References and Notes

1. W. E. Parry, *Journal of a Voyage for the Discovery of a Northwest Passage* (Murray, London, 1821; reprinted by Greenwood Press, New York, 1968).
2. Some of the more informative references and pictures published since 1945 are: R. E. Lacy, M. A. Ellison, S. E. Ashmore, *Weather* **9**, 206 (1954); G. H. Liljequist, *Norwegian-British-Swedish Antarctic Expedition 1949–52 Scientific Results*, vol. 2, part 2, *Halo-Phenomena and Ice Crystals* (Norsk Polorinstitutt, Oslo, 1956); R. Scott, *Weather* **15**, 309 (1960); J. R. Blake, *Australian National Antarctic Research Expeditions*, ser. A, vol. 4, *Solar Halos in Antarctica* (Department of External Affairs, Melbourne, 1961); R. T. P. Whipple, *Weather* **21**, 132 (1966); E. C. W. Goldie and J. M. Heighes, *ibid.* **23**, 61 (1968); P. P. Hattinga Verschure, *ibid.* **26**, 532 (1971); W. J. D. Tucker, *ibid.* **27**, 240 (1972); G. P. Konnen, *ibid.* **28**, 258 (1973); P. P. Hattinga Verschure, *ibid.*, p. 300.
3. C. Magomo and C. W. Lee, *J. Fac. Sci. Hokkaido Univ.* **2**, 321 (1966). A good introductory survey article on snow crystal forms is by C. Knight and N. Knight, *Sci. Am.* **228**, 100 (January 1973).
4. A. B. Fraser, *Phys. Unserer Zeit* **3** (No. 1), 2 (1972).
5. R. A. R. Tricker, *Introduction to Meteorological Optics* (American Elsevier, New York, 1970).
6. W. J. Humphreys, *Physics of the Air* (Dover, New York, 1964).
7. R. G. Greenler and A. J. Mallmann, *Science* **176**, 128 (1972).
8. A. W. Hogan, *J. Appl. Meteorol.* **14**, 246 (1975).
9. See a standard optics textbook; for example, M. Born and E. Wolf, *Principles of Optics* (Pergamon, Oxford, ed. 4, 1970), pp. 38–42.
10. This is a refinement of our earlier treatment (*7*) where we used some additional approximations of the beam cross section for skew rays. The changes make no noticeable difference in the appearance of the circumscribed-halo simulations.
11. E. C. W. Goldie, *Weather* **26**, 391 (1971).
12. P. Putnins, *Meteorol. Z.* **51**, 321 (1934).
13. Actually Putnins has light incident on the crystal from the right and so would label these the 1-5 and 2-6 arcs.
14. K. O. L. F. Jayaweera and G. Wendler, *Weather* **27**, 50 (1972).
15. In all the simulations discussed before this the reference plane shown in Fig. 2 was oriented perpendicular to the line of sight to the sun; that is, the simulations were sun-centered and would match the perspective of photographs in which the sun was centered in the picture. The simulations of Fig. 11 are made with the reference plane perpendicular to a line of sight to a point just below the arc, which is in the center of the photograph, to match the perspective of the photograph. Similarly, the simulations of Fig. 12 are made to match the perspective of the photograph in that figure.
16. One of the authors (J.R.M.) received summer support from the National Science Foundation's Undergraduate Research Program. Computer support was provided by the graduate school of the University of Wisconsin–Milwaukee, and publication costs were supported by grant DDP 76-18593 from the National Science Foundation.

Economic Models in Ecology

The economics of resource allocation provide a framework for viewing ecological processes.

David J. Rapport and James E. Turner

Ecological processes have traditionally been studied from several vantage points. One approach focuses on energy flows through ecological communities from primary producers to consumers at higher trophic levels (*1*). Another approach considers species interactions in terms of population dynamics (*2*). A third explores the geographical distribution of species and the relationship between species diversity and area (*3*).

None of these approaches, however, explicitly address what some (*4, 5*) have regarded as one of the central problems of ecology—the ways in which scarce resources are allocated among alternative uses and users. This question is, of course, fundamental to economic thinking (more specifically to microeconomic theory) and it is for this reason that we have recently seen the introduction of essentially economic models and modes of thought in ecology (*6–21*). In some cases economic models and concepts have been transferred directly across disciplinary boundaries (*5, 7, 10–14, 16–18*), while in other instances ecologists have rediscovered economic principles in an ecological context (*6, 8, 9, 15, 19, 20, 21*).

These developments have occurred in a number of diverse areas of ecology, including models of optimal foraging (*6–8, 11, 12, 15, 16, 21*), reproduction strategies (*9, 12, 19, 20*), territoriality (*10*), altruism (*20*), and social caste systems (*17*). Viewed as a group these and other recent contributions may lay the foundations for an approach to ecology in terms of an economics of natural communities. In this article we review how economic analysis has contributed to our understanding of ecology and show how a comprehensive framework for economic analysis of ecological phenomena may emerge.

That economic principles are relevant to the study of ecology is by no means a new idea. H. G. Wells, Julian Huxley, and G. P. Wells (*22*) in their treatise *The Science of Life* defined ecology as biological economics or an extension of economics to the whole world of life. For these authors, economics is "the science of social subsistence, of needs and their satisfactions of work and wealth. It tries to elucidate the relations of producer, dealer, and consumer in the human community and show how the whole system carries on. Ecology broadens out this inquiry into a general study of the give and take, the effort, accumulation and consumption in every province of life" (*22*, p. 961).

In the history of science, biological-economic analogies have played a significant role. Malthus (*23*) borrowed from "the laws of natural increase in the animal and vegetable kingdom" in forecasting a dismal economic future for mankind. Darwin (*24*), as is well known, received a critical inspiration for formulating his theory of evolution by means of natural selection from a reading of Malthus's essay on population. It occurred to Darwin that not only man, but all other species too, are engaged in a struggle for existence owing to their requirement for limited resources, and that those species that evolved ways to use resources more efficiently would be favored in their struggle for survival.

Dissatisfied with the predominance of mechanical analogies in economic thinking, the economist Alfred Marshall (*25*), writing at the turn of this century, insisted that the Darwinian concept of natural selection is also the most important economic principle, and he frequently asserted that, as economics became a mature science, biological analogies would displace mechanical analogies. Some years later John Maynard Keynes (*26*) made the observation that the Darwinian "principle of survival of the fittest could be regarded as a vast generalization of Ricardian economics."

Several other examples of biological-economic analogies may be cited (*27*), but among the most colorful was Adam Smith's frustrated attempt to extend the invisible hand to the economy of nature

---

Dr. Rapport is environmentalist in the Office of the Senior Advisor on Integration, Statistics Canada, Ottawa, Ontario, Canada K1A 0T6; Dr. Turner is associate professor in the Department of Mathematics, McGill University, Montreal, Canada.

(*28*). In an early chapter of *The Wealth of Nations*, Smith concluded that while "a philosopher is not in genius and disposition half so different from a street porter, as a mastiff is from a greyhound, or a greyhound from a spaniel . . . those different tribes of animals, however, though all of the same species, are of scarce any use to one another. . . . The effects of those different geniuses and talents, for want of the power or disposition to barter and exchange, cannot be brought into a common stock, and do not in the least contribute to the better accommodation and conveniency of the species."

Numerous economic models have made their appearance in theoretical ecology within the past decade (*6–21*). If one adopts the classical definition of economic activity provided by Lionel Robbins (*29*), namely, that "any act has an economic aspect if time and the scarce means necessary to the achievement of one end involves the relinquishment of their use in the achievement of another," the applicability of economic concepts and models to resource allocation aspects of ecosystems can be shown to be rather pervasive. To place these diverse economic-ecological concepts and models into a coherent framework we group them into the three essential components of economic resource allocation systems—consumption, production, and consumer-producer interactions (*30*).

Consumer Behavior in Natural Communities

A plethora of theoretical models of the economics of consumer choice in natural communities now exists (*6–8, 11, 15, 16, 21, 31, 32*). Generally, these studies seek to determine the optimal feeding strategies of predators maximizing total energy intake, reproduction rates, or some other aspect of fitness.

It has been possible to use directly simple microeconomic models to describe important aspects of optimal foraging behavior (*7, 11, 16, 31*). The problem facing a consumer in terms of classical microeconomics is to choose the bundle of goods that maximizes utility within the budget constraints. Figure 1a illustrates a solution to this problem for the two goods case. Here the budget line is determined by the consumers' income constraints and the prices of goods A and B. The budget line forms the boundary between those bundles of goods obtainable and unobtainable by the consumer in a given time period. Benefits from consumption are represented by a family of indifference contours or isoclines, each isocline indicating those bundles of goods A and B of equal satisfaction to the consumer. The solution to the dilemma of consumer choice is given by the tangency of the "highest" isocline with the budget line (*33*). The ecological model in Fig. 1b was derived directly from this economic model. Here the budget constraint (denoted as consumption frontier) is determined by a complex of ecological parameters (time and energy allocated to foraging, the ease of prey capture, prey abundance, competition among predators for prey). As in Fig. 1a, the budget constraint separates the alternative consumptions possible from those that are not and the family of fitness contours indicates the contributions of alternative prey combinations to the predators' welfare (*34*). The predators' best strategy is to consume that prey combination determined by the tangency of the highest fitness contour with the consumption frontier (*35*). The circumstances under which predators may shift from "generalist" to "specialist" strategies or from specialization on one prey type to another are readily determined within this context. In this regard a change in relative prey abundance acts as a change in relative prices for consumers. As Pulliam (*31*) points out, this economic model underscores the importance of relative prey abundance.

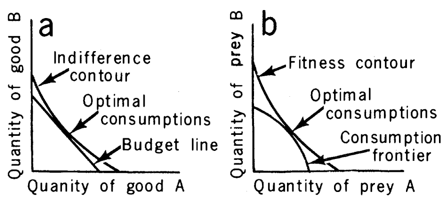

Fig. 1. (a) Optimal consumer. Tangency solution to maximize utility subject to budget constraint. (b) Optimal forager. Tangency solution to maximize fitness subject to consumption possibilities. Both (a) and (b) are in terms of rates of consumption per unit time.

The concepts of substitute and complement resources, so basic to economic analysis, also play an important role in characterizing a predator's response to changes in prey abundance. If prey resources are "perfect" substitutes, slight changes in their relative abundance can cause a predator to switch from one prey type to another (*7, 11, 36*).

Laboratory experiments with predator-prey systems offer support for several of the assumptions and hypotheses derived from the economic foraging model. In experiments with protozoa, the ciliate *Stentor coeruleus* was fed on paired combinations of four prey species—two algal and two nonalgal species (*37*). Stentor food preferences were highly consistent (transitive), in that the stentor preferred nonalgal to algal prey and was indifferent in choosing among alternative algal species or alternative nonalgal species. In another set of experiments (*38, 39*), stentors' responsiveness to relative prey abundance (corresponding to relative prices in economics) was determined. Stentors increased their degree of preference for those prey types which became relatively more abundant (*40*). If greater abundance is interpreted in terms of reduced costs of capture or digestion, the stentor acts as a rational consumer, increasing its demand for relatively lower priced goods.

In order to determine the possible adaptive significance of food preference in stentor, glycogen accumulation, starvation times, and reproductive rates were measured in stentors maintained on alternative diets (*38*). In those cases in which stentor was indifferent to alternative prey combinations, it reproduced equally well on either prey type alone or on a combination of prey types fed sequentially. However, in the cases where stentor selected a particular combination of prey types in a nonrandom fashion, it reproduced better on a mixture of prey than on either prey type alone. These results suggest that stentor food preferences are highly adaptive, enabling this opportunistic species to increase its growth rate by exploiting complementary food resources in an economically efficient manner.

Holmberg (*41*) conducted similar experiments with the spider predator *Pardosa vancouveri* feeding on *Tenebrio* larvae, *Drosophila* adults, and young *Oncopeltus*. He found not only consistent (and nearly absolute) food preferences but also a correlation between food preferences and indicators of fitness. When spiders were fed preferred prey types their weight gain and size gain were significantly greater than achieved on alternative prey species. In those cases where spiders were indifferent to two prey types, there were no significant differences in any of the benefit criteria tested.

Simple microeconomic consumer behavior models have also been used to interpret field data on foraging. Tullock (*16*), in analyzing Gibbs' data on the predation by coal tits on insect larvae, concluded that the coal tit's behavior can be compared to that of a careful shopper. When the bird locates a region of high larval density it expends less energy in pine cone tapping per larva consumed. Therefore, a downward sloping demand function for larva in terms of coal tit energy expenditure can be inferred.

We now turn to examples of foraging models developed from within ecology which correspond to aspects of consumer economics. Among these is MacArthur's theory of the economics of consumer choice (*21*). MacArthur considered the economics of species behavior as an essential ingredient for understanding biogeographical patterns. He postulated that a forager will have "a fairly clear statistical expectation of the resources it will come upon" and that the expected yield to the predator in terms of grams of successfully captured prey per unit time will be maximized. From these postulates he derived the result that prudent predators should "pursue an item if and only if during the time the pursuit would take it would not expect to locate and catch a better item." This result as stated is an ecological equivalent of the opportunity cost concept familiar in many economic analyses.

In Schoener's development of the theory of foraging strategies (*15*), an explicit economic orientation is adopted at the outset. His optimal foraging framework consists of "choosing a currency—what is to be maximized or minimized, choosing the appropriate cost-benefit functions, and solving for the optimum." The parallel set of ideas in microeconomic theory is to specify measures of welfare (utility), budget constraints, and solve for the optimum (the tangency solution in the economic model). Schoener identifies two extreme strategists: energy maximizers and time minimizers. The energy maximizer allocates all its foraging time to prey capture, selecting prey in such a manner as to obtain the maximum net energy gain for the time expended on foraging. A time minimizer seeks a specified energy requirement, minimizing the time expended to obtain it.

In a review of optimality principles in ecology Cody (*6*) develops a model which focuses on generalist versus specialist strategies. A generalist consumes all prey species encountered (no preferences) while a specialist consumes only the prey type conferring maximum fitness. Using an economic cost-benefit analysis Cody finds that, as the proportion of preferred prey types available in a given habitat declines, a generalist strategy becomes more profitable to the organism. This is due to the increased costs (in terms of waiting time and energy expended for search) of being a selective (specialist) predator.

The foregoing examples serve to demonstrate that not only have some optimal foraging models in ecology been suggested by analogous models in consumer economics, but also that ecologically derived models can readily be reinterpreted in terms of the economics of consumer behavior. These models emphasize aspects of the problem of choice faced by many general predators, and yield insight into predator strategies such as those of energy maximizers, time minimizers, specialists, and generalists.

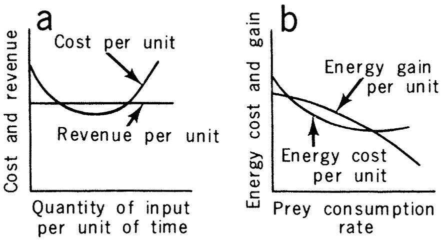

Fig. 2. (a) Economic cost and revenue per unit input as functions of input rate. The firm may profitably process inputs, for example, labor, land, capital, for some intermediate range of input rate where the average cost per unit of input is less than the average return on the input's contribution to the firm's output. (b) Energy cost and gain per unit of consumption as functions of consumption rate. Net reproduction can occur in the range where the cost of obtaining energy inputs is less than the assimilated energy derived from them.

Production in Natural Communities

The economics of production in natural communities covers a very broad spectrum of topics. Production to the ecologist is generally considered in terms of the manufacture of biomass either by growth or reproduction processes. From an economic perspective one desires to know the nature of the production function, that is, the relationship between factors of production (ecological equivalents to the economist's land, labor, and capital) and growth or reproductive output. Other questions concern the allocation of energy between growth and reproduction (*9, 42*), the optimal division of labor in social caste systems (*17*), and strategies for territorial defense (*10*).

As in consumer choice theory, microeconomic models have been transferred rather directly to ecology in elucidating aspects of producer behavior. Consider for example the models shown in Fig. 2, a and b, in which the theory of the firm has been used in a description of the relationship between foraging activity and population growth (*12*). Both firms and organisms (viewed here as producers) are faced with the problem of determining the optimal quantities of inputs required for production per unit time.

A predator maximizing its net energy gain by consuming the quantity of prey that yields the largest difference between total energy gain and total energy cost is behaving in a similar fashion to a firm which seeks to employ the quantity of input that generates the largest difference between the total value of its product-added and its total costs. This economic perspective when applied to ecology enables one to relate the quantity and quality of available food resources to optimal consumption rates and population growth. For example, it has been shown with this approach that energy maximizing and time minimizing strategies converge as food becomes scarce (*12*). Further, this type of cost-benefit model permits one to explore the dependence of population growth on the quality and quantity of food resources and energy conversion efficiencies. Oster (*18*), in his development of the economics of the intricate relations between foraging and reproduction in bumblebee colonies, makes use of this structure of ideas. He describes the bee colony as analogous to the economy of a firm, relating the optimal population to the energy gains from harvesting activities (a complex function of flower density and nectar quality and quantity) and the energy costs of foraging activities and reproduction.

Schoener's optimal foraging models (*15*) should also be recalled here since they provide a striking example of the discovery in ecology of the economist's marginal cost—marginal revenue analysis of profitability. Schoener measures both costs and benefits in terms of offspring. As a predator feeds it incurs decreasing marginal benefits from ingesting lower quality foods and from less efficient conversion of food to offspring. At the same time the organism incurs increasing marginal costs, which here are measured in terms of offspring forgone by inadequate time for necessary reproductive activities such as courtship, nest building, and defense. The optimal time allocated to foraging is determined where marginal benefits equal marginal costs. Schoener's analysis is also similar to one economist's conceptualization of the household as a small factory which combines "capital goods, raw material and labor to clean, feed, procreate and otherwise produce useful commodities" (*43*).

Parental investment theory (*20*) furnishes another example of explicit economic analysis in describing aspects of production in natural communities. Viewing reproduction as an investment process, Trivers considers the contribution of each parent in terms of time and energy expenditures for all activities concerned with preparing for raising young. He suggests that monogamy, polygamy, and parental desertion can all be understood in terms of the relative parental investment made by each parent over time. For example, if the investment by females in offspring is large relative to males, a male may do better (in evolutionary terms) by deserting the female and engaging in polygamous behavior. In this case the expected return on a number of investments (in offspring of more than one female) exceeds the expected return of a single extensive investment (that is, including not only mating but also the care of offspring). Similar economic arguments are used to explain why male birds in most cases are more brightly colored and aggressive than females. Since females bear the brunt of the parental investment, they are the "scarce resource" in the production process and therefore there is a strong selective pressure for characteristics enabling males to compete for this limiting resource. It is interesting that in those species where male investment in a single brood of offspring is relatively large (Phalaropodidae and polyandrous species) the females are more brightly colored, aggressive, and exhibit polygamous behavior.

Life history strategies of species have also been viewed in terms of economic principles of investment behavior. Gadgil and Bossert (*9*) examined the returns (again in the currency of offspring) from allocations of energy to growth and reproduction. They pointed out that while a higher reproductive effort in a given year yields a higher expected number of surviving offspring, this is at the cost of lower adult survival probabilities and less adult growth. These costs reduce expected contributions to offspring in succeeding years. The exact forms of the cost and gain functions yield strategies ranging from repeated reproduction (iteroparous organisms) to "big-bang" reproduction in which a very large number of offspring are produced all at one time (semelparous organisms) (*44*). In all cases Gadgil and Bossert argue that natural selection "would tend to an adjustment of the reproductive effort at every age such that the overall fitness of the life history would be maximized" (*9*). In a similar manner, the investment decisions of individuals or firms take into account the opportunity costs of investment in terms of forgone consumption or reduced liquidity, and attempt to maximize benefits (profits, utility) over time.

In extending formal models of optimal life history strategies to more complex cases, Schaffer (*19*) has shown that "an optimal life history maximizes for each age class the expected fecundity at that age plus the sum of all future expected fecundities, each discounted by an appropriate power of e^{-m} where m is Fisher's Malthusian parameter." In this formulation the Malthusian parameter serves the function of an interest rate. Students of economics will recognize that the expected returns from a given investment are generally discounted to present value by the rate of interest.

Organisms, like firms, may change their "technology" in response to changes in resource availability. Heinrich (*45*) describes the foraging activities of the bumblebee in these terms. If nectar is abundant, the bee employs a high (energy) cost-gathering technique (flight), while the bee switches to a low-cost process (walking or crawling) when the flower density is low. Another example of the effect of resource availability on techniques of resource acquisition is provided by Cody's description of Mohave desert flocks (*6*). These flocks are more cohesive and better organized when food supplies dwindle than when food is abundant. Cody speculates that the change in behavior in response to resource scarcity serves to increase the success rate of gathering resources by regulating the return time of the group to the regeneration time of the resource.

Another aspect of the economics of production is the spacial relationships between the location of the producer and the location of resources gathered. This area of microeconomic theory has its origin in Losch's classic work on the economics of location (*46*). Using principles developed by Losch, Hamilton, and Watt (*10*) proposed a general theory of refuging systems which explores the relationships of the size of defended territory to the resources available, and spacing patterns of individuals or groups to the temporal and spacial pattern of the resource. Their approach enables one to account for the empirical finding that as the size of the group inhabiting a central location increases it becomes less probable that the foraging territory will be defended. In a recent review, Covich (*47*) discusses a wide range of similarities between economic and ecological location models, and demonstrates how economic concepts can be used to investigate the determinants of the shapes of foraging areas.

The division of labor in social insect societies is another area of ecological production amenable to economic analysis. In what he terms the "ergonomics" of insect societies, Wilson (*17*) has demonstrated how classic microeconomic techniques of linear programming are well suited to explain the division of labor among social insect castes. He considers the optimal number of castes and the proportion of workers in each caste required for the insect colony to function efficiently. This focus is the biological equivalent of the choice of types and proportions of land, labor, and capital by the firm. In social insect societies the objective function might be the production of queens at minimal energy cost (*18*). Wilson contends that in relatively constant environments the optimal number of castes should not exceed the number of separate tasks (defense and foraging, for example), and in general it is advantageous for the species to evolve so that in each mature colony there is one caste specialized to respond to each kind of contingency (*17*). A fluctuating environment can make a particular caste uneconomical and favors generalists over specialists even if the functions the caste performs remain as important as before.

Other aspects of the ergonomics of social insects have recently been explored by Oster (*18*) using the economics of contracts pioneered by the 19th-century economist Edgeworth (*48*). Within this explicit microeconomic framework, Oster shows how a reallocation of energy and population between castes in a given colony can increase the productivity of both castes. However, as in the standard economic models, after a certain degree of trading resources, a given caste (or contracting party in economics) can only improve its position at the expense of another.

Producer and Consumer Interactions as an Ecological Market

Writing several decades before Darwin, the geologist Lyell described population interactions in terms of a buffering effect, recently reinterpreted by Egerton (*49*) as "a biological example of the law of supply and demand." Today, reference to the role of supply and demand factors as elements in the balancing of predator-prey interactions is commonplace (*50–52*). Holling (*53*), for example, draws a specific analogy between predator-prey interactions and the supply and demand for land. Unsuccessful bidders for land are analogous to unsuccessful predators, and the behavior of both depends on the quality and availability of substitute resources. The supply of prey is regenerated by a reproduction process while land supply is governed by a resale process.

The economist Boulding has raised the question: "What, if anything, in the biosphere corresponds to the concept of a price system, and especially to an equilibrium price system, in economics?" (*51*). Energy has often been referred to as the currency of life, but as an answer to Boulding's query it is cumbersome because the energy cost of obtaining a particular prey type will differ for every species of predator (*54, 55*). A conceptually simpler approach considers prey density as equilibrating the availability of food supplies with the demands of predators (*13, 52*). In Fig. 3, the familiar supply-demand model from economics is compared with the harvest-yield model in ecology. For economic markets (Fig. 3a) "partial equilibrium" occurs at the price for which supply equals demand. In this classical economic model (*30*) [one which pertains to the agricultural sector of less-developed countries today as well as to foreign exchange and stock exchange markets (*56*)], if supply exceeds demand sellers lower prices to dispose of surplus goods. Conversely, if demand exceeds supply buyers bid up prices until the equilibrium price $\hat{p}$ is obtained. In ecological markets (Fig. 3b) the harvest function represents the total demand of all predators in a given habitat for a particular prey type as a function of prey density. The yield function indicates the number of prey available to predators at each prey density. If the prey harvest exceeds yield prey density declines, while if yield exceeds harvest prey density increases. The intersections of harvest and yield functions can generate stable, unstable, semistable, and multiple equilibriums as in the economic market models (*52*). From this representation of ecological producer-consumer interactions, the relation between prey density and predation rates of a single predator species (the functional response) (*53*) was extended to situations involving a community of predator and prey species interactions (*13*). The community is described in terms of moving attractor points, defined for each population and for the entire ecosystem. A change in abundance for a given prey species leads to adjustments in prey densities throughout the community through a series of interrelated harvest-yield function interactions. If the time constants of these interactions were specified it would be possible to explore stability and resilience properties of natural communities in these terms.

Just as theories of producer and consumer behavior have given rise to the theories of supply and demand, respectively, in economics, it can be shown that theories of biological production (in terms of energy gains and costs) and optimal foraging underlie the yield and harvest functions in ecology. The yield is governed by a delicate balance of energy gains and costs. As the density of the population increases, there may be both enhancement and competitive effects, these altering the profits to each of the individuals and, thus, their reproductive potential (*12*). The harvest is affected by changes in either the consumption opportunities or consumer preferences (*11*). Thus, models of ecological markets derived from theories of reproduction and optimal foraging have a parallel structure to models of economic markets derived from theories of producer and consumer behavior.

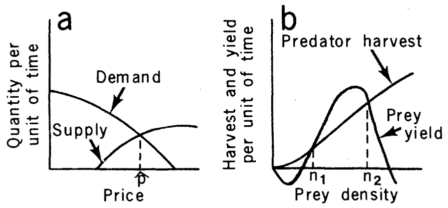

Fig. 3. (a) Supply and demand as functions of commodity price. In this case there is one intersection of the supply and demand curves. This intersection determines the market price ($\hat{p}$) and the quantity of goods purchased. (b) Prey yield and predator harvest as functions of prey density. There are two intersections of the harvest and yield functions in the above case. The first of these, n_1, is unstable. Should the prey population density decline below n_1 it would become extinct. Thus n_1 has been termed the extinction threshold. If the prey population exceeds n_1, it approaches the stable equilibrium n_2.

Economic models of consumer choice, reproductive strategies, and predator-prey interactions that fulfill the functions of the basic microeconomic processes of consumption, production, and exchange, respectively (*57*), have been described. We now turn briefly to a comparison of economic and ecological models of competition. Ecologists have placed primary emphasis on the partitioning of resources by competitors (*21, 58*) and the effects of competition on population numbers (*2, 5*). Economists have been more concerned with the efficiency of resource utilization (*30*). In both areas the stability of competitive interactions and the diversification of competitors to avoid the direct effects of competition have been of considerable interest.

Transfers of elements of competition theory from economics to ecology and from ecology to economics have occurred (*5, 14, 59*). Economic competition models have provided an energetic substructure for ecological population dynamics (*5, 14*), by relating classical Lotka-Volterra competitive outcomes to parameters such as the quality of the resource, and the efficiency with which the resource is exploited. Ecological models of competition (*59*) have served to introduce concepts of resource partitioning and ecological niche into the economic theory of the firm.

Uncertainty and Evolution

In the preceding sections, economic models of consumption, production, and exchange have been reinterpreted to describe corresponding ecological processes. Although these models embodied many simplifying assumptions about economic behavior (for example, perfect information, rationality) they served to provide a rudimentary framework for relating economic and ecological concepts and principles. In this section we consider how more realistic models of economic and ecological behavior take into consideration factors such as uncertainty and habitual behavior. Finally we consider evolutionary mechanisms in economic and ecological systems.

The assumption of optimal behavior on the part of economic agents has played a major role in the development of simple economic models (*60*). The validity of this assumption has subsequently been challenged in experimental studies of consumer behavior, in theories of decision-making and management, in economic anthropology, and in other areas (*61*). Consumers obviously do not have complete information concerning the consumption possibilities and the benefits of consumption. Producers equally face an uncertain and variable market for their products. Even when information is available, the consumer or producer may not have the computational ability to make optimal choices in the time available.

These objections to the assumption of optimal behavior in the narrow sense of making the best choice from all possibilities apply with equal force to other species of consumers and producers. Optimal behavior may be a limiting case to be expected only in those situations in which the consumer or producer does indeed have complete information or in which habits of consumption or techniques of production have evolved (by a trial and error procedure) over a considerable period of time in a predictable environment. While the consumption choices of predators are subject to natural selection, it should be noted that this does not imply that consumption choices in present environments are necessarily the most appropriate for survival and reproduction.

Johnson (*62*) has explored a number of ways in which introducing elements of uncertainty in economic analysis blurs the crisp precision of simple economic models. Johnson discusses the fact that, in the face of uncertainty, (i) households do not know the specific amounts of income they will receive in any given period in the future, nor do they know the time shape of their income stream, (ii) the household does not know its exact life-span, (iii) household tastes and preferences may change because of unforeseen and seemingly random events (for example, illness or changes in family size) as well as systematic factors such as aging, and (iv) the future course of prices, interest rates, and other parameters to the household are not known with perfect certainty. Analogous phenomena obviously pertain to consumers in natural communities. For example, foragers do not usually know their future foraging opportunities with certainty, or their exact life-span. Thus, for consumers in both natural (*21*) and human communities there may be statistical expectations of future conditions. These expectations are themselves subject to uncertainty and change.

An alternative assumption to optimal behavior of economic agents is satisficing behavior. A satisficer examines alternative courses of action and then chooses the first one that satisfies a set of minimal requirements (*61, 63*). The satisficing model is useful in explaining empirical data such as those collected by Wolpert (*64*) on farm productivity in one area of Sweden indicating that "less than half the area had performances more than 70 percent of the optimum" [see Haggett (*65*)]. This is attributed in part to "the simple fact that Swedish farmers were not aiming at optimum productivity but merely at a satisfactory (but suboptimal) level." Haggett points out the necessity of developing locational models on satisficer rather than optimizer principles. This approach may also prove useful for understanding the economics of populations in natural communities subject to variable conditions.

Another modification of traditional economic models would include a consideration of threshold behavior. Since the costs of acquiring information and determining the responses to changes in the environment may be considerable, organisms may be responsive only to stimuli which exceed thresholds rather than responsive to continuous variation in the environment. In economic models of consumer behavior, the central importance of threshold behavior has been examined by Devletoglou (*66*). In ecological models of predator-prey interactions, the importance of threshold behavior has long been recognized. For example, in the concept of search image "a predator does not learn and remember the worth of a food unless it reaches some threshold abundance (both relative and absolute). Thus foods below this density threshold are eaten proportionally less than when common . . ." (*53*).

Alchian (*67*) has reformulated the theory of the firm using an approach that "embodies the principles of biological evolution and natural selection by interpreting the economic system as an adaptive mechanism which chooses among exploratory actions generated by the adaptive pursuit of 'success' or 'profits.' " Alchian (*67*), and later Enke (*68*), Simon (*61*), Winters (*69*), and Lloyd *et al.* (*59*) argue that profit maximization is a poor single criterion for the behavior of the firm because of inadequate knowledge of opportunities and the uncertainty of the environment. Instead, they develop theories of reinforcement of successful (profitable) behavior and elimination of unsuccessful behavior.

A Transdisciplinary Focus

Economic models of ecological processes contribute a distinctive point of view to ecology. Optimal foraging, population growth, competition, life history strategies, and other ecological phenomena are brought into a common focus in terms of resource allocation processes. Natural communities are viewed in terms of the economics of consumption, production, and mechanisms for bringing into balance producer-consumer activities. This framework is suggestive of the Wells, Huxley, and Wells definition of ecology as biological economics (*22*). Microeconomic principles pertaining to the household, the firm, and markets have been related to their ecological theory counterparts.

Macroeconomic questions—the determinants of total economic activity (ecological productivity), its growth, and fluctuations—are also of obvious interest to ecologists. Hannon (*70*) has already described the energy and nutrient structure of total ecological activity in terms of the Leontieff input-output matrix.

Similarly, macroecological questions may prove of some interest to economists. For example, a study of how natural communities come to grips with resource limitations and achieve a no-growth economy (*55, 71*) may provide guidance for the management of human communities faced with the challenge of making the transition to a steady state economy.

What are the limitations of the comparative approach to economics and ecology? It is readily apparent that at a detailed level of analysis the fields are hardly isomorphic. Surely the organization of man's technology and society differs qualitatively from physiological, genetical, or behavioral rules governing the behavior and social organization of other species. At a finer level of detail the ecology of each species is unique as is the economics of each nation, industry, and firm.

It is at a more general level of description of ecological and economic systems that many similarities have been proposed. Holling (*50*) points to the limits to resources and limits to the responses of organisms to their resources as a fundamental similarity between ecological and economic systems. He further asserts that the diversity of interactions, historical components, spatial characteristics, and structural properties give social and ecological systems a similar degree of complexity which permits one to use the tools, approaches, and languages interchangeably among them. Although our exposition has stressed the manner in which ecology can be viewed in terms of economic principles, it is clear as we have noted in passing, that transfers have been made in both directions. It is, therefore, our belief that deep common principles underlie both fields enabling both economics and ecology to benefit from such transdisciplinary efforts.

A common framework for economic and ecological processes should make possible extensive transfers of concepts and theories between these fields. In this regard, the approach developed here contributes to the goals of general systems theory which attempts to unify areas of knowledge by searching for those "models, principles, and laws which apply to generalized systems irrespective of their particular kind, elements, and the forces involved" (*72*). The general systems viewpoint has been implicit in the work of many authors who have used economic or biological analogies in other disciplines. The 19th-century sociologist Emile Durkheim (*73*) wrote that the concept of the division of labor, for example, "applies to organisms as to societies . . . [and] is no longer considered only as a social institution that has its source in the intelligence and will of men, but is a phenomenon of general biology whose conditions must be sought in the properties of organized matter. The division of labor in society appears to be no more than a particular form of this general process, and societies, in conforming to that law, seem to be yielding to a movement that was born before them, and that similarly governs the entire world."

The existence of common ecological-economic models suggests that it is possible to unify methodologies, concepts, and theories which have independently developed in the two fields (*74*). This prospect should be of interest to strategic planners and managers of our resources. Communications between those whose concerns are with economic well-being and those who strive for ecological balance would be improved if common resource allocation principles were identified.

References and Notes

1. R. I. Lindemann, *Ecology* **23**, 399 (1942).
2. A. J. Lotka, *Elements of Physical Biology* (Williams & Wilkins, Baltimore, 1925); V. Volterra, *Mem. Accad. Naz. Lincei* **2**, 31 (1926); G. F. Gause, *The Struggle for Existence* (Williams & Wilkins, Baltimore, 1934).
3. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, N.J., 1967).
4. P. H. Klopfer, *Behavioral Aspects of Ecology* (Prentice-Hall, Englewood Cliffs, N.J., 1962). Klopfer suggests that the ecologist's fundamental questions concern the allocation of a finite amount of space and energy among species and the temporal dimension of this distribution. León and Tumpson (*5*) suggest that "The classical models of interspecific competition are phenomenological, that is, they purport to describe the trajectories followed by the abundances of both competitors, without specifying either mechanisms or the dynamics of what the competition is for, that is, resources. Yet the different outcomes of competition inferred from these models are most often interpreted in terms of resources."
5. J. A. León and D. B. Tumpson, *J. Theor. Biol.* **50**, 185 (1975).
6. M. L. Cody, *Science* **183**, 1156 (1974).
7. A. Covich, *Conn. Acad. Arts Sci.* **44**, 91 (1972).
8. J. M. Emlen, *Am. Nat.* **100**, 611 (1966); *ibid.* **102**, 385 (1968).
9. M. Gadgil and W. H. Bossert, *ibid.* **104**, 1 (1970).
10. W. J. Hamilton III and K. E. Watt, *Annu. Rev. Ecol. Syst.* **1**, 262 (1970).
11. D. J. Rapport, *Am. Nat.* **105**, 575 (1971).
12. ——— and J. E. Turner, *Ecology* **56**, 942 (1975).
13. ———, *J. Theor. Biol.* **51**, 169 (1975).
14. J. E. Turner and D. J. Rapport, in *Mathematical Problems in Biology*, P. Van den Driessche, Ed. (Springer-Verlag, New York, 1974), pp. 236–240.
15. T. W. Schoener, *Annu. Rev. Ecol. Syst.* **2**, 369 (1971).
16. G. Tullock, *Am. Nat.* **105**, 77 (1971).
17. E. O. Wilson, *Sociobiology* (Harvard Univ. Press, Cambridge, Mass., 1975).
18. G. Oster, *Am. Nat.* **110**, 215 (1976).
19. W. M. Schaffer, *Ecology* **55**, 291 (1974).
20. R. L. Trivers, in *Sexual Selection and the Descent of Man 1871–1971*, B. Campbell, Ed. (Aldine, Chicago, 1972), pp. 136–179.
21. R. H. MacArthur, *Geographical Ecology* (Harper & Row, New York, 1972).
22. H. G. Wells, J. Huxley, G. P. Wells, *The Science of Life* (Doubleday, Garden City, N.Y., 1933).
23. T. R. Malthus, *Population: The First Essay* (reprinted) (Univ. of Michigan Press, Ann Arbor, 1959).
24. C. Darwin, *The Origin of Species by Means of Natural Selection* (Murray, London, 1859).
25. A. Marshall, *Principles of Economics* (Macmillan, London, 1920).
26. J. M. Keynes, *The End of Laissez-Faire* (Hogarth, London, 1927).
27. See, for example, correspondence between Marx and Engels, in *Marx and Engels on Malthus* (Lawrence & Wishart, London, 1953).
28. A. Smith, *The Wealth of Nations* (Dent, London, 1910), p. 16.
29. L. Robbins, *An Essay on the Nature and Significance of Economic Science* (St. Martin's Press, New York, 1932).
30. C. Lloyd, *Microeconomic Analysis* (Irwin, Homewood, Ill., 1967).
31. H. R. Pulliam, *Am. Nat.* **108**, 59 (1974); *ibid.* **109**, 765 (1975).
32. J. M. Emlen and M. G. R. Emlen, *ibid.* **109**, 427 (1975); R. H. MacArthur and E. P. Pianka, *ibid.* **100**, 603 (1966); F. B. Gill and L. L. Wolf, *ibid.* **109**, 491 (1975).
33. In some cases a nontangency solution is obtained involving complete specialization in one type of good.
34. The fitness contours resemble Levins' concept of the adaptive function developed for a description of optimal phenotypes in changing environments [R. Levins, *Evolution in Changing Environments* (Princeton Univ. Press, Princeton, N.J., 1967)].
35. As in the economic model, nontangency solutions can also occur. If the consumption frontier is convex to the origin, the predator's optimal diet would be complete specialization on one prey type.
36. León and Tumpson (*5*) have shown the relevance of these concepts (substitute and complement resources) in models of ecological competition for resources. MacArthur (*21*) independently derived the notion of complementary resources in his competition model.
37. D. J. Rapport, J. Berger, D. B. Reid, *Biol. Bull. (Woods Hole, Mass.)* **142**, 103 (1972).
38. D. J. Rapport, in preparation.
39. Some of the data in (*38*) from these experiments have been given by W. Murdoch, S. Avery, M. E. B. Smyth, *Ecology* **56**, 1094 (1975).
40. Food preferences were not confounded with prey availability. Preference was determined by comparing food uptake in single and mixed cultures. Details of the method can be found in D. J. Rapport and J. E. Turner, *J. Theor. Biol.* **26**, 365 (1970).
41. R. G. Holmberg, in preparation.
42. W. M. Schaffer, *Ecology* **55**, 291 (1974).
43. G. S. Becker, *Econ. J.* **75**, 493 (1965).
44. Repeater producers allocate some energy to reproduction for many periods during their life cycle and comprise the majority of perennials, while "big-bang" reproducers "have a reproductive effort of zero for many ages followed by the suicidal reproductive effort of one. This category includes a few organisms such as the pacific salmon or the bamboo tree" (*9*).
45. B. Heinrich, *Sci. Am.* **228**, 96 (April 1973).
46. A. Losch, *The Economics of Location* (Yale Univ. Press, New Haven, Conn., 1963).
47. A. Covich, *Annu. Rev. Ecol. Syst.*, in press.
48. Edgeworth's theory of contracts [see Oster (*18*)] involves the famous Edgeworth box diagram within which trades among two parties possessing given proportions of two commodities can be analyzed. Edgeworth showed that trading resources could improve the welfare position of both parties up to the point that the "contract curve" was obtained. Further reallocations along the contract curve involve the improvement of one party's welfare at the expense of the other's.
49. F. N. Egerton, *Q. Rev. Biol.* **48**, 322 (1973).
50. C. S. Holling, *Brookhaven Symp. Biol.* **22**, 128 (1969); D. Pimentel, *Science* **159**, 1432 (1968); L. A. Real, *Theor. Pop. Biol.* **8**, 1 (1975).
51. K. E. Boulding, in *Challenging Biological Problems*, J. A. Behnke, Ed. (Oxford Univ. Press, London, 1972), p. 366.
52. D. J. Rapport and J. E. Turner, in *Mathematical Problems in Biology*, P. Van den Driessche, Ed. (Springer-Verlag, New York, 1974), pp. 206–209.
53. C. S. Holling, *Mem. Entomol. Soc. Can.* **45**, 5 (1965).
54. For a discussion of ecological markets in terms of energy price, see Hannon (*55*). Hannon develops the concepts of marginal product pricing in the ecosystem in terms of energetics. His underlying view of biological components as economic production units is strikingly similar to the theory of production in this article [see (*12*)].
55. B. Hannon, *J. Theor. Biol.* **56**, 253 (1976).
56. Hannon (*55*) points out that the economic conditions for perfect competition are probably better satisfied in natural communities than in economic systems.
57. It should be noted that while predator-prey interactions are hardly a mutually beneficial economic exchange, they contain the essential elements of economic market transactions, namely, an interaction of supply and demand factors. In this case supply is of course involuntary. A more exact economic analog in ecological systems is flowering plant–pollinator interactions.
58. T. W. Schoener, *Science* **185**, 27 (1974); in preparation; *Theor. Pop. Biol.* **6**, 265 (1974).
59. C. Lloyd, D. J. Rapport, J. E. Turner, in *Adaptive Economic Models*, R. H. Day and T. Groves, Eds. (Academic Press, New York, 1975), p. 119.
60. W. J. Baumol, *Economic Theory and Operations Analysis* (Prentice-Hall, Englewood Cliffs, N.J., 1961).
61. H. A. Simon, *Models of Man* (Wiley, New York, 1957).
62. M. B. Johnson, *Household Behavior: Consumption, Income and Wealth* (Penguin, Middlesex, England, 1971).
63. H. A. Simon, *Am. Econ. Rev.* **49**, 253 (1959); W. Isard, *General Theory: Social, Political, Economic and Regional* (MIT Press, Cambridge, Mass., 1969).
64. J. Wolpert, *Ann. Assoc. Am. Geog.* **52**, 176 (1964).
65. P. Haggett, *Locational Analysis in Human Geography* (St. Martins Press, New York, 1966).
66. N. E. Devletoglou, *Consumer Behavior* (Harper & Row, London, 1971).
67. A. A. Alchian, *J. Polit. Econ.* **58**, 211 (1950).
68. S. Enke, *Am. Econ. Rev.* **41**, 566 (1951).
69. S. Winters, in *Adaptive Economics Models*, R. H. Day and T. Groves, Eds. (Academic Press, New York, 1975), p. 73.
70. B. Hannon, *J. Theor. Biol.* **41**, 535 (1973).
71. E. P. Odum, *Science* **164**, 262 (1969).
72. L. V. Bertalanffy, *General Systems Theory* (Braziller, New York, 1968). See also M. D. Mesarovic, Ed., *Views on General Systems Theory* (Wiley, New York, 1964); I. Laszlo, *Relevance of General Systems Theory* (Braziller, New York, 1972); R. Rosen, *Optimality Principles in Biology* (Plenum, New York, 1967); in *Adaptive Economic Models*, R. H. Day and T. Groves, Eds. (Academic Press, New York, 1975), p. 39.
73. E. Durkheim, *The Rules of Sociological Method* (Collier-Macmillan, London, 1938).
74. H. A. Regier, P. L. Bishop, D. J. Rapport, *J. Fish. Res. Board Can.* **31**, 1683 (1974); H. A. Regier and D. J. Rapport, in *Proceedings of Symposium on Biological Evaluation of Environmental Impact* (Presidents Council on Environmental Quality, in press).
75. We thank D. Bloomberg, A. Covich, C. Lloyd, E. Rapport, T. Schoener, G. Tullock, A. Turnbull, P. Wollheim, and several anonymous reviewers for critical comments on the manuscript. We thank H. Regier for continuous encouragement and R. Holmberg for permission to use unpublished material. We acknowledge the support of the Canada Council through its I. W. Killam senior research fellowship program. This fellowship was held at Simon Fraser University, British Columbia, Canada.