\rho$  is a vector of age-specific caloric need, as a fraction of the neediest class. This variable ranges from 0 to 1.

The food ratio is the ratio of realized production to baseline consumption, where “baseline” refers to the case where there is no reduction in demographic rates due to hunger:

$$E = \frac{Y A_m F}{J N \rho}.$$

The population in the following year can be calculated from the current one through the effect of  $E$  on the age-specific rates of fertility ( $m_x(E)$ ) and survival ( $p_x(E)$ ), where  $x$  represents the annual age class. In practical terms this is easiest done through software that allows the construction of a population projection matrix. R code to do these calculations was written by the Winterhalder lab and is available at [github.com/puleston/spacelim](https://github.com/puleston/spacelim).

Once the equilibrium food ratio has been determined (or approximated), it can be used to calculate the equilibrium population size:

$$\hat{N}_m = \frac{A_m}{(Hk\hat{\phi}) \log\left(\frac{\hat{E}_m}{E}\right)},$$

where  $\hat{\phi}$  is the value of  $\phi$ , the worker ratio, determined using the equilibrium population structure, and  $\hat{E}_m = Y H k \hat{\phi} / J \hat{\rho}$ , representing the theoretical maximum of the food ratio, given equilibrium population structure. Here  $\hat{\rho}$  is the value of  $\rho$ , the consumption ratio, calculated from the equilibrium population structure. The equilibrium population structure  $\hat{\mathbf{u}}$  is determined from the equilibrium food ratio and the responsiveness of fertility and survival rates to hunger.

The first paper in the Tuljapurkar series describes and interprets the basic food-limited case in which a population may expand into infinite space. The second examines the dynamics of a food-limited population within a finite or space-limited agricultural landscape, and the third analyzes the effects on the model of environmental stochasticity. The series is parameterized to represent the dryland sweet potato field system on the Kohala Peninsula of Hawai'i Island (USA) in the time before European contact (Kirch et al. 2012). Subsequent analyses usually have taken these parameters as defaults, generally representative of demographic and agroecological conditions in prehistory, while adjusting them selectively to explore new questions. The reader should consult the original papers for further technical details.

In application the space-limited approach to preindustrial agricultural population ecology is employed as an iterative computer-based simulation, each cycle representing an annual time step. The core feedback loop is represented within the dashed line in Fig. 16.1. A description of the model's dynamics can begin with the population's total size,  $N$ , and its age structure, the latter indexed in 1-year increments. Knowing the parameter values of the age-specific food requirements, the program calculates a total food requirement. At the same time, using assumptions about the age-specific social organization of work, it calculates age-specific labor availability and its total. The total food available, the comestible agricultural output, is calculated using information about labor and the agroecological environment of production. This calculation is based on the total area cultivated by the labor available and the production potential per unit area. The total food requirement relative to total food available completes calculation of the food ratio,  $E$ .

Moving around to the left side of Fig. 16.1,  $E$  then determines age-specific fertilities and mortality rates achieved by the population's subsistence efforts, updating with new births and deaths the age-specific groups that comprise the total population,  $N$ . The general shapes of the relationships between survival and fertility and food availability for  $E \leq 1$  are shown in the upper left of Fig. 16.1.

The space-limited model tracks age structure, but it does not track sex for purposes of work, consumption, births, or mortality. Following the practices of single-sex demography, we adjust by allowing only half of the fertile age classes to give birth. Because the model calculates age-specific birth and death rates, it does allow us to track several standard measures of population welfare, such as food availability, total fertility rate, average life span, and survival to a particular age (Fig. 3 in Puleston et al. 2014).

The simulation allows us to represent socio-cultural determinants of subsistence work by specifying what fraction of the available labor by age group is engaged in agriculture. In the agroecological environment component, the model uses a conversion from labor (in hours per day) into an area of land cultivated. This can be made conditional on the technologies available, the environment, and the method and nature of cultivation employed. Assuming labor is applied at its maximum efficiency, this determines the greatest cultivable area. Total food production, based on potential yields per unit area of land, can be set to represent environmental features such as climate and soils.

In the space-limited case that we describe here, land is finite (total agricultural land area). As more of it gets put into use, the efficiency of production decreases as a consequence of competitive inefficiencies. This is calculated using the fraction of land under cultivation. While the population is small, each new farmer has little trouble finding and utilizing an accessible, salubrious, contiguous, and unoccupied plot. But, as the landscape begins to fill up, this becomes more difficult. In terms adopted by Wood (1998), this captures the declining marginal productivity of labor. However, we might also reach back further to Malthus and Ricardo and take it to represent the declining marginal productivity of land. In Box 16.1 we provide a more formal, mathematical description of this and other model elements.

Set upon a course of population growth, this system ultimately achieves a stable equilibrium at which births and deaths balance and population ceases to grow. At this equilibrium an additional individual cannot provide food sufficient to meet her/his needs. The food ratio at which this occurs cannot be derived analytically, but it can be approximated (Eq. (6) in Puleston and Tuljapurkar 2008)

or determined numerically. Using the native Hawaiian population parameters mentioned earlier, found in Lee and Tuljapurkar (2008), the equilibrium food ratio, or  $\hat{E}$ , is 0.67. Given fertility and survival rates reasonable for a preindustrial agricultural population, and food distributed proportional to need, at the Malthusian equilibrium, individuals would be subsisting on a diet of 67% of the kilocalories they would need for maximal fertility and survival. Once the equilibrium food ratio has been determined, it can be used to find the equilibrium population size. This maximum sustainable population depends on the cultivable area available, its productivity under agriculture, and assumptions about labor. This dependence on context makes it a *variable*; unlike carrying capacity ( $K$ ), it is not stated a priori.

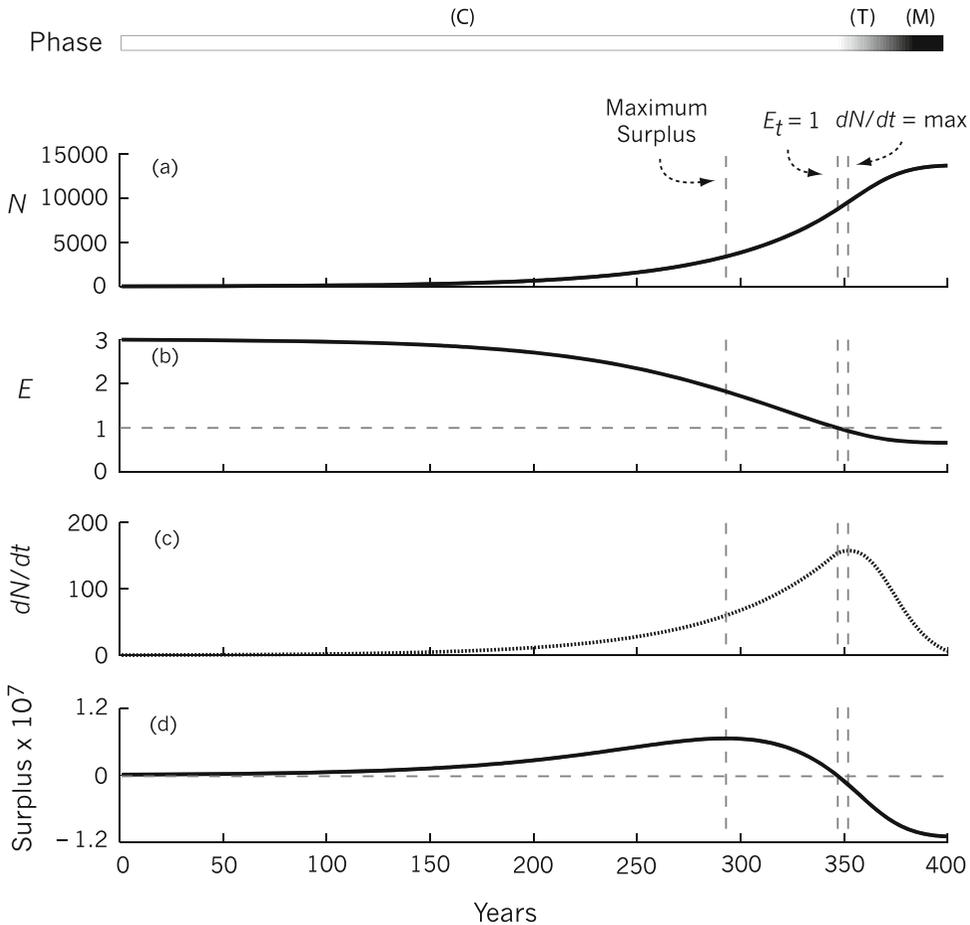
The various components of the food-limited approach are amenable to modification; versatility is one of its virtues. Considered in terms of our earlier history, it links demography, in the form of statements about fertility and mortality, to population dynamics over time, in the form of size, density, and age structure, and finally, to agroecology, represented by environmental potential of land as realized through social organization of labor, food production, and consumption. The interactions of these parameters and variables are represented in quantitative terms and may be modeled as a time series. Importantly, many of the parameters and variables we have described are empirically observable and measureable, not abstractions. The approach has been used to examine population growth trajectories, their phases and timing (Puleston et al. 2014), the potential for agricultural taxation in prehistoric states and its impact on the welfare of the farming population (Puleston and Tuljapurkar 2008; Winterhalder and Puleston 2018), and the risk-minimizing utility of storage facilities in a variable environment (Winterhalder et al. 2015). Extensions to more fully bring Boserupian processes into the model are possible. The availability of enhanced mathematical methods such as Leslie matrices and computational programming resources such as MATLAB<sup>®</sup> allow us to simulate the outcome of multiple interacting variables. Malthus knew of their mutual significance, but he must scarcely have imagined possibilities for their dynamic synthesis.

## Space-Limited Insights and Their Archaeological Significance

### *Properties of a Population Growth Trajectory*

An important result of this approach is more detailed and realistic insight into the growth trajectories of founding populations or those recovering from a significant population decline. The founder case, for instance, might be a small group of Polynesian voyaging canoes with a mixed-sex crew landing on an unoccupied island. We would like to know how long it takes for the population to fill the agricultural space available to it and its experience as it increases in size and approaches and then reaches zero net growth. The space-limited approach is well suited to this type of investigation. In Fig. 16.2 we assume an egalitarian population in a constant environment large enough and sufficiently productive to allow a larger population than the initial number of settlers. No migrants arrive after the founders and the age-specific allocation of work is fixed, as are agroecological methods and technology. We of course could elect to vary any of these fixed conditions to explore model predictions more broadly. For the moment, however, we choose to make the simplifying *ceteris paribus* assumption (keeping all else constant, see Boyer 1995) in order to focus on the underlying patterns.

Having landed in a salubrious environment with 1000 ha of arable land available, the earliest colonizers ( $N = 20$ ) are able easily to meet their subsistence needs. Their vital rates are not diminished by food shortfalls or the effects of hunger. This period of growth, when  $E \geq 1$ , we call the *copial* phase (Fig. 16.2, white phase bar labeled (c)). As measured by infant mortality, life expectancy, and the absence of hunger, quality of life is high. Total food production is limited by the size of the labor pool, but the population is capable of covering its consumption and producing a surplus, food in



**Fig. 16.2** The space-limited population growth trajectory. The simulation begins with a founding population of  $N = 20$  occupying a frontier with 1000 ha of arable land. Panel (a) shows the population growth time series,  $N$ ; (b) shows the value of the food ratio,  $E$ , the variable determining vital rates; (c) shows the instantaneous rate of change in  $N$  as a function of time, i.e., whether growth is accelerating or decelerating; and, (d) depicts the capacity of the population to produce a surplus, given constant work effort. The copial (C, white), transitional (T, increasing gray), and Malthusian (M, black) phases of the trajectory are demarcated at the top. Not depicted: the Malthusian phase would continue indefinitely unless behavior changed or the system was disturbed in some manner. Further details in the text

excess of the amount needed to avoid hunger. The general condition is one of abundance, even as key variables are changing.

As the population moves through the copial phase, the food ratio (panel b) remains  $>1$  although it is dropping continuously as the population expands.  $E$  first falls below 1 in year 347, signaling the initiation of shortfalls. The copial phase founding population grows in total size very slowly for almost half of the 400-year series shown, then at a more rapidly accelerating pace until year 352. Year 352 marks the inflection point in curve (a) and the last increment of positive acceleration in the rate of change (c). There is a 5-year lag between the onset of hunger and deceleration of growth due to age structure effects.

The *transition* phase (Fig. 16.2, T) begins with the first experience of hunger in year 347. The food ratio has dropped below 1 and the growth rate begins to decline. The transition phase typically passes quickly, and the drop in quality of life measures is remarkably abrupt (Puleston et al. 2014). From abundance, it takes on only two to three generations for the population to reach an experience

of hunger so severe that life spans of 45 years under copial conditions have fallen to 30 years by the transition's end. The number of live births to a woman who lives through her childbearing years falls by more than half. The transition ends with growth rate stabilized at an effective value of zero.

The third and final phase of the population trajectory is the *Malthusian* phase (M). The population is at or very near its equilibrium size of 13,509; food availability is two-thirds of that which would sustain optimal vital rates ( $\hat{E} = 0.67$ ). Without some external perturbation or changes in environment or the population's behavior, this state would continue indefinitely. The Malthusian population is generally larger than predicted by a simple conversion of potential calories to people because such calculations typically assume everyone in the population is fully fed ( $\hat{E} = 1$ ) and the level of food required sometimes is not adjusted for subadult age classes.

Our last panel (d) traces surplus production under the assumption of constant agricultural work effort, set to 5 h/day for all working-age individuals, over the full period of growth. We recognize that constant effort may be counterfactual if Chayanov (1977) is correct that peasants expend only as much subsistence effort as is needed to adequately supply their households. Nonetheless, it is useful as a modeling assumption for revealing key dynamics and potentials. As it expands, population begins to produce more food than it consumes. This surplus peaks at year 293 and drops to zero at year 347, when  $E$  falls below 1. It becomes negative thereafter. A counterintuitive result of the model is that a population's potential to generate a surplus with modest effort, not entailing a reduction in demographic welfare, is at its maximum when the population is quite small, only 25% of its ultimate size (3382 of 13,509) and nearly a century before it reaches its maximum size.

Some of the more interesting and robust results of this approach regard the timing of these phases (Fig. 16.2, Phase bar). Under a wide range of starting assumptions, the copial phase (C) lasts about 350 years, meaning that some 14 generations live and grow free of hunger-driven reductions in vital rates. The dramatic impact of the transition phase (T) suggests that founding populations are at risk of an endogenously generated crisis beginning approximately 350 years after their arrival. A population that has spent many generations in a state of sufficiency, if not plenty, is forced suddenly to confront serious shortfalls.

These patterns are quite different from those predicted by the phenomenological Verhulst-style, logistic approach. In the Verhulst conceptualization, a founding population would experience a continuously increasing "pressure" from the moment it arrives, a pressure set ultimately by an assigned carrying capacity ( $K$ ). For a population starting from zero, the inflection point in the S-shaped growth curve is predetermined to be midway from the initiation to the conclusion of its growth; this also is the point of maximal sustainable yield (Winterhalder et al. 1988).  $K$  is not easily tied to specific properties of demography, work, or environment, making case-specific empirical assessment and interpretation difficult. By contrast, in the space-limited approach, the more significant demographic events occur late in the growth period; they are not gradual, but are disruptively abrupt; and they are not predetermined by an a priori parameter like  $K$ , but are emergent from observable properties of vital rates, labor, and the environment of agroecological production.

We predict that a small agricultural population arriving in a geographically circumscribed area of anything but the meanest agroecological potential should be able to grow at maximum rates for approximately 350 years. This will be followed by approximately 50 years of difficult transition to a replacement growth rate and equilibrium. This 400-year span is robust across wide ranges of the size of the founding population and the area of available for agriculture (Puleston et al. 2014). The prehistoric settlement of Pacific islands represents an ideal situation in which to assess this pattern and timing; the results are encouraging. Researchers have found evidence in multiple locations of a crisis or transition, occurring approximately 400 years after initial settlement. Archaeologist Pat Kirch describes three separate studies of early Hawaiian populations that are consistent with the pattern of Fig. 16.2 (2012, pp. 164–168). In agreement with the early work of archaeologist Bob Hommon (1976), Kirch finds that the richer agricultural regions were occupied first, and they become fully utilized within about 400 years. At this point settlement and land use patterns shift to less

productive and more labor-intensive agricultural zones. Referring to growth trajectories that began about 1100 AD Kirch writes:

The transition to the second phase of Hawaiian demographic history may have occurred rapidly. By approximately 1500, high-density levels had been achieved over all the best agricultural lands. Marginal leeward slopes in areas like Kahikinui, and Kohala on Hawai'i Island were already being converted into vast rain-fed agricultural field systems. The rate of population growth began to fall dramatically until it leveled off, closer to a steady replacement rate. (Kirch 2012, p. 169)

Likewise, Rapa Nui (Easter Island) was probably settled at about 1200 AD (Hunt and Lipo 2008) and saw rapid expansion in land use, as evidenced by the summed probability densities of obsidian hydration-dated material, until between 1600 and 1700 AD (Stevenson et al. 2015). After 1600 the population appears to halt its expansion into more marginal areas and even begins to abandon them, shifting its efforts to make more intensive use of productive lands. The pattern suggests that the behaviors regarding settlement and land use that were dominant for the first 400 years were fairly quickly replaced in the century following. Opportunities to observe founding population and their subsequent growth with closely documented archaeological evidence are rare, and examples such as these increase our confidence in the dynamics and parameter values of the space-limited model.

### *Population in an Unpredictably Variable Environment*

Various features of human subsistence behavior likely are adaptations to reduce the hazards of food shortfalls caused by stochastic variability in environmental factors affecting subsistence production. An example is central place food sharing by hunter-gatherers (Jaeggi and Gurven 2013); another is dispersion by an agricultural household of small field plots over an agricultural landscape in order to minimize the likelihood that localized environmental insults like a hailstorm can affect all of them at once (Goland 1993). Such behaviors can be quite effective in mitigating unpredictable food shortfalls (Winterhalder 1990), but they can also be unavailable or fail. We can investigate the consequences of such failure for population welfare by modifying the space-limited model to incorporate stochastic yields. We change the parameter potential production/unit area (Fig. 16.1) from a fixed value to one randomly drawn at each iteration of the model from a distribution of possible values. The average yield is kept the same. The resulting simulations suggest that environmental variability can have profound and sometimes counterintuitive effects on human population dynamics and welfare (Table 16.1).

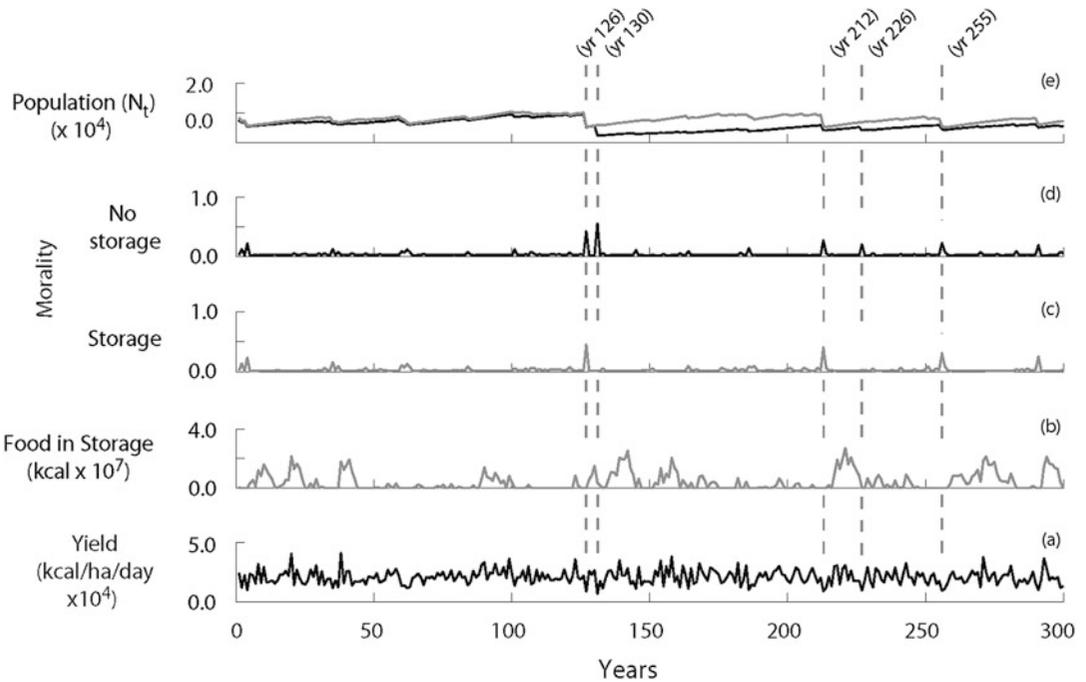
These patterns emerge (Table 16.1; Fig. 16.3). If environmental productivity is stochastic instead of constant, mean long-run population size declines even though mean long-run yield remains unchanged. The magnitude of this decline is a function of the magnitude of the environmental variation. At the same time, long-term average food availability, measured by the food ratio,  $E$ , actually *increases* with a fluctuating food supply. Average measures of welfare such as life span also improve. At first encounter these results appear paradoxical; how can the affliction of randomly fluctuating harvests improve a population's average welfare? The explanation lies in the interactional dynamics of environment and demography. We assume for illustration that environmental yield varies according to a symmetrical distribution, production shortfalls of a particular degree having the same odds as surfeits of that degree. If this is the case, the demographic response generally is *not* symmetrical due to differential response rates of mortality and fertility in the face of shortfall and abundance. Population size can fall quickly but it recovers only slowly.

With the population at equilibrium, any food shortfall is the equivalent of famine; it suppresses reproduction and elevates mortality, perhaps strikingly. A decline in total population pushes it back toward and perhaps well into the copial phase where food is abundant and welfare high. Once the shortfall has abated, renewed growth starts moving the population back toward equilibrium, but recovery occurs at its usual slow pace (Fig. 16.2a). The return of Malthusian conditions may be

**Table 16.1** The effects of storage. The table summarizes the results of multiple iterations of the space-limited model under various assumptions regarding the ability of the population to store surplus food, and presence of obligatory set-asides (e.g., seed or tribute) in the face of yield variability

Condition	Storage	$E$	$N$	Frac $E > 1$	$e_0$ (years)	Death rate	Granary (kcal/year)
Baseline (non-stochastic)	No	0.67	13,509	0.00	30.0	0.033	–
Stochastic CV = 0.3; no set-aside	No	0.85 (0.31)	10,565 (0.10)	0.26	35.3 (0.34)	0.033(0.83)	–
	Yes	0.87 (0.34)	11,208 (0.11)	0.29	35.4 (0.34)	0.033 (0.85)	$6.11 \times 10^8$ (2.32)
Stochastic CV = 0.3; 22% set-aside	No	1.06 (0.43)	6058 (0.25)	0.50	37.9 (0.31)	0.033(1.28)	–
	Yes	1.11 (0.49)	7970 (0.16)	0.51	37.8 (0.32)	0.033 (1.25)	$1.46 \times 10^9$ (1.48)

Notes: “set-aside” refers to any food produced but not available for consumption, including that stored as seed and that given as tribute. “Frac  $E > 1$ ” is the fraction of years in which production exceeds need.  $e_0$  is life expectancy at birth. Death rate is the number of annual deaths divided by the size of the population at the start of that year. Numbers in parentheses are standard deviations.



**Fig. 16.3** A time series of near-equilibrium population dynamics given unpredictable variability in yields, for populations that do or do not practice inter-annual food storage. To represent environmental variability, yields (production potential/unit area; Fig. 16.1) are drawn randomly from a symmetrical gamma distribution with a mean yield of 21,000 kcal/ha/day and a CV of 0.3 (panel a). Panel (b) shows the amount of food in storage, a function of whether or not the preceding several years’ harvests provided a normal surplus. The spikes in panels c (storage) and d (no storage) indicate the magnitude of famine-induced mortality associated with years of particularly low agricultural yields. Finally, panel e traces the population history of the food-storing group (gray) and the group not storing food (black). The years and events highlighted by vertical dashed lines are described in the text; more detailed interpretation and mathematical and programming details can be found in Winterhalder et al. (2015)

many years in the future. Periodic famines are punctuated events that suppress population size and result in higher welfare for the majority of copial, non-famine years. Even moderate environmental stochasticity, such as a yield coefficient of variation of 0.2, is enough to regularly drive a population from Malthusian back into copial phase conditions. Of course, a year or two of serious famine is a disaster for those experiencing it, but it may be followed by generations of relative prosperity for the survivors. This dynamic inverts normal sensibilities. Benign environments, continuously salubrious one year to the next, may be the most continuously ruthless in imposing the misery of Malthusian conditions.

Inter-annual storage of surplus in early agricultural societies is thought to have offered preindustrial populations a degree of risk-minimizing control over food availability in variable environments (Halstead and O'Shea 1989). While this may be the case in some contexts, the benefits to a population living near or at its Malthusian equilibrium can be fickle. In a further modification to the stochastic version of the space-limited model, we allow the population to store excess food in years of high production and to withdraw food from those stores to help meet needs in years of production shortfall. This can stabilize the total food available (Fig. 16.1) and thus elevate the average size of the population and its average well-being (Winterhalder et al. 2015). The magnitude of these effects increases with increasing variability in yields.

The general result gives support to the idea that storage is adaptive, but examination of the specifics reveals important qualifications. For instance, if several years of mediocre yields or shortfalls cluster together, there may be no excess of food with which to replenish depleted stores; granaries sometimes are empty, offering no protection. Further, the observed improvement in well-being from storage may result not from the availability of a buffer against famine but as a consequence of famines being *more severe*. The coincidence of an unusually large population, its size enhanced by years of successful use of storage, and a particularly severe shortfall exposes the population to fewer but more deadly famines. The shortfall will be especially acute if harvests immediately prior to the famine have not filled the granaries. Severe mortality spikes can reset the population far into the earliest reaches of the copial phase, in which for a long period food again will be plentiful and welfare high. Storage can abet the paradox that we observed earlier. It may improve the long-run subsistence and demographic welfare of a population not by consistently preventing crises but by ensuring that the rare crisis, when it occurs, is more deadly.

We summarize in Table 16.1 by comparing demographic properties of our baseline scenario at Malthusian equilibrium (see Fig. 16.2) with those derived from the last 300 years of ten 700-year simulations with stochastic yields. We focus on a sample period late in the simulation in order to get past effects of initial conditions and to approximate the same time frame as the enduring Malthusian equilibrium of the non-stochastic case. Our comparisons set the yield coefficient of variation (CV) at 0.3, with and without a fixed set-aside for seed and/or taxes. Stochasticity and, independently, storage increase the average food ratio ( $E$ ). Stochasticity and set-asides both reduce average population size ( $N$ ), whereas storage independently has a positive effect. The average food ratio ( $E$ ) and, indeed, the fraction of years the population experiences an adequate food supply ( $\text{Frac } E > 1$ ) is elevated by stochasticity and, independently, by set-asides and storage. The average risk of death in each of the scenarios is the same, although variability is not. While overall mortality remains constant, that risk can be more or less concentrated in time as a function of famine frequency and severity.

Figure 16.3 illustrates a single of the 300-year time series, chosen to illustrate the impact of storage on system dynamics. The distribution of randomly drawn (independent and identically distributed) agroecological yields is depicted in panel (a). Panel (b) shows the amount of food held in storage at the point of inter-annual carry-over, just prior to a new harvest. With unpredictable yield variability, granaries often are empty or hold only small reserves; years of ample storage tend to occur in clusters of approximately 10 years duration. Panels (c) and (d) record population mortality with and without storage, respectively, and panel (e) traces the size of the resulting populations, with storage (gray) and without (black).

In these three centuries of simulation, there were 5 years of particularly bad agricultural yields (years 126, 130, 212, 226, 255). Crop failures in years 130 and 226 follow periods in which stored foods have accumulated, the reserves successfully buffering the production shortfall, thus eliminating for the provident the mortality spike affecting the population without storage. However, bad harvests in years 126, 212, and 255 follow on mediocre yields which have left the granaries empty or nearly so; the provident suffer as well. Perhaps ironically, the mortality spike actually is greater for the food-storing population in years 212 and 255. Being larger size, the food-storing population actually is more susceptible when the famine occurs. From the start of the time series through the famine in year 126, the two populations track one another closely in size. However, the non-storing population has the bad luck to suffer a second mortality spike in year 130, and, growth being slow, it remains smaller through the last 170 years despite the greater impact on the food-storing group of poor yields years 212 and 255. This time series reinforces generalizations we described earlier, and it demonstrates how chance events in unlikely combinations impart unique histories to population dynamics.

### ***Modeling Sociocultural Determinants of Vital Rates***

So far we have modeled a natural fertility and mortality population, one not exercising voluntary control over vital rates. The impacts food shortfalls are experienced through what Malthus would call “positive” checks, those acting after an increase has resulted in exposure to disease, malnutrition, or hunger. Positive checks generally are characterized as physiological. It is possible, however, that early societies developed sociocultural norms and practices affecting fertility and survival by age. Delay of marriage or fertility exposure would be an example. Malthus would call this a “preventive” check, one acting *before* fertility is limited by hunger. We can represent preventive checks in the space-limited model by altering the curves (see Fig. 16.1) representing the *elasticities* of fertility and survival relative to food availability. An elasticity is a measure of the sensitivity of one variable to another, weighted to convey a proportional response. An elasticity of 1, for example, means that a 10% increase in a particular parameter (or variable) results in a 10% increase in the variable of interest; an elasticity of 0.5 means the same 10% parameter increase yields a 5% increase in the response variable. Elasticities may be negative, indicating an antagonistic response.

The elasticities of age-specific fertility and survival adopted in the resource-limited model could be formed so that they affect fertility at levels of subsistence production well above the experience of hunger, that is, at  $E > 1$ . For instance, with refinement such a scenario could be used to model demographic transitions. We, however, continue to focus on responses after  $E$  falls below 1. If the elasticity of the fertility response is increased to represent volitional suppression of fertility in hard times, there of course is no change in the copial phase of growth. But as soon as the population enters the transition phase, realized fertility begins to fall more quickly than it would in the default scenario, in which fertility remains unconstrained. This leads to a number of changes at equilibrium. The population is smaller and it is less hungry, suffers less infant mortality, and has a longer life expectancy. We could in fact make the elasticities of fertility large enough that the population equilibrates almost immediately after crossing into the transition phase, coming to equilibrium with only a limited impact on diet.

Puleston et al. (2017) included such a scenario in simulations of the maximum population on Rapa Nui (Easter Island) before European contact. Rapa Nui is an iconic (Diamond 2005) and contested (Hunt and Lipo 2009; Mulrooney et al. 2010) example of societal collapse due to unrestrained ecological exploitation. This debate makes it critical to understand the size and demographic circumstances of the Island’s population over time. Puleston and his co-authors find that, with near-perfect fertility control and egalitarian subsistence, the maximum island population size is reduced by an average of 37%, relative to a population without such control. The simulations show that

infanticide, documented in some populations as a response to scarcity of resources (Smith and Smith 1994), has an almost identical demographic signature to fertility control acting before conception. In effect, it would be difficult to distinguish these mechanisms for fertility control from population data.

Population equilibrium is achieved by the convergence of birth and death rates. While we usually imagine sociocultural controls as targeting fertility, it is worth considering how behavioral responses to hunger might affect age-specific rates of mortality across the life span. Food can be withheld as well as foregone. Ethnographic accounts of contemporary nonindustrial populations suggest that exiling, abandonment, or killing of the elderly in situations that include resource shortages is mentioned in 20–30% of societies examined (Foner 1993), although details understandably are scarce. Lacking good data, we nonetheless can use our food-limited model to examine the population dynamics of socially induced mortality. It comes as a relief to your authors that the long-term, population welfare benefits of systematic geronticide are minimal, particularly when weighed against the potential social and personal costs (Puleston and Tuljapurkar 2008). Geronticide has no effect on the equilibrium experience of hunger, it generates a very small decrease in equilibrium population size, and it results in a small reduction in the average age of the population, as older individuals are supplanted at equilibrium by younger ones. This of course is a largely hypothetical exercise, but it reveals that fertility control will be much more effective as a long-term population control measure than will geronticide.

### *Surplus, Taxation, and Sociopolitical Hierarchy*

The space-limited model also can be modified to address issues arising in the study of social evolution, such as the origins of social differentiation and political stratification. As an example, we focus on the impact on agrarian producers of taxes extracted by political authorities (Winterhalder and Puleston 2018). We use “tax” as a gloss for any form of taking of goods or labor, such as tallage, tribute, or corvée, and, for simplicity, we focus on net loss incurred by producers after any return to them through redistribution. What is taxed disappears from the system being analyzed, whatever benefits it may provide to the offstage apparatus of the state.

Theories about the origins of political hierarchy often incorporate the concept of surplus, the definition and nature of which has spurred impassioned debate (e.g., Pearson 1957; Harris 1959, current review in Morehart and de Lucia 2015). From a dynamic population ecology perspective, the focus of these debates on the ways in which surplus is extracted and its political uses once available to a polity is incomplete. It misses essential parts of a dynamic system. Agrarian producers provide the work, but they necessarily are consumers, their labor capacity is not uniform, and they come with families and households of old and young of both sexes who are products of cross-generational patterns of population growth and replacement. Adaptations of the space-limited model help us to take account of these features while also defining in more precise terms the relationship between the extraction of goods and/or labor, the impacts on the agricultural class, and, ultimately, the consequences for the dependent political class.

We define the normal surplus as production of food in excess of an operational conception of need, corresponding in our model with production in excess of that required to make at least  $E = 1$ . This only can occur in the initial copial phase of growth or in subsequent repetitions of the copial phase induced perhaps by environmental variability. To produce a normal surplus, the agricultural population may be required to expend extra labor effort, but they do not otherwise suffer a diminished quality of life as measured by food sufficiency or demographic indicators. As we noted above, the copial surplus can be significant with modest effort; it is maximized when the producer population is still relatively small, about 25% of its equilibrium size and between 250 and 300 years into its growth (Winterhalder and Puleston 2018). At this point the marginal agricultural productivity of labor is high, and the total consumption requirement of the worker population is relatively low.

Although the peak of this normal surplus is fairly broad and thus prolonged (Fig. 16.2d), an excess of food above  $E = 1$  is ephemeral. The agrarian population is well fed and thus continues to grow toward its Malthusian equilibrium. As the marginal productivity of labor falls while the population's consumption requirements climb, the normal surplus is extinguished.

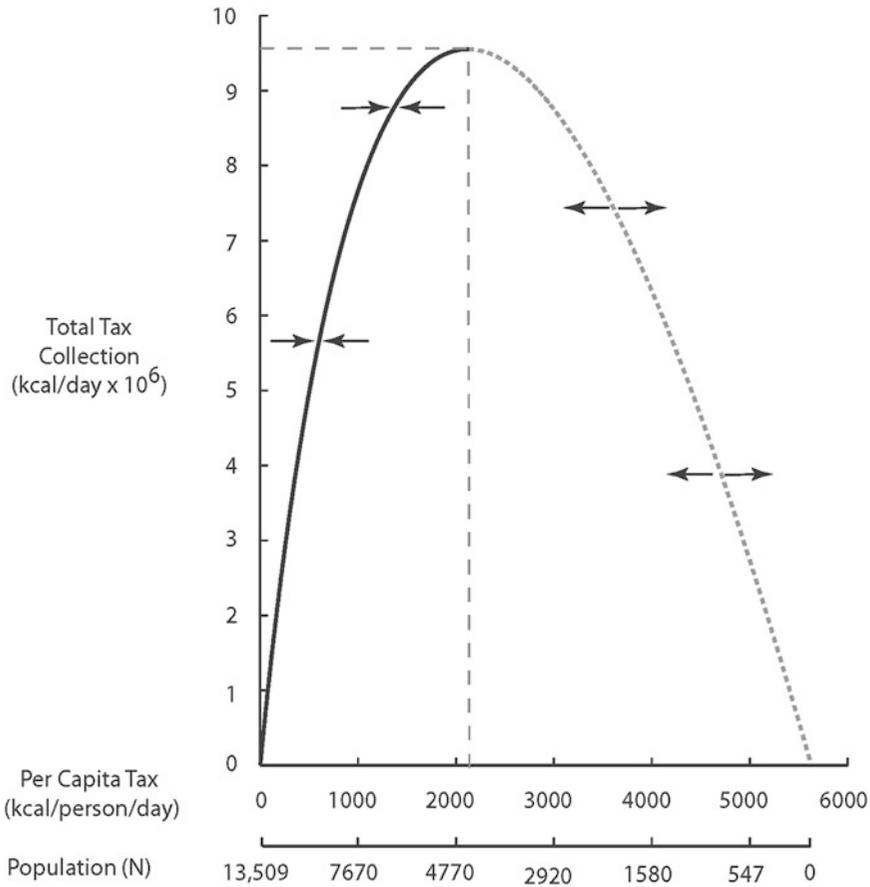
The normal surplus may nonetheless be an overlooked but important element in social evolution. Allen (1997), for instance, downplays the importance of population in the development of the Upper Egyptian state because its realm was underpopulated at the time. Our modeling suggests the contrary possibility. Relative underpopulation may have been key in providing a significant normal surplus which could be taxed without severe impacts on the welfare of the agrarian population (discussion in Winterhalder and Puleston 2018), surplus that was critical in underwriting state development.

At the Malthusian equilibrium, elite resource extraction has different characteristics than in the copial phase. For this reason we avoid in this circumstance the word surplus. In a constant Malthusian situation, taxation causes the producer population to be smaller, as fewer resources are available to feed it. The demographic state of well-being at equilibrium and particularly its poor measures of demographic welfare remain unchanged (Puleston and Tuljapurkar 2008). Taxation reduces stable population size but it does not affect an already poor quality of life.

Under Malthusian conditions there exists an intermediate optimum at which the total tax that can be collected from an agrarian population is maximized. We explain with reference to Fig. 16.4. The two x-axes depict the inverse relationship between a per capita tax rate, from zero to 6000 kcal/person/day, and the associated equilibrium population density. If taxes are zero, we recover the population of 13,509, its full equilibrium size (see Fig. 16.2); as taxes remove ever greater amounts of production, the agrarian population becomes less and less able to feed itself, and its numbers necessarily must diminish. Focusing on equilibrium outcomes, the product of the size of the population and the per capita rate of taxation generates a parabolic-like curve of total tax collected. Given our baseline parameter values, this curve peaks at a population of 4507, a tax rate of 2119 kcal/individual/day, and it generates an elite income of 9,550,000 kcal/day.

Allowing for producer consumption and population dynamics brings to light a trade-off neglected in debates about the political economy of state origins: elites cannot have both a large income from their agrarian producers and a large population of them. Further, the parabolic shape of this equilibrium relationship indicates that any level of total tax collected other than the maximum can be produced by two combinations of tax rate and population size. For reasons that we detail in Winterhalder and Puleston (2018), low rates at larger population sizes (solid line) are stable to small temporary perturbations of agrarian population size or accidents of over/under tax collection. High rates at smaller population sizes are unstable (dashed line) to these possibilities. At high rates of taxation (dashed line), perturbations that diminish the number of producers without a concomitant reduction in the total tax being collected set the agrarian population on a course to extirpation; a perturbation that induces an increase in its size sets it on a path to the corresponding stable equilibrium. Considering these stability properties, we generally would expect to find a population subject to a fixed total tax on the left, or low rate/high numbers, portion of the curve.

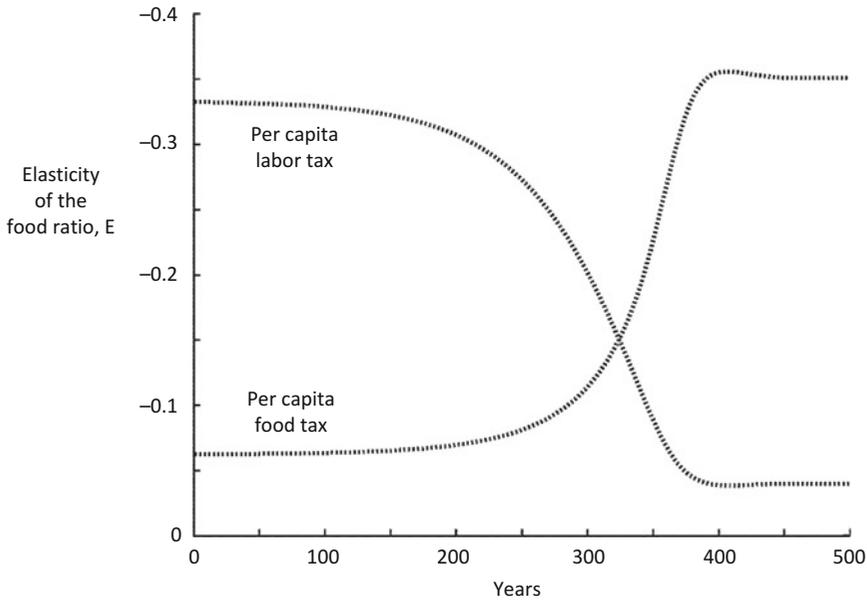
The equilibrium size of the agrarian population drops dramatically as the rate, and thus total tax, increases. At the point of maximum elite income, the agrarian population is only 33% (4507/13,509) of its untaxed size. Likewise, if a ruler were to impose a total burden  $>9.55 \times 10^6$  kcal/day, the agricultural population cannot both pay their tax burden and feed themselves and their families at a level that allows replacement. Agrarian collapse would follow. Traditional political ecology approaches to agrarian revenue generation have suggested that a state that maximized its agrarian population would simultaneously be maximizing its potential income in the form of taxes. But this conclusion applies neither to the potential of a normal surplus during the copial phase, nor to the potential for exploitation through taxes collected near or at a Malthusian equilibrium among producers. Even the tax-collecting despots of antiquity were subject to the dynamics of demography and population ecology.



**Fig. 16.4** Total tax collection as a function of per capita tax rate and population size at equilibrium. Note that the double x-axes run in opposite directions and that the population axis is not on a linear scale, a result of the nonlinear relationship between tax rate and population. Total tax collection is given by combinations of  $N$  times the per capita tax rate. The solid black arc on the left side of the arc represents stable equilibrium combinations, whereas dashed line arc on the right side represents unstable combinations. The arrows indicate the direction of population change if a small perturbation were to displace the population from either of the equilibria. Discussion in the text; full mathematical and related details in Winterhalder and Puleston (2018)

The space-limited approach also suggests that the form in which obligations are met will be important. Extraction of surplus or taxes could take the form of agrarian produce, as discussed above, or the ruling class could require contributions in the form of labor. A labor obligation might entail craft production for elites or maintenance of religious monuments. We model a labor obligation as removing some fraction of the time devoted to sustenance production of the individual without altering consumption requirements. Model dynamics indicate that exploitation in the form of goods and labor has quite different impacts on the welfare of the producers. This difference depends on where the population is in its growth trajectory (Fig. 16.5).

Early in the population’s growth, unused land is abundant, there is little or no inefficiency due to competition, and the marginal productivity of labor is high. Consequently, it is relatively easy to produce food in abundance, without impacts on demographic welfare. As the population approaches equilibrium, these conditions invert. Little open land remains available, inefficiencies due to crowding are increasing, the marginal productivity of labor is low, and food is scarce. As a result of these contrasts, when the population is small, labor is valuable, but calories are easily produced and just as



**Fig. 16.5** Impact of per capita labor and food taxation on the food ratio ( $E$ ) over the course of population growth. The y-axis values show the relative, negative effect of either form of taxation, measured as the elasticity of its impact on  $E$ . The relative severity of taxation inverts as a consequence of population growth. Taxation in agrarian produce is less onerous to small and growing populations; taxation in labor is less onerous to populations approaching their Malthusian equilibrium. Further discussion in the text; mathematical and related details in Winterhalder and Puleston (2018)

easily given up. Conversely, when it is large, calories are precious but labor is redundant and costly to feed. We depict this inversion of impacts with elasticities (defined above) in Fig. 16.5. The y-axis values are negative because any degree of increase in taxation imposes some burden, reducing  $E$ . Nonetheless, the burden is greater for taxation in labor than in produce at low population densities, early in growth, and it inverts late in that growth.

If the persistence and competitive success of prehistoric states depends on the efficiency of their resource generation and the forbearance of their agrarian-producing population, we would predict greater likelihood of success for those that adopt tax policies consistent with this outcome. It also suggests that states requiring labor for armies or the construction of public works or state monuments will be able to call upon that labor with diminished impact on the agrarian production if it is in the late stages of a growth trajectory. This casts doubt, for instance, on the hypothesis that the Maya collapse that ended the Classic Period was precipitated by an irrational choice of leadership to deflect labor from agriculture into the building of monuments (e.g., Culbert 1988).

Rulers and their administrators in pre-modern states faced a variety of choices in the design of their policies for collecting surplus or imposing taxes. The choices they made had population ecology consequences, some of them quite difficult to discern, for their revenue-generating success and the size, persistence, and welfare of the agrarian populations upon which they depended. To cite one additional insight from space-limited modeling, we probably can take as a given that state authorities faced pressures to generate greater and greater revenues. A dramatic example comes from Gutiérrez (2013, p. 158): “I estimate that over these thirty-six years of Aztec domination, the tribute requirement for the Tlapa province increased by 947 percent . . .” Some success in meeting such demands, at some risk, potentially could result from fine-tuning the tax burden (Fig. 16.4). It would help to correctly assess the form of contribution—goods or labor—with the least impact on the producers (Fig. 16.5).

Winterhalder and Puleston (2018, their Figs. 3 and 5) show that the opportunities for enhancing state income by reducing producer consumption (food consumption practices, Fig. 16.1) or increasing producer labor time (age-specific social organization of work) are limited and subject to decreasing margins. By contrast, innovations that increase yield without extra labor (production potential/unit area) provide a near-linear increase in the potential for income (elasticity  $\approx 1$ ), if they can be developed in a continuous fashion. Territorial expansion that increases access to arable land (total agricultural land area) offers a direct proportional increase in revenue potential (elasticity = 1). This may be a reason that territorial expansion is such a regular feature of early polities (Spencer 2010; also this volume).

### ***Better Integrating Boserup into Our Models***

Malthus emphasized the power of environmental and economic circumstances to impede population growth, dwelling on the human misery this entailed. Boserup, in contrast, emphasized the power of population growth to provoke changes in agroecological practices and economy that lessened or circumvented altogether such impedance to growth, mitigating the associated impacts on demographic welfare. Malthus was writing before Darwin and trying to explain why things don't change much if at all, whereas Boserup was writing long after Darwin and attempting to account for observations of rapid, historical developments in agricultural practices. Viewed as competing theories for much of the last half century, the current trend is to accept that they are complementary and should be combined. It is evident that an evolutionary anthropology needs both selection pressure for adaptive change coupled to models showing why and how it might occur and with what effectiveness.

Contemporary accounts synthesizing Malthus and Boserup commonly take a narrative form. For instance, Kristinsson and Júlíusson (2016) argue that with increasing cultural complexity, human societies become more readily adaptable. As a result they concurrently undergo a shift from Malthusian to Boserupian regimes of population response. Four archaeological case studies—Göbekli Tepe, Tiwanaku, Iceland, and Rapa Nui—are mustered in support of their observation that processes of agroecological intensification replace those of Malthusian determinism. Examples of more mathematically based Boserupian models can be found in Lee (1988) and Cohen (1995). These models constitute thought experiments designed to probe gaps between our understanding of resource limitation and recent trends in human super-exponential growth. Such models are necessary because, as we have emphasized, reliable *intuitive* assessment of population ecology dynamics can be quite difficult.

As an indication of future directions, we point to the integrative potential of the space-limited model depicted in Fig. 16.1. Broadly speaking, the left side of the schematic holds the elements, demography and population, central to Malthus, whereas the right holds the elements—labor, the agroecological environment, and yields—central to Boserup. To make use of this observation and formally incorporate Boserup into the space-limited model, we could, for instance, place a portion (%) of the total agricultural land area into fallow and create a function to diminish the fallow portion as a function of the food energy ratio ( $E$ ). The output of this function would measure intensification. Two parameters of the present model, production potential/unit area and cultivated/unit of labor, would be reformulated as variables, the first as an increasing and the second as a decreasing marginal function of some form. While simple enough to state, each of these changes would require detailed empirical investigations and analytical judgments to implement. For instance, at what point in a population growth trajectory do we expect our extensive farmers would feel compelled to shorten fallow? What marginal increases in yield arise from this effort, and how quickly can new methods of intensification be developed and implemented? Innovation modeling focused on the development of new cultural traits (Creanza et al. 2017, p. 7783) could come into play in these efforts.

As such questions indicate, devising a population ecology model is as much a process of research as is interpreting and then assessing its output against evidence. But, even assuming these questions settled, the coding done, and the model poised to run, we would hesitate to predict the outcome with confidence. Our experience with the significantly simpler model of Fig. 16.1 has impressed upon us the difficulty of correctly anticipating from intuition the dynamic behavior of population ecology systems. Surprises are among the good reasons for using models.

## From Simulation Models to Evolutionary Archaeology

The methods described here were applied first to the islands in the Pacific. This is not accidental. Islands have been used to better understand demographic, environmental, and evolutionary processes since Darwin and Wallace (Darwin 1989 [1839]; Wallace 1998 [1881]). Archaeologist Pat Kirch, among others, has argued that islands represent wonderful natural experiments in cultural evolution. “[In] the Pacific, history has given us an unparalleled opportunity to compare what literally hundreds of societies have wrought, at times in highly similar environments, at times in strikingly different ones” (2000, p. 324; see also Vitousek 2004). Many of these groups spread quite quickly from a single parent culture, sharing language, foods, ideas about religion, social organization, and farming until time, distance, ecological context, and biological and cultural evolutionary processes caused their development to diverge. This history and diversity facilitates the comparative analyses essential to understanding evolutionary change.

The island of Hawai’i, for example, has been well characterized ecologically, and, although many questions remain, we have some record of what life was like before the arrival of Europeans. Hawai’i is small enough that it was at times ruled by a single individual but large enough to support a complex society. The archaeology of Hawai’i provides insight into the timing of colonization, the pattern of agricultural extensification and intensification, and the history of sociopolitical developments on the island (Kirch 2010). In the areas that have been studied most carefully, there was a single dominant form of food production, a subsistence base relying on unirrigated sweet potatoes, which can be modeled as a function of local soil and climate variables.

Ladefoged et al. (2008) applied space-limited modeling ideas to the question of variance in population growth rates and food production as a function of land quality across a highly subdivided landscape on the Kohala Peninsula on Hawai’i. They find that the region was not subdivided to maximize quality of life for the inhabitants, but instead to optimize surplus production and reduce its variability under the direction of local chiefs who were themselves subordinate to more powerful chiefs. In the same region, Kirch et al. (2012) tested the predictions of food-limited demography against data on residential patterns and land use across time and space. The study concludes that although the archaeological data are coarse with respect to chronology, the pattern supports the space-limited model’s predictions of exponential growth followed by a rapid transition to equilibrium in the core areas. Populations in more marginal areas may still have been expanding at the time of European contact.

The space-limited demographic model also has been applied to Rapa Nui (Easter Island). Some researchers have argued Rapa Nui underwent a collapse before the first contact with Europeans (e.g., Diamond 2005), whereas others have argued that a population decline occurred only after contact (e.g., Rainbird 2002). Stevenson et al. (2015) have examined the chronological pattern of obsidian hydration-dated material at three sites on the island, assuming the probability density of these artifacts across time was indicative of intensity of human occupation and use. The food-limited demographic model was parameterized for the island and then run under different combinations of assumptions. The results suggest that although there is evidence for a precontact decline in land use and, by extension, in

population, the pattern varied across the landscape. Land use intensity declined earliest in the poorer agricultural regions but was maintained at high levels in better soils until after European contact. Rather than a straightforward example of “ecocide,” the data describe a population that faced an ecological crisis and adapted its behavior to the changing context. They abandoned agriculture where sustainable returns were too small to justify their use and intensified where marginal returns allowed it.

More recently modeling was used to estimate the maximum sustainable population on Rapa Nui. Puleston et al. (2017) combined a carefully parameterized food-production model with the demographic model. Under reasonable assumptions regarding agricultural productivity, the maximum population size clusters around 17,500 individuals, lending support to the idea that the island’s population had in fact declined significantly by the time observers made careful estimates, decades after regular contact with Europeans.

In an independent line of inquiry, this one in a continental context, Anna Prentiss and colleagues have pursued evidence of population ecology interactions at the Bridge River Village site in British Columbia. Bridge River was occupied by a fisher-forager population from about 1800 B.P. to 100 B.P., with at least one long period of abandonment. Prentiss et al. (2014) find evidence in support of reductions in quality of life at the village level synchronized with regional and local declines in salmon populations. In a detailed study of the stratigraphy of a single house, Prentiss et al. (2018) examine predictions made regarding the relationship between food storage and population trajectories. The evidence suggests that the local population goes through the phases described in Puleston et al. (2014) and that the use of storage pits conforms to the predictions of Winterhalder et al. (2015). The population appears to have increased over time to a peak density with evidence of a plentiful food supply during this growth phase. Fish and deer were processed in the village, indicating that they were acquired nearby and transported home whole. In the next phase of occupation, the population appears to be much diminished, fish and deer are more likely to be acquired at a distance sufficient that they were processed in the field, storage pits become more common, and dogs are being used as a managed food resource. It is unclear whether the peak of population was sustained through active population control (i.e., a Malthusian preventive check), but the later phase has signs of a classical resource-limited population afflicted by the unhappy constraints of Malthus’s positive checks.

## Concluding Thoughts

Population is a common factor in the wide-ranging renaissance of research traditions in evolutionary anthropology (Creanza et al. 2017; papers in this volume). Like surplus, population has a high-profile role in archaeologists’ attempts to explain the major socioeconomic transformations of human history, from the origins of agriculture (Cohen 1977) to the development of states (Carneiro 1970). And, like surplus, the use of population causation in these contexts has provoked intense debates for almost as long (Cowgill 1975; Vaesen et al. 2016).

In these debates population growth generally has been assumed to be of the form modeled by Verhulst, a continuous and unidirectional phenomenon of increase. Carried into archaeological discourse, population has functioned as a slowly increasing pressure, one that eventually catalyzes the particular transformation of interest. We argue that it will be necessary for archaeologists to revisit the old debates with insights more firmly grounded in the dynamics of population ecology. The space-limited model shows us that population sometimes is not what it has seemed. Normal surplus is greatest when population size is small; food storage can make famines worse; a salubrious environment threatens population welfare to a greater degree than an unstable one; a state cannot have both a large agrarian population and a large income from it. Evolutionary archaeology requires a well-developed understanding of the mechanisms giving rise to such observations. It necessarily will be based in developing approaches that integrate into formal models—space-limited and those arising from other approaches—the insights and variables featured in both of Malthus and Boserup.

**Data Sharing Statement** The data sets (R code) generated and/or analyzed during the current study are available at [github.com/puleston/spacelim](https://github.com/puleston/spacelim).

## References

- Allen, R. C. (1997). Agriculture and the origins of the state in ancient Egypt. *Explorations in Economic History*, 34, 135–154.
- Anderies, J. M. (2000). On modeling human behavior and institutions in simple ecological economic systems. *Ecological Economics*, 35, 393–412. [https://doi.org/10.1016/S09218009\(00\)00221-4](https://doi.org/10.1016/S09218009(00)00221-4)
- Boserup, E. (1965). *The conditions of agricultural growth: The economics of agrarian change under population pressure*. New York: Aldine.
- Boyer, P. (1995). *Ceteris paribus* (all else being equal). In J. Brockman & K. Matson (Eds.), *How things are: A science tool-kit for the mind* (pp. 169–175). New York: William Morrow and Company.
- Brander, J. A., & Taylor, M. S. (1998). The simple economics of Easter Island: A Ricardo-Malthus model of renewable resource use. *The American Economic Review*, 88, 119–138.
- Brown, G. R., & Richerson, P. J. (2014). Applying evolutionary theory to human behavior: Past differences and current debates. *Journal of Bioeconomics*, 16, 105–128. <https://doi.org/10.1007/s10818-013-9166-4>
- Carneiro, R. L. (1970). A theory of the origin of the state. *Science*, 169, 733–738.
- Chayanov, A. V. (1977). On the theory of non-capitalist economic systems. In R. H. Halperin & J. Dow (Eds.), *Peasant livelihood: Studies in economic anthropology and cultural ecology* (pp. 257–268). New York: St. Martin's Press.
- Cohen, J. E. (1995). Population growth and earth's human carrying capacity. *Science*, 269, 341–346.
- Cohen, M. N. (1977). *The food crisis in prehistory: Overpopulation and the origins of agriculture*. New Haven, CT: Yale University Press.
- Cowgill, G. L. (1975). Population pressure as a non-explanation. In A. C. Swedlund (Ed.), *Population studies in archaeology and biological anthropology: A symposium* (pp. 127–131). Washington, D.C.: Society for American Archaeology.
- Creanza, N., Kolodny, O., & Feldman, M. W. (2017). Cultural evolutionary theory: How culture evolves and why it matters. *Proceedings of the National Academy of Sciences*, 114, 7782–7789. <https://doi.org/10.1073/pnas.1620732114>
- Culbert, T. P. (1988). Collapse of classic Maya civilization. In N. Yoffee & G. L. Cowgill (Eds.), *The collapse of ancient states and civilizations* (pp. 69–101). Tucson, AZ: University of Arizona Press.
- Darwin, C. (1989). *Voyage of the beagle*. London: Penguin Books.
- Diamond, J. M. (2005). *Collapse: How societies choose to fail or succeed*. New York: Viking Penguin.
- Foner, N. (1993). When the contract fails: Care for the old in nonindustrial cultures. In V. L. Bengtson & W. A. Achenbaum (Eds.), *The changing contract across generations* (pp. 101–117). New York: Aldine de Gruyter.
- Freeman, J., & Anderies, J. M. (2012). Intensification, tipping points, and social change in a coupled forager-resource system. *Human Nature*, 23, 419–446. <https://doi.org/10.1007/s12110-012-9154-8>
- Glassow, M. A. (1978). The concept of carrying capacity in the study of culture process. In M. B. Schiffer (Ed.), *Advances in archaeological method and theory* (pp. 31–48). New York: Academic.
- Goland, C. (1993). Field scattering as agricultural risk management: A case study from Cuyo Cuyo, Department of Puno, Peru. *Mountain Research and Development*, 13, 317–338.
- Gutiérrez, G. (2013). Negotiating Aztec tributary demands in the *Tribute Record of Tlapa*. In K. G. Hirth & J. Pillsbury (Eds.), *Merchants, markets, and exchange in the pre-Columbian world* (pp. 141–167). Washington, D.C.: Dumbarton Oaks.
- Halstead, P., & O'Shea, J. M. (1989). *Bad year economics: Cultural responses to risk and uncertainty*. Cambridge: Cambridge University Press.
- Harris, M. (1959). The economy has no surplus. *American Anthropologist*, 61, 185–199.
- Hommon, R. J. (1976). *The Formation of Primitive States in Pre-Contact Hawai'i*. Doctoral Dissertation, University of Arizona, Tucson, AZ.
- Hunt, T. L., & Lipo, C. P. (2008). Evidence for a shorter chronology on Rapa Nui (Easter Island). *The Journal of Island and Coastal Archaeology*, 3, 140–148.
- Hunt, T. L., & Lipo, C. P. (2009). Revisiting Rapa Nui (Easter Island) "Ecocide". *Pacific Science*, 63, 601–616.
- Hutchinson, G. E. (1978). *An introduction to population ecology*. New Haven, CT: Yale University Press.
- Jaeggi, A. V., & Gurven, M. (2013). Natural cooperators: Food sharing in humans and other primates. *Evolutionary Anthropology: Issues, News, and Reviews*, 22, 186–195. <https://doi.org/10.1002/evan.21364>
- Kirch, P. V. (2000). *On the road of the winds: An archaeological history of the Pacific Islands before European contact*. Berkeley, CA: University of California Press.

- Kirch, P. V. (2010). *How chiefs became kings: Divine kingship and the rise of archaic states in ancient Hawai'i*. Berkeley, CA: University of California Press.
- Kirch, P. V. (2012). *A shark going inland is my chief: The island civilization of ancient Hawai'i*. Berkeley, CA: University of California Press.
- Kirch, P. V., Asner, G., Chadwick, O. A., Field, J., Ladefoged, T., Lee, C., et al. (2012). Building and testing models of long-term agricultural intensification and population dynamics: A case study from the Leeward Kohala Field System, Hawai'i. *Ecological Modelling*, 227, 18–28.
- Kögel, T., & Prskawetz, A. (2001). Agricultural productivity growth and escape from the Malthusian trap. *Journal of Economic Growth*, 6, 337–357.
- Kohler, T. A., Bocinsky, R. K., Cockburn, D., Crabtree, S. A., Varien, M. D., Kolm, K. E., et al. (2012). Modelling Prehispanic Pueblo societies in their ecosystems. *Ecological Modelling*, 241, 30–41. <https://doi.org/10.1016/j.ecolmodel.2012.01.002>
- Kohler, T. A., & van der Leeuw, S. E. (2007). Introduction: Historical socio-natural systems and models. In T. A. Kohler & S. E. van der Leeuw (Eds.), *The model-based archaeology of socio-natural systems* (pp. 1–12). Santa Fe, NM: School for Advanced Research Press.
- Kristinsson, A., & Júlíusson, A. D. (2016). Adapting to population growth: The evolutionary alternative to Malthus. *Clodynamics: The Journal of Quantitative History and Cultural Evolution*, 7, 37–75. <https://doi.org/10.21237/C7clio7130171>
- Ladefoged, T. N., Lee, C. T., & Graves, M. W. (2008). Modeling life expectancy and surplus production of dynamic pre-contact territories in leeward Kohala, Hawai'i. *Journal of Anthropological Archaeology*, 27, 93–110.
- Lake, M. W. (2014). Trends in archaeological simulation. *Journal of Archaeological Method and Theory*, 21, 258–287. <https://doi.org/10.1007/s10816-013-9188-1>
- Lee, C. T., Puleston, C., & Tuljapurkar, S. (2009). Population and prehistory III: Food-dependent demography in variable environments. *Theoretical Population Biology*, 76, 179–188.
- Lee, C. T., & Tuljapurkar, S. (2008). Population and prehistory I: Food-dependent population growth in constant environments. *Theoretical Population Biology*, 73, 473–482.
- Lee, R. D. (1986). Malthus and Boserup: A dynamic synthesis. In D. Coleman & R. Schofield (Eds.), *The state of population theory* (pp. 96–130). New York: Basil Blackwell.
- Lee, R. D. (1988). Induced population growth and induced technological progress: Their interaction in the accelerating stage. *Mathematical Population Studies*, 1, 265–288. <https://doi.org/10.1080/08898488809525278>
- Malthus, T. R. (2003). *An essay on the principle of population: Text, sources and background, criticism* (2nd ed.). New York: W. W. Norton.
- Mayhew, R. J. (2014). *Malthus: The life and legacies of an untimely prophet*. Cambridge, MA: Harvard University Press.
- Morehart, C. T., & de Lucia, K. (2015). Surplus: The politics of production and the strategies of everyday life, an introduction. In C. T. Morehart & K. de Lucia (Eds.), *Surplus: The politics of production and the strategies of everyday life* (pp. 3–43). Boulder, CO: University Press of Colorado.
- Morgan, C. (2014). Is it intensification yet? Current archaeological perspectives on the evolution of hunter-gatherer economies. *Journal of Archaeological Research*, 23, 163–213. <https://doi.org/10.1007/s10814-014-9079-3>
- Mulrooney, M. A., Ladefoged, T. N., Stevenson, C. M., & Haoa, S. (2010). Empirical assessment of a pre-European societal collapse on Rapa Nui (Easter Island). In P. Wallin & H. Martinsson-Wallin (Eds.), *The Gotland papers: Selected papers from the VII international conference on Easter Island and the Pacific: Migration, identity, and cultural heritage* (pp. 141–154). Gotland: Gotland University Press.
- Nagase, Y., & Uehara, T. (2011). Evolution of population-resource dynamics models. *Ecological Economics*, 72, 9–17. <https://doi.org/10.1016/j.ecolecon.2011.09.003>
- Pacheco-Cobos, L., Grote, M. N., Kennett, D. J., & Winterhalder, B. (2015). Population and environmental correlates of maize yields in Mesoamerica: A test of Boserup's hypothesis in the milpa. *Human Ecology Interdisciplinary Journal*, 43, 559–576. <https://doi.org/10.1007/s10745-015-9771-z>
- Pearson, H. W. (1957). The economy has no surplus: Critique of a theory of development. In K. Polanyi, C. M. Arensberg, & H. W. Pearson (Eds.), *Trade and market in the early empires: Economies in history and theory* (pp. 320–341). New York: The Free Press.
- Prentiss, A. M., Cail, H. S., & Smith, L. M. (2014). At the Malthusian ceiling: Subsistence and inequality at Bridge River, British Columbia. *Journal of Anthropological Archaeology*, 33, 34–48.
- Prentiss, A. M., Foor, T. A., Hampton, A., Ryan, E., & Walsh, M. J. (2018). The evolution of material wealth-based inequality: The record of housepit 54, Bridge River, British Columbia. *American Antiquity*, 83, 598–618. <https://doi.org/10.1017/aaq.2018.56>
- Puleston, C., Ladefoged, T. N., Haoa, S., Chadwick, O. A., Vitousek, P. M., & Stevenson, C. M. (2017). Rain, sun, soil, and sweat: A consideration of population limits on Rapa Nui (Easter Island) before European contact. *Frontiers in Ecology and Evolution*, 5, 69. <https://doi.org/10.3389/fevo.2017.00069>

- Puleston, C., & Tuljapurkar, S. (2008). Population and prehistory II: Space-limited human populations in constant environments. *Theoretical Population Biology*, *74*, 147–160.
- Puleston, C., Tuljapurkar, S., & Winterhalder, B. (2014). The invisible cliff: Abrupt imposition of Malthusian equilibrium in a natural-fertility, agrarian society. *PLoS One*, *9*, 1–13. <https://doi.org/10.1371/journal.pone.0087541>
- Rainbird, P. (2002). A message for our future? The Rapa Nui (Easter Island) ecodisaster and Pacific island environments. *World Archaeology*, *33*, 436–451.
- Roman, S., Bullock, S., & Brede, M. (2017). Coupled societies are more robust against collapse: A hypothetical look at Easter Island. *Ecological Economics*, *132*, 264–278. <https://doi.org/10.1016/j.ecolecon.2016.11.003>
- Smith, E. A., & Smith, S. A. (1994). Inuit sex-ratio variation: Population control, ethnographic error or parental manipulation? *Current Anthropology*, *35*, 595–624.
- Spencer, C. S. (2010). Territorial expansion and primary state formation. *Proceedings of the National Academy of Sciences*, *107*, 7119–7126. <https://doi.org/10.1073/pnas.1002470107>
- Stevenson, C. M., Puleston, C., Vitousek, P. M., Chadwick, O. A., Haoa, S., & Ladefoged, T. N. (2015). Variation in Rapa Nui (Easter Island) land use indicates production and population peaks prior to European contact. *Proceedings of the National Academy of Sciences USA*, *112*, 1025–1030. <https://doi.org/10.1073/pnas.1420712112>
- Stocking, G. W. (1968). On the limits of “presentism” and “historicism” in the historiography of the behavioral sciences. In G. W. Stocking (Ed.), *Race, culture, and evolution: Essays in the history of anthropology* (pp. 1–12). New York: The Free Press.
- Szulga, R. S. (2012). Endogenous population and resource cycles in historical hunter-gatherer economies. *Cliodynamics: The Journal of Quantitative History and Cultural Evolution*, *3*, 234–270.
- Tkachenko, N., Weissmann, J. D., Petersen, W. P., Lake, G., Zollikofer, C. P., & Callegari, S. (2017). Individual-based modelling of population growth and diffusion in discrete time. *PLoS One*, *12*, e0176101. <https://doi.org/10.1371/journal.pone.0176101>
- Vaesen, K., Collard, M., Cosgrove, R., & Roebroeks, W. (2016). Population size does not explain past changes in cultural complexity. *Proceedings of the National Academy of Sciences*, *113*, E2241–E2247. <https://doi.org/10.1073/pnas.1520288113>
- Verhulst, P.-F. (1838). Notice sur la loi que la population suit dans son accroissement. *Correspondances Mathématiques et Physiques*, *10*, 113–121 [English translation, Vogels, M., Zoeckler, R., Stasiw, D. M., & Cerny, L. C. 1975. *Journal of Biological Physics*, *3*(4), 183–192].
- Vitousek, P. M. (2004). *Nutrient cycling and limitation: Hawai'i as a model system*. Princeton, NJ: Princeton University Press.
- Wallace, A. R. (1998). *Island life*. Amherst, MA: Prometheus Books.
- Winterhalder, B. (1990). Open field, common pot: Harvest variability and risk avoidance in agricultural and foraging societies. In E. A. Cashdan (Ed.), *Risk and uncertainty in tribal and peasant economies* (pp. 67–87). Boulder, CO: Westview Press.
- Winterhalder, B. (2002). Models. In J. P. Hart & J. E. Terrell (Eds.), *Darwin and archaeology: A handbook of key concepts* (pp. 201–223). Westport, CT: Bergin & Garvey.
- Winterhalder, B., Baillargeon, W., Cappelletto, F., Daniel Jr., I. R., & Prescott, C. (1988). The population ecology of hunter-gatherers and their prey. *Journal of Anthropological Archaeology*, *7*, 289–328.
- Winterhalder, B., & Goland, C. (1997). An evolutionary ecology perspective on diet choice, risk, and plant domestication. In K. J. Gremillion (Ed.), *People, plants, and landscapes: Studies in paleoethnobotany* (pp. 123–160). Tuscaloosa, AL: University of Alabama Press.
- Winterhalder, B., & Lu, F. E. (1997). A forager-resource population ecology model and implications for indigenous conservation. *Conservation Biology*, *11*, 1354–1364.
- Winterhalder, B., & Puleston, C. (2018). The exchequer's guide to population ecology and resource exploitation in the agrarian state. *Cliodynamics: The Journal of Quantitative History and Cultural Evolution*, *9*, 40–83.
- Winterhalder, B., Puleston, C., & Ross, C. (2015). Production risk, inter-annual food storage by households and population-level consequences in seasonal prehistoric agrarian societies. *Environmental Archaeology*, *20*, 337–348. <https://doi.org/10.1179/1749631415Y.0000000025>
- Wood, J. W. (1998). A theory of preindustrial population dynamics: Demography, economy, and well-being in Malthusian systems. *Current Anthropology*, *39*, 99–135.