Title
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Permalink
https://escholarship.org/uc/item/40r7w9wp

Journal
Samfundsøkonomen, 4

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Publication Date
2002

Peer reviewed

Evolutionary Social Science: The Behavioral Ecology Approach

Evolutionary social science applies theory and method developed in evolutionary biology, anthropology, psychology and economics to understand adaptive variation in human behavior, particularly social behavior. Hypotheses and models about resource use, mating and parenting strategies, and cooperation and competition are derived from evolutionary theory, and empirically tested to understand how humans adapt to their diverse natural and social environments.

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Introduction

There are several approaches in the evolutionary social sciences (Smith et al, 2001), the most prominent ones being human behavioral ecology (HBE), evolutionary psychology, and cultural evolution (or dual transmission) theory. All these approaches combine theory and methods from a number of different academic disciplines. From evolutionary biology they draw mathematical or graphical models anchored in basic principles of evolution by neo-Darwinian natural selection. From neoclassical economics they adopts concepts and analytical techniques such as optimisation, marginal value analysis, and game theory. Various research methods are drawn from the conventional social sciences (anthropology, economics, psychology, etc.) as well as from animal behavior. In empirical research, HBE tends to emphasize ethnographic methods (extend-ed recording of behavioral observations in their immediate socio-environmental context, often in small communities), whereas evolutionary psychology is more reliant on data collection via surveys or laboratory experiments. Dual transmission theory has not yet developed a significant body of empirical research.

This review will concentrate on summarizing theory and findings in HBE, with limited reference to research in the other two primary traditions of evolutionary social science.

Behavioral ecology is a branch of the larger field of evolutionary ecology, the study of evolution and adaptive design in ecological context. Evolutionary ecology emerged as a distinct field in the 1960s, and includes topics ranging from the structural and behavioral traits of organisms to the organization of ecological communities. The first textbooks on be-

havioral ecology appeared in late 1970s and early 1980s, and there is now a voluminous literature, including monograph series, specialized journals, and a number of field-defining volumes edited by Krebs and Davies (e.g., 1997, and earlier).

Researchers in anthropology use the theory developed in animal behavioral ecology as a tool to understand human behavior, considering humans as one more (though admittedly unique) evolved species. The HBE approach began to emerge slowly in the 1970s, and accelerated rapidly in the 1990s (Winterhalder and Smith 2000). Since it incorporated material and methods from the much older tradition of ecological anthropology, and paid attention to the roles of intentionality, social complexity and cultural evolution, the development of HBE required that it adapt and extend biological approaches to better fit human materials and problems (Smith and Winterhalder 1992). We will summarize some fundamental theoretical principles that characterize HBE (and behavioral ecology generally), and then describe selective HBE research problems, grouped into several topical categories.

Theoretical Framework

The adaptationist program (Mayr 1983) in contemporary evolutionary biology proposes that natural selection has designed organisms to respond to local social and environmental conditions in fitness-enhancing ways. From this starting point, behavioral ecologists formulate and test formal models incorporating several components. These generally include an adaptive *goal* (which the strategy under consideration is designed to optimize), a *currency* (for measuring the relevant costs and benefits – see Glossary), a set of *constraints* (characterizing the social and environmental context in simplified form – see Glossary) and a *decision set* (the range of behavioral options considered). Different evolutionary goals may require different optimisation methods – deterministic, stochastic, or dynamic methods, or game-theoretic analysis.

Because they focus on behavior, and particularly social behavior with a strong cultural component, human behavioral ecologists must analyze a much more labile and causally complex set of phenomena than an evolutionist studying, for example, primate anatomy or the foraging behavior of birds. HBE generally attempts to explain such complex patterns of cultural and behavioral variation as forms of *phe-*

notypic adaptation (see Glossary) to diverse social and ecological conditions. The research strategy focuses on understanding variation in behavior that occurs within short time spans (less than a lifetime), or that accumulates over a few generations through cultural evolution, rather than genetic evolution over many generations. HBE researchers test predictions about the match between environmental conditions or payoffs and behavioral variation; less attention has been paid to the developmental or learning mechanisms that create or maintain this match.

The link between phenotypic or cultural adaptation and genetic evolution is provided by positing that the former is guided by »decision rules.« These decision rules are presumed to be pan-human cognitive adaptations that have evolved by natural selection in order to generate behavioral variation that is sensitive to environmental context. In the language of game theory, decision rules are usually conditional strategies (see Glossary) that take the general form »In context X, adopt one behavioral tactic; in context Y, switch to the other tactic,« and so on. For example, in many cultures, it is common for some men to have multiple wives simultaneously, a practice termed »polygyny.« The polygyny threshold model (Figure 1) hypothesizes that female mate choice follows the evolved decision rule »If the bachelor suitor has at least half the resources of an already-married suitor, accept his offer; otherwise, become the second wife of the married suitor.« Behavioral variation arises as individuals match their conditional strategies to their particular socioecological settings.

In common with many scientific fields, HBE research is strongly theory-driven. The research strategy is built around simple and general mathematical models of particular phenomena. Any given model is designed to answer a particular set of questions – e.g., What is the optimal set of prey to harvest? How much should a parent invest in male versus female offspring? Models are used to generate hypotheses that can then be tested empirically, and the results of these tests indicate whether the model appears to correctly capture essential features of the phenomenon being investigated, needs significant modification, or should be discarded. As an area of research develops, sets of related models are linked together to form a body of theory covering a relatively broad domain.

A ideal HBE explanation combines models of

Figure 1
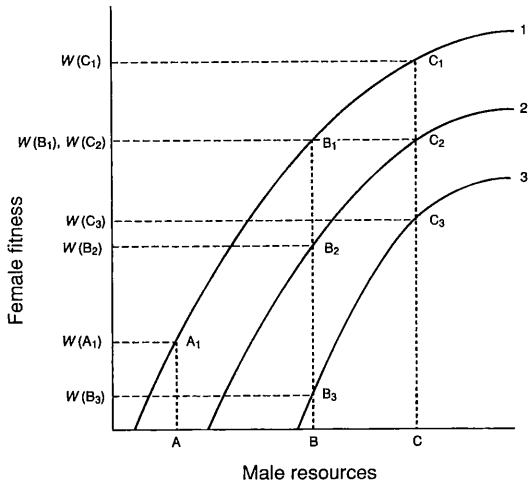
The polygyny threshold model. When female fitness is at least partially a function of the resources controlled by her mate, females may benefit reproductively by mating polygynously with males who control greater amounts of resources. In the hypothetical example graphed here, a female who became the third wife of a male controlling **C** resources would obtain higher fitness [$W(c_3)$] than if she were to be the married monogamously to a male controlling **A** resources or the second wife of a male controlling **B** resources, but would have higher fitness if married monogamously to a poor male controlling **A** than being the third wife of a male controlling **B**.

circumstance and models of mechanism (Winterhalder 1997). Models of circumstance ask how socioecological factors shape the costs and benefits associated with alternative behavioral strategies in a given domain; for example, high amounts of variation in male resources should favor polygyny. Models of mechanism attempt to specify how natural selection, or a variant such as sexual, kin, or cultural selection, will act on these costs and benefits. By combining these two elements, the HBE approach avoids some of the problems associated with functionalist explanation in the social sciences. In particular, neo-Darwinian theory identifies a restricted set of units, costs, and benefits that will play a significant role in evolutionary processes (for example,

ruling out strategies that increase longevity without increasing number of surviving descendants or other genetic kin).

In order to achieve generality, most HBE models are designed to be as simple as possible. They aim to capture the essential features of an adaptive problem, and thus analyze complex socioecological phenomenon in a relatively reductionist fashion. HBE models are thus caricatures of reality intended to be heuristic tools, rather than realistic descriptions of the cognitive or ontogenetic processes that produce human behavior. This sacrifice of realism is made in order to obtain the compensating benefits of increased generality, analytical tractability, and clear empirical appraisal.

More specifically, HBE research often assumes that the details of genetic, phylogenetic, and cognitive mechanisms do not, to a first approximation, seriously constrain human adaptive responses to ecological variation. This strategic shortcut, known as »the phenotypic gambit« (Grafen 1984), is taken because it makes it much easier to build and test general (widely applicable) models, focused on adaptive design. In this regard, it is broadly similar to the »complete information« assumption often made in economic decision models. A model of foraging strategy that was designed specifically for bats, for example, might be made more accurate and realistic by incorporating model representations of echolocation and the specific nutrient composition of insect prey, but it would then be of little use for understanding foraging behavior in birds, bees, or wolves. The phenotypic gambit may of course be wrong in any particular case; for instance, humans may, as some evolutionary psychologists claim, be too easily attracted to sugar and fats for our own good because in our ancestral environments these nutrients were rare and of high adaptive value. Ignoring such evolved biases might lead to erroneous interpretations of the adaptive value of diets in modern populations. On the other hand, humans seem to have the cognitive and cultural abilities needed to rather quickly produce adaptive responses to many novel environmental conditions (including, in the present example, dieting regimes, gymnasiums filled with exercise equipment, and nutritional and medical knowledge for dealing with the threats posed by overeating). Given the present state of our knowledge about human behavioral adaptation, it is probably too early to draw any firm con-

clusions about the overall validity of the phenotypic gambit.

Empirical Research
Production
HBE research can be grouped into three broad topical areas: production, distribution, and reproduction. Analyses of production – resource acquisition behavior – draw from »optimal foraging theory,« a family of models initially developed by biologists that borrows heavily from neoclassical economics. Optimal foraging models address resource selection, time allocation, and movement between different habitat sectors or »patches.« By far the most popular has been the prey choice model (PCM), which nicely exemplifies the HBE research strategy.

PCM predictions test our assumption that foragers have the goal of choosing the set of available prey types that, under given environmental conditions, yields the maximum value per unit foraging time. Because it can be readily measured and is quite general, the currency usually used is the net energy acquisition rate (i.e., calories acquired minus calories expended, per person-hour). Net acquisition rate is appropriate if foragers are time-limited (i.e., gain more from freeing time for other activities than from harvesting additional resources), energy-limited (i.e., gain more from additional units of harvest than from reduced foraging time), or face foraging conditions that expose them to hazard levels greater than those they experience when not foraging (e.g., predation, higher risk of injury, or climate stress). Thus, contrary to common intuition, energy return rate may be adaptively important even if food is relatively abundant, as long as there is an opportunity cost associated with the time or risk exposure involved in foraging.

The PCM predicts that diet breadth will shrink as high-ranking prey become more abundant, but that increased abundance of any resources lying outside of the optimal set will not cause it to be harvested. (As an analogy, think of piece-work; a person paid by the piece will only make time-consuming pieces that pay less per hour worked if she cannot get enough orders for higher-paying pieces, and the abundance of low-return pieces she could sell should have no influence on her decision.) These and other predictions, as well as those derived from other optimal foraging models, have been tested us-

ing extensive field data collected among a variety of hunter-gatherer populations, from deserts to jungles to coastal areas, and from tropical to arctic climes (reviews in Kaplan and Hill 1992; Winterhalder and Smith 2000). The theory is relatively successful in explaining observed patterns of prey choice and patch use, though it appears that meat is more highly valued than the caloric equivalent in plants, and that men and women have different decision rules (see below).

The optimal foraging framework is increasingly being used by archaeologists to study shifts in subsistence patterns in prehistoric populations in response to such factors as technological change, climatic fluctuations, prey depletion due to overharvesting, and human population growth. It has illuminated why children harvest different resources than adults in the same society (one important reason seems to be their smaller size and strength, which limits the rate at which they encounter and harvest resources), why foragers do or do not conserve resource species, and why some resources are processed at the harvest or kill site and others transported whole back to camp, and why foragers in various parts of the world have independently engaged in a process of plant and animal domestication leading to agricultural production systems (review in Winterhalder and Smith 2000).

Given the universal and recurrent short-term need for metabolic energy, it is reasonable to assume that foraging strategies which maximize the net acquisition rate of energy while foraging have higher fitness, at least within broad limits. We should expect selection to favour cognitive mechanisms and culturally-inherited rules of thumb that produce behaviors keyed to this goal. However, most optimal foraging models are general enough that the currency could be any rate measure of resource value – protein capture, raw-material value, monetary return, or prestige. For instance, recent applications of the PCM have examined the circumstances under which sexual selection might favour different currencies for males and females (Bliege Bird 1999). Some applications have even used information return rate as the currency in very modern contexts: library scientist Pamela Sandstrom (1994) finds that foraging theory provides useful guidelines for optimising searches by library patrons, while computer scientists Pirolli and Card (1995) argue that foraging models are applicable to

analysis and design of effective information-gathering tools for the world-wide web and other large-scale, patchy informational databases.

Distribution
Foraging models concern themselves with the short-term production decisions of individuals. However, for humans and their hominid ancestors, the harvest and/or consumption of resources generally occurs in a social group, a context adding a host of theoretical and empirical challenges.

Cooperative subsistence efforts may offer several advantages: increased per capita resource harvest rate, reduced variation in harvest rates, reduced losses to competitors, and increased vigilance in predator detection. However, group foraging can also increase local resource competition and depletion. Even where cooperation is beneficial, modeling has shown that optimal group size may be unstable due to conflicts of interest between existing members and potential joiners. (For example, even if parties of two offer the highest per-capita return rate in deer hunting, I might selfishly wish to become the third group member, thus driving down the returns of the first two members, if the per-capita returns in a group of three are higher than those I can get from solitary foraging.) Once groups form, they provide the context for complex social dynamics, including competition and conflict over labour contributions and division of the harvest, any of which may affect production in ways not anticipated by simple foraging models.

The conditions favouring different kinds of resource transfers have been the focus of considerable research in HBE. Unlike most other primates, human foragers and agriculturalists often harvest resources of sufficient »package size« (e.g., large game) or in sufficient bulk (e.g., an agricultural crop) that some combination of transfer to those without the resource and storage for later use is likely. There are a variety of models to study this (Winterhalder 1997), each making somewhat different assumptions about the socioecological circumstances specified (e.g., group size, information flow, frequency of interactions among the individuals involved, the nature of the resource), and the evolutionary mechanism invoked (e.g., individual, kin, sexual, group or cultural selection). Simple individual-level selection will generate transfer by scrounging (also known as »tolerated theft«) when those

not possessing a resource packet benefit more by taking portions than the holder can benefit by defending them. Voluntary resource sharing is usually modeled in terms of the delayed, cost-benefit calculus of reciprocal altruism. For example, if resource harvest is unpredictable and relatively unsynchronised, harvesters might benefit by pooling the catch and thereby minimizing subsistence risk (variance in resource consumption). A very different type of explanation invokes costly signaling: by successfully harvesting and then distributing difficult-to-capture resources, individuals may reliably signal their skill or other socially-valued qualities, benefiting themselves as well as potential allies, mates, or competitors who gain useful information about the provider as well as food (Smith and Bliege Bird 2000; Gintis et al. 2001; Hawkes and Bliege Bird 2002).

There are several empirical studies assessing the explanatory power of one or more of the resource transfer models. Collectively, these studies indicate that transfer behaviors are much more diverse and context-specific than has been appreciated in the standard ethnographic literature. These studies also suggest that transfer behaviors are probably multicausal in origin, the result of several selective pressures whose relative importance depends on the situation (Winterhalder 1997).

Reproduction
While classical sociobiology analyzed reproductive behavior in terms of factors inherent in sexual reproduction, such as genetic relatedness and gamete asymmetry, HBE analyzes variation in reproductive behavior as a function of local ecological context (Borgerhoff Mulder 1992). In contrast to evolutionary psychology, HBE posits that this variation involves phenotypic tracking of current circumstances, rather than the playback of relatively »hard-wired« species-, sex-, or age-specific behavioral routines that were adaptive in our remote evolutionary history. Nevertheless, HBE approaches overlap considerably with these other two traditions and with certain versions of cultural evolution , as well as with less explicitly Darwinian fields such as demography and reproductive ecology.

The central concept in HBE studies of reproductive strategies is the principle of allocation (Hill 1993): any effort (time, energy, resources) allocated to one domain (for example, enhancing personal

survival and maintenance) cannot be allocated to another domain (for example, reproduction). Mating and parenting together constitute reproductive effort, and models often assume that effort allocated to mating cannot be allocated to parenting (and vice versa). Thus, the principle of allocation can be used to define a set of key tradeoffs that are amenable to study with optimisation models.

The distribution of key resources strongly shapes the behavior of males and females, generally through different routes. If some males can monopolize resources necessary for female survival and reproduction, they can use this control to attract mates, or to compete with other males for social dominance. As we mentioned above, polygyny and increased variance in male mating success is the predicted result. Male resource control coupled with female mate choice is the basis for the polygyny threshold model (Figure 1). The outcome predicted by the simplest versions of this model is an »ideal free distribution,« in which the number of mates per male will match the resources each male can offer, and female fitness will be equal across mateships.

The polygyny threshold model has received broad support in empirical tests among a variety of human societies, though with various qualifications (Borgerhoff Mulder 1992; Winterhalder and Smith 2000). The male-controlled resources may be political rather than economic. Coercion by mates or by relatives may severely constrain female choice. Females mated polygynously may face reduced reproductive success due to competition with co-wives, though this may be compensated in the next generation if the sons of polygynously-married women have increased chances of inheriting wealth and mating polygynously themselves.

Polygyny has been a common form of marriage in the great majority of societies in the ethnographic and historical records (just consult the Old Testament for examples). Even in societies where monogamy is legally prescribed, extramarital mating and remarriage biased towards wealthier or more powerful males creates a situation of effective polygyny. Human behavioral ecologists have also analyzed monogamous systems, especially those involving social stratification and dowry, as well as the rare but intriguing polyandrous case. »Serial polyandry,« in which women remarry to find better mates, is presumably much more common (Hrdy

1999) but has only recently begun to be studied in detail (M. Borgerhoff Mulder, personal communication)

Whatever form the mating system takes, human offspring require extensive and extended parental care. This »parental investment« (Trivers 1972) begins with gestation and, among humans, can continue beyond the parent's death (via bestowing of land, wealth, and other forms of inheritance). HBE analyses ask how the amount and timing of such investment might vary according to social and environmental constraints. Most research is concerned with one of three categories: birth spacing, differential investment in offspring (by sex or expected reproductive value), and interactions between mating and parenting.

Since parental time and resources are finite, higher fertility rates should result in less parental investment per offspring and may eventually reduce total reproductive success. This insight provided the basis of the optimal clutch-size model first developed by behavioral ecologists to study reproduction in nesting birds, but easily generalized to apply to any species with parental investment, including humans (Figure 2.a). This model predicts that beyond a certain point, increased fertility (larger clutches, or shorter interbirth intervals) will result in reduced overall parental reproductive success.

Nicholas Blurton Jones (1986) used this approach to show that among the !Kung San hunter-gatherers of southern Africa, interbirth intervals much shorter than the actual mode of 4 years resulted in increased offspring mortality, sufficient to cause a net loss in expected reproductive success. One attempt to replicate the !Kung results among Ache foragers of Paraguay failed, possibly because Ache offspring mortality is less sensitive to variation in interbirth interval (Hill and Hurtado 1996; but see Strassmann and Gillespie 2002).

Parental investment affects a child's health, survival and future mating success, and thus the parents' inclusive fitness. Parental fitness payoffs depend on three sets of variables: (1) the genealogical relatedness between parent (or other caregiver) and offspring, (2) the effect of investment on the expected reproductive value of the offspring (as well as present and future siblings), and (3) the effect of investment on the caregiver's own reproductive value. Sets (2) and 3) are more directly affected by ecological variables, and hence are at the center of HBE

Figure 2
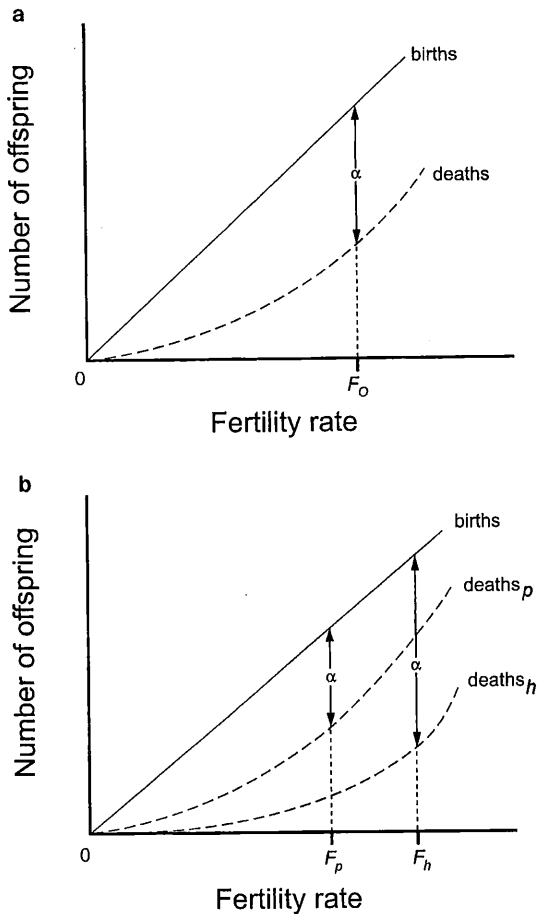
A graphical model of optimal fertility rate. Solid lines represent fertility rate (births per unit time), while dashed lines represent mortality as a function of fertility rate, the latter curving upwards to represent the effect of increasing competition among offspring for parental investment. The net difference between these two curves is the number of surviving offspring, with a local peak at a. The model assumes that selection favours maximizing a given the constraints a parent faces, and hence favours an optimal fertility rate F_o. Graph (a) considers a single parent. Graph (b) models two parents with different constraints and hence different offspring mortality curves as a function of fertility (parental investment). A poorly-endowed parent suffers higher offspring mortality at a given fertility rate, and hence a lower optimal fertility rate F_p than a more highly-endowed parent with optimal fertility rate F_h.

analyses (Voland 1998; various authors in Cronk et al. 2000).

HBE analyses of broader life history topics center on such categories as the timing of growth and maturation, sub-adult and adult dispersal strategies, the onset of reproduction, the timing of reproductive events (e.g., birth spacing, weaning, menopause), mortality patterns, and senescence. Most such research thus far has focused on four topics: (1) links between production and reproduction, (2) reproductive effort and maturation, (3) menopause and extended human lifespan, and (4) evolutionary analysis of the so-called demographic transition (reduction in fertility and family size with modernization). The first three of these topics are given exemplary treatment in an extended case study by Hill and Hurtado (1996; see also Hawkes et al. 1997; Hill and Kaplan 1999), while (4) is reviewed by Borgerhoff Mulder (1998).

Conclusions

Evolutionary social science applies contemporary Darwinian theory and ethnographic and ethological methods to understand the evolutionary origins and adaptive variation in human behavior, particularly social behavior. One approach within evolutionary social science, human behavioral ecology (HBE), combines elements from a number of different academic disciplines, including anthropology, economics, animal behavior, and evolutionary biology. In HBE, formal models anchored in basic principles of evolution by natural selection are used to derive hypotheses concerning how humans adapt to past or present natural and social environments. Predictions are then tested with ethnographic, historical, and archaeological data. HBE research assumes that human decision-making is guided by evolved »decision rules« or conditional strategies, but focuses primarily on behavioral variation and adaptive consequences, rather than on the underlying cognitive mechanisms.

While much has been learned in the relatively short time (circa two decades) in which HBE research has been carried out, the field is in its infancy, and many fundamental issues remain unresolved. These unresolved issues include the degree to which contemporary behavioral variation (particularly that in industrialized societies) is adaptive, the role played by cultural inheritance, and the evolutionary mechanisms (e.g., kin selection, group se-

lection, costly signaling, reciprocal altruism, etc.) and selective environments that have shaped various aspects of human nature. New and promising methodological developments such as risk-sensitive models, dynamic programming, and agent-based models are receiving greater attention, as is the more mechanistic question of how individuals actually achieve the adaptive responses predicted and often found in HBE research.

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Glossary of Terms

Conditional strategy: In game theory, a rule that specifies responding in one of several ways, depending on environmental cues (e.g., if it is a cloudy morning, pack an umbrella) or on the player's current state (if I am bad at math, don't major in economics).

Currency: The units in which costs and benefits of different options are defined theoretically or measured empirically; while evolutionary theory specifies *inclusive fitness* as the ultimate currency, both decision-makers and analysts often use proximate currencies (such as mating success, food harvest rate, etc.).

Constraint: Any factors which determine the possible options, costs, benefits, and abilities of individual decision-makers; a key element in any optimisation or game-theoretical analysis.

Decision rule: A pan-human (universal) adaptation that evolved by natural selection and guides behavioral variation to adapt it to environmental context; for example, a predisposition that makes one prefer to behave in ways that locally increase food acquisition rate or social status. Decisions rules are often modelled as *conditional strategies*.

Inclusive fitness: Net rate of gene replication realized through both direct descendants (offspring) and through the effect of one's actions on the *reproductive success* of close genetic kin.

Marginal value: Additional value (fitness, food capture, wealth, etc.) obtained through an additional unit of investment (of time, effort, energy, wealth, etc.)

Parental investment: Any expenditure that enhances the expected *reproductive success* of a given offspring while reducing the parent's ability to invest in other existing or future offspring.

Phenotypic adaptation: Actions or changes in condition (e.g., tanning) that take place within an individual's lifetime and without genetic change, but which enhance that individual's ability to survive and reproduce.

Polygyny: A form of polygamy involving marriage or sustained sexual coresidence of one man and two or more women simultaneously; a less common form of polygamy is polyandry (simultaneous marriage or mating of one woman and two or more men).

Reciprocal altruism: A social relationship wherein a donor pays a cost to help a beneficiary who profits disproportionately (e.g., sharing one's catch with an unsuccessful forager), and is repaid in the future when fortunes are reversed, generating a net fitness gain to both parties.

Reproductive effort: Any actions or changes in condition (e.g., ovulation) that directly increase the probability of reproduction; subdivided into mating effort and *parental investment*, and distinguished from somatic effort.

Reproductive success: Some measure of the number of surviving offspring (e.g., all offspring surviving to maturity).

Scrounging (tolerated theft): Extraction of resources from a producer by a non-producer (other than a dependant) through begging, coercion, or some other means of imposing costs on the producer.

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BioEconomics Comes of Age

What links economics and biology? First, humans form a biological species. Second, both disciplines assume agents optimize subject to constraints. Third, both recognize the fallacy of aggregation. Fourth, both assume people are self-interested maximizers. Fifth, game theory has assumed central importance in both disciplines. The last development has led us to understand that most people are not self-interested, but rather are strong reciprocators.

Herbert Gintis, External Faculty, Santa Fe Institute and Professor Department of Economics, University of Massachusetts

Introduction

»Nothing in biology makes sense except in the light of evolution,« the great Russian geneticist Theodore Dobzhansky once noted. Charles Darwin, the discoverer of evolution by natural selection, spent many years pondering the data he collected on the distribution of bird species in the Galapagos Islands. Only after reading Thomas Malthus' *An Essay on the Principle of Population* did the idea of natural selection come to him. Alfred Russel, the codiscoverer of evolution by natural selection, reported that he too had come to the idea upon reading Malthus. But of course Thomas Malthus, along with Ricardo and Adam Smith, was one of the founders of the English Classical school in economics. Thus, in a figurative sense, we can say that *nothing in biology makes sense except in the light of economics*.

The influence is not all in one direction. The great French economist Quesnay, whose models of flows between agriculture and industry laid the basis for the English Classical school, was inspired by Harvey's model of the circulation of the blood in the human body.

The natural affinity linking economics and biology stems from several factors. First, humans form a biological species, so it is completely natural that ways of understanding nonhuman species will have some applicability to understanding humans. Second, and flowing from the first, both disciplines use the notion that agents optimize subject to constraints to explain their behavior. In biology, what is optimized is »fitness,« while in economics it is »utility.« In biology, the constraints involve physiology and resources, while in economics the constraints are income and wealth. Third, both disciplines recognize that the aggregate effects of the optimizing behavior of members of a population may be quite different from the intentions of the individuals involved, so a population-level analysis is needed – population biology on the one hand, and general equilibrium analysis on the other.

Self-Interest in Economics and Biology

The fourth factor in the affinity between biology and economics is that both disciplines systematically explain cooperation in terms of individually selfish behavior. In economics, the story is doubtless well known to the readers of this journal. It started with Bernard Mandeville's (1714) *The Fable of the Bees; or, Private Vices, Publick Benefits* which directly inspired Adam Smith's notion of the *invisible hand*. »It is not from benevolence of the butcher, the brewer, or the baker,« wrote Adam Smith, »that