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Human Adaptation and Energetic Efficiency

Eric Alden Smith¹

A lack of consensus on the general adaptive significance of energetic efficiency can be shown to exist in ecology and anthropology. After briefly reviewing key studies in optimal foraging theory and ecological anthropology, a model is presented which includes the following elements: (1) an equation of adaptive success with reproductive fitness, within an optimality framework; (2) a definition of energy limitation consistent with this framework; (3) a distinction between efficiency of energy capture and efficiency of energy use in achieving other goals; (4) a multiple definition of energetic efficiency that distinguishes purely energetic measures (output/input) from rate measures (energy captured per unit time); (5) the inclusion of time budgeting as a primary adaptive constraint; (6) a quantitative demonstration that increased output/input ratios do not consistently predict an increase in net energy captured, and are poor measures where time is a constraint. The general conclusion is that where energy is limiting, increased efficiency in the rate of energy capture will be adaptive because more net energy will be made available; where energy is not limiting, an increased net capture rate may still confer increased adaptive success, since time and labor energy are freed from energy-capture activities and can be devoted to achieving other adaptive goals. But while energetic efficiency, properly defined, is shown to have general adaptive significance in all cases where time or energy are constraints, considerations of adaptive optimality preclude the general equation of energetic efficiency and adaptive success.

KEY WORDS: energetic efficiency; adaptation; behavioral ecology; optimal foraging theory.

INTRODUCTION: THE CONTROVERSY

An examination of the literature on the relation of energetic efficiency and human adaptation discloses an unresolved controversy over whether traits

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promoting increased energetic efficiency are universally adaptive. Not only is there no agreement on the correct answer to the question: “Is there a consistent relationship between energetic efficiency and adaptation?” – there is no agreement on how to go about answering this question systematically. Yet the question has significant implications for research in human ecology, and until the issues are clarified much time will be devoted to factional struggles.

The roots of the “universalist” view of energetic efficiency go back at least to 1922, when A. J. Lotka published a paper on the energetics of evolution. Lotka set forth various postulates on the relation between natural selection and energy flow in biological systems, in particular arguing for the universal validity of the following principle:

In the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favorable to the preservation of the species. (1922: 147)

This principle followed from his belief that “the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy” (Lotka, 1922). Currently, the strongest exponent of Lotka’s principle is H. T. Odum (1971, 1974), who interprets Lotka as having virtually translated Darwinian fitness into energetic terms:

Lotka indicated that the maximization of power (energy per unit time) for useful purposes was the criterion for natural selection. Darwin’s evolutionary law thus developed into a general energy law. (1971: 32)

Although other proponents of the adaptive value of energetic efficiency have often phrased the purported connection in less universal terms, the assumption that adaptation will generally maximize some form of energetic efficiency has become very widespread among biologists, human ecologists, and anthropologists. Some, however, refute the universality of the efficiency paradigm, among them L. B. Slobodkin:

The concept of efficiency as such relates to energy, while the concept of effectiveness relates to adaptation. That is, an animal may be effective at hiding or effective at searching for food in the sense that it does these acts well and in the way that is appropriate to whatever environmental problems it may face. The energetic cost or lack of energetic cost associated with these acts may prove of interest if energy is, as a matter of fact, limiting. The conditions under which energy is limiting can also be specified, but there is not any formal necessity for a connection between effectiveness and efficiency. Effectiveness may or may not involve optimization or maximization of some function relating to energy. (1972: 294)

Thus, the argument goes, activities or situations relevant to adaptive success, such as parental care or predator detection, must be performed effectively, that is, effectiveness will be selected for. The degree to which these activities are energetically efficient would seem to be tied to the prevalence of energy limitations in past or present environments of the population being studied. Ac-

according to Vayda and McCay (1975: 296), when a population is not energy-limited and is threatened by other sorts of hazards, "then the effectiveness of the organism's response to those problems and not the energy expended in making the response is the important subject matter."

An energetic efficiency model of some sort has informed human ecology research in a number of areas, including, for example, studies of hunter-gatherer foraging strategies (Lee, 1969; Yellen and Harpending, 1972; Rogers and Black, 1976; Harpending and Davis, 1977; Winterhalder, 1977); the pattern of food production and dung use in highland Peru (Thomas, 1973; Winterhalder *et al.*, 1974); archaeological "least effort" models of settlement patterns and subsistence strategies (Wilmsen, 1973; Wobst, 1974; Jochim, 1976; Perlman, 1976); and the conduct of warfare in small-scale societies (Rappaport, 1968; Harris, 1975: 259ff; Durham, 1976a). At the same time as this "energetic trend" seems to be gathering momentum in human ecology, more criticism of the assumed relationship between energetic efficiency and adaptation is being heard, paralleling the criticisms in general ecology noted above (cf. Vayda and McCay, 1975).

The issues raised by this conflict are both complex and important. However, one must consider the possibility that neither position has correctly and rigorously related adaptation and energetic measures such as efficiency. As I will attempt to demonstrate, considerations of optimum time-budgeting alone may favor some kinds of energetically efficient traits, *depending on the way one defines and measures energetic efficiency*; yet energetic efficiency cannot be simply equated with adaptation. But before this argument is developed, some definitions of key terms and a discussion of the theoretical framework guiding it must be presented.

GENERAL THEORY

An Approach Via Evolutionary and Ecological Theory

In order to examine the relation of energetic efficiency to human adaptation it is imperative to decide what theoretical framework and operational measures are contained in the concept of adaptation. Within the broad field of human ecology, adaptation has become an almost magical word, a concept that is either protean in meaning or else is really several different concepts traveling under the same semantic label. Since social scientists from Herbert Spencer on have developed adaptation theory somewhat independently of biologists (Alland and McCay, 1973), and since biologists themselves have often disagreed on the factors involved in adaptation (Williams, 1966; Stern, 1970), this situation should not be surprising. To reduce this confusion several recent attempts have been made to establish a consistent measure of adaptation in

human ecology, whether this be maintenance of homeostasis, survival, goal satisfaction, or reproductive fitness (e.g., Alland, 1975; Alland and McCay, 1973; Durham, 1976b).

Lacking space to discuss these various measures, I will refer to W. A. Durham's formulation (1976b) as a guide to the adaptive framework I will employ in analyzing energetic efficiency arguments. Briefly, an adequate theory of adaptation must not only enable us to identify adaptations and adaptive processes, describe and measure them, and predict responses from specified environmental alterations; it must also provide solid deductive explanations for the existence of specific adaptive responses and general adaptive capabilities. In other words, it should specify not only the goals or end states of adapting organisms, but also how they came to have such goals and the capabilities for achieving them. This theory should be equally capable of defining and measuring maladaptive traits or processes, and their associated selective forces. At present, only neo-Darwinian theory can even approach these requirements, in my opinion.

The specific body of theory most relevant to the central question addressed here has been developed in evolutionary behavioral ecology (a field well reviewed in Pianka, 1974), and includes a set of hypotheses and models that generally go under the name of "optimal foraging theory" (Pyke *et al.*, 1977). Based on neo-Darwinian theory coupled with sophisticated models of environmental variance, and emphasizing a rigorous deductive approach, this approach should prove highly useful for research into fundamental questions of energy flow and adaptation.

Optimal foraging theory, as the name implies, is concerned with building and testing models of *optimal* strategies of energy acquisition. The concept of optimality, originally borrowed from microeconomics, is central to contemporary evolutionary theory, where it is recognized that natural selection operates on complex organisms in complex and variable environments, so that questions of adaptive response to any one problem or opportunity involve many other sets of adaptive responses and environmental factors (Cody, 1974). Since the complexity of most environmental situations leads to a multitude of constraints, the theoretically optimal solution favored by natural selection will balance various conflicting and/or interdependent demands (e.g., for growth, reproduction, avoiding hazards, capturing energy, competing, cooperating) in order to maximize fitness. However, in behavioral ecology most models of optimal choice that employ energy as a cost-benefit currency assume the maximization of energetic efficiency *per se*. One might first consider the conditions under which this simplifying assumption is valid.

As an example, discussions of human foraging strategies often assume that the strategic goal is effort minimization or the maximization of energetic efficiency, as if energy captured vs. energy expended were the *only* relevant consideration in assessing the adaptive value of foraging strategies. But a more

valid approach would recognize that the situation is considerably more complex. In the words of Eric Pianka (1974: 108), a foraging strategy

involves the ways in which an animal gathers matter and energy. This matter and energy constitute the profits gained from foraging, in that they are used in growth, maintenance, and reproduction. But foraging has its costs as well: thus, a foraging animal may often expose itself to potential predators and much of the time spent in foraging is rendered unavailable for other activities, including reproduction. An optimal foraging strategy maximizes the differences between foraging profits and their costs. Presumably natural selection, acting as an efficiency expert, has often favored such optimal foraging behavior.

A study of lion foraging energetics (Caraco and Wolf, 1975) has demonstrated that lion group size is adjusted to a hierarchy of ecological factors, of which energetic efficiency is only one; energetic efficiency is maximized in some situations, but lions adapt to changing circumstances by "optimizing group size, balancing foraging efficiency against other determinants of fitness" (p. 350).

Published models of optimal foraging behavior focus on several types of strategies and utilize various measures of energetic efficiency. Of particular relevance here are those dealing with three aspects of energy-capturing behavior: optimal food choice, optimal use of habitat sectors or "patches," and optimal spatial distribution. The basic assumption of optimal food choice models is that food sources can be ranked by an organism in terms of the relative contributions of different choices to reproductive fitness. Various optimum food choice models focus on "food value" (Emlen, 1973: 169, 1966; Rapport, 1971), time-and-energy budgets (Schoener, 1971), and prey selection strategies (Charnov, 1976a; Slobodkin, 1968, 1974; Schoener, 1969). Optimal use of a patchy environment is sometimes modeled in terms of energetic efficiencies, since environments characterized by different types of resource patches present problems for efficient energy capture (MacArthur and Pianka, 1966; Royama, 1970; Tullock, 1971; MacArthur, 1972; Pianka, 1974: 207ff). Finally, various attempts have been made to relate spatial distribution of animal populations to resource distribution in terms of energetically efficient strategies. Thus, general models of group size, dispersion patterns, and degree of territoriality have been presented (Brown, 1964; Hamilton and Watt, 1970; Brown and Orians, 1970; Schoener, 1971) and field data have been used to test and support these models (McNab, 1963; Horn, 1968; Schoener, 1968; Smith, 1968; Wolf *et al.*, 1975).

Models of optimal foraging behavior posit optimum solutions to the problems of efficient capture and use of energy within the context of maximizing reproductive fitness. The implicit assumption in many cases is that energetic efficiency is closely enough identified with fitness that selection will tend to maximize it (at least under the conditions prescribed by the model). However, several different measures of energetic efficiency are used in these studies, and in most cases no direct measures of energy capture or expenditure are available. Furthermore, with one or two exceptions, none of the studies has any measure

of potential or actual energy limitation, or of a correlation between reproductive fitness and energetic efficiency.

As discussed above, Slobodkin (1972) and other critics of the “universalist” view have argued that where the availability of energy is not an adaptive constraint, there is no reason to expect selection for energetic efficiency, and in fact some reason to expect counter-selection in the face of competing goals. With regard to activities that do not capture energy, it seems clear that selection will maximize *effective* attainment of goals relevant to adaptive success, and that *efficient* solutions will be of overriding adaptive importance only in energy-limited situations. The question of whether this caveat holds for activities that *capture* energy (e.g., foraging, agriculture, fuel procurement) needs to be reexamined. In particular, I will attempt to demonstrate that one of Slobodkin’s examples (“searching for food”) will be more effective (for adaptive success) if it is more energetically efficient in some way.

Definition of Key Variables

“Energetic efficiency” is a term that has had multiple, sometimes contradictory, uses and meaning in the ecological literature (cf. Kozlowski, 1968; E. P. Odum, 1971; Ricklefs, 1973: 651). Of the various ecosystem, population, and individual organism measures that have fallen under this rubric (e.g., trophic assimilation efficiency, production efficiency, growth efficiency), I will focus on measures that refer to individual efficiency in capturing energy, and on those that seem to be closely related to adaptation in the framework developed above. An ecosystem focus (such as on the efficiency with which energy is transferred between trophic levels) makes sense if one is concerned with proximate mechanisms and processes. If the inquiry is concerned with adaptation and the ultimate (evolutionary) origins of traits controlling energy flow, then the focus must be on the characteristics and possible strategies of individuals and social groups.

As has been argued elsewhere, the bulk of selective forces (and therefore of adaptive change) is concentrated at the level of individuals and kin groups (see Williams, 1966, 1971; Lewontin, 1970; and Wilson, 1973 with reference to evolutionary biology; and Alland and McCay, 1973; Durham, 1976b; and Richerson, 1977 for an extension to cultural adaptation and human ecology). Furthermore, natural selection acts to maximize individual fitness, but the traits thus selected for are not necessarily additive with respect to higher levels of biological organization. This lack of additivity is primarily due to the basic role of *reproductive* competition in the evolutionary process (competition between individual genetic lineages for greater representation in future generations), which often results in *ecological* competition (competition over resources). For example, selection at the individual level for increased energetic efficiency may

lead simultaneously to population growth and resource scarcity, resulting in a decline of average (population-wide) energetic efficiency in spite of continued selective advantage for individual efficiency; and the competing evolutionary goals of members of different species may result in a depression of the efficiency of energy transfer across trophic levels (e.g., selection for predator detection and escape strategies, the evolution of distasteful forms and their mimics, etc.).

Since both supporters and critics of energetic efficiency models stress energy limitation as a key variable, this concept should be defined both rigorously and consistently. Depending on the specific level of adaptation being discussed, energy limitation can mean a number of things. If the framework is neo-Darwinian adaptation, two possible (and potentially interchangeable) meanings are relevant: (1) an individual organism is energy limited if and only if an increase in energy intake will positively affect its reproductive fitness; (2) a population is energy limited if and only if its growth rate would show a positive increment with an increase in energy intake. Such a definition has limitations (especially for operationalizing the measurement of energy limitation via fitness depression), but it is very useful for constructing models and analyzing problems in the context of evolutionary theory.

Note that a neo-Darwinian or demographic notion of energy limitation does not necessarily include such phenotypic situations as chronic or periodic hunger, a lower rate of energy consumption as compared with some average standard, or the presence of starvation (though these may sometimes occur along with fitness depression and thus be correlated with energy limitation in the demographic sense). This is because many such phenotypic conditions may be too temporary to affect fitness, or alternatively, organisms may evolve strategies that avoid evolutionarily wasteful events such as overproduction and subsequent lowered fitness of young in energy-limited situations (cf. Lack, 1968). Energy limitation as defined here does not mean that trophic energy is necessarily being captured at any maximal rate, but simply that the given mode of exploitation is constrained (by competition, available daylight, technology, social organization, or whatever) to the extent that fitness is limited by the amount of energy captured and consumed.

Within other adaptive frameworks, such as those mentioned in an earlier section, energy-limited may be defined differently. Focusing on individual homeostasis, for example, it might be defined in terms of such variables as the presence of caloric malnutrition, while for homeostasis at the population level it might include demographic variables. No one measure is adequate for analyzing all types of adaptive process, in both proximate (functional) and ultimate (evolutionary) causal frameworks. However, a clear and narrow definition is necessary when working in any one adaptive framework, in order to make valid deductive inferences for the construction and testing of general theory.

A Simple Model

As will be discussed below, one can distinguish between measures of energetic efficiency that consider only energetic costs and benefits (input vs. output) and those that include a measure of time (acquisition rates). It therefore follows that energy-capturing strategies can be analyzed in terms of what is efficient on purely energetic grounds or in terms of efficient budgeting of both time *and* energy. The differences have not only formal significance, but important theoretical and empirical implications concerning the relation of energetic efficiency to adaptation.

A simple model (and notational system) will facilitate the discussion of these issues. The relevant variables are time spent foraging or acquiring energy in any fashion (T_a), energy expended during this time (E_e), and energy acquired during this time (E_a). With these three variables, the basic parameters of energetic efficiency can be identified: output/input efficiency (F) is the ratio of energy acquired to energy expended ($F = E_a/E_e$); net energy is their difference ($E_a - E_e$); and by introducing time considerations, we can define rates of gross acquisition ($R_g = E_a/T_a$) and net acquisition ($R_n = [E_a - E_e]/T_a$).² (For convenience, these and various other variables and parameters are listed and defined in Table I.)

We can now turn to an examination of the relative merits of these various measures of energetic efficiency. Gross acquisition rate, R_g , is simply a measure of energy captured per unit time (E_a/T_a), and omits any measure of energy expended (E_e). Accordingly, R_g does not necessarily covary with the other measures of efficiency (R_n or F) or with net energy (E_n), since any variance in E_e will change the values of these later measures. In fact, since gross acquisition rate does not specify the energetic costs of capturing energy, it is not an adequate measure of efficiency at all (though it is frequently used as such, often being termed "foraging success"). The assumption usually is made that gross and net acquisition rates would be highly correlated in any particular case. While it may be true that in many cases energy-capturing strategies could alter so as to increase or decrease R_g without affecting the rate of energy expenditure, it is at least equally probable that the opposite could occur. That is, an increase in R_g might be purchased via an increased expenditure of energy (E_e) during some time period T_a , and this could conceivably lead to a decrease in F (output/input efficiency) or R_n (net acquisition rate), or even a net loss of available energy (E_n). Insofar as is practical, then, other measures should be used in preference to gross acquisition rate in assessing energetic efficiency.

² A hypothetical example may clarify these relationships. An Eskimo male hunting for seal spends 100 minutes at a breathing hole and going to and from this site and camp. During this hunt, he captures one seal (with a caloric value of 10,000 kcal), and expends a total of 500 kcal of his own energy on this task (an average of 5 kcal/min). By the definitions given, we have an acquisition efficiency of $10,000/500 = 20.0$, a gross acquisition rate of $10,000/100 = 100$ kcal/min, and a net acquisition rate of $10,000 - 500/100 = 95$ kcal/min.

Table I. Variables and Parameters Relating to Energetic Efficiency*Variables*

E_a = energy acquired during some period of acquisition time
 E_e = energy expended in acquiring any E_a
 T_a = acquisition time for any E_a (and the associated E_e)
 T_o = time available for activities other than energy capture
 W = fitness (or some correlate thereof)

Parameters

E_n = net energy acquired = $(E_a - E_e)$
 R_g = gross acquisition rate = (E_a/T_a)
 F = output/input efficiency = (E_a/E_e)
 R_n = net acquisition rate = $(E_a - E_e)/T_a$

Output/input efficiency (parameter F , the ratio of E_a to E_e) is a purely energetic measure. The limitations of such a time-free measure, as compared to a rate measure of efficiency, need to be emphasized. It can easily be shown that this ratio does not consistently predict the values of net energy captured (E_n), net rate of energy acquisition (R_n), time invested in energy capture (T_a), or time remaining for other activities (T_o). Given two cases where arbitrary values are assigned to E_a and E_e , set $E_{a1} = 10x$, $E_{e1} = 5x$, $E_{a2} = 3x$, and $E_{e2} = x$. Since $F = E_a/E_e$, then $F_1 = 10x/5x = 2.0$, and $F_2 = 3x/x = 3.0$. Since $E_n = E_a - E_e$, then $E_{n1} = 10x - 5x = 5x$, and $E_{n2} = 3x - x = 2x$. Since $R_n = E_n/T_a$, then $R_{n1} = 5x/T_a$, and $R_{n2} = 2x/T_a$ (assuming in this arbitrary example that acquisition times in the two cases are the same length). Thus, although in this example $F_1 < F_2$, it so happens that $E_{n1} > E_{n2}$, and $R_{n1} > R_{n2}$. Furthermore, since F includes no time measures, both T_a and T_o can vary independently of F (increasing the chance that changes in F will not correspond to changes of R_n in direction or magnitude).

To summarize thus far, both output/input efficiency (F) and net acquisition rate (R_n) can be increased by changes that decrease energy expenditure or increase energy acquired during bouts of energy capture, but only R_n measures the amount of net energy captured in any fixed period of time in a mathematically consistent manner. The conclusion that can be drawn from these results is that these two types of "energetic efficiency" (what I have termed output/input efficiency and net acquisition rate), while overlapping in the variables that define them and in their use in the literature, must be distinguished in assessing the adaptive value of energy-capturing strategies.

Having emphasized the importance of using a net rate measure of efficiency, we can turn to the major issue: when and why is an increase in this rate adaptive? If energy is limiting, by the definition given earlier, fitness (or some correlate of fitness) is a direct function of available net energy. In simplest terms,

$$W = f_1(E_n) \quad (1)$$

such that an increase in E_n will lead to an increase in W . Net energy is a component of the net rate of energy acquisition:

$$R_n = (E_a - E_e)/T_a = E_n/T_a \quad (2)$$

and by transposition, $E_n = (R_n)(T_a)$. It follows that Eq. (1) can be rewritten in terms of these identities as

$$W = f_1(R_n)(T_a) \quad (3)$$

and that fitness can be increased either by devoting more time to acquiring energy (increasing T_a) or by increasing the net rate of acquisition (R_n). Insofar as Eq. (1) applies (fitness is solely limited by net energy captured), it is of adaptive advantage to increase the total time spent acquiring energy (ΣT_a); but since devoting more time to capturing energy decreases time potentially available for other activities, at some point fitness will begin to decrease as ΣT_a continues to increase.

To make this point more explicit, let us turn to the limiting case where fitness is a function of time available for activities other than the capture of energy:

$$W = f_2(T_o) \quad (4)$$

If we assume that ΣT_a and T_o account for the total time budget, then $\Sigma T_a + T_o = 1$, and $T_o = 1 - \Sigma T_a$. Since any $T_a = E_n/R_n$ [by transposing Eq. (2)], then

$$T_o = 1 - \Sigma(E_n/R_n) \quad (5)$$

This last equation simply states that T_o can be increased (and ΣT_a decreased) either by maintaining the same efficiency and thus capturing less net energy (decreasing E_n), or by increasing the efficiency of energy capture such that the same net energy is obtained in less time (increasing R_n). The former option is only adaptive as long as total E_n is in surplus, and at some point this option will decrease net energy to the point that E_n (rather than time available for other activities) is limiting. In other words, to increase T_o by decreasing E_n and maintaining a constant efficiency eventually pushes the system out of the domain of Eq. (4) and back into the energy-limited domain defined by Eq. (1). The option of increasing T_o by increasing the net rate of acquisition (R_n) does not have this "equilibrating" effect, and thus increasing R_n by increasing E_a or decreasing T_a is theoretically the only strategy that increases fitness under either an energy-limited or time-limited regime without leading directly to oscillation between these two regimes.

In summary, the logic of this admittedly simple model predicts that where available (net) energy is limiting, fitness can be increased by holding energy acquisition time (T_a) constant and increasing the net rate of acquisition (R_n). Where time (but not net energy) is limiting, Eq. (4) predicts that fitness can be increased by holding E_n constant and reducing T_a , resulting in an increased net

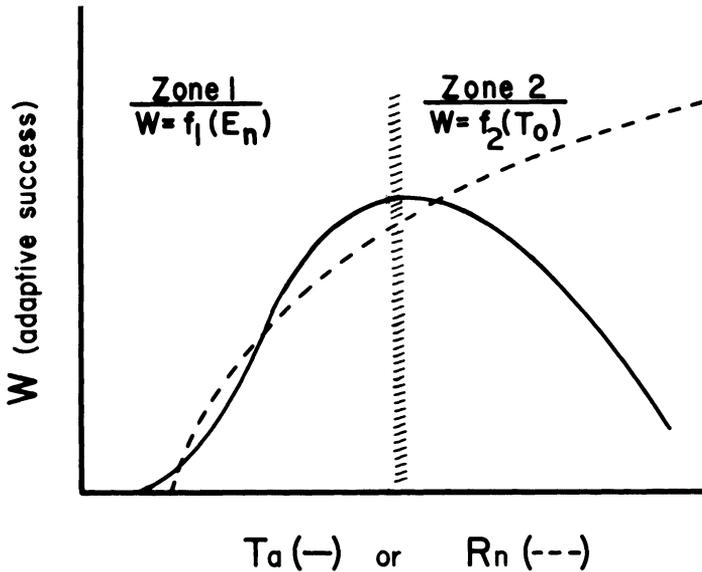


Fig. 1. Hypothetical fitness curves in relation to total net energy (E_n) and apportionment of the time budget (T_o vs. T_a). The relative positions of the R_n and T_a curves are arbitrary.

rate of acquisition (R_n) as well. The shifting between domains of energy-limitation and time-limitation is illustrated graphically in Fig. 1.

Proponents and critics of the universal adaptiveness of energetic efficiency agree that increasing the total net energy captured is adaptive for the energy-limited case, and my analysis supports this view. However, even in this case a rate measure of efficiency should be used rather than a purely energetic ratio of output to input, for reasons detailed above. When energy is not limiting, an increase in net acquisition rate frees time from energy acquisition to devote to any activities that are relevant to adaptive success, and thus increased energetic efficiency in this sense is predicted to be generally adaptive in all cases where time is an important adaptive constraint.³ Where there are neither time nor energy constraints on adaptive success, an increase in net acquisition rate would be of no adaptive value, but this limiting case would seem to be rather rare.

Of course, it is possible in any particular case that increased efficiency is purchased at too great a price in terms of the net benefit to fitness (if, for

³ Time is here defined to be an adaptive constraint when the manner in which time is budgeted for various activities has a significant effect on reproductive success, such that the total time invested in energy acquisition (ΣT_a) could not be increased without a reduction in fitness.

example, a more efficient strategy is also more risky). But the model presented here has shown that energetic efficiency has a more general adaptive significance than those who have focused on energy limitations have argued, but for different reasons than Lotka supposed. This last point – and indeed the whole distinction between purely energy-efficient, purely time-efficient, and time-and-energy-efficient strategies of energy capture – has generally been overlooked in the controversy over energetic efficiency and adaptation.

IMPLICATIONS FOR EMPIRICAL STUDIES

The concepts of energy flow and/or energetic efficiency are central to energy-based approaches to social evolution (Cottrell, 1955; H. T. Odum, 1971; Odum and Odum, 1976), the cultural evolutionism of White (1949, 1959) and others (cf. Sahlins and Service, 1960), and the cultural materialism espoused by Harris (1968, 1975). Vayda and McCay (1975), following Brookfield (1972: 46), have detailed some of the criticisms of a “calorific obsession” in ecological research: they question the validity of the “basic assumption that all living organisms compete ultimately for energy and therefore that adapted organisms will be energetically efficient ones” (Vayda and McCay, 1975: 295). The parallel “assumption that nutritional energy is a significant environmental problem (a limiting factor) for all human populations, with subsistence systems providing the solution to it,” has also been attacked as a “fallacy” (Little and Morren, 1976:22). Yet neither those who proclaim the importance of energy in human adaptation nor their critics have adequately considered the difference between efficiency in capturing energy and efficiency in using energy to achieve other goals, or the difference between purely energy-efficient strategies and strategies that are efficient in terms of both time and energy.

Several populations that have been subjected to more or less detailed energy-flow studies will be briefly discussed, in order to indicate some of the implications of the present analysis for their results. Of these examples, one case exhibits strong signs of chronic energy shortage (Nuñoa Quechua), one group has a history of acute energy shortages but no such shortage at present (Boreal Forest Cree), and two are cases where energy is probably not limiting in any way (!Kung San and Tsembaga Maring).

Nuñoa Quechua

Thomas (1973) conducted a detailed study of energy flow in relation to patterns of food production, distribution, and demography among a Quechua Indian population inhabiting a highland region in southern Peru. This study used an output/input measure of efficiency exclusively (a common practice in human energy flow studies) to compare the efficiencies of various crop regimes, domestic

animal production, product exchange with outside (lowland) groups, and division of labor. A later study also examined patterns of dung use for fuel and fertilizer (Winterhalder *et al.*, 1974). Thomas presented substantial physiological and ecological evidence that trophic energy is limited for this population, though no demographic measure of energy limitation was attempted (however, out-migration appears to be quite high, as would be expected if local energy or other resources were limiting fitness).

The value of any analytic concept (such as energetic efficiency) for studies of human adaptation lies in its ability to account for patterns of choice or variability in human behavior. While the arguments presented by Thomas and his associates are not uniformly powerful, a considerable array of Nuñoan behavioral patterns seem to be at least partially explained by the assumption that energetic efficiency of food production is maximized, under the given constraints of the local technoeconomic system. The main strategies employed by this population to increase energetic efficiency include the following: (1) key plant and animal domesticates, adapted to different altitudes, are planted or pastured so as to maximize productivity; (2) locally produced high-protein foods (as well as wool and hides) are exchanged with lowlanders for low-protein high-calorie foods (producing a net caloric yield); (3) a heavy reliance is put on child labor in family production, and for these tasks children produce equivalent amounts with a lower energy cost than adults; (4) adults emphasize sedentary subsistence tasks in daily activity (a correlate of point 3); (5) dung use as fertilizer and as fuel corresponds with optimal choices predicted by an efficiency model.

An energetic-efficiency approach is used to illuminate the adaptive significance of choices Nuñoa people make with respect to resource selection and production, division of labor, work patterns, and exchange with other populations. While empirical output/input ratios and net capture rates for any one resource *may* be equivalent in Nuñoa, the demonstration that this is so would strengthen the interpretation of Nuñoan food production in energetic terms. In any case, the Nuñoa population seems to be an example of energy-maximizing (vs. time-minimizing) in human adaptation (cf. Schoener, 1971: 376ff). Due to the chronic energy shortage that probably exists in this population, we could expect Nuñoans to respond to increased energy availability by increasing the total energy captured rather than by decreasing time invested in energy capture. Sufficient acceleration of out-migration or land redistribution might create such an increase in available energy, and thus provide a possible test case for a central prediction of energetic efficiency theory.

Boreal Forest Cree

Winterhalder (1977) analyzed the foraging practices of a contemporary Boreal Forest Cree population subsisting on a combination of wild game and store food, using both net capture rates and output/input ratios as measures

to examine four broad aspects of foraging strategy: (1) diet breadth; (2) use of space in a heterogeneous environment; (3) the scheduling of foraging effort (both daily and seasonally); and (4) the distribution of social units (foraging group sizes). Winterhalder specifically tests hypotheses derived from several models of optimal foraging theory and evolutionary ecology, including MacArthur and Pianka's (1966) optimal diet breadth and optimal patch choice models, Horn's (1968) model for dispersion and aggregation under different resource-distribution regimes, and Charnov's (1976b) marginal value theorem for foraging in a patchy environment.

According to Winterhalder, the Boreal Forest Cree employ several main strategies to maximize the energy return on time and energy invested under different environmental conditions. First, prey choice is altered (seasonally or over shorter periods) in response to changes in prey distribution and abundance as well as changes in search and pursuit costs, in such a way as to generally maximize the efficiency with which energy is captured. Secondly, the choice of which patch type to forage in is based on the expectable energetic return on foraging, given the geometry of the environmental mosaic and the alternatives available at any one time. Finally, the decision to leave any patch and forage elsewhere seems to be based on the expected productivity of alternative patches, in the manner predicted by Charnov (1976b) – though here Winterhalder acknowledges that the supporting data are largely qualitative and therefore the confirmation is weaker than in the previous cases. It should be pointed out that although the Boreal Forest Cree have a history of acute, periodic energy shortages dating at least to the fur-trade era, and thus energy has been a periodic limiting factor via depressed fertility and starvation, at present there is no evidence that food energy is a limiting factor at all. Accordingly, this case is probably a good human example of a “time-minimizing” approach to efficient energy capture [to use Schoener's (1971: 376) phrase]; thus we can predict that any increase in available energy would lead to reduced foraging time, and not to any increase in the total energy captured by this population.

In Winterhalder's study, energetic costs and benefits are used to subsume a whole series of complex, diverse, and interrelated factors that help shape Cree foraging behavior, such as weather conditions, habitat diversity, prey behavior, aboriginal and industrial hunting and transport technology, prey distributions in time and space, work effort, and seasonal cycles. Without the use of time and energy as basic cost-benefit measures, it would have been very difficult or impossible to consider such a wide range of determinants. While these measures may be imperfect, it seems doubtful that any others would allow equivalent generality and precision. Furthermore, the fact that a careful and relatively rigorous analysis of Cree foraging strategies supports the energetic-efficiency assumptions of optimal foraging, even though energy is not in this case limiting, suggests that those who argue that energy is of limited relevance for studies of human adaptation might reconsider their position.

!Kung San

Although detailed studies of energy flow and foraging effort among the !Kung have not been published, published studies often assume that !Kung foragers attempt to minimize effort and maximize energy captured in foraging periods, though such an assumption may not be explicitly stated (cf. Lee, 1968, 1969, 1972; Yellen and Harpending, 1972). Vayda and McCay (1975: 296ff) argue that since the !Kung are probably not energy-limited, we would do better to focus on more relevant adaptive problems, such as water shortage. In this case, however, constraints on the availability of water and food energy are interrelated, such that adaptive responses to each cannot really be considered separately (Lee, 1969: 59ff).⁴

This interrelation of water availability and foraging strategy occurs because permanent water sources are few, and food must be sought in proximity to these sources during the dry season:

Since Bushman camps, of necessity, are anchored to water sources they can exploit only those vegetable foods that lie within a reasonable walking distance of water. Food sources that lie beyond a reasonable walking distance are rarely exploited. (Lee, 1969: 56)

It is important to note that Lee defines a “reasonable walking distance” for foraging in terms not of the maximum distance water can be carried, but in terms of a radius within which a round trip does not exceed 1 day – beyond this, the time and energy costs of overnight trips away from water are considered generally too high to justify. Adaptation to the problem of scarce water is certainly a special problem for the !Kung, as Vayda and McCay argue, but it does not follow that energetic efficiency and effective responses to nonenergetic adaptive problems can be assumed to be competing or unrelated goals. During the dry season, the clustering of camps around waterholes means that food in the vicinity becomes scarce, and !Kung foragers must walk greater distances and expend more energy in order to maintain an adequate intake (Lee, 1969: 73). Indeed, water scarcity for the !Kung is not an absolute scarcity at all, but a scarcity in relation to food sources, or in other words, an environmental constraint on foraging efficiency. Lee puts it this way:

it is possible to summarize the basic principle of Bushman foraging strategy in a single statement: At a given moment, the members of a camp prefer to collect and eat the desirable foods that are the least distance from standing water. (1969: 59-60)

⁴In fact, the caloric nutrition of !Kung San foragers is at present controversial (Truswell and Hansen, 1976: 190; Marshall, 1968: 94). Lee *may* have been misled on this point by: (1) measuring only caloric intake, not expenditure; and (2) measuring this caloric intake only over a period of a few weeks, and not in the season of greatest scarcity for both food and water.

Such a strategy might not maximize the energetic efficiency of foraging, but it certainly fits the predictions of efficiency theory, although !Kung foraging must be more complex than Lee has stated it to be.

A more general point that can be derived from the arguments I have presented is that *if* !Kung foraging strategies are analyzed in terms of energetic efficiency, a measure of net acquisition rates should be used, rather than output/input ratios or gross acquisition rates [Lee (1969) used this last measure], regardless of the degree of energy limitation present. It follows directly that any foraging strategy that increased the net *rate* of energy capture would free time and energy from foraging so that other problems relevant to !Kung adaptive success (such as obtaining water, acquisition of mates, maintenance of social networks, etc.) could be dealt with more effectively.

Tsembaga Maring

Vayda and McCay (1975: 297) also use the example of the Tsembaga Maring, a population whose energy flow system has been extensively studied by Rappaport (1968, 1971). They argue that since the Tsembaga are not energy-limited their adaptive problems cannot fruitfully be analyzed in terms of energetic efficiency. However, it is not clear that the relevance of energy to Tsembaga adaptation can be so easily dismissed.

In the first place, the great bulk of Tsembaga subsistence is based on root crops; as Rappaport (1968: 63) notes, these are a primary source of calories but are poor in most other nutrients. Accordingly, it is valid to analyze root-crop production strategies and land-tenure systems in energetic terms — although Rappaport's reliance on output/input ratios rather than on net rates of energy capture is theoretically incorrect. Assuming that the Tsembaga are indeed not energy-limited, there is no clear adaptive advantage in their increasing the energetic efficiency of their horticulture solely to maximize the net energy captured. But if the same net output can be obtained with less work, time and energy may be freed from energy production that can then be directed toward the attainment of other goals that are important to Tsembaga adaptation.

Rappaport has presented evidence indicating direct competition between such goals and that of maximizing overall energetic efficiency. The Tsembaga raise pigs for eventual consumption, the caloric efficiency of which has been estimated at less than 1:1 in output/input terms. Such low efficiency, which is unexplainable if adaptive success were equated directly with energetic efficiency, is explained in terms of the role of pigs in providing scarce protein and fats in the diet. According to Rappaport (1968: 63), the Tsembaga in this case “make an investment of energy and get a return of nutrients that are extremely important, but not primarily as a source of energy.” While no one has conclusively demonstrated that pig-raising is a Tsembaga response to protein/fat scarcity,

the low return on their energetic investment revealed in Rappaport's data strongly suggests this possibility. If so, increased energetic efficiency in pig production would either provide more protein, or reduce the time and energy invested in obtaining the same amount, either of which might be of adaptive advantage. While considerations of energetic efficiency may not tell us why the Tsembaga raise pigs with little or no net energy gain, it may tell us why they do not raise pigs in any number of possible ways that would result in a *less* efficient conversion of time and effort into pigs.

I am not arguing that human ecological research need always focus strongly or even partially on energy flow or efficiency. But if an attempt is made to analyze the subsistence strategies of a population, the universal applicability of energy and time as general measures of costs and benefits makes an energetic efficiency approach very useful. There is no need to establish beforehand that energy is limiting, although the possibility that other dietary constraints (e.g., protein, iodine) are of overriding importance should be considered. To be sure, studies that simply demonstrate the energetic efficiency of subsistence systems in various human populations are of less value than research that uncovers major constraints on efficiency maximization or that connects energetic efficiency with significant questions in ecological and anthropological theory. The value of energy and time as general "currencies" for measuring or analyzing adaptive strategies can be demonstrated in other kinds of analyses [for instance, the analysis of spatial organization, territoriality, and social boundaries – see Dyson-Hudson and Smith (1978)] without regarding energy as a universal and ultimate measure of adaptive success. I have not raised the issue of whether increasing the total energy flow controlled by a social group is universally adaptive or a prime mover in cultural evolution [the view expounded in the cultural evolutionism of White (1959)]. Nor have I directly considered the view that labor energy (as opposed to trophic energy) is a generally scarce or limiting factor in human adaptation (see Morren, 1977). While this analysis has implications for these viewpoints, space limitations and a desire to maintain a central focus on energetic efficiency preclude examining them.

SUMMARY

Lotka's belief that energy was the fundamental object of evolutionary competition led him to postulate that the maximization of energetic efficiency was virtually an adaptive universal. While certain contemporary ecologists have adhered to this view and expanded on it, critics have pointed out that energy availability is not a universal adaptive problem, and have argued from this that neither the amount of energy nor the efficiency with which it is captured or put to use need be of great adaptive significance. The issue has thus focused to

a great extent on the degree to which energy limitations are important adaptive constraints. As I have tried to argue, this focus on energy limitations overlooks some important issues concerning energetic efficiency and general adaptive trends. In particular, I have presented an analysis that: (1) differentiates cases in which energy alone is the primary adaptive constraint from cases in which time and energy are constraints, (2) separates efficiency of energy *capture* from efficiency of energy *use* in accomplishing other goals, and (3) defines different types of energy limitation and different levels of adaptation. The main conclusion is that, where energetic efficiency is defined so as to include time constraints (i.e., as a net acquisition rate), the matter of energetic limitations is to some degree irrelevant, and energetic efficiency (properly defined) thus has general adaptive significance.

The whole controversy over the importance of energetic limitations has in a sense made us overlook the fact that adaptation to varied and heterogeneous environments always must eliminate grossly inefficient strategies. As Bruce Winterhalder (personal communication) has pointed out, if a human population does not exhibit overt signs of energy limitations, this could mean one of two things: either energy is so abundant that virtually any strategy of capture is sufficient; or, in fact very efficient strategies have evolved and should be of interest irrespective of a current absence of energy shortages. The latter possibility would suggest that strategies of low efficiency were selected against and eliminated in the history of the individual or population.

While the presence or absence of energy limitations does not serve to define the adaptive value of increased energetic efficiency, this distinction does have significance for analyzing the *uses* to which increased efficiency will be directed. Basic predictions deduced from the analysis presented above include: (1) in energy-limited systems, an increase in energetic efficiency (net acquisition rate) will be adaptive because it means that the total net energy available to the system can be increased without devoting more time to its capture; (2) in all systems where energy is not limiting but time is a significant constraint on adaptive success, increased energetic efficiency (net acquisition rate) will be adaptive because this will allow the same amount of net energy to be captured in less time. In other words, *energy-limited organisms should increase their energetic efficiency in order to increase total net energy captured, while non-limited organisms should increase their energetic efficiency in order to minimize the time spent acquiring energy*. The same or similar conclusions have been independently stated by evolutionary ecologists (Schoener, 1971: 376; Orians, 1971: 516).

It must be stressed that the conclusion that certain types of energetic efficiency are adaptive regardless of the degree of energetic limitations does not mean that energetic efficiency will be universally maximized. In the first place, as discussed above, what is selected for at one level of organization (e.g., the individual or kin group) does not automatically increase at other levels of

organization (the population, species, or ecosystem). Furthermore, other adaptive constraints and environmental fluctuations make it unlikely that the general-purpose goals of adaptation (survival, homeostasis, or Darwinian fitness, depending on the analytic framework) can be equated with a single variable such as energy or a single parameter such as energetic efficiency.

However, one should not automatically assume that other adaptive goals invariably compete with the efficient capture and use of energy. Consider the following statement from a recent textbook in ecology:

It is a mistake to believe that animals and plants have all evolved primarily as efficient converters of energy. The pressures of natural selection are pressures for survival, and survival may sometimes be more concerned with the efficient use of nutrients, ensuring that individuals mate, safe overwintering, or swift growth and dispersal, than with the efficient use, or even collection, of energy. (Colinvaux, 1973: 233)

This statement has been cited (Vayda and McCay, 1975) to support the assertion that, where energy is not limiting, other adaptive goals will conflict with the attainment of efficiency in the capture of energy. I would challenge the assumption that the attainment of various adaptive goals automatically or generally competes with energetic efficiency: if such efficiency results in more time available to invest in achieving other goals (as it will if we are talking about efficiency in *rates* of energy capture), it can hardly be assumed to be competitive. Once again, the question of time budgeting must be carefully considered before this judgment can be accepted in any specific case.

In conclusion, neo-Darwinian optimization theory is an important and useful tool in ecological research, whether we are focusing on humans or any other species. Energetic efficiency is one possible parameter of adaptive optimization, and models employing time and energy as "proximate currencies" facilitate comparison of many different cases, and thus the construction of general theory. However, efficient energy capture and use are only one type of factor that can affect adaptive success, and it must be stressed that energy has no real deductive priority over other factors. While energetic efficiency models might not account for many aspects of adaptation in any specific case, a measure of the degree to which energetic efficiency is maximized may be very helpful in indicating other ultimate forces that structure behavioral adaptation.

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version will eventually appear that more fully recognizes Dr. Thomas's contribution (Smith and Thomas, n.d.). The paper has also greatly benefitted from the criticisms and suggestions of Bill Durham, Bruce Winterhalder, and two anonymous reviewers. An earlier version was presented at a Columbia University Anthropology Seminar, November 1976, and at an Anthropology Department Colloquium, University of Massachusetts at Amherst. I received financial support from Cornell University during the writing (and rewriting) of this work.

REFERENCES

- Alland, A. (1975). Adaptation. *Annual Review of Anthropology* 4: 59-73.
- Alland, A., and McCay, B. (1973). The concept of adaptation in biological and cultural evolution. In Honigman, J. (ed.), *Handbook of Social and Cultural Anthropology*. Rand-McNally, Chicago, pp. 143-178.
- Brookfield, H. C. (1972). Intensification and disintensification in Pacific agriculture: A theoretical approach. *Pacific Viewpoint* 13: 30-48.
- Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bulletin* 76: 160-169.
- Brown, J. L., and Orians, G. H. (1970). Spacing patterns in mobile animals. *Annual Review of Ecology and Systematics* 1: 239-262.
- Caraco, T., and Wolf, L. (1975). Ecological determinants of group sizes of foraging lions. *American Naturalist* 109: 343-352.
- Charnov, E. L. (1976a). Optimal foraging: Attack strategy of a mantid. *American Naturalist* 110: 141-151.
- Charnov, E. L. (1976b). Optimal foraging: The marginal value theorem. *Theoretical Population Biology* 9: 129-136.
- Cody, M. L. (1974). Optimization in ecology. *Science* 183: 1156-1164.
- Colinvaux, P. A. (1973). *Introduction to Ecology*. Wiley, New York.
- Cottrell, F. (1955). *Energy and Society*. McGraw-Hill, New York.
- Durham, W. H. (1976a). Resource competition and human aggression: A review of primitive war. *Quarterly Review of Biology* 51: 385-415.
- Durham, W. H. (1976b). The adaptive significance of cultural behavior. *Human Ecology* 4: 89-121.
- Dyson-Hudson, R., and Smith, E. A. (1978). Human territoriality: An ecological reassessment. *American Anthropologist* 80: 21-41.
- Emlen, J. M. (1966). The role of time and energy in food preferences. *American Naturalist* 100: 611-617.
- Emlen, J. M. (1973). *Ecology: An Evolutionary Approach*. Addison-Wesley, Reading, Mass.
- Hamilton, W. J., III, and Watt, K. E. F. (1970). Refuging. *Annual Review of Ecology and Systematics* 1: 263-286.
- Harpending, H., and Davis, H. (1977). Some implications for hunter-gatherer ecology derived from the spatial structure of resources. *World Archaeology* 8: 275-283.
- Harris, M. (1968). *The Rise of Anthropological Theory*. Crowell, New York.
- Harris, M. (1975). *Culture, People, Nature*. Crowell, New York.
- Horn, H. S. (1968). The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). *Ecology* 49: 682-694.
- Jochim, M. A. (1976). *Hunter-Gatherer Subsistence and Settlement. A Predictive Model*. Academic Press, New York.
- Kozlovsky, D. G. (1968). A critical evaluation of the trophic level concept. I. Ecological efficiencies. *Ecology* 49: 48-60.
- Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Lee, R. B. (1968). What hunters do for a living, or, how to make out on scarce resources. In Lee, R. B., and DeVore, I. (eds.), *Man the Hunter*. Aldine, Chicago, pp. 30-48.

- Lee, R. B. (1969). !Kung Bushman subsistence: An input-output analysis. In Vayda, A. P. (ed.), *Environment and Cultural Behavior*. Natural History Press, Garden City, N.Y., pp. 47-79.
- Lee, R. B. (1972). !Kung spatial organization: An ecological and historical perspective. *Human Ecology* 1: 125-147.
- Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics* 1: 1-18.
- Little, M. A., and Morren, G. E. B., Jr. (1976). *Ecology, Energetics, and Human Variability*. W. C. Brown, Dubuque, Iowa.
- Lotka, A. J. (1922). Contributions to the energetics of evolution. *Proceedings of the National Academy of Sciences (U.S.A.)* 8: 147-188.
- MacArthur, R. H. (1972). *Geographical Ecology*. Harper and Row, New York.
- MacArthur, R. H., and Pianka, E. R. (1966). On optimal use of a patchy environment. *American Naturalist* 100: 603-609.
- Marshall, L. (1968). Discussion. In Lee, R. B., and DeVore, I. (eds.), *Man the Hunter*. Aldine, Chicago.
- McNab, E. K. (1963). Bioenergetics and the determination of home range size. *American Naturalist* 97: 133-140.
- Morren, G. E. B. (1977). From hunting to herding: Pigs and the control of energy in montane New Guinea. In Bayliss-Smith, T. P., and Feachem, R. G. (eds.), *Subsistence and Survival, Rural Ecology in the Pacific*. Academic Press, New York, pp. 273-315.
- Odum, E. P. (1971). *Fundamentals of Ecology*. 3rd ed. Saunders, Philadelphia.
- Odum, H. T. (1971). *Environment, Power, and Society*. Wiley, New York.
- Odum, H. T. (1974). Energy, ecology and economics. *CoEvolution Quarterly* 1: 8-16.
- Odum, H. T., and Odum, E. C. (1976). *Energy Basis for Man and Nature*. McGraw-Hill, New York.
- Orians, G. H. (1971). Ecological aspects of behavior. In Farner, D., and King, J. (eds.), *Avian Biology*, Vol. 1. Academic Press, New York, pp. 513-546.
- Perlman, S. M. (1976). *Optimum Diet Models and Prehistoric Hunter-Gatherers: A Test on Martha's Vineyard*. Ph.D. thesis, University of Massachusetts, Amherst.
- Pianka, E. R. (1974). *Evolutionary Ecology*. Harper and Row, New York.
- Pyke, G. H., Pulliam, H. R., and Charnov, E. L. (1977). Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology* 52: 137-154.
- Rappaport, R. A. (1968). *Pigs for the Ancestors*. Yale University Press, New Haven.
- Rappaport, R. A. (1971). The flow of energy in an agricultural society. *Scientific American* 224(3): 116-132.
- Rappaport, D. J. (1971). An optimization model of food selection. *American Naturalist* 105: 575-588.
- Richerson, P. J. (1977). Ecology and human ecology: A comparison of theories in the biological and social sciences. *American Ethnologist* 4: 1-26.
- Ricklefs, R. E. (1973). *Ecology*. Chiron Press, Newton, Mass.
- Rogers, E. S., and Black, M. B. (1976). Subsistence strategy in the fish and hare period, Northern Ontario: The Weagamow Ojibwa, 1880-1920. *Journal of Anthropological Research* 32: 1-43.
- Royama, T. (1970). Factors governing the hunting behavior and selection of food by the great tit (*Parus major* L.). *Journal of Animal Ecology* 39: 619-668.
- Sahlins, M., and Service, E. (eds.). (1960). *Evolution and Culture*. University of Michigan Press, Ann Arbor.
- Schoener, T. W. (1968). Sizes of feeding territories among birds. *Ecology* 49: 123-141.
- Schoener, T. W. (1969). Models of optimal size for solitary predators. *American Naturalist* 103: 277-313.
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369-404.
- Slobodkin, L. B. (1968). How to be a predator. *American Zoologist* 8: 43-51.
- Slobodkin, L. B. (1972). On the inconstancy of ecological efficiency and the form of ecological theories. *Transactions of the Connecticut Academy of Sciences* 44: 291-305.

- Slobodkin, L. B. (1974). Prudent predation does not require group selection. *American Naturalist* 108: 665-678.
- Smith, C. C. (1968). The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. *Ecological Monographs* 40: 349-371.
- Smith, E. A. and Thomas, R. B. (n.d.). Energetic efficiency and adaptation. In Thomas, R. B., and Harris, L. D. (eds.), *Energy Flow and Human Adaptation*. In preparation.
- Stern, J. T., Jr. (1970). The meaning of "adaptation" and its relation to the phenomenon of natural selection. In Dobzhansky, T., Hecht, M. K., and Steere, W. C. (eds.), *Evolutionary Biology*, Vol. 4. Appleton-Century-Crofts, New York, pp. 39-66.
- Thomas, R. B. (1973). *Human Adaptation to a High Andean Energy Flow System*. Occasional Papers in Anthropology, No. 7, Department of Anthropology, Pennsylvania State University, University Park, Pennsylvania.
- Truswell, A. S., and Hansen, J. D. L. (1976). Medical research among the !Kung. In Lee, R. B., and DeVore, I. (eds.), *Kalahari Hunter-Gatherers*. Harvard Univ. Press, Cambridge, pp. 166-194.
- Tullock, G. (1971). The coal tit as a careful shopper. *American Naturalist* 105: 77-80.
- Vayda, A. P., and McCay, B. J. (1975). New directions in ecology and ecological anthropology. *Annual Review of Anthropology* 4: 293-306.
- White, L. A. (1949). *The Science of Culture*. Grove Press, New York.
- White, L. A. (1959). *The Evolution of Culture*. McGraw-Hill, New York.
- Williams, G. C. (1966). *Adaptation and Natural Selection*. Princeton University Press, Princeton, N.J.
- Williams, G. C. (ed.). (1971). *Group Selection*. Aldine, Chicago.
- Wilmsen, E. N. (1973). Interaction, spacing behavior, and the organization of hunting bands. *Journal of Anthropological Research* 29: 1-31.
- Wilson, E. O. (1973). Group selection and its significance for ecology. *BioScience* 23: 631-638.
- Winterhalder, B. P. (1977). *Foraging Strategy Adaptations of the Boreal Forest Cree: An Evaluation of Theory and Models from Evolutionary Ecology*. Ph.D. thesis, Cornell University, Ithaca, N.Y.
- Winterhalder, B., Larsen, R., and Thomas, R. B. (1974). Dung as an essential resource in a highland Peruvian community. *Human Ecology* 2: 89-104.
- Wobst, H. M. (1974). Boundary conditions for Paleolithic social systems: a simulation approach. *American Antiquity* 39: 147-178.
- Wolf, L. L., Hainsworth, F. R., and Gill, F. B. (1975). Foraging efficiencies and time budgets in nectar-feeding birds. *Ecology* 56: 117-128.
- Yellen, J., and Harpending, H. (1972). Hunter-gatherer populations and archaeological inference. *World Archaeology* 4: 244-253.