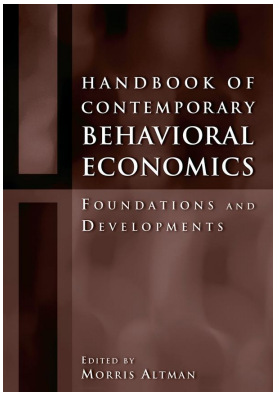

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Morris Altman

How to Do as Well as you Can

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PART 3

DECISION MAKING

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CHAPTER 14

HOW TO DO AS WELL AS YOU CAN

The Psychology of Economic Behavior and Behavioral Ecology

STEPHEN E.G. LEA

This essay seeks to locate the emerging discipline of behavioral economics by setting out a general point of view about the relationships between three disciplines. It is not primarily a summary or an introduction to the literature of a particular part of behavioral economics, but it does provide samples of research literature that illustrate its general theme.

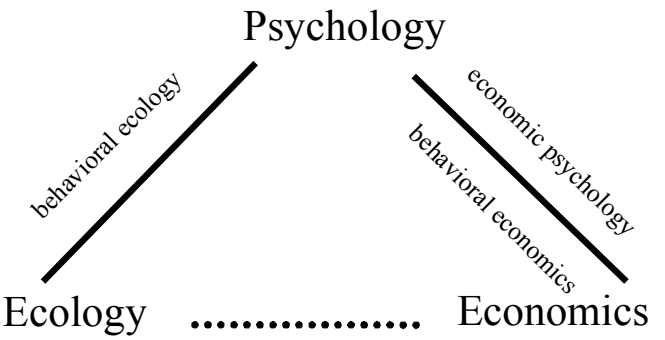
The point of view expounded in this essay is simple. It is that the sciences of ecology, economics, and psychology overlap more than has been realized; that there are problems, important in both scientific and social terms, that can be solved only by using psychological analysis along with economic analysis, ecological analysis, or both; and that if we are to make progress with this kind of interdisciplinary approach, we need paradigms different from those currently most often used.

In part of its argument, at least, this essay stands in the mainstream of other contributions to this handbook. All the present essays share, in one way or another, the view that psychology and economics have something important to do with each other. But this essay is about the meeting of three disciplines, not two, and its arguments about the relation between psychology and ecology will have less supportive context in the rest of the book. They may perhaps be less immediately persuasive, especially as they refer as much to animal psychology as to human psychology. It should be recognized at once that the essay is making the implicit assertion that there is some psychological unity across species, although of course it also recognizes the essential psychological differences between humans and other animals.

Since this essay is written by someone who is, by training, a psychologist, psychological analysis may tend to take pride of place here. But that is not to say that it is in any way more important, or more fundamental, than the ecological or economic approach. The thrust of the argument is the need for more interdisciplinary work, and that will not be furthered by mere disciplinary imperialism—trying to pretend that psychology could "take over" economics, or vice versa.

It might be expected that a balanced presentation of the relations between three disciplines would be structured as a triangle, with each discipline relating to the other two. In practice, however, this essay largely discusses the relations between psychology, on one hand, and ecology and economics, on the other: the structure of the discussion is illustrated by Figure 14.1. It is a key part of the argument that psychology relates to both ecology and economics in essentially the same way, while the relation between ecology and economics is rather different. However, at the end of the essay, that third side of the triangle is briefly reviewed.

Figure 14.1 **Relations Between the Disciplines of Psychology, Ecology, and Economics**



This essay shares its title with the Lister Lecture given by the author in 1983 to the British Association for the Advancement of Science, the foremost public showcase for science in the United Kingdom. Returning to that title more than twenty years later provides an opportunity to reexamine themes expounded in the lecture and see how they have progressed after two decades—a period that has seen crucial developments both in behavioral economics and in behavioral ecology, with those two interdisciplinary areas moving strongly toward the mainstream. In 1983 it seemed necessary both to demonstrate and to justify an upsurge in interdisciplinary activity that was beginning to involve psychology in both economic and ecological analyses—to point to both intellectual and institutional developments, as well as events in the world, that were making economic psychology and behavioral ecology active research areas and familiar concepts. Now, and especially in the context of the present volume, that argument scarcely needs making.

However, it remains worth asking why interdisciplinary research areas develop. Do they arise at times when the mainstreams of traditional disciplines are running dry of research openings, forcing the ambitious to the fringes? In the middle of the twentieth century a standard biochemistry textbook offered a cynic's definition of biochemists as men who talk about chemistry to biologists, about biology to chemists, and about women among themselves. It is not just the sexist humor that has dated irreversibly: the subsequent history of biochemistry has triumphantly refuted the author's skepticism about his own discipline. By 1948, when that book was first published, both chemistry and biology had reached a stage of development where, for further progress in certain well-defined directions, they needed each other, and half a century later we have seen how the new science of biochemistry has transformed our understanding of life and of human society.

The argument of the present essay is that by about 1975 a similar point had been reached in the relations of psychology with both economics and ecology. Some of the traditional concerns of psychology, particularly in the areas of instrumental behaviors (human and animal), could no longer be tackled without using the kind of approach characteristic of economics or ecology. And some of the traditional concerns of economics and ecology, such as the response of consumers to changes in price and income, and of foraging animals to the availability of food, were ripe for the sort of empirical input about the attitudes and behavior of individuals that only a psychological approach could provide. A quarter of a century further on, it is possible to look at the progress that has been made in forging interdisciplinary links.

PSYCHOLOGY AND ECONOMICS, PSYCHOLOGY AND ECOLOGY

Before considering the substance of interdisciplinary work, however, it is necessary to look a little more systematically at the nature of the relationships between the three disciplines with which this essay is concerned—at least in their traditional, monodisciplinary forms.

Two things mark off psychology from either economics or ecology: a difference of subject matter and a difference of approach. At first glance, it might seem that the really fundamental difference is that of subject matter. If we are interested in individual behavior and mental life, that makes us psychologists. If we are interested in the movements of scarce resources, of money and goods, around whole social systems, that makes us economists. If we are interested in the interactions of whole species of animals with the other species that constitute their biological environment, that makes us ecologists.

A second glance makes it clear that these differences are relatively superficial. On one hand, societies and species are made up of individuals, so the behavior of economies or species are products of individual behavior, and the leading theories in both fields attempt to derive the behavior of aggregates from the behavior of individuals. On the other hand, the prevailing economic or ecological situation has an important influence on every individual within it. Consequently, long before the institutions of economic psychology and behavioral economics came into existence, there were areas in which both economists and psychologists were taking an interest. The motivation and incentive for work behavior is an obvious example. Similarly for psychology and ecology: both have a long-standing interest in feeding behavior, for example. What makes an approach to a problem ecological or economic rather than psychological is not the problem under consideration but the framework within which the problem is viewed.

That framework is partly a matter of the other problems that form the context for looking at any one particular problem. An economist approaching the incentive to work sees employment as one more situation in which a commodity is bought and sold, so it can be compared with the purchase and sale of goods and services. A psychologist sees it as one more situation in which people enter into social relations, so the workplace can be compared with the family, the neighborhood, and other scenes of interpersonal interaction. Similarly with feeding behavior: an ecologist might see it as one way in which the numbers and fitness of animals of one species are acted on and act upon the numbers of other species, to be compared with competition for space or the spread of disease. A psychologist, on the other hand, might see it as one variety of motivation or reinforcement, to be compared, perhaps, with sexuality or curiosity.

Much more important, however, is the theoretical lens through which any problem is viewed. Psychologists, by and large, are low-level theorists. Faced with a new phenomenon, or a new area of study, our first inclination is to collect some data. When we have a fair amount of data in hand, we usually try to produce a descriptive generalization rather than interpreting the data in terms of any wide-ranging theory. When we do carry out a theory-driven investigation, the theory in question is normally quite specific, not part of some grand general approach to the whole of psychology. One psychologist might inquire, for example, whether Maslow's (1970) hierarchical theory of motivation applies to the employment situation, but another could regard Maslow as wholly irrelevant to the problem without thereby ceasing to be a psychologist.

Both economists and ecologists behave very differently. Each discipline has its grand theory, which is part of, and characteristic of, an economic or ecological approach to any problem whatever. In the case of economics, it is the theory of rational decision making; in the case of ecology, it is Darwin's theory of the evolution of species by natural selection. There are differences, both in substantive content and in logical status, between these two theories. But in

terms of their relations to psychology, both say somewhat the same thing. They say that individuals—animal or human—will do the best they can. Economists tend to describe this as behaving "rationally," ecologists as behaving "optimally," but each discipline has powerful reasons for expecting it to happen.

So when either an ecologist or an economist approaches a new phenomenon or a new problem area, his or her first urge is not to set up a study and collect some data. It is to apply the grand theory and find out what ought to happen. That "ought" has two senses. In the first sense, it asks what the predictions of the grand theory are. In the second, it asks how the individual animal or person should behave if he, she, or it is to do as well as possible in the given situation. That is not to say that either ecologists or economists do not collect data. No one would ever have supposed that of ecologists, but a reader of elementary economics textbooks might be forgiven for thinking it of economists. Most elementary treatments of the discipline, and even some of its most prestigious research, pay no attention to the huge masses of econometric data that are constantly being collected and analyzed, charting the effects of changes in prices, incomes, and other conditions on important economic behaviors such as hours worked, amounts of goods and services bought and sold, and amounts of money saved. One of the major changes over the past twenty years, however, has been that economics has become an empirical discipline in an additional sense, through the rapid development of a lively subdiscipline of experimental economics, crowned in 2002 by the award of the Nobel prize to Vernon Smith "for having established laboratory experiments as a tool in empirical economic analysis, especially in the study of alternative market mechanisms."

But though both ecology and economics are genuinely empirical disciplines, they are both theory-driven in a sense that psychology is not. It is possible to ask, "What does economic theory say about this question?" and obtain a coherent answer. If you then ask, "And what does psychological theory say?" the only reasonable answer would be "Which psychological theory?" This fact imposes an asymmetry on the relationship between the disciplines; it has also led to the tacit adoption of a paradigm for behavioral investigation of economic questions that has frequently been unhelpful.

THE PITFALL OF THE RATIONALITY QUESTION

The fact that economics and ecology as disciplines are unified by a coherent theory sets a snare in the path of the psychologist who becomes interested in the sorts of questions studied by ecologists or economists. All too readily, psychologists see themselves as able to produce the data by which the assumption of rationality or optimality can be tested, so that the role of psychology is testing (and probably refuting) that assumption. Most psychologists believe that humans or animals faced with real economic or ecological problems will not, in fact, do as well as they can. Data from other situations, and any one of the numerous low-level theories psychology can muster, make this seem obvious.

Twenty years ago, it was necessary to spend a good deal of time clearing the issue of the rationality question out of the way. At that point it still virtually formed a paradigm, in the sense in which Kuhn (1962) used that term. When economic psychology approached a new research area, the tendency was to marshal ideas, theories, and data into those that support rationality and those that oppose it. All too often the result looked like a contest between psychology and economics, or between psychology and ecology. Increasingly, however, economic psychologists have taken the view that this way of looking at the area is fundamentally misguided (e.g., Lea 1994). Not only does a pro- and anti-rationality paradigm tend to set up oppositions between

disciplines when what is needed is collaborative effort, but it rests upon a misconception about the nature and role of the rationality or optimality assumption in the first place.

Part of the problem is the multitude of different things we might mean when we say that behavior is rational. For the present essay, a particularly important distinction is between descriptive and procedural rationality (Simon 1978). If we are using rationality as a description, we describe a behavior as rational if it is the one that would be performed by an ideally logical decision maker, armed with all the available information, and able to calculate from it what the best thing to do is—what Gigerenzer and Goldstein (1996) call a "Laplacean demon." But if we are using rationality to define a procedure, we would mean that the person taking the decision was or was seeking to be such an ideally logical decision maker, that is, that the person used rational forethought in coming to a decision: there is then no commitment as to how successful the decision maker has been. It is obvious that descriptive rationality and procedural rationality do not entail each other. On one hand, the kind of cognitive limitations that Simon has constantly pointed out means that people who are seeking to be rational will almost necessarily fail to equal the performance of the Laplacean demon. On the other hand, we can envisage that entirely mechanical processes, such as could be conferred on animals by the evolution of instincts, might produce optimal behavior in particular situations without any need or possibility of reflective forethought (cf. Lea 1978).

Ecologists have always been perfectly clear about the status of rationality (more usually called optimality in the ecological context) within their theorizing. The theory of natural selection leads them to expect that optimality will hold, more or less, at the descriptive, behavioral level. It makes no prediction whatever about the mechanism underlying that behavior. Ecologists will readily agree that even if an animal's foraging behavior agrees with an optimal model, it is still unlikely that the animal is consciously working out the best possible way to get food. It is much more likely that some mechanism other than rational forethought is responsible for producing rational behavior. In other words, the word *rationality* confuses two things that biologists have learned, by painful experience, to keep separate: functional explanations and mechanistic explanations. When we have specified the function of some organ or piece of behavior, we have indeed explained it in one important sense. We have provided what is often called an ultimate explanation—an explanation within the terms of evolutionary theory. But we have not provided a proximate explanation until we have also specified the mechanism by which the function is exercised. As an aside to the present argument, we should note that we also need a third sort of explanation, a developmental account, specifying how the individual organism develops from not having that organ or behavior as an embryo to possessing it in the full adult form. Behavioral economics also needs its developmental arm, and the attempt to discover the socialization processes that underlie adult economic behavior has been one of the more fruitful avenues for interdisciplinary research (cf. Harbaugh, Krause, and Berry 2001; Webley 2004).

Compared with ecology, mainstream economic thinking has in general not been so clear about the distinction between ultimate and proximate causation. It has used the human capacity for rational forethought as a guarantee that rationality will provide an appropriate descriptive account of behavior, and that argument is unsound. It is not in doubt that humans can use rational forethought. But the fact that I have feet does not mean that I necessarily stand up all the time, nor does the capacity for rational forethought mean that all behavior will be governed by it. And even when I do think rationally, I may not be able to mobilize all the information that the ideal decision maker would use, or to process it in the time available—to return to Simon's fundamental point about the external and internal bounds for rationality.

Of course, within economics there are alternative arguments according to which human economic

behavior can be expected to be rational at the descriptive level. In the case of firms rather than individuals, competition processes will impose a kind of selection not unlike that spurring genetic evolution in animals: firms that behave optimally will be more likely to survive in such a climate than suboptimal firms, which will be bankrupted, so the remaining firms will all behave in ways that seem fairly rational (Hirshleifer 1977). However, as Cyert and March (1963) point out, such competitive pressures are often ineffective outside periods of dire financial stringency, and the recent history of the dot-com boom and the behavior of firms such as Enron shows how very far from optimality firms' behavior can get—even if in the longer run a competitive nemesis is waiting for them.

Such arguments show some awareness of the distinction between proximate and ultimate causation. Furthermore, within economics there have always been dissident voices, arguing for a more nuanced concept of rationality (e.g., March 1978). But still one can find economics and psychology being set up as rival systems for explaining behavior, one assuming rationality and the other denying it. To economic psychology, such contests are or should be wholly irrelevant. What matters to an economic analysis is to characterize the rational behavior in a given situation. What matters to a psychological analysis is the mechanism producing rational behavior, or (more usually) something like it, or (unusually) something quite unlike it. The two questions are almost entirely independent. This is one reason why asking whether or not observed performance is rational is a poor way to approach the psychological foundations of economic behavior.

However, the most important reason for rejecting "testing rationality" as a paradigm for interdisciplinary research is that mainstream economics treats the assumption of rationality in a rather special way. When it discovers some aspect of economic behavior that is manifestly irrational, it does not reject the assumption; instead, it changes the definition of rationality. For example, all authorities agree that people are too much inclined to accept present gain at the cost of future loss. One simple way in which this "excessive time preference" (in economic terms) or "failure to delay gratification" (in psychological terms) can be made consistent with rationality is simply by specifying a subjective discount rate that is different from the objective rate at which an abstractly rational decision maker would discount the future (e.g., Friedman 1963), or, if no single subjective discount rate will do the job, a subjective discount function different from the exponential decay function implicit in standard rationality (for example, the hyperbolic form proposed by Ainslie 1992). Psychologists sometimes feel there is something unsatisfactory about this tinkering with rationality. On the contrary, it is simply a device to enable the apparatus of economic theory to work, to produce descriptive accounts of the sense in which behavior is rational.

According to this formalist view, rationality within economics is not a theory to be tested. It is a framework within which behavior can be described and smaller-scale theories about it tested. A psychological approach that sets itself to test rationality is therefore doomed to irrelevance within an interdisciplinary perspective (Lea 1994).

Everything that has been said here about the relation between psychology and economics applies with equal force to the relation between psychology and ecology. But in this respect, at least, one is preaching to the converted in the case of ecology; the status of the optimality assumption within ecology is much better understood by both psychologists and ecologists than the status of the rationality assumption within economics.

ALTERNATIVE FRAMEWORKS FOR ECONOMIC PSYCHOLOGY

If we cannot organize a fruitful interdisciplinary discussion around the rationality question, what structure can we use? Are there any alternative paradigms? Much of the rest of this essay is taken up with the discussion of two possibilities, which are complementary rather than competing.

First, we could opt for a division of roles between psychology and economics. We give to economics its traditional role of describing behavior in terms of rationality: of finding rational models that are consistent with at least the gross facts of observed behavior (or, in other words, of finding how the simple assumption of rationality must be modified and fleshed out if it is to be a valid description of behavior). We then give to psychology the task of discovering the mechanism and the process of development that gives rise to more or less rational behavior. This is very much the solution that has been adopted in the ecological case. This will be referred to below as the "function/mechanism" or "ultimate/proximate explanation" paradigm.

Within this paradigm, it is very plain that psychology can and should tell you *how* to do as well as you can. Economics or ecology will tell you what the best thing to do is; psychology will furnish the mechanism by which to produce this rational or optimal behavior, or the nearest approach to it that you can manage with the cognitive resources you have. It will do so whether we are talking about the immediate mechanism of one small instance of behavior or the process of lifetime development that produces the behavioral tendencies that in turn solve problems in the optimal way.

The second alternative refers back to the point made earlier in this essay, that disciplines are separated not by their subject matter but by the manner in which they approach it. Psychology focuses on the individual. Economics and ecology both focus on the structured whole, the society within which the individual must live. Within the social sciences generally, there have always been two ways of seeking to understand both individuals and societies. One is the atomistic approach, which starts from the individual and attempts to understand the entire society as the aggregation of the knowable behaviors of individuals. The alternative is the organic approach, which starts from the entire society, treating it as an entity with behavior of its own and laws of its own governing that behavior, and attempts to understand the individual as a product of the knowable behavior of the society he or she lives in. Applying these two broad approaches to the narrower context of economic behavior, it is evident that we can either start from the choice behaviors of individuals and try to aggregate them so as to understand the entire economy, or we can start from the behavior of the economy as a system and try to deduce individuals' economic behavior. It is important to recognize that though psychology focuses on the individual while economics focuses on the system, it is not the case that psychology is atomistic while economics is organic. True, there are tendencies in those directions. But Anglo-American economics, at least, is almost as atomistic in its general trends as Anglo-American psychology; microeconomic theory is the field par excellence of the analysis of system-level economic phenomena in terms of individual choice behaviors. The doctrine of "consumer sovereignty" means nothing else but that the entire behavior of the economy can be predicted from the choice behavior of individual consumers: in the words of the 1990s Ford Europe slogan lifted from a Queen lyric, "Everything we do is driven by you."

A more radical proposal for a framework within which to study economic psychology, therefore, involves accepting that atomistic and organic approaches to society both have validity—that they are complementary rather than competing—and furthermore that both economics and psychology make use of both. In other words, there is a dual causation both of individual economic behavior and of large-scale economic phenomena. Both are caused partly by processes operating at the level of the entire economy and partly by processes operating at the level of the individual. Lea, Tarpy, and Webley (1987) developed this approach more fully. We called it the "dual causation paradigm"; it is in many ways a simplified version of the basic model for economic psychology set out by Van Raaij (1981) in the first issue of the *Journal of Economic Psychology.*

This might seem a modest proposal, since it simply recognizes some obvious realities. In

practice, however, it is quite radical, because rejecting the assumption of unidirectional causation means accepting a range of methodological difficulties. Once we accept that economic behavior is embedded within a social system, we have to accept that many investigations of economic behavior are likely to give inconclusive or misleading results. Dual causation implies circular causation, that is, feedback processes. Where social feedback is negative, causal processes that have been discovered in isolated systems (e.g., the laboratory) will often fail to have any effect when we study them in their original societal context. Even more unsettling, where social feedback is positive, effects may occur for which there is very little apparent cause. Biochemists must constantly make the distinction between in vitro and in vivo behaviors of reagents; behavioral economists need to draw the same distinction—and, like biochemists, not reject laboratory results because they cannot be reproduced on the societal scale. It is impossible to understand a social process without understanding the individual processes that make it up, even if in the social context those individual processes do not reach the same logical end points as they do in the laboratory.

Everything that has been said in this essay so far has been abstract. The remainder of the essay reviews the use of both these alternative frameworks in three specific, concrete areas where psychology overlaps with economics and ecology. In terms of their nonpsychological content, the first belongs purely to ecology, the second is a hybrid of ecological and economic questions, and the last is purely economic. Each of them is examined with the aid of the two paradigms just discussed. It will quickly become apparent that the two approaches are by no means mutually exclusive. It is especially important to realize that they are not alternative theories to be tested against one another. Even the rationality-question paradigm, which we earlier rejected as a general key to understanding, will turn out to have some place in the ensuing discussions.

THE PSYCHOLOGY OF FORAGING

As an ecological example, we shall consider the case of foraging for food and, more particularly, of optimal foraging theory.

This case is particularly easily analyzed within the function/mechanism paradigm. Ecology has always been interested in feeding, for food availability is one of the major factors with the potential to limit the numbers of any animal species. MacArthur and Pianka (1966) first stated clearly a very simple idea that has been immensely influential. Each animal species, they argued, has been produced by natural selection. The efficiency of foraging—hunting for food, whether animal or vegetable—will have a powerful influence on the fitness of any animal, that is, on the number of descendants it manages to leave. Natural selection implies that any behavior that increases foraging efficiency, so as to give one animal a competitive edge over its neighbors, will be selected for strongly. In fact, this selection pressure is likely to be so strong that all the animals in the species will end up as optimal foragers within their own particular environment: they will become so efficient that no further improvement is possible. At any rate, there will be no way an individual can improve without changing radically the sort of animal it is.

This idea is a special case of the general claim that natural selection will produce descriptively rational behavior. It forms the core of what has become known as optimal foraging theory. That theory is only interesting, however, because we can add substantially to that core. It proves to be possible to specify the optimal foraging "strategy" in a number of environments that are at least reasonable approximations to the infinitely complex real environment in which real foragers live. For example, we can consider an environment that contains a number of different kinds of prey, differing both in their food value and the time it takes to eat them; the general optimal foraging

theory is then specialized to provide an optimal diet model. Or we can consider an environment that contains perceptible patches within which some food is to be found, but between which there is only barren land across which the forager must travel to get from patch to patch; we then generate a patch selection theory (Charnov 1976). Or we can consider an environment that contains a central "home," where the forager feeds its young or stores food for later consumption, and more or less distant feeding grounds, and develop a theory for the central-place forager (Orians and Pearson 1979).

The obvious move is then empirical: go out into the field, study some real animals' foraging behavior, and see whether it is as optimal foraging theory suggests that it should be. In the years following MacArthur and Pianka's paper, there have been almost innumerable studies doing just that, either in wholly natural situations or in reasonable approximations to them arranged in the laboratory. An early example was Goss-Custard's extensive studies of redshank feeding in the mud of English estuaries. Goss-Custard (1977) found that redshanks' selection between different kinds of prey was much more affected by the availability of the better kinds of prey than by the availability of the worse kinds (this is one of the more surprising predictions of optimal diet models). On the other hand, the redshank occasionally sampled all kinds of prey, whereas theory predicts that, provided they are present in sufficient density, only the better kinds will be taken.

Initially, optimal foraging theory was almost wholly an affair for behavioral ecologists. But then psychologists began to take an interest. A number of people asked themselves whether the predictions of optimal foraging theory would hold for animals working in the quite unnatural, abstract conditions of the psychological laboratory, as well as under more natural circumstances. Using rats and pigeons and the conventional apparatus and procedures of the operant conditioning laboratory, it was quickly demonstrated that there was nothing special about the natural environment. Collier and Rovee-Collier (1981) showed that optimal foraging theory provided a good prediction for the behavior of rats in a Skinner box when choices were structured to resemble those facing natural foragers; Lea (1979) obtained the same result from pigeons and extended the experiment to various situations in which laboratory animals are known to behave suboptimally from the point of view of maximizing the rate of food intake; and Abarca and Fantino (1982) brought these experiments within the context of a general mechanistic approach to animal choice, delay-reduction theory.

All empirical tests of optimal foraging theories are, in one sense, raising the question of the validity of rationality assumptions. But the general trend has been away from questions of optimality as such, toward a much healthier concentration on the mechanism by which either optimal or nearly optimal behavior is produced. This is a question to which psychologists have a great deal to contribute, because that mechanism must necessarily involve some learning, and animal learning is one topic on which psychologists have gathered a great many data and a great many ideas.

Even the simple kinds of foraging problem described above require some level of learning. Optimal behavior varies according to the densities of different kinds of prey in different places, and in a changing environment these must be learned from day to day and even from minute to minute. The operant psychology that emerged from B.F. Skinner's analysis of instrumental learning provided simple tools by which the learning of such parameters could be studied (cf. Dow and Lea 1987; Killeen et al. 1996). Conversely, the general need of animals to forage optimally provided a much-needed ecological and evolutionary context and anchoring for the principles of operant psychology, which had previously seemed a wholly artificial creation.

However, consideration of the needs of foraging animals has contributed a great deal more to the study of animal learning than just providing an adaptive rationale for the well-understood principles of classical and operant conditioning. In the final quarter of the twentieth century, the

psychological study of animal learning was dominated by a new approach, usually referred to as "animal cognition" (Pearce 1997; Vauclair 1996): instead of trying to derive everything from a bottom-up analysis of behavior, psychologists have been taking cognitive analyses and concepts that are effective in the study of human mental life and seeing whether they can be applied effectively to other animals. Part of the thrust of this approach is to consider why and how human cognitive capacities may have evolved. A particularly powerful way to do this is to consider species that have unusual foraging needs and to investigate whether these are matched with unusual cognitive capacities.

So, for example, in seeking to investigate memory processes in animals, psychologists and zoologists have turned their attention to species that cache food in times of abundance and recover their caches in times of scarcity. From the point of view of memory, the most interesting cachers are those that make a large number of small hoards, because (for obvious reasons to do with preventing cache robbery) such caches cannot be marked in any way, nor can they be placed where they could be discovered by smell or other public cues. The animals must rely on a private cue to take them back, sometimes months later, to the cache sites, and the only obvious candidate is pure memory. The memory load this implies can be severe, because the caches that some animals make are very numerous: Clark's nutcracker, a bird of the American West, has been calculated to cache 20,000 to 100,000 seeds each autumn, in caches containing between one and fourteen seeds each (Vander Wall 1990, 300–5), while in England the gray squirrel needs to hide and recover around 3,000 nuts each year in order to survive the winter (Macdonald 1997). Here the ecology of foraging sets a problem, and comparative psychologists have set themselves to solve it by seeking to find out the cognitive mechanisms (e.g., Kamil, Balda, and Olson 1994) and even the brain structures (e.g., Basil et al. 1996) underlying these exceptional performances. It turns out that scatter-caching species do have exceptional memories when compared with otherwise similar animals that do not cache, and that these abilities are mirrored in an enlarged hippocampus, a part of the brain that in birds and nonhuman mammals seems to have a specialized function as a spatial memory store.

From an evolutionary point of view the most interesting cognitive adaptations are those that we find in the animals most closely related to ourselves, and which might therefore pave the way for the emergence of human intelligence. Here a good example would be some recent work on food processing techniques in chimpanzees and gorillas (Byrne, Corp, and Byrne 2001; Corp and Byrne 2002a, 2002b). One might expect the great apes, as the most intelligent animals in their environments, to have a wide choice of food sources. In fact they do not: Byrne and colleagues show that they survive thanks to their ability to exploit foodstuffs that other species can make no use of, such as thistles and *Saba florida* fruits, because the apes alone have the manual dexterity and learning ability that enable them to prepare for eating plants that are well protected by their structure against less intelligent predators.

So far our study of foraging has given us plenty of evidence of the way in which ecology specifies the optimal behavior, and psychology looks for evidence of how individual animals forage as well as they can. The function/mechanism paradigm for economic psychology or behavioral ecology has been well to the fore. But is there any place for the second alternative, the dual causation paradigm? Clearly there is. At the broadest level, the evolution of specialist brain structures and cognitive mechanisms, as in squirrels or great apes, changes the range of behaviors that an individual can emit. But there are also top-down, societal influences that are important on the much shorter time scale of an individual forager's lifetime. What is optimal for a given individual depends on the qualities and quantities of prey present and the skills that the individual has acquired in the course of its development, but it does not depend only on these individual and

environmental factors: it also depends on the society in which the individual lives. Goss-Custard, Cayford, and Lea (1998) showed that early in the autumn, juvenile oystercatchers feeding on the mussel beds of the River Exe estuary could make a substantial contribution to their food intake by robbing other birds of mussels those birds had already opened; by October, however, the victims of such kleptoparasitism became sharply more aggressive, shifting the juvenile birds' balance of advantage toward foraging for themselves (at which they were in any case becoming more adept).

Just as social processes affect foraging, so the foraging situation may affect social structure. An early study was carried out in the laboratory by Goldstein, Johnson, and Ward (1989), using rats in a large arena that contained eight operant conditioning setups, each with a lever and a food dispenser, as in a conventional Skinner box. The cost of food at different places in the environment could be controlled precisely by setting up schedules of reinforcement to determine when food would be delivered. The rats could move freely from one lever/dispenser combination to another. The researchers were therefore able to study the number of rats feeding at any one station, and show that the distribution of animals depended on the schedules of reinforcement used and their parameters—for example, the more presses required to obtain each pellet, the more dispersed the rats tended to be. This is a demonstration at a small scale, and on a moment-to-moment basis, of something that is almost certainly critical on the large scale and over the evolutionary time frame: the differences of social structure between species within related groups are probably best understood in terms of differences in their characteristic prey distribution (Clutton-Brock and Harvey 1977; Wrangham 1979).

In the study of animals' foraging behavior, we have seen a most fruitful collaboration between psychologists and ecologists, psychological analysis and ecological analysis. If psychologists had confined themselves to trying to prove that foraging behavior was not optimal and ecologists had confined themselves to defending optimal foraging theory at all costs, very little progress would have been made. What, though, of human foraging, and how it might have impacted on our cognitive evolution?

It is taken for granted among evolutionary psychologists that the evolution of modern humans took place within a hunter-gatherer economic system. Ethnographers have shown that standard optimal foraging theory provides a good basis for describing the foraging of modern hunter-gatherers (e.g., Winterhalder and Smith 1981). The repeated, small-scale decisions of gathering will therefore have had the opportunity to shape the course of human cognitive evolution. Gigerenzer and Goldstein (1996) argue that evolution will tend to produce decision-making heuristics that compensate for the inevitable bounds on our rationality by allowing us to make nearly optimal decisions nearly all the time. It is in the demands of early human foraging that we should look for the details of the selective pressures that have produced those heuristics.

HOARDING AND SAVING

The second example of an overlap area involves both ecology and economics. It starts not very far from optimal foraging theory but ends in one of the most central areas of modern economic theory.

Anyone who has ever kept a golden hamster will know that these charming little creatures, though generally excellent pets or laboratory subjects, do have a number of irritating habits. Chief among these is their tendency to remove their food supply to some place of their own finding. This is not the scatter hoarding of squirrels, considered in the last section, but larder hoarding—the establishment of a large single store of food, usually in the animal's nest. Hamsters' capacity for transporting and hoarding food is astonishing and famous. Lanier, Estep, and

Dewsbury (1974) report that the local name for the golden hamster in its native Syria translates as "father of saddlebags," and that hamster nests have been found containing sackfuls of grain. Similar behavior is shown by the other species of hamster—for example, the English name for these animals comes from the verb *hamstern,* which in Germanic languages means "to hoard," and this was first applied not to the golden hamster but to the similar but larger European black-bellied hamster. All species of hamster are anatomically adapted for hoarding—the food pouches in their cheeks can carry several grams of food, and when they depouch a load it is difficult to tell that the food has even been touched.

It is not hard to guess at some potential ultimate explanations of the behavioral and anatomical traits that result in larder hoarding. Presumably, the tendency to hoard enables hamsters to forage more efficiently. When food is in good supply, they can gather as much as they can carry and store it in their nests. When food is hard to find, they need not forage at all, but can consume their hoards. This will work whether the variations in food supply occur from day to day or from season to season. Over a year or a lifetime, a hoarding animal can manage with spending only a fraction of the time above ground that a nonhoarder would have to spend, and for a slow-moving, burrow-nesting, fat, succulent animal such as a hamster, time spent foraging means time above ground, during which the hamster is all too likely to fall victim to some predator animal's foraging efforts.

The effects of hoarding on hamsters' behavior are fairly startling. For example, unlike other animals of similar size and generally similar environment, hamsters are only weak hibernators: since they can live off their hoards during the winter, they have no need to minimize energy consumption or to build up internal food stores in the form of fat. Furthermore, unlike almost all other animals that have been studied, golden hamsters do not respond to an enforced fast by eating more on recovery days, so that their weight remains low for several days after a single day's deprivation of food (Silverman and Zucker 1976). But if the opportunity to hoard is available, Siberian hamsters respond to food deprivation by adding to their hoards (Bartness and Clein 1994).

This second finding gives us a hint that the mechanisms controlling food intake may be very different in hamsters from those familiar to psychologists from their work with rats. At once our alternative paradigm for economic psychology or behavioral economics is activated. It is fairly clear that hoarding is a special way in which hamsters come near to doing "as well as they can" in terms of getting food out of the environment. Have we here another situation where psychology can ask how the animal does as well as it can.

But hamsters' hoarding is not just a problem in the interaction of psychology and ecology. There is in fact a considerable psychological literature on the hoarding behavior of rats, stemming from a paper by Wolfe (1939). Rats do not hoard anything like as much or as spontaneously as hamsters (Waddell 1951), but they can be persuaded to do so—for example, by current or previous food deprivation, by low temperatures, or by providing food in the form of inconveniently large pellets (Whishaw and Tomie 1989). The early work on hoarding came, in fact, from the heyday of rat psychology, and its authors saw themselves as not merely investigating rats: they were seeking a model of human saving behavior and general possessiveness. Although the belief in that kind of applicability of animal data to human psychology is now thoroughly and rightly unfashionable, it is not so unreasonable in this particular case. Economists trying to account for saving behavior usually include in the list of motivations to save something like "pure miserliness" (Keynes 1936)—in other words, the mere instinct to hoard. If we want to know what a hoarding instinct looks like, the behavior of hamsters seems a promising place to start.

In an effort to get a grip on the simultaneously ecological, psychological, and economic ques-

tions posed by hamsters' hoarding behavior, we carried out a series of experiments in which we manipulated the cost of food to hamsters (Lea and Tarpy 1986). The hamsters lived in Skinner boxes, where they could always earn food by pressing on a lever, and they had a little nesting box in which they slept and where they could make a hoard. We varied the cost of food by varying the number of responses the hamster had to make to earn each pellet of food. If you do that systematically, you end up being able to plot a curve of the number of food pellets taken against the cost per pellet, which is what an economist would call a demand curve (see also Hursh 1980; Lea 1978, 1981). In one of our experiments, we varied the price from a fairly low value (six presses per pellet) up to the point where the hamsters virtually stopped pressing the lever (usually twenty-four or forty-eight presses per pellet). Each day we observed how many pellets had been taken, and by counting those hoarded in the nest box, we knew how many had been eaten. But we also stole the hamster's entire hoard—in economic terms, we imposed a 100 percent daily wealth tax. We got three very interesting results.

Unlike other animals, as the price of food went up, hamsters did not greatly increase the amount of work they did, so the number of pellets they earned declined. However, the number of pellets actually eaten was not greatly affected by price. What fell off (and it fell off very dramatically) was the number of pellets hoarded. Similar results were obtained, with different experimental procedures, by Day and Bartness (2003) in Siberian hamsters: making food more expensive to get sharply reduced the amount hoarded. On the other hand, we found that our "wealth tax" did not affect hoarding in the slightest, and the hamsters did not respond to the theft of their hoards by hoarding less. Indeed, Phillips, Robinson, and Davey (1989) found that artificially depleting golden hamsters' hoards led them to hoard more rather than less.

That last finding clearly shows that the hamsters' behavior was not optimal (and the detailed data relating to the other results confirmed this). But to make much of this fact, as the rationality-question paradigm would lead us to, would be to miss the most interesting points. The hamsters' indifference to the "wealth tax" shows that their hoarding is, indeed, largely instinctive. Presumably, hamsters must lose some of their hoards under natural conditions, but the loss must be sufficiently regular for there to be no adaptive advantage for a hamster in taking account of the rate of loss. It does not always pay to be too clever—it may not be optimal for an animal to be equipped to deal with every contingency. If the environment is sufficiently reliable, then an instinctive response to some of its stimuli will be more certain and often quicker than a more comprehensive response that depends upon learning.

Furthermore, the first two findings show that even under the drastic and quite unnatural manipulation of daily total hoard loss, the hoarding behavior was still functional. When food costs increased, the hamsters were able to maintain food intake more or less intact without increasing their work output, even without being allowed to feed from their hoards, just by sacrificing the hoarding behavior. An economic psychologist is reminded of some of the results of Cyert and March (1963) on behavior within firms and other organizations. When financially hard times come around, firms ensure their survival by dropping procedures and laying off staff that are not strictly necessary, such as personal secretaries for executives. This is not to say either that hoarding has no function for hamsters or that executives have no need of secretaries. It is just that these luxuries can be dispensed with temporarily, and it is adaptive to do so in difficult times. They form a kind of behavioral buffer against environmental variation.

Once again we have seen how ecological considerations can tell us the function of a behavior, psychological considerations can throw light on the mechanisms that produce it, and both disciplines stand to gain from an interdisciplinary approach. And in this case, the economic dimension is also present. I would not wish to push the golden hamster very far as a model of human savers.

Its indifference to the "wealth tax," though, recalls the fact that, at least with single-figure inflation, individuals in the economy normally regard inflation as a sign of hard times and respond to it by increasing their saving behavior (Katona 1975, ch. 9). Both these trends are against received economic wisdom, according to which mild inflation is a normal accompaniment of economic growth, while increases in inflation make it more worthwhile to spend than to save. Katona explained these "irrationalities" by saying that people treat a reserve of savings almost like a consumer durable good: it is one of the things, like kitchen machinery and cars, that we aspire to own as we grow more affluent. Thus people dislike inflation, because it devalues their savings, but save more during it, so as to maintain their savings' value. But suppose we are, just a little, merely instinctive savers like the hamster. Might we not then continue to save anyway, no matter what the slings and arrows of outrageous macroeconomics might do to our hoard? It is not clear that there are any data that could demonstrate that this account is any less satisfactory than Katona's.

All this discussion of hoarding has been in terms of the function/mechanism paradigm. But saving has its social dimension too, as the last paragraph reminded us. Human beings are not hamsters. Katona was interested in saving precisely because of its potential macroeconomic impact: if a sufficient number of consumers increase or decrease the proportion of their income that they save, that has a deflationary or expansionary effect on the entire economy. But economic psychology has now gathered a very considerable amount of data on the individual processes underlying saving and the factors that affect them (Wärneryd 1999). We know that if inflation, or wealth tax, goes to extremes, we will change the way we save, or stop saving altogether, and inflation and taxes are properties of the economy as a whole. Dual causation is virtually axiomatic in the study of saving.

PSYCHOLOGY AND MONEY

In the third illustration that we shall consider, the social dimension becomes paramount, and we shift definitively from considering behavioral ecology to economic psychology and behavioral economics proper.

For most of the first century of academic psychology, few psychologists took any interest in money. Yet psychologically speaking, it is fascinating stuff—and not only for those few unfortunates who develop a pathological attraction to it. Anthropologists have found that a wonderful variety of objects can be used as money: everyone has heard of cowrie shells, and cows and bales of cloth make a sort of sense; but what about two-meter granite boulders, or woodpecker scalps? In present-day society, most forms of money are utterly valueless in themselves, and many forms (e.g., entries in the memories of bank computers) are utterly abstract. Yet we rely on money totally and unthinkingly for day-to-day purposes, and only with great reluctance do we rely on anything else for year-to-year purposes (one of the most unpopular features of high inflation is the way it requires people who merely want to maintain the purchasing power of their savings to think about investment strategy). And, to take an example that will be developed more fully below, we resist any attempt to interfere with it. There are interesting macroeconomic arguments as to whether or not it would be to the United Kingdom's advantage to join the euro zone, and no doubt they have some influence on the government, but it is beyond doubt that the key issue in the public debate is the British public's almost visceral attachment to the pound sterling (Routh and Burgoyne 1998). This has led to the different outcome of the political question about the euro in the United Kingdom as compared with most other European Union states, where the macroeconomic background is not very different but the emotional context certainly is (Müller-Peters 1998). We have recently reviewed some of the oddities of human behavior toward money and

concluded that they are so odd that we have to consider money as functioning, in part, as a drug, not just as a neutral tool (Lea and Webley in press).

Over the past twenty years, the rise of economic psychology as an organized interdisciplinary study has filled some of the gaps in a psychological study of money, to the point where it is possible to have a serious textbook devoted to the subject, written by two of the United Kingdom's most prolific and eminent social psychologists (Furnham and Argyle 1998). However, there is still much work to do, and the study of the psychology of money is a good illustration of the danger of naive thinking about other disciplines. In terms of the simplest possible economic analysis, modern money is valuable to an individual only as a means of exchange or a store of value. Its only use is to be got rid of as soon as possible, in exchange for real goods or services, or to be saved for a specific purpose. In reality, money is itself an economic good, something that is only available in restricted amounts: there is a demand for money, a supply of money, and a market in money. Here a naive concentration on the rationality question would easily lead psychologists astray: we might find the demand for money and the desire to possess money irrational, and imagine that we had scored a point against economic theory. In practice, the concept of economic rationality is quite rightly adjusted to allow for the need to hold money stocks.

The alternative paradigms we have proposed prove to be much more fruitful. Consider first the distinction between function, on one hand, and mechanism and development, on the other. The very oddness of modern money as a phenomenon has led quite a number of psychologists to ask how children come to learn how to use it. One of the classic questions in the study of economic socialization has been the way concepts of money develop, and this is readily posed within the framework of Piaget's general approach to cognitive development (e.g., Danziger 1958). These studies are quite illuminating, and could in principle be of practical use to parents trying to educate their children in the effective management of money—a subject on which there is a huge self-help literature (e.g., Whitcomb 2000) but still almost no academic research, or at least none that has given rise to reliable positive results. But these early studies of children's understanding of money missed an important point, which is brought to light more clearly within the dual causation paradigm (see Lea, Tarpy, and Webley 1987, 325–26). The Piagetian psychologists of money treat money as a given, almost the way they treat aspects of the physical universe. But money is actually a social creation. Its continued existence depends upon the way individuals behave to and with it. The "cognitive equilibrium" that the Piagetians see as the end of development need not, in principle, be found within existing institutions. In terms of the dual causation paradigm, the Piagetians are being, Continental-fashion, too organicist. They are giving too little weight to the fact that individuals not just are determined by the economic whole but also help to determine it.

To illustrate how individuals can determine economic institutions we can return to the example of people's resistance to new forms of money, and to one specific example, the effects of the replacement of notes by coins. Hussein (1985) investigated what happened in the United Kingdom when the £1 note was replaced with a coin in 1983. She was interested in the possibility that, because it was a coin, it would be spent faster than £1 notes—a process Duncan (1975) suggested might contribute to inflation. To this end, Hussein rewarded volunteers in an irrelevant experiment with a payment of £1, made either by coin or note, and marked all the coins and notes with an ultraviolet pen. She then recalled the volunteers the next day and checked the contents of their purses and wallets. Sure enough, everyone's £1 coins disappeared in less than a day, while the majority of those who had received a £1 note still had it; in another study, Hussein found that the lifetime of a £1 note in purse or wallet averaged 1.1 to 4.0 days. At the time, however, it hardly required this degree of sophistication to tell us that the £1 coins were psychologically different

from notes and that people's attitudes toward them were strong enough to affect the economic processes. When the coins were first introduced, many people simply refused to take them when they drew money from banks or got change in shops, with the result that six months after their introduction, less than a third of those minted were in circulation. In the United States, an attempt to introduce a dollar coin in 1979 essentially failed, and the coins simply did not circulate (Caskey and St. Laurent 1994); by the late 1990s, the only large-scale use of this coin, the Susan B. Anthony dollar, was to pay fares on a few urban transit systems, as in Chicago—coins that were intended as legal tender had fallen to the status of special-purpose tokens. The U.S. Mint introduced a new "golden" dollar coin in 2000 but has felt it necessary to mount a strong propaganda campaign to persuade people to use it: there is even a "Coin Coalition" that has been set up to advocate for wider use of the new coin, joining together major commercial and public corporations from the New York City Transit Authority to the International Carwash Association. At the time of writing (2005), the circulation of the golden dollar appears to be minimal.

The reasons for people's odd behavior in the face of currency changes are surely open to psychological investigation. It is often said that £1 coins did not initially seem valuable, or that the Anthony dollar was confusable with the quarter. But new coins nowadays are carefully researched before production (e.g., Bruce et al. 1983), so these objections seem more likely to be rationalizations of less superficial objections. Economic psychological research has thrown some light on those deeper processes. In the first place, though the rejection of new coins seems odd, it is not necessarily irrational: Caskey and St. Laurent (1994) showed there are real costs in using new forms of money, especially when few other people are doing so, so there are economic reasons why take-up may be slow at first and can fail if a critical level of usage is not reached. Second, both pound and dollar are the defining units of their national currencies, so perhaps changes affecting them are particularly susceptible to interference from factors of national pride, which Müller-Peters (1998) showed to be a key factor in attitudes toward the introduction of the euro. The detailed psychological analysis that has been carried out, Europe-wide, in connection with this particular currency change (see Pepermans, Burgoyne, and Müller-Peters 1998) goes much further than dismissing any difficulties as "irrational"; by recognizing that behavior toward money is both a product of and a cause of the societal phenomenon of money, it becomes possible to understand it.

CLOSING THE TRIANGLE: ECOLOGICAL AND ENVIRONMENTAL ECONOMICS

What, though, of the third possible relation between our three disciplines, that between economics and ecology? The very similarity of the words suggests that there must be a relationship; according to the *Oxford English Dictionary,* the word *ecology* was coined in imitation of *economy,* and we can see how its nineteenth-century inventors would have wanted to parallel the economy of nature against the national and international economy, seeing both as systems in which huge numbers of elements and processes were held in an equilibrium that was relatively resistant to disruption but subject to continual progressive forces.

Whatever the derivation of the words, however, ecology is not a derivative or subset of economics, but rather the reverse, in two important senses. From the point of view of individual people, economics is just human ecology: it is the economy that specifies how we gain access to resources and how we impact on our environment. But at the macro level, the human economy is embedded in the planetary ecology, dependent, on it and impacting on it.

Two subtly different disciplines have sprung up to study the relations between the two, envi-

ronmental economics (e.g., Field and Field 2001) and ecological economics (e.g. Söderbaum 2000). The distinction is not hard and fast, but as a general rule academics and practitioners calling themselves environmental economists are likely to be found assessing the environmental impact of proposed economic developments, on the large or small scale, or alternatively the economic impact of proposed environmental developments such as the designation of national parks. They would tend to see the environment as a scarce resource that can be studied through the methods of economics, the science of scarce resources. This leads to an attempt to follow a value-neutral approach, setting out ecological and economic costs and benefits of different courses of action, often with a leaning toward market solutions or at least toward minimizing interference with the market. Those calling themselves ecological economists, on the other hand, would be more likely to be pursuing a normative, policy-oriented approach, driven by the belief that economic developments must be sustainable within the planetary ecology, and considering the Earth as a single economic and ecological system whose productive capacity is limited and needs to be understood. For example, Costanza et al (1997) argued that the contribution of the planet to economic production should be recognized, and calculated that at a conservative estimate, the economic value of ecosystem services was around U.S. $33 trillion, twice the total of the world's gross national products. Ecological economists thus tend to take a nonstandard, critical approach to conventional economics, and their approach has some points in common with that of economic psychologists (Lea 2001).

CONCLUSION

We have seen that psychologists interested in interacting with either economics or ecology face the difficulty of getting a data-driven discipline to interface with one where theory, and in particular a single all-pervading theory, plays a larger role. We have also seen that there are ways in which that difficulty can be overcome: many essays in the present book give evidence that it is being overcome successfully in the case of economics, and in this essay we have reviewed some of the ways it which it is being overcome successfully in the case of ecology. It might be thought that psychologists interested in interacting with both economics and ecology face a double difficulty, but in fact the links that exist between the two disciplines open up both a specialized possibility and a general one. From a specialized point of view, psychologists have a contribution to make to the study of the human behaviors through which the economy interacts with the planetary ecology. Individual preferences underlie the choice between technologies or activities that are relatively benign or relatively damaging to the environment, and economic psychologists have consistently shown an interest in areas such as green consumption (see the survey by Beckmann 1999) and ethical investment (see, for example, Lewis et al. 1998), where such preferences can be studied.

More generally, however, we need to realize that if economics is human ecology, the sorts of considerations that govern behavioral ecology will also govern economic psychology. The parallels I have been seeking between these two interdisciplinary endeavors are not accidental. All animals are adapted to behave in ways that enable them to survive in their ecological niches, and the human economy is our ecological niche. It has changed so fast in the past 10,000 years that no genetic adaptation process could keep up: to a significant extent we all have to deal with the Internet-age economy using Stone Age psychology. Perhaps our difficulties with money are in part a result. But I would argue that the differences between a natural economy and a modern one are more superficial than fundamental. What is fundamental is that we are immersed in a network of flows of scarce resources, more or less in equilibrium, which we both influence and are influ-

enced by. Within that network, rational or optimal behavior will provide a rough prediction of actual behavior; we have to understand psychology, however, if we are to know the limits of that prediction, and the mechanisms through which animals or humans, in their different environments, do as well as they can.

NOTE

An earlier version of this essay formed a keynote address at the September 2003 conference of the International Association for Research in Economic Psychology, Christchurch, New Zealand. It is a reflectively updated form of a paper of the same title given as the Lister Lecture to the British Association for the Advancement of Science, Brighton, United Kingdom, August 1983. The writing was completed while the author was a visiting scholar in the Department of Psychology of the University of California, Berkeley, United States, and thanks are due to Dr Lucia Jacobs for facilities there.

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