Genetic Feedback and Human Population Regulation

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Abstract Human population growth has been identified as a primary cause of ecologically destructive phenomena and, if left unchecked, will threaten the survivability of the human species. It has been demonstrated that genetic feedback is the mechanism by which species achieve ecological balance. The present analysis shows the applicability of this mechanism to human population regulation. In this model, the traits of behavior and culture are explained as following a four step process, similar to, and nested within genetic evolution. As species extinction is part and parcel of evolution, and environmental circumstances are changing rapidly, the population regulatory change that would take place on the genetic level of integration would be human extinction. However, the change on the cultural level, requiring a revision of the social contingency from "food production must be increased to feed a growing population" to "food production increases cause population increases," would lead to human sustainability.

Keywords Agriculture · Ecology · Evolution · Extinction · Food availability · Food production

Introduction

Many leading scientists and public organizations are concerned about the deterioration of natural resources and the environment caused by rapidly increasing human numbers and activities (Pimentel et al. 1998). As population size and consumption levels increase, basic natural resources are depleted. The increase in the number of humans is responsible for amounts of pollutants dumped into land, water, and atmosphere. It is well understood that escalating human population is fueling the acceleration of all environmental problems (Pimentel et al. 1998; Hopfenberg and Pimentel 2001).

Although human numbers have more than doubled since 1960, much of the scientific and lay literature holds to the perspective that food production must be increased to feed a growing population (Hopfenberg and Pimentel 2001). For example, Young (1999) noted that current UN projections predict that the population of developing countries will rise to about eight billion by 2025 and nine billion by 2050. He then asserted, "It is widely recognized that massive agricultural development will be needed to feed this added population." Cakmak (2002) stated that food production on presently used land must be doubled in the next two decades to meet the food demands of a growing world population.

However, Gilland (2002) has pointed out that the global supply of food calories per capita rose from 2,420 kcal per day in 1958 to 2,808 kcal in 1999 (see endnote). Furthermore, it has been clarified that human population growth is a function of food supply (Farb 1978; Quinn 1992, 1996; Hopfenberg and Pimentel 2001; Hopfenberg 2003). McQueen (2000) showed that while world food production currently exceeds requirements, distribution problems leave about 800 million people malnourished. These distribution problems have increased along with the increasing global population (Hinrichsen 1997; Rosset et al. 2000). If the history of the Green Revolution has taught us one thing, it is that increased food production goes hand in

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hand with greater hunger (Rosset et al. 2000). Thus, rather than ameliorate the population problem and the tragedy of malnutrition and starvation, increases in global food production have, in fact, precipitated population growth and malnutrition difficulties.

Should agricultural expansion continue as predicted, 10^9 ha of natural ecosystems could be converted to agriculture by 2050 (Tilman et al. 2001; Jenkins 2003). The commensurate habitat destruction would cause unprecedented ecosystem simplification, loss of ecosystem services, and species extinctions. Indeed, forest conversion for agriculture expansion is the most salient signature of civilized human occupation of the earth's land surface (Carr 2004). Pimentel (2001) pointed out that humans are currently utilizing more than 50% of total biomass produced in the world, leaving less for other species and increasing their likelihood of perishing. Additionally, there exists a growing sense of "common fate" between humans and other animal species regarding sustainability and even survivability (Myers 1996; Liu et al. 1997). Pimm et al. (1995) showed that recent extinction rates are 100 to 1,000 times their pre-human levels. They further stated that "If all species currently deemed 'threatened' become extinct in the next century, then future extinction rates will be ten times recent rates." It is not a far logical leap to determine that, if human population and resource use continues to grow and we continue to kill off our neighbors in the biological community, one of the many species facing extinction will be the human. Thus, the impact of civilized humanity on the rest of the biological community can be seen as lethal to the point of destroying our own ecological support.

Non-human creatures certainly perform lethal acts, from herbivore grazing to carnivore hunting to bacterial and viral infection. Yet these actions typically do not undermine these species' ecological support. When they do, species may face extinction, which is part and parcel of evolution. One way of understanding the process by which populations attain ecological balance has been termed the genetic feedback mechanism of population regulation.

The mechanism of genetic feedback in population regulation can best be understood in the context of the general evolutionary process. In this process, a distribution of characteristics, physical or behavioral, gain expression and are selected through environmental effects such as rates of obtaining resources and predation, and, ultimately, reproductive success (Darwin 1859; Dawkins 1989; Baum 2003). One characteristic that the populations of all species share is the propensity to increase their numbers to the level of food availability and other density-dependent limiting factors, together known as the carrying capacity of the environment. Carrying capacity is therefore the "ecological magnet" that draws population numbers to it. Another characteristic that species share is the tendency to maximize their use of environmental resources and minimize their expenditure of energy. Regulation of population size, which serves to maximize and maintain a species' ecological support, ensures the species' survivability.
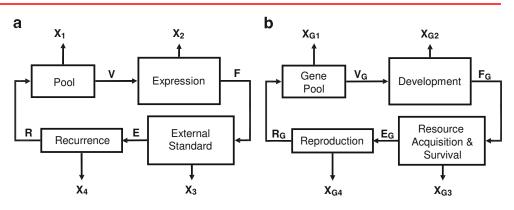
Several studies have shown that the genetic feedback mechanism functions to regulate populations (Pimentel 1961; Pimentel and Soans 1970; Pimentel et al. 1975; Levin and Pimentel 1981). Population density influences selective pressure, which, in turn, influences genetic makeup. Furthermore, evolution of one species occurs in a coevolutionary context. In other words, evolution is not a phenomenon isolated to a single species or population at a given point in time. Evolutionary changes in one species often involve changes in others. For example, Olson and Pimentel (1974) demonstrated that changes in a host's resistance to a parasite changed the population dynamics of the parasite.

The relationship of genetic feedback to population dynamics and reproductive choice seems to become clouded when more complex organisms are considered. Organisms which are capable of making behavioral (operant) or cultural adjustments may appear to be immune from genetic feedback as a population regulatory mechanism because the capacity to make some regulatory choices is already in place. However, these capacities have, as their underpinnings, biological structures determined by the species genetic makeup. Thus, even operant and cultural behavior, insomuch as these behaviors may determine the individual or species' survivability, feed back to and, therefore, influence genetic makeup. The present analysis illustrates the relationship between the genetic, behavioral and cultural feedback systems and their impact on population dynamics in the context of the general evolutionary process.

The General Evolutionary Process

The general evolutionary process consists of four basic transformation operations viz.: pooling, expression, external standard, and recurrence. Figure 1a is a graphic representation of this cycle (Baum 2003). A *pool* produces a pattern of frequencies, which constitutes the essential element of variation in the evolutionary process. For example, in the case of genetic selection (shown in Fig. 1b), the gene pool produces the range of genetic variants known as genotype. Again, the result of the pooling operation is a distribution of suitable variants designated by the variable *V*. The transform distribution *V* then becomes the operand for the next transformation. The variable *X*, further identified by a numerical subscript for the purpose of this discussion, represents those variants that are not adequate as operands.

Fig. 1 a The general evolutionary process flow chart; b the general evolutionary process chart applied to genetics

The next transformation, designated *expression*, yields the transform distribution F. This expression process occurs through environmental interactions, for example, development in the case of genetic evolution. The course of development contributes to the physical expression of genetic potential, known as phenotype. The transform distribution F then becomes the operand for the *external standard* operation. This operation may be seen as a set of "if-then" contingencies which generates E, the distribution of external effects. Again, an example drawing upon genetics is the case of coat pigmentation. If the distribution F represents the range of pigmentation variants, the external standard operation serves to select coloring that blends with the organism's surroundings, thus providing adequate camouflage. The if-then contingency can be stated as follows: if pigmentation adequately matches the organism's surrounding, then the organism is more likely to survive. If there is a change in climate such that the surrounding flora changes color, the distribution of E will shift in the direction of pigmentation that matches the altered surrounding. Those pigmentations that do not adequately match the surroundings stand to be eliminated and are designated by the variable X_3.

In the next stage of the cycle, the distribution E becomes the operand for the *recurrence process*. The result of this process is R, which is the new distribution of variants to be added to the pool for the next iteration. Identifying a recurrence process that is separate from pooling accounts for the variability in recurrence itself. Although fidelity in the recurrence process must be high in order to ensure transmission, it does not have to be perfect. In fact, perfect fidelity would eliminate the variability that produces novel traits to be selected or eliminated in the cycle. For example, in genetic evolution, the recurrence process accounts for events such as mutation, which produces novel attributes that may ultimately prove to be adaptive. Again, among the distributions resulting from each operation, are those on the continua that are inadequate to serve as operands for the next transformation process, designated in the figures by the variable X.

The general evolutionary process provides the foundation for understanding physical and behavioral changes in a population over time. The process is, in effect, a circuit in which the variation of a characteristic is altered through feedback from the environment. This feedback involves the selection of physical and behavioral traits at each stage in the process. In addition to genetically determined physical and behavioral traits, the general evolutionary process provides the theoretical underpinnings for understanding operant behavior (Skinner 1938). Included under the rubric of operant behavior is the special class called cultural behavior.

Behavioral and Cultural Evolution

The experimental analysis of behavior is a level of integration and a field of study in its own right (Lee 1988). However, behavior is a phenomenon that, in fact, rests upon and is nested within genetic evolution (Skinner 1981; Baum 2003). In addition, operant behavior, i.e., behavior selected by its consequences, follows the same basic evolutionary process previously described (Skinner 1938, 1981). The case of behavioral selection is illustrated inside the dotted box in Fig. 2. The pooling operation or behavior pool generates the distribution of behavior available in the organism's repertoire and is designated by the variable V_B, where the subscript B stands for behavior. Through stimulus control and/or induction, a range of behavior is emitted. For example, the presence of a light switch, a discriminative stimulus, sets the stage for a range of behavior. However, this range is much narrower than the person's entire behavioral repertoire V_B. The distribution of behavior, F_B, emitted in the presence of the light switch, is then subject to the consequences prescribed by the "reinforcement contingencies" operation. Again, a contingency can be seen as an "if-then" formula. For example, the if-then contingency might be: if the light switch is operated correctly the light will come on. The illumination of the room reinforces the particular light-switching behavior that
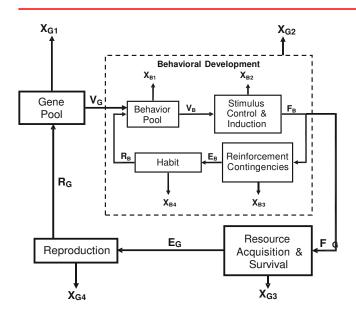
Fig. 2 The behavioral (operant) evolutionary process as nested within the genetic evolutionary process

was emitted by the person. The range of behaviors designated by X_{B3} in Fig. 2 might consist of behaviors not sufficient to operate the light switch (think of someone's difficulty operating a new dimmer switch). Baum (2003) proposed a recurrence process termed *Habit*, which accounts for the reproduction of behavior and the inherent variation. This variation accounts for novel behavior, analogous to mutation in genetic evolution.

As the ability to emit operant behavior is an organismic feature, it necessarily has genetic underpinnings. That operant behavior has its own feedback process indicates that, within limits, iterations of the operant cycle may proceed independent of genetic evolution and can occur numerous times in multiple contexts over the lifetime of an individual. However, since the capacity to emit operant behavior has a genetic foundation, the operant feedback system must be nested within the genetic process. Figure 2 shows operant behavior as part of the development transformation within genetic evolution since the range of behavior that emerges from the development /operant process ultimately impacts the ability of the organism to acquire resources and survive. Thus, a range of variants emerges which may be adequate to serve as operands for the next transformation operation in genetic evolution (F_G). In some instances, the reinforcement contingencies may be equivalent to the resource acquisition contingencies. Nevertheless, the operant system is nested within the genetic system.

A special class of operant behavior, cultural behavior, is a product of evolution that presumably enhances the survivability of a population. Although distinguishable as a class of behavior, cultural behavior can be seen as operant in that it is ultimately selected by its consequences. Culture can be distinguished from other operant behavior using two criteria. First, cultural practices are defined as such if a group, versus an entire species, exhibits them. That is, the practices exist in the repertoire of a group or subgroup. Second, cultural practices are transmitted from one individual to another and may occur in different individuals at the same time. On the other hand, other operant behavior dies with its possessor. If the behavior is transmitted to others, it is considered cultural. As with all complex behavior, culture has nested within it other operant behavior that together, form the complex pattern.

The mechanism of cultural evolution, as with other operant behavior, follows the same general evolutionary process. As seen in Fig. 3, a culture pool gives rise to a distribution designated as V_C. This distribution then becomes the operand for the development transformation process that, in this case, involves *Modeling and/or Rule Giving*. In culture, the external standard operation involves *Social Contingencies*. The recurrence process involves Transmission of practices from individual to individual. The evolution of culture, as with other operant behavior, can be seen as being nested within genetic evolution (see Fig. 4).

Taken together, genetic, cultural and operant processes are seen as nested and each process follows the same basic evolutionary pattern. Cultural behavior, which contains modeling and rule giving, involves other more molecular operant processes. Again, Fig. 3 shows operant behavior as accounting for the modeling and rule giving transformation and nested within culture. Similarly, Fig. 4 shows cultural
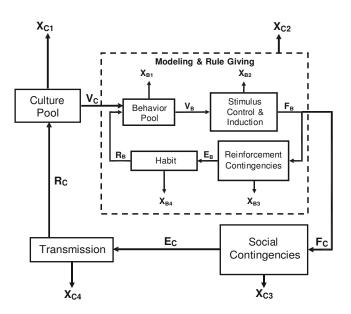

Fig. 3 The behavioral (operant) evolutionary process as nested within the cultural evolutionary process
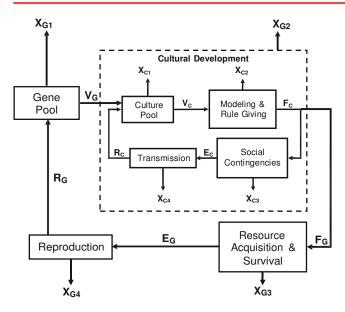
Fig. 4 The cultural evolutionary process as nested within the genetic evolutionary process

behavior as accounting for the cultural development transformation and nested within the genetic evolutionary process.

Although the genetic, operant and cultural feedback systems are ultimately interdependent and integrated, the iterations of these systems can proceed at various rates. For example, the operant and cultural feedback circuits may occur many times within an individual lifetime, while genetic evolution must proceed over generations. Because of this lack of one to one reliance, it is conceivable that behavior fostered at one level of integration may be eliminated at another. An example is a cult that socially reinforces suicide pacts. Although this behavior may be reinforced through social contingencies in the cultural evolutionary process, it clearly does not meet the genetic evolutionary process contingency for survival, and the cult stands to be eliminated. The distribution following this transformation is accounted for by X_{G3}. Similarly, a group like the Shakers had a social contingency of reinforcing sexual abstinence. However, at the genetic transformation process of reproduction, the entire distribution is accounted for by the variable X_{G4} and the group was ultimately eliminated.

Explanations of the occurrence of organisms' traits and behavior can be classified as either proximate or ultimate (Dawkins 1989; Baum 2003). The upper two boxes of each level of integration in the figures represent proximate explanations, while the lower two boxes represent ultimate explanations. Proximate explanations answer "how" questions. For example, how do biological or behavioral traits occur. Ultimate explanations answer why or "how come" questions. For example, why do these traits occur (Alessi

1992). Although both proximate and ultimate explanations are necessary for a full understanding of evolutionary phenomena, changes in the selecting environment, which impact the two latter processes, i.e., external standard and recurrence, can be said to ultimately account for changes in traits and behavior. Again, the overall effect of the feedback process is the fostering of survivable, i.e., adaptive traits and the elimination of those variants that are not adequate.

Among the characteristics of a species is the size of its population. The larger the population, the fewer the resources available to individuals, impacting the *resource acquisition and survival* transformation in the genetic evolutionary process. Thus population size itself ultimately has a bearing on genetic evolution, i.e., changing selective pressure. This impact affects the range of genetic variants that, in turn, affects population regulation. The contingency mechanism of population regulation has been termed negative feedback (Alessi 1992; Quinn 1996).

Negative Feedback in Population Regulation

It has been repeatedly demonstrated that population growth proceeds in a sigmoidal fashion relative to carrying capacity (Wilson 1971; Cohen 1995). When population size is low relative to carrying capacity, growth rate increases. As the population size approaches the asymptote of the carrying capacity, growth slows. At the asymptote of carrying capacity, population size does not remain constant but fluctuates. This is due to the fact that carrying capacity fluctuates. The mechanism of population dynamics can be best understood in terms of negative feedback.

In the biological community, the contingency governing ecological negative feedback takes the following course: An increase in resources, i.e., food availability, causes an increase in population. The effect of this population increase is that resources per individual become scarce. This decrease in resources per individual precipitates stabilization, followed by the inception of a declining trend in the population size. The result of this population decline is that the resources are replenished. This replenishment then begins the negative feedback cycle again (Hopfenberg and Pimentel 2001).

As the organic material that composes living beings comes only from food, whether this is self-generated, as with green plants, or obtained through ingestion, it can be concluded that the level of food availability defines the carrying capacity or absolute upper limit for the population of any species, and all species will increase their number until approaching this limit (Pimentel 1966). The dynamic balance maintained between food and feeder populations in the natural community mitigates all of the other limiting factors (Pimentel and Pimentel 1996). Darwin (1859) noted

the effect of food availability on population size. In his chapter 'The Struggle For Existence' he pointed out that food is a critical element that limited animal populations. He also noted the "numerous recorded cases of the astonishingly rapid increase of various animals in a state of nature, when circumstances have been favorable to them during two or three following seasons."

Recent studies have indicated that food is the necessary and sufficient carrying capacity variable that accounts for human population growth (Farb 1978; Quinn 1992, 1996; Pimentel and Pimentel 1996; Hopfenberg and Pimentel 2001; Meritt 2001). Hopfenberg (2003) applied the logistic model of population dynamics to the human population for the years 1960–2000. Using food production data as the sole measure of carrying capacity, he found that the resultant estimate of human population was in accord with actual population numbers. Of course, ongoing increases in food production, and the resultant growth in the human population, have not been limited to the past 40 years. The cultural shift that put a premium on increasing production occurred approximately 10,000 years ago with the onset of the agricultural revolution (Farb 1978; Quinn 1992; Cohen 1995; Hopfenberg and Pimentel 2001).

Ford (1931) stated that "numerical increase inevitably prepares the way for reduction, and the reverse; so giving rise to fluctuations in numbers, with alternating periods of high and low variability." Ford and Ford (1930) and Ford (1931) was also the first to point out the importance of genetic changes in population dynamics and specifically as a cause of population fluctuations. Thus, he combined the concept of negative feedback with species' genetic changes. As negative feedback in population dynamics is part and parcel of the *resource acquisition and survival* transformation in the genetic evolutionary process, it ultimately affects the genetic makeup of species (Pimentel 1961). The influence of negative feedback on a species' genetic makeup is called the genetic feedback mechanism of population regulation.

Genetic Feedback and Population Regulation: The Coevolutionary Process

Often, changes in the selecting environmental contingencies of one species are the result of changes in another (Pimentel et al. 1978). As the external standard in genetic evolution involves the acquisition of food and defense against predators, a large part of the dynamics are between food and feeder populations. In 1927, Elton concluded that "the whole structures and activities of the (biological) community are dependent on the questions of food supply." That the external standard operation in the genetic evolutionary process involves the acquisition of resources highlights this

point. Therefore, evolutionary changes in one species may affect the environmental contingencies which influence the evolutionary changes in another. This coevolutionary process many times occurs between food and feeder populations. Even competition for territory, both within and between species, and occurring independent of immediate food supply levels, has its evolutionary root in competition over food supply (Darwin 1859).

For example, Pimentel (1988) examined various herbivore population control mechanisms and coevolution. He found that when herbivores exert sufficient selective pressure on their hosts, hosts evolve such defenses as toxic chemicals, protective physical factors and nutrient deficiencies that tend to limit the feeding pressure of herbivores. Similarly, as these defenses cost the host in terms of vital resources, some balance is achieved between the costs of the defenses and the benefits for the host in reducing herbivore feeding. Fenner and Myers (1978) noted the example of the coevolutionary changes in the myxomatosis virus parasite and the European Rabbit (Oryctolagus cuniculus) in Australia. In contrast to the effect on the forest rabbit, the introduced virus produced a rapidly lethal disease in the European rabbit. Over time, the interactions of the virus parasite and the rabbit host evolved. The virus developed avirulence and the rabbit resistance to virus attack. The mechanism of genetic change in this case was hypothesized by Levin and Pimentel (1981) as due to interdemic selection. Since transmission of the virus was dependent on mosquitoes that fed only on living rabbits, rabbits that lived longer, both through resistance and infection with avirulent type parasites were available for infection. In other words, because the virulent type parasites destroyed the food resource of their carrier organism, i.e., their ecological support, faster than the avirulent type, the avirulent type were more likely to meet the genetic external standard contingency of *resource acquisition and survival*.

Cultural *vs*. Genetic Extinction

Virus lethality is proximally determined by the virus' genetic makeup. Changes in viral lethality that stem from population growth, feedback pressure and host resistance achieve balance in the virus–host system. These changes in viral lethality are understood as manifest on the genetic level of integration. It is the nature of viruses that multiple generations and large populations occur over a relatively short period of time. Unlike the human, as the virus does not exhibit behavioral (operant) or cultural traits, the trait flexibility of the virus is manifest only at the genetic level of integration.

There is, of course, a human correlate of viral lethality. In addition to necessary predation and defense, human

lethality has extended to a virtual arms race against threats to future perceived needs (Palumbi 2001). In fact, human lethality has increased to the point that our own ecological support is threatened. Human actions are the cause of what we consider to be environmental/ecological problems, and rapid human population growth is arguably the most detrimental (Pulliam and Haddad 1994). In fact, escalating human population is fueling the acceleration of all environmental problems.

Since human impact on the environment can be seen as being a result of traits manifest on the behavioral and cultural levels of integration, the changes that need to occur in order to achieve ecological balance can take place on the behavioral and cultural levels. However, if changes do not take place on these levels, they may, in the end, take place on the, behaviorally-less-flexible, genetic level of integration.

It is important to remember that behavioral, cultural and genetic evolution are nested and work in concert, producing the adaptive features of species and individuals. The recurrence process, whether this is genetic, behavioral, or cultural, must occur with high fidelity. However, perfect transmission is not required. In fact, slightly imperfect transmission is necessary for survival. Otherwise, the *range* of variants would eventually cease to exist and only one "invariant" would emerge. Subsequently, any significant change in the selecting environment would result in the extinction of the behavior, culture, trait, or species.

Lack of cultural variability is precisely the situation in which the human species finds itself. Except for a tiny minority of tribal peoples on the planet, the human species can be seen as participating in a monoculture. This monoculture, called civilization (Quinn 1992; Cohen 1995), has as its foundation, the basic feature of continually increasing food production. As Cohen (1995) stated, "The ability to produce food allowed human numbers to increase greatly and made it possible, eventually, for civilizations to arise." Farb (1978) pointed out that "intensification of production to feed an increased population leads to a still greater increase in population." He also asserted "the population explosion, the shortage of resources, the pollution of the environment, exploitation of one human group by another, famine and war—all have their roots in that great adaptive change from foraging to production." Farb's statement makes clear that the "adaptive change from foraging to production" is coming into focus as one that has provided some relatively short-term benefits and many long-term difficulties. These difficulties may ultimately lead to an environment that is no longer capable of sustaining human life (Pimm et al. 1995). Meritt (2001) expanded on the problematic features of civilization. He asserted:

"With a genuinely ecological understanding of how humanity fits in with the rest of nature, the filters

through which we see our increase culture can finally be removed. The result is the uncovering of a complex of cultural traits, including total reliance on agriculture, the ultracompetitive interspecies practices that surround that reliance and the institutionalized ownership of food as a means to keep people from abandoning civilization. This complex arose along with increase culture itself and serves to perpetuate it. An additional and most significant result is the expansion of our prevailing paradigm to include not just physical growth and structural complication but a preference for those very traits. Thus, we cling to these traits rather than being able to give them up when their costs outweigh their benefits. This preference has insidiously prevented us from being able to even recognize our paradigm as a paradigm. Instead, we came to conceive our civilized way of life as the one right and possible way to live, incapable of contemplating a shift and, in any case, undesirous of one."

The features of "our increase culture," mentioned above, can be seen as belonging to the *social contingencies* transformation in the cultural evolutionary process (see Fig. 4). It appears that these social contingencies which advocate growth, particularly the ecological falsehood that there is a "need to increase food production to feed a growing population (Daily 1995; Tilman et al. 2001)," has lead to a variety of ecological ills and could lead to human extinction. However, if the variable X_{C3} in Fig. 4 were to account for the range of variants, X_{C3} would lead, not to an extinction of culture itself, but to a revised social contingency that would include understanding the need for halting agricultural increases, and limits to growth. If this does not occur, the result will be one of severely limited resources, impacting the *resource acquisition and survival* transformation at the genetic level of integration. The entire range of variants for humans might then be accounted for by the variable X_{G3}, or biological extinction.

Recent studies have indicated that the sixth great extinction is currently taking place (Pimm et al. 1995). It is not difficult to imagine that the human species may eventually be one of many moving towards extinction, especially because of, not in spite of, our great numbers. However, a choice is evident. Either the cultural behavior, which involves primarily the socially reinforced paradigm that increased food production and growth are necessary, needs to be extinguished (X_{C3}) or the human species itself is at risk of extinction (X_{G3}). The choice is similar to the one faced by the cult members previously mentioned. Either opt out of the suicide-pact cult and lose membership (X_{C3}), or maintain membership at the expense of survival

(X_{G3}). Given the psychological, social, biological and environmental problems that our "increase culture" has produced, it seems that a cultural shift would serve to ameliorate these conditions (Quinn 1992, 1996; Hopfenberg and Pimentel 2001; Hopfenberg 2003).

Coda

The notion of cultural change is in keeping with the understanding of the evolutionary process itself. Evolution is the mechanism through which adaptations appear and maladaptive traits extinguish. All that currently exists in the biological community is a function of evolution. As such, population dynamics can be seen as the foundation of the evolutionary process. As some species grow in biomass, others necessarily diminish due to the reality of finite biological resources. Thus, the physical reality of the earth is that growth is limited. Therefore, unlimited growth is, by definition, unsustainable. Continued human population growth threatens species, including ourselves (McKee et al. 2003; McKee 2004). As long as we pursue growth, fueled by increasing food production, we simply deepen the hole out of which we must climb (Meritt 2002) and our own extinction may be the outcome.

Diamond (2005) drew as vital the distinction between cultural and biological survival as the two are typically seen as one and the same. It is almost universally assumed that biological survival hinges on the strength of our civilization's social contingencies. That was "the lesson" taken from the two world wars and the nuclear age that followed: we would survive as a species only if we learned to get along and resolve our disputes peacefully, i.e., behave in a more civilized manner, even though these terrible events were a product of civilized culture itself. The fact is, we can perceive ourselves to be law-abiding, peace-loving, tolerant, inventive, committed to freedom and true to our own values and still behave in ways that are biologically suicidal. The two kinds of survival are separate (Gladwell 2005). Changing civilization's biologically destructive social contingency that promotes increases in food production and limitless growth to one that recognizes that food production increases lead to population increases, and embraces the notion of physical, ecological and biological limits, would be adaptive and life sustaining.

References

Alessi, G. (1992). Models of Proximate and Ultimate Causation in Psychology. American Psychologist 47: 1359–1370 doi:10.1037/0003-066X.47.11.1359.

Baum, W. M. (2003). Behavior and the General Evolutionary Process. Available from http://cogprints.ecs.soton.ac.uk/archive/00001051/00/Behavior_and_the_General_Evolutionary_Process.htm (Accessed 12 December 2003).

Cakmak, I. (2002). Plant Nutrition Research: Priorities to Meet Human Needs for Food in Sustainable Ways. Plant and Soil 247: 3–24 doi:10.1023/A:1021194511492.

Carr, D. L. (2004). Proximate Population Factors and Deforestation in Tropical Agricultural Frontiers. Population and Environment 25: 585–612 doi:10.1023/B:POEN.0000039066.05666.8d.

Cohen, J. E. (1995). How Many People Can the Earth Support? Norton, New York.

Daily, G. C. (1995). Restoring Value to the World's Degraded Lands. Science 269: 350–354 doi:10.1126/science.269.5222.350.

Darwin, C. (1859). On the Origin of Species By Means of Natural Selection, Random House, New York, USA, (Modern Library edn., 1998).

Dawkins, R. (1989). The Selfish Gene. Oxford Univ. Press, Oxford, New Ed.

Diamond, J. (2005). Collapse: How Societies Choose To Fail or Succeed. Viking, New York.

Elton, C. S. (1927). Animal Ecology. Sidgwick and Jackson, Ltd., London.

Farb, P. (1978). Humankind. Houghton Mifflin, Boston.

Fenner, F., and Myers, K. (1978). Myxoma virus and myxomatosis in retrospect: the first quarter century of a new disease. In Kurstak, E., and Maramorosch, K., (eds.). Viruses and Environment. 3rd International Conference on Comparative Virology, Mont Gabriel, Quebec, pp. 539–570.

FAOSTAT (Food and Agriculture Organization of the United Nations). (2004). FAOSTAT. Available at: http://faostat.fao.org.

Ford, E. B. (1931). Mendelism and Evolution. Methuen, London.

Ford, H. D., and Ford, E. B. (1930). Fluctuations in Numbers and Its Influence on Variation in Meliteaaurinia. Rott (Lepidoptera). Transactions of the Entomological Society of London 78: 345–351.

Gilland, B. (2002). World Population and Food Supply Can Food Production Keep Pace with Population Growth in the Next Half-Century? Food Policy 27: 47–63 doi:10.1016/S0306-9192(02)00002-7.

Gladwell, M. (2005). The Vanishing. The New Yorker 80: 4170–73.

Hinrichsen, D. (1997). Winning the food race. Population. Reports. Series M (13). Available from http://www.jhuccp.org/pr/m13edsum.stm (accessed March 2003).

Hopfenberg, R. (2003). Human Carrying Capacity is Determined by Food Availability. Population and Environment 25: 109–117 doi:10.1023/B:POEN.0000015560.69479.c1.

Hopfenberg, R., and Pimentel, D. (2001). Human Population Numbers as a Function of Food Supply. Environment, Development and Sustainability 3: 1–15 doi:10.1023/A:1011463231976.

Jenkins, M. (2003). Prospects for Biodiversity. Science 302: 1175–1177 doi:10.1126/science.1088666.

Lee, V. (1988). Beyond Behaviorism. Erlbaum, Hillsdale, NJ.

Levin, S. A., and Pimentel, D. (1981). Selection of Intermediate Rates of Increase in Parasite-Host Systems. The American Naturalist 117: 413–421 doi:10.1086/283708.

Liu, J. H., Bonzon-Liu, B., and Pierce-Guarino, M. (1997). Common Fate Between Humans and Animals? The Dynamical Systems Theory of Groups and Environmental Attitudes in the Florida Keys. Environment and Behavior 29: 87–123 doi:10.1177/001391659702900104.

McKee, J. K. (2004). Brother, Can You Spare A Species? The Reporter Spring:6–9.

McKee, J. K., Sciulli, P. W., Fooce, C. D., and Waite, T. A. (2003). Forecasting Biodiversity Threats Due to Human Population Growth. Biological Conservation 115: 161–164 doi:10.1016/S0006-3207(03)00099-5.

McQueen, R. E. (2000). World Population Growth, Distribution and Demographics and Their Implications on Food Production. Canadian Journal of Animal Science 80: 229–234.

Meritt, M. S. (2001). The unsustainability and origins of socioeconomic increase. Unpublished master's thesis, The City University of New York, New York. Available from http://www.potluck.com/offerings/increase.pdf (accessed November 2004).

Meritt, M. S. (2002). The Case Against Growth. Scientific American 286: 12.

Myers, N. (1996). Environmental Services of Biodiversity. Proceedings of the National Academy of Sciences, USA 93: 2764–2769 doi:10.1073/pnas.93.7.2764.

Olson, D., and Pimentel, D. (1974). Evolution of Resistance in A Host Population to An Attacking Parasite. Environmental Entomology 3: 621–624.

Palumbi, S. R. (2001). Humans as The World's Greatest Evolutionary Force. Science 293: 1786–1790 doi:10.1126/science.293.5536.1786.

Pimentel, D. (1961). Animal Population Regulation by the Genetic Feed-Back Mechanism. The American Naturalist 95: 65–79 doi:10.1086/282160.

Pimentel, D. (1966). Complexity of ecological systems and problems in their study and management. In Watt, K. (ed.), Systems Analysis in Ecology. Academic, New York, pp. 15–35.

Pimentel, D. (1988). Herbivore Population Feeding Pressure on Plant Hosts: Feedback Evolution and Host Conservation. Oikos 53: 289–302 doi:10.2307/3565527.

Pimentel, D. (2001). The Limitations of Biomass Energy. Encyclopedia on Physical Science and Technology. Academic, San Diego, 159–171.

Pimentel, D., and Pimentel, M. (1996). Food, Energy and Society, rev. edn. University Press, Boulder, CO.

Pimentel, D., and Soans, A. B. (1970). Animal Populations regulated to carrying capacity of plant host by genetic feedback. In denBoer, P. J., and Gradwell, G. R. (eds.), Dynamics of Populations. Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeek, The Netherlands, pp. 313–326.

Pimentel, D., Levin, S. A., and Olson, D. (1978). Coevolution and the Stability of Exploiter-Victim Systems. The American Naturalist 112: 119–125 doi:10.1086/283256.

Pimentel, D., Levin, S. A., and Soans, A. B. (1975). On the Evolution of Energy Balance in some Exploiter-Victim Systems. Ecology 56: 381–390 doi:10.2307/1934968.

Pimentel, D., Giampietro, M., and Bukkens, S. G. F. (1998). An Optimum Population for North and Latin America. Population and Environment 20: 125–148 doi:10.1023/A:1023367211000.

Pimm, S. L., Russell, G. J., Gittleman, J. L., and Brooks, T. L. (1995). The Future of Biodiversity. Science 269: 347–350 doi:10.1126/science.269.5222.347.

Pulliam, H. R., and Haddad, N. M. (1994). Human Population Growth and The Carrying Capacity Concept. Bulletin of the Ecological Society of America 75: 141–157.

Quinn, D. (1992). Ishmael. Bantam/Turner, New York.

Quinn, D. (1996). The Story of B. Bantam/Turner, New York.

Rosset, P, Collins, J, and Lappé, FM (2000). Lessons from the Green Revolution. Tikkun 15(2):52.

Skinner, B. F. (1938). Behavior of Organisms. Appleton-Century-Crofts, New York.

Skinner, B. F. (1981). Selection by Consequences. Science 213: 501–504 doi:10.1126/science.7244649.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D., and Swackhamer, D. (2001). Forecasting Agriculturally Driven Global Environmental Change. Science 292: 281–284 doi:10.1126/science.1057544.

Wilson, E. O., and Bossert, W. H. (1971). A Primer of Population Biology. Sinauer, Sunderland, MA.

Young, A. (1999). Is There Really Spare Land? A Critique of Estimates of Available Cultivable Land in Developing Countries. Environment, Development and Sustainability 1: 3–18 doi:10.1023/A:1010055012699.

Per capita food availability, measured as grain production, peaked in 1983/84 and has continually declined since (FAOSTAT 2004). However, because population numbers change as a function of carrying capacity, an elevated food supply will precipitate a population increase, leading to per capita food supply numbers that are in dynamic equilibrium with population numbers. Thus, with a food supply that is elevated relative to population, the population will increase and per capita food must eventually decrease (Cohen 1995; Hopfenberg 2003). See www.panearth.org for further explication.