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ARTICLES

Analyzing Adaptive Strategies: Human Behavioral Ecology at Twenty-Five

BRUCE WINTERHALDER AND ERIC ALDEN SMITH

INTRODUCTION

Human behavioral ecology (HBE) began in the mid-1970s with the application of optimal foraging models to hunter-gatherer decisions concerning resource selection and land use. In the 25 years since, the field has developed and successfully adapted evolutionary ecology theory and methods to a wide range of topics important to archaeology and to anthropology generally. In this review we examine the basic theory and its extensions to children's foraging, conservation biology, demographic transitions, domestication and agricultural origins, the evolution of menopause, field processing and central place foraging, life history, male-female division of labor, mating tactics and fertility decisions, and resource intensification. Work on resource acquisition continues, but has been extended from foragers to pastoral and agricultural production systems. Studies of resource distribution, and especially intragroup processes of resource competition and transfers, now supplement and enrich those of resource production. Demographic and life history analyses have begun to show how ecological factors of production and distribution relate to those of mortality, fertility, and life course.

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Key words: behavioral ecology; foraging strategies; human adaptation; human evolution; human life history; reproductive strategies

Besides providing a comprehensive view of the field, we hope to demonstrate that HBE has established itself as a progressive research tradition,[1] a question we take up in our conclusion. We note that this review supplements others. Two edited collections summarized the state of HBE in the early 1980s[2] and early 1990s;[3] shorter reviews have appeared as well.[4–6] A pending collection carries us to the late 1990s.[7] Reviews of HBE generally,[8,9] as well as life history and demography,[10–12] maturation,[13] primate life span and litter size,[14] mating strategies,[15,16] reproductive ecology,[17,18] resource transfers,[19] resource conservation,[20] and division of labor[21] have appeared previously in this Journal.

Evolutionary ecology studies "evolution and adaptive design in ecological context."[22] As a distinct field, evolutionary ecology emerged in the 1960s with the work of Charnov and Orians,[23] Hutchinson,[24,25] Lack,[26] MacArthur and Pianka,[27] MacArthur and Levins,[28] MacArthur,[29] Orians,[30,31] and others. Textbooks on evolutionary ecology appeared in the 1970s, covering topics from the structural and behavioral traits of organisms to the organization of ecological communities. Evolutionary ecology shares fuzzy boundaries with evolutionary genetics, community ecology, animal behavior, and decision theory. When applied to the analysis of behavior, evolutionary ecology is conventionally termed "behavioral ecology." Behavioral analyses have been an integral element of evolutionary ecology from the beginning, treating topics such as foraging strategies,[27] mating systems,[30] and spatial organization and competition.[32] The first textbooks on behavioral ecology appeared in late 1970s[33] and early 1980s.[34] There now is a voluminous literature, including monograph series, dedicated journals (e.g., *Evolutionary Ecology*, and *Behavioral Ecology and Sociobiology*), and a widely read, state-of-the-art series of volumes,[35–38] each edition with a new set of papers.

Human behavioral ecology applies evolutionary ecology models and concepts to the study of human behavioral diversity. HBE began in the mid-1970s with a small set of interpretive papers[39–41] and independent dissertation projects. Initially centered on foraging theory and hunter-gatherer studies, HBE has expanded over the last 25 years to encompass diverse topics and subsistence systems (Fig. 1). Although a second generation of HBE researchers is now in academic positions, the field is young enough that its initiators remain the majority of those publishing in it.

HBE's early goals were to set the cultural ecology of Steward,[42] particularly as developed in his hunter-gatherer work[43] and as represented in later studies such as those by Lee,[44] on a sounder theoretical footing by allying it to emerging, neo-Darwinian approaches to behavior. From the start, the proposed alliance was a somewhat wary and selective one. To varying degrees, there were attempts to distance this anthropological effort (sometimes termed "socioecology"[2]) from the sociobiology of Wilson,[45] and

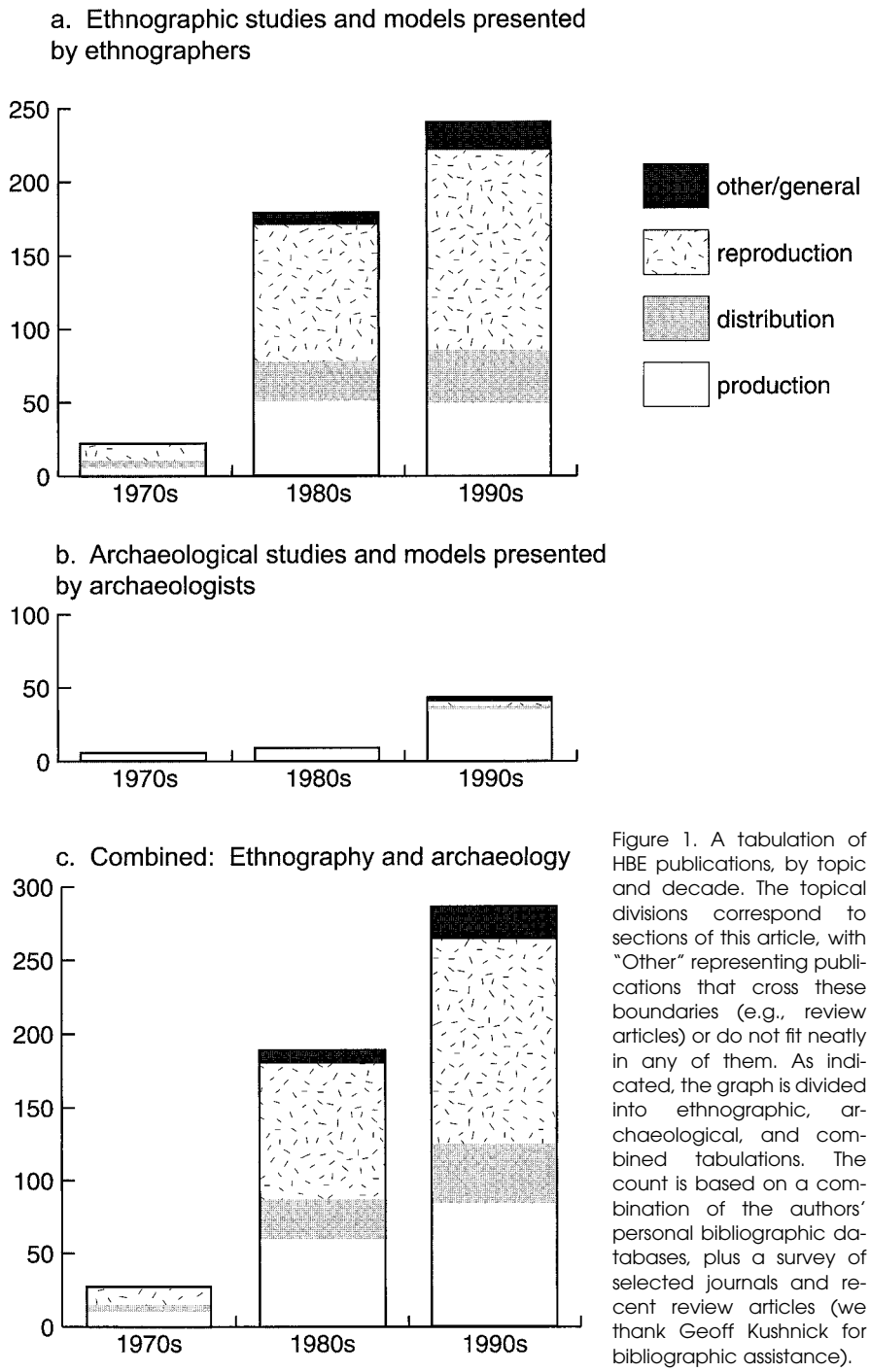

Figure 1. A tabulation of HBE publications, by topic and decade. The topical divisions correspond to sections of this article, with "Other" representing publications that cross these boundaries (e.g., review articles) or do not fit neatly in any of them. As indicated, the graph is divided into ethnographic, archaeological, and combined tabulations. The count is based on a combination of the authors' personal bibliographic databases, plus a survey of selected journals and recent review articles (we thank Geoff Kushnick for bibliographic assistance).

more recently from the approach known as evolutionary psychology (see Box 1).

THEORY AND METHOD IN HBE

HBE is an anomaly within sociocultural anthropology due to its hypothetico-deductive research strategy and its neo-Darwinian theoretical sources. HBE derives testable hypotheses from mathematical or graphical models anchored in basic principles of evolution by natural selection. Emphasizing generality, most HBE models strive to be as simple as possible. They seek to capture the essential features of an adaptive problem, and neglect to some degree the myriad ancillary variables of concern in the more particularist tradition of anthropology.[70] HBE assumes that complex socioecological phenomenon are most fruitfully studied in a reductionist rather than holistic fashion.

However, the methods of HBE and anthropology overlap in a common concern with ethnography: the extended recording of behavioral observations in their immediate socioenvironmental context, often in small communities in remote and materially impoverished conditions, supplemented with data collected by survey, interview, or archival research. Here the uncluttered predictions of simple models meet the messy reality of fieldwork and participant observation. Although HBE is more committed to quantitative methods that reliably document observable behavior than is sociocultural anthropology generally, it is rare that key variables can be controlled, samples randomized, or replication achieved. HBE researchers share field methods with their sociocultural colleagues, but within a theoretical and epistemological framework that is alien to that field.

HBE is an anomaly within sociocultural anthropology due to its hypothetico-deductive research strategy and its neo-Darwinian theoretical sources. HBE derives testable hypotheses from mathematical or graphical models anchored in basic principles of evolution by natural selection.

A complete HBE explanation combines models of circumstance and models of mechanism.[71] *Models of circumstance* ask, "How do socioenvironmental factors shape the costs and

Box 1. HBE Compared to Some Closely Related Fields[a]

	Behavioral ecology	Evolutionary psychology	Dual inheritance theory
Explanatory focus	Behavioral strategies	Psychological mechanisms	Cultural evolution
Key constraints	Ecological, material	Cognitive, genetic	Structural, information
Temporal scale of adaptive change	Short-term (phenotypic)	Long-term (genetic)	Medium-term (cultural)
Expected current adaptiveness	Highest	Lowest	Intermediate
Hypothesis generation	Optimality and ESS models	Informal inference	Population-level models
Primary hypothesis-testing methods	Quantitative ethnographic observation	Survey, laboratory experiment	Mathematical modeling and simulation
Favored topics	Subsistence, reproductive strategies	Mate choice, sex differences	Cooperation, maladaptation

[a] Modified from Smith.[46]

HBE is only one of several distinct approaches to evolutionary analysis of human behavior that have developed in recent years; other prominent ones include evolutionary psychology and dual inheritance theory. Here we offer a brief comparison with these two fields.[46–49]

Evolutionary psychology (EP) aims to uncover the evolved "psychological mechanisms that underpin human . . . behavior," and "the selective forces that shaped those mechanisms"[50] (see reviews[51–54]). EP posits that human behavior is guided by specialized cognitive modules rather than "general purpose" mechanisms that work across multiple behavioral domains. It argues that these modules evolved in the EEA (environment of evolutionary adaptedness), and are designed to produce very specific outcomes that may no longer be adaptive in modern (post-paleolithic) environments. Based on these assumptions, some evolutionary psychologists[55–57] have actively criticized behavioral ecologists for studying adaptive patterns in contemporary nonforaging contexts, and for measuring degree of adaptation via fitness outcomes or correlates.

Dual inheritance theory (DIT) views culture and genes as providing separate (but linked) systems of inheritance, variation, and hence evolutionary change.[58–63] Most DIT practitioners posit that the spread of cultural information is affected by multiple forces, including natural selection (differential fitness of culturally inherited variation), decision-making (based on genetically or culturally evolved preferences and constraints), and transmitter influence or prominence. They differ in the relative strengths or attention they give to these various forces.

In contrast to classical forms of cultural evolutionism[64,65] and to *evolutionary archaeology*,[66,67] DIT practitioners posit that cultural evolution is embedded in and constrained by genetically evolved psychological propensities. They often build these assumptions into explicit mathematical models. Since cultural inheritance differs from genetic inheritance in key ways (e.g., nonparental transmission, multiple transmission events over a lifetime), the evolutionary dynamics of culture will also differ in important but analytically understandable ways. Hence, genetically nonadaptive cultural evolution is possible, and may be likely in hierarchical and modern bureaucratic societies. However, this divergence of cultural and genetic evolution can cut both ways: several DIT theorists[60,68,69] posit that mechanisms of cultural evolution often find ways of *improving* on adaptive outcomes compared to what can be achieved by ordinary genetic evolution plus phenotypic adaptation.

Although EP, DIT, and HBE are often portrayed as competing alternatives, a case can be made for viewing them as complementary.[46,48,49] Competition is fueled by different assumptions, analytical methods, and alliances with other disciplines, as well as by ordinary academic politics. Complementarity between the three styles is increasingly recognized, however, and can be fostered by taking advantage of differences in their methods of investigation (e.g., observation vs. experiment), empirical foci (e.g., psychological vs. behavioral vs. cultural), selection of constraints (cognitive, ecological, informational), time scales of adaptation, and behavioral domains (see table, above). There are limits to this complementarity, however. A behavior cannot simultaneously be the product of a genetically programmed cognitive algorithm that no longer produces adaptive results, a product of a culturally inherited meme that persists because it has a high replication rate, and a product of phenotypic adaptation that is optimally geared to local environmental conditions. Nevertheless, these hypotheses could be simultaneously true for *different* behavioral domains or instances.[46]

benefits associated with potential alternatives in this behavioral category?" *Models of mechanism* require that we specify how natural selection, or a variant such as sexual or kin selection, will act on these costs and benefits. By combining these two elements, the HBE approach avoids some of the problems associated with sociological functionalism.[3] In particular, neo-Darwinism restricts the range of units, costs, and benefits that we expect to have causal salience in evolutionary processes.

HBE usually frames the study of adaptive design in terms of *decision rules*[72] or *conditional strategies:* "In context X, do α; in context Y, switch to β." For example, the polygyny threshold model[30,73] assumes that female mate choice has evolved to follow the 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 diverse socioenvironmental settings. More generally, HBE assumes that the details of genetic, phylogenetic, and cognitive mechanisms do not, to a first approximation, seriously constrain human adaptive responses to ecological variation.[74]

PRODUCTION: FORAGING BEHAVIOR AND RESOURCE SELECTION

Analyses of resource selection and harvesting behavior—"production" in economic terms—formed the greater part of the HBE literature through the 1980s (see Fig. 1). This research draws from "optimal foraging theory" (or OFT).[75,76] Although OFT was initially developed by biologists, anthropologists have made some original theoretical contributions in recent years.[77] OFT consists of a family of models addressing resource selection, time allocation, and habitat movement or "patch choice." By far the most popular of these foraging models has been the diet breadth or prey-choice model.[78] We focus on this particular model to illustrate the logic of the HBE approach in general.

Prey Choice: An Example of the HBE Approach

As with all HBE models, the prey-choice model incorporates a *goal* (optimize net acquisition rate), a *currency* (for measuring the relevant costs and benefits), a set of *constraints* (characterizing the social and environmental context), and a *decision* or *alternative set* (the range of behavioral options to be examined).

Different evolutionary goals may require different optimization methods, and HBE analyses may draw on either deterministic, stochastic, or dynamic optimization, as well as on game-theoretic analysis.[79] The prey-choice model typically uses a deterministic optimization approach, and it specifies which resource types can be harvested most efficiently from among those available in a given locale. Prey-choice model predictions test our assumption that foragers have the *goal* of responding to changing environmental constraints with choices that optimize net yield.

Because it can be readily measured and is quite general, the *currency* used in the prey-choice model is usually the net acquisition rate of energy. Net acquisition rate can be used when 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).[80–85] Thus, net acquisition rate may be important even if food energy is not strictly limiting (see Smith,[81] contra Vayda and McCay[86]).

The *constraints* of the prey-choice model include those endogenous to the forager, such as the information available, cognitive processing capacities, and technology, as well as exogenous factors such as the distribution, density, and nutritional content of the available resources. In applying the model, all constraints but one are considered to be relatively fixed. The remaining constraint becomes the independent variable that predicts choices among the *decision set*. For instance, the independent variable might be the encounter rate with various resource types. Other constraints (e.g., foraging technology, information processing) could take this role, depending on their rate and degree of change, and the researcher's interest.

The *alternative set* in the prey-choice model is the diet combinations (or breadth) achieved by stepwise addition of resources which have been ranked by their pursuit and handling profitability (or 1, 1 + 2, 1 + 2 + 3, etc.). Diet breadth is said to expand as more resources are added to the optimal set, i.e., those pursued on encounter.

Given the universal and recurrent short-term need for metabolic energy, it is reasonable to assume that foraging strategies that maximize the net acquisition rate of energy *while foraging* have higher fitness, at least within broad limits. We should expect selection to favor cognitive mechanisms (and culturally inherited rules of thumb) to 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, material need, monetary return, or prestige. Recent applications of the prey-choice model have examined the circumstances under which sexual selection might favor different currencies for males and females (see Sexual Division of Labor, below).

Although we abbreviate their presentation, it is important to keep in mind that all hypotheses or interpretations discussed in the balance of this paper are derived from models constructed of this same set of elements: an evolutionary goal, a currency, constraints, and an alternative set.

Ethnographic Applications and Extensions of OFT

A small set of ethnographic analyses have tested basic OFT models among hunter-gatherers.[87,88] These range from primarily qualitative and heuristic applications to detailed, quantitative analyses of foraging decisions.[89–92] Specific applications explain shifts in subsistence patterns

Box 2. Leapfrogging From Prehistoric to Postmodern: Foraging for Information on the World Wide Web

Foraging theory has established a secure place in archaeological analyses of economic decisions in prehistoric societies. Much of the ethnographic use of these models has focused on the subsistence behavior of extant hunter-gatherers, pastoralists, or, less commonly, agriculturists (see Production: Foraging Behavior and Resource Selection). One can imagine applications in urbanized, industrial economies, although we know of few specific studies. For instance, taxi drivers act as predators seeking to optimize the benefit-to-cost ratio of encountering and "harvesting" their prey. Routinely, they must decide whether to actively search or to use a sit-and-wait, ambush tactic, when to leave a patch that is declining in its yield, etc. In an actual study, political scientists Gray and Lowery[98] make a preliminary case that behavioral ecology models of group formation can be used to examine competition and alliance formation among political groups lobbying state legislatures.

One of the more interesting recent applications leaps directly to the hunter-gatherers of the postmodern world: software engineers are using HBE theory to analyze and optimize patterns of "information foraging" on the internet. Computer scientists Pirolli and Card[99] argue that foraging theory models are applicable to the analysis and design of effective information-gathering mechanisms from the world wide web and other large-scale, patchy, informational databases. In a similar analysis, library scientist Pamela Sandstrom[100] suggests that foraging theory will be important for her field, as librarians seek to optimize the search capacities of their patrons.

This presents us with one of those marvelous, time-transcending ironies that appeal to postmodernist sensibilities: information-seeking readers may have found this paper because their internet software or library reference services use HBE principles designed originally to understand the subsistence-seeking behavior of prehistoric hunter-gatherers.

over time, in response to such factors as changes in technology,[93,94] climatic fluctuations,[95] the availability of imported substitutes (wheat flour) for resources with high handling costs (grass seed harvesting among Australian Aborigines),[96] or hunting companions.[97]

Fieldwork application of OFT models to several long-standing and some novel research questions illustrates how HBE has stimulated important new research (Box 2).

Children's foraging

Children exhibit different levels of foraging effort and self-provisioning across hunter-gatherer groups (Fig. 2). The !Kung are low-effort foragers whose children do almost no productive work. Among the Hadza, even young children provide substantial portions of their food needs in some seasons of the year. Using cost-benefit measures derived from OFT, Blurton Jones,[101] Blurton Jones et al.,[102] and Hawkes et al.[103] argued that these differences occur because Hadza country periodically offers children higher returns than their !Kung counterparts, and Hadza children are less likely to get lost or be attacked by predators.

The question of why children differ from adults in their foraging choices and net acquisition rate is currently a matter of debate. Working with Hadza, Blurton Jones et al.[104] suggest that children select different resources because of their lesser upper-body strength, not because of limitations of cognition or experience. In contrast, Kaplan et al.[12] propose that humans have evolved to specialize in nutrient-dense resources that are difficult for children to procure and process. Effective use of these resources, they argue, requires maturity, experience, and lengthy skill acquisition.

Figure 2. Among Mikea forager-farmers of southwestern Madagascar, children provide for much of their own subsistence needs through tuber foraging. Wild tubers are the dietary basis for many Mikea households, especially during years of agricultural shortfall. The potential impact of self-provisioning by children on socioecological adaptations of hominids and contemporary hunter-gatherers is an active area of HBE inquiry. Photograph courtesy of Bram Tucker.

Bird and Bliege Bird[105] show that Meriam children foraging for shellfish on tropical reef-tops quickly learn to pursue an optimal set of prey which, given their slower travel speeds and lesser strength, differs from the optimal set taken by adults in the same environment. In this case, body size rather than cognitive or experiential constraints explain the differences between adult and child foraging strategies. In some environments, children are able to forage quite effectively and match OFT predictions, even if their different capabilities require that they diverge from the resources selection of their parents.

Nonforager applications

Behavioral ecologists have now successfully applied optimality and selectionist logic to horticultural[106,107] and pastoral[108] production systems. Dynamic optimization analysis has been used to examine the cost-benefit trade-offs faced by pastoralist families deciding between inexpensive, high-fertility but environmentally sensitive small stock, and expensive, low-fertility but reliable large stock.[109] Data from several East African societies (Somali, Twareg, Meidob, Turkana) fit the model predictions well.[110,111] Because they manage the movement and feeding of their herds, pastoralists such as the Fulani can be analyzed as making foraging decisions on behalf of their domestic stock.[112] Models of patch choice and optimal information-sharing have also been employed in an industrialized context, to help explain the behavior of Alaskan commercial fishermen.[113]

Conservation biology

Some writings portray indigenous peoples as living in ecological harmony with their environments and carefully conserving resources against overexploitation. Others cite archaeological examples of apparent anthropogenic extinction, and argue that sustainability may be due more to low population densities, simple technologies, or absence of markets than to ecological restraint.[114,115] This interpretive disagreement is partly an empirical problem—evidence is scant—and it is partly due to unclear definitions and ambiguous relationships between observed behaviors and inferences. Sustainable harvests have been cited in favor of conservation when they may be incidental to good hunting tactics or a consequence of other constraints. For instance, rotation of hunting ranges has been cited both as conservation behavior (tracts recently hunted are allowed to "rest," while more productive patches are being exploited),[116,117] and as a tactic to maximize yields through optimal movement among patches.[82,93,118,119]

Figure 3. The Huaorani Indians of Ecuador's Amazon forest use blowguns and darts tipped in curare poison to hunt monkeys and birds from the canopy. Access to firearms and markets has changed the dynamic between indigenous hunters and their faunal prey in ways being investigated by behavioral ecologists. At its best, this work integrates anthropology, evolutionary ecology, population ecology, and conservation biology. Photograph courtesy of Flora Lu.

Alvard[20] and Hames[120] use foraging theory to address these issues (Fig. 3). Alvard[20] defines as conservationist any resource use restraint that sacrifices short-term yield and fitness gains in order to realize long-term benefits from heightened sustainability or yield. Because OFT models identify precisely the behaviors expected by short-term optimization, they provide the null hypothesis against which conservation can be assessed. The Piro horticulturalist-foragers of lowland Peru select prey species matching the prediction of shorter-term optimization models, irrespective of their vulnerability to overexploitation and depletion.[121] When moving through depleted zones near to villages in order to hunt in more favorable distant areas, Piro (Peru)[122] and Yanomamö and Ye'kwana (Venezuela)[120] foragers do not forego opportunistic chances to harvest individuals of valuable but overexploited species. Piro do not selectively avoid the more productive sex-age classes in favor of those minimizing impact on population sustainability.[123] Further, as prey become depleted, tropical foragers increase the time they spend hunting, opposite what would be predicted under the conservationist view.[120,124]

Some important modeling work has examined how population dynamics and production strategies interact.[125,126] For instance, simulation has been used to show how the different parameter values for population density, foraging effort, and resource selection strategies of hunter-gatherers interact with the sustainability and population dynamics of the resource on which they depend.[127,128] For example, if a predator exploits two profitable species that differ in their intrinsic rate of increase ("r"), the low "r" species of the pair is vulnerable to depletion and local extinction.

Behavioral ecologists have now successfully applied optimality and selectionist logic to horticultural and pastoral production systems.

Three characteristics of resources—open access, high abundance relative to need, and a reproductive potential lower than evolved human discount rates[129]—may help to explain why genuine conservation of game appears to be rare in indigenous societies.[20] OFT

Figure 4. Huaorani females in the lowland tropical forests of northeastern Ecuador return from the garden burdened with manioc tubers and cuttings. Although the men assist in garden clearing and weeding, much of the horticultural work is done by women, a typical division of labor. Quantitative, ethnographic studies of time allocation have illuminated the work patterns and subsistence contributions of different sex-age groups, e.g., the young females pictured here, but a satisfactory explanation for male-female division of labor seen in foraging and forager-horticulturalist societies has remained elusive. Photograph courtesy of Flora Lu.

allows us to isolate the costs and benefits that must be assessed in order to separate incidental from genuine conservation, in ethnographic[130] and in archaeological[131,132] contexts. Combined with population ecology models, OFT provides insights into the dynamic processes linking foraging decisions to their impacts on resource populations.[128] Various social constraints (including inequalities in social power) may fundamentally alter the trade-off between efficiency and conservation.[133] More generally, success in solving contemporary environmental problems may require appreciation of our evolved dispositions with respect to patterns of self-interest and temporal discounting in the use of resources.[134–136]

Sexual division of labor

Overall, ethnographic tests and interpretive applications of OFT models have been reasonably successful over a broad range of systems. But failures of model predictions can be a stimulus to research as well. An example is the ongoing debate over the male-female division of labor in many foraging societies (Figs. 3, 4). In some groups, men pursue resources (e.g., large game) that yield a high variance, entail greater between-household sharing, and have greater protein and fat content than the resources preferentially harvested by women. This dimorphism in foraging strategy may be due to male-female complementarity in household provisioning and macronutrient balance,[137–139] or it may reflect male status competition and mating investment.[21,140,141] The debate among these alternatives (and intermediate possibilities) has been protracted, and no clear resolution is in sight (see below, Parenting-Mating Strategy Interactions).

Archaeological Applications and Extensions

Archaeological uses of OFT have been hampered by the fact that direct tests of the models require data on individual decisions, taken in behavioral time. In contrast, the recoverable archaeological record consists of material remains that aggregate over multiple foragers and foraging episodes. The data only indirectly reflect behavior and are further obscured by various taphonomic factors. However, there has been progress in revising OFT predictions to fit the archaeological context.[142] In addition, ethnoarchaeological applications have been devised to serve as a bridge between the short time-frame of foraging models and the extended time-frame of prehistorians.[143–145]

Residential movement

Drawing on archaeological observations from the Owens Valley, Zeanah[146] (see also Kelly[88]) has developed a central place foraging (CPF) model that predicts when hunter-gatherers who travel from their residence (A) to a distant site (B) to gather resources logistically, should reverse the pattern and relocate to that second site, making logistic foraging trips back to (A).

Field processing

Archaeologists also have adapted CPF models to predict when resources will undergo *field processing* to remove low utility portions prior to their transport back to a camp.[77,91,147] Transport of an unprocessed resource takes less handling time in the field and thus allows for more round trips, but some part of the carried load has little or no value. Field processing before transport lessens the number of round trips per unit time, but the load is composed of high-value materials only. Given estimates of load capacities, processing costs, and the utilities of high and low value portions,[148] the model predicts the travel distance at which field processing becomes the best option. Separating nut meats or shellfish from their shells, edible animal tissues from low utility skin, carapace, and hooves, or high-grade stone tool material from low-quality matrix at a quarry are potential examples. Similar analyses shed light on how the distribution and composition of prehistoric faunal remains will be shaped through selective processing and transport.[149,150]

Intensification

According to the prey-choice model, as the forager's encounter rate with high profitability resources declines, overall foraging efficiency falls and the best-choice diet expands to encompass previously neglected types of lower and lower profitability. Encounter rates with the most desirable resources might decline due to a number of reasons, including forager population growth and resource overexploitation. Empirical studies of hunter-gatherers stimulated by foraging theory have shown that low-ranked resources typically are difficult-to-catch or difficult-to-process items such as small game, nuts, and seeds.

Prehistorians have combined these observations on foraging logic, costs, and benefits, to give a new and more specific purchase to an old idea: resource intensification or, more specifically, the *broad spectrum revolution*. For instance, Broughton[131,132] and Broughton and Grayson[151] have shown a remarkably consistent pattern through late Holocene archaeological sites in northern California. Although the precise timing and the species set differ by site and environmental zone, in each case harvests of highly ranked species (e.g., sturgeon, elk, white-tailed deer) drop steadily relative to low-ranked species (e.g., shellfish, acorns, small mammals). Other evidence (e.g., declining size of the species presumed to be subject to heavy exploitation; indicators of increasing human density) is consistent with a hypothesis of resource depletion and diet breadth expansion. Alternative explanations for these changes—new technology, of climate or habitat change affecting resource population densities—can be rejected. Whereas acorns once suggested the easy bounty of the California environment, experimental archaeology studies coupled to OFT models suggest that acorn use marks the latter stages of a long period of declining production efficiency.[152] In a like study, Edwards and O'Connell[153] use foraging theory to evaluate the plausibility of several hypotheses for the relatively late appearance of "broad spectrum" seeds in the diets of arid-zone Australian Aborigines.

Stiner et al.[154,155] use a similar OFT approach in their study of human population growth and resource intensification in early Middle- to Upper- and Epi-Paleolithic sites in Italy and Israel. Their analysis turns on the implications of two categories of small game. In one category are "slow," easily caught and processed, high profitability species with low fertility and thus, low resistance to exploitation. Tortoises and marine shellfish are "slow." The other category consists of "fast," more difficult to catch, low profitability species with high fertility and thus high resistance to exploitation. Partridges, hare, and rabbits are "fast." In the sites examined, "slow" species appear steadily in the archaeofaunal record throughout the Middle Paleolithic but are increasingly supplanted in importance by "fast" species in the Upper and Epi-Paleolithic. The Middle-Paleolithic pattern is consistent with a mobile, low-density population of human foragers, opportunistically harvesting high-value "slow" species without the exploitation intensity that would cause their extirpation. Increasing human density and greater sedentism in the Upper and Epi-Paleolithic are interpreted from the diminishing size and apparent depletion of easily harvested "slow" species and their replacement in the foraging schedule with low profitability, "fast" small game. Biotic communities were relatively stable through the examined changes in harvests, eliminating one alternative explanation for the pattern.

Given their life history variability and potential disparities in their ranking as resources, small game may prove to be more sensitive indicators of basic changes in the prehistoric foraging economy than are the large game species that typically command the most archaeological attention.

Given their life history variability and potential disparities in their ranking as resources, small game may prove to be more sensitive indicators of basic changes in the prehistoric foraging economy than are the large game species that typically command the most archaeological attention. Stiner et al.[154,155] paleoanthropoloical offer a too rare example of the potential contribution of behavioral ecology models to interpretation.

Domestication and agricultural origins

Recent work shows that OFT may be useful in understanding the conditions under which domestication and agricultural production might emerge and spread.[156–159] The cost-benefit trade-offs recognized in OFT models underwrite a set of hypotheses concerning the circumstances in which prehistoric agriculturalists would adopt or domesticate new crops, and their impact on existing agro-ecological relationships in the prehistoric southeastern United States. For instance, maize remained a minor component of garden production for some 600–1,000 years after its introduction into the Midwest and Midsouth, but it quickly came to dominate production after its later arrival in the interior Southeast.[160] The use of acorns declined relative to hickory nuts coincident with the emergence of plant husbandry in upland regions of the Cumberland Plateau, eastern Kentucky.[161]

GROUPS AND RESOURCE TRANSFERS

Foraging models concern themselves with the short-term production decisions of individuals. The input variables to these models are environmental factors such as the profitability, density, distribution, and re-

sponse to exploitation of potential resources. Foraging models are the only models a Robinson Crusoe would need. However, for humans in general, their hominid antecedents, and many other species, the harvest and/or consumption of resources likely occurs in a group. Attention to the resulting social interactions adds the evolutionary dynamics of resource distribution to those of production.

Models

Group-based subsistence efforts may offer several advantages: 1) increased per capita encounter rate with resources, 2) reduced variation in encounter rates, 3) reduced losses to competitors, and 4) increased vigilance and predator detection.[162] Nonetheless, modeling has shown that optimal group size itself may be unstable due to conflicts of interest between existing members and potential joiners.[163,164] Once groups exist, they provide the context for complex social dynamics, including competition and conflict.[165] Here we focus on resource transfers, which are fundamental to these social dynamics and are well-studied in HBE.

Hand-to-mouth feeding provides no incentives to food transfers beyond provisioning of related infants and juveniles until they are competent as independent foragers. However, the situation is different if group members harvest one or more of their resources as a divisible "packet," a unit large enough that it cannot be consumed immediately by the individual holding it. The technical equivalent of this condition is that the value of the packet is subject to short-term, diminishing marginal returns to the individual possessing it.[166] This virtually guarantees that portions of the packet will be valued differently by different group members. Given this model of circumstance, a variety of evolutionary mechanisms may come into play.[71]

All resource transfer models address a common causal circumstance, the unsynchronized acquisition of valuable resource packets by individuals within a group. The models differ primarily in their structural refinements (e.g., to what extent are the group members genetically related, or in an ongoing social relationship? What cost-benefit constraints are present? What is the nature of the resource?), and in the evolutionary mechanism they apply (e.g., individual, inclusive, sexual, or group selection). Simple individual-level selection will generate transfer by *scrounging*[167] (also known as tolerated theft[168]) when those not possessing a resource packet benefit more by taking portions than the holder can benefit by defending them. Resource *sharing* eliminates the involuntary element of coercion, replacing it with the delayed, cost-benefit calculus of reciprocal altruism.[169] In *by-product mutualism*[170] the individual discovering or possessing a resource obtains a net gain as a result of others participating in its capture, defense, or consumption. In this case, short-term cooperation is mutually beneficial, and defection or cheating, so important to reciprocal altruism, is not an issue.

Costly signaling,[171–173] a form of by-product mutualism, is another potential mechanism for resource transfers.[174] By successfully harvesting and then distributing difficult or dangerous-to-capture resources, individuals reliably signal their prowess, benefiting themselves as well as participants who gain both food and useful information.[141] In *trade* or *exchange*,[175] individuals swap unlike resources or services because both, by marginalist logic, stand to gain by doing so. The *show-off hypothesis*[176] is a transfer model built on the mechanism of sexual selection. Male hunters target high value, high-variance resources, despite unfavorable average returns and losses to group-wide sharing, because they are able to translate the resulting "social attention" into other benefits such as enhanced mating opportunities. Finally, inclusive fitness selection should lead to transfers through *kin-provisioning* that balances costs and benefits against degrees of relatedness. If individuals produce significant parts of their diet unpredictably, *risk minimization* is among the important benefits of resource transfers.[177,178]

Ethnographic Studies

There are several empirical studies assessing the relative importance of one or more of the proposed resource transfer hypotheses. Those that exist diverge on which mechanism appears to be causally dominant: scrounging and the show-off hypothesis,[179] trade,[175,180] kin-provisioning,[181] reciprocity-based risk-minimization,[182,183] and costly signaling.[141] Collectively, these studies leave the impression that transfer behaviors are much more diverse and situationally specific than has been appreciated in the standard ethnographic literature on "sharing." These studies also suggest that transfer behaviors are probably multicausal in their origin, the result of several selective pressures acting concurrently, their relative causal importance depending on the situation. Labor exchange has been less studied, but may show comparable diversity of forms and the same range of causal influences.[184–186]

Archaeological/Prehistoric Studies

Provisioning by grandmothers

In conventional wisdom, the features by which *Homo erectus* is believed to anticipate later hominids—male-female division of labor, lengthy juvenile dependence, nuclear families, and central place foraging—developed from a pattern in which males provisioned their offspring through large-game hunting (viz., the *hunting hypothesis*). O'Connell et al.[187] question this scenario and present an alternative, the *grandmother hypothesis*. In their model, the development of more arid and seasonal environments following 1.8–1.7 million years ago reduced the capacity of juveniles to provision themselves with easily gathered fruits, as occurs in most primate species and some hunter-gatherers. This put pressure on their caretaking mothers, who turned to a low-ranked food source which was plentiful and geographically widespread, but which demands adult skill and strength to harvest and process: tubers. The growing demands of provisioning their developing offspring with tubers sharply constrained adult female birth intervals and consequently their fertility. According to the grandmother hypothesis, this constraint provided an opportunity for selection: aging female relatives of these moth-

ers could offset declines in their own fitness by stepping in to provision their grandchildren, especially the offspring of their daughters. Comparative life history studies of existing vertebrates[188] suggest that a variety of features might have followed: reduced juvenile mortality, delay to age of maturity, larger size, shortened birth intervals (higher fertility), and larger group size. This also makes grandmothering a leading evolutionary hypothesis for the extended, postmenopausal female life span of hominids,[189–192] which would evolve and be maintained by natural selection if women near the end of their life span gain inclusive fitness by investing in their grandchildren (or other close relatives still in or before their reproductive prime).

If correct, the grandmother hypothesis shows that neither big-game hunting nor male feeding of a female and her children is required to explain key features of hominid emergence. The hypothesis combines foraging theory observations on the gathering tactics of Hadza mothers and their children[193,194] and life history patterns suggested by comparative studies and the models of Charnov and Berrigan.[14] The precise form and plausibility of the hypothesis depend substantially on research stimulated by HBE.

Transfers and the exploitation of large game

Paleoanthropologists[195] sometimes argue that it was the active hunting of big game that provided the opportunity and incentive for food sharing. In this view, big game were a resource made available to hominids by technological or cognitive advances late in our evolutionary history. However, a good HBE case can be made for the reverse: only with the evolution of reciprocity or exchange-based food transfers did it become economical for individual hunters to target large game. The effective value of a large mammal to a lone forager—what could be eaten and converted directly to inclusive fitness on the short term—probably was not great enough to justify the cost of attempting to pursue and capture it, even if unrelated group members benefited through tolerated theft. However, once effective systems of reciprocity or exchange augment the effective value of very large packets to the hunter, such prey items would be more likely to enter the optimal diet.

Given social foraging and harvest of large-packet resources, both of which are archaeologically visible, the variety of evolutionary mechanisms that can generate intragroup transfers suggests that they will be both commonplace, and diverse in form and function, among our hominid ancestors. Comparative ethological and ethnographic evidence is consistent with this prediction.[196] Resource transfer models also expand our sense of appropriate currencies beyond kilocalories, perhaps modifying optimal resource selection. Some prey types may be valued precisely because they are dangerous, rare, and costly to obtain,[141] e.g., the albino deerskins, red woodpecker scalps, and giant obsidian blades displayed in certain Native Californian ceremonies.[197] Intragroup resource transfer models give HBE analytical linkages between the original production focus of OFT and the dynamic social realm of resource distribution.

If correct, the grandmother hypothesis shows that neither big-game hunting nor male feeding of a female and her children is required to explain key features of hominid emergence.

REPRODUCTION: MATING, PARENTING, AND LIFE HISTORY STRATEGIES

While classical sociobiology[198,199] analyzed reproductive behavior in terms of factors inherent in sexual reproduction, such as genetic relatedness and gamete asymmetry, HBE analyses focus on variation in reproductive behavior as a function of local ecological context. And in contrast to evolutionary psychology,[200] HBE posits that this variation involves phenotypic tracking of current circumstances, rather than the playback of species-, sex-, or age-specific behavioral routines that were adaptive in our remote evolutionary history (see Box 1).[201,202] Nevertheless, HBE approaches overlap considerably with these other two traditions and with certain versions of cultural evolution, as well as with less explicitly neo-Darwinian fields such as demography[203] and reproductive ecology.[204]

HBE analyses of reproductive behavior can be divided into three broad areas: mating, parenting, and life history.[205–207]

Mating Strategies

The distribution of key resources strongly shapes the distribution of males and females, generally through different routes.[208,209] 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. Polygyny and increased variance in male mating success will result. Male resource control coupled with female-initiated mate choice is the basis for the "polygyny threshold" model[30] referred to earlier. The outcome predicted by the simplest versions of this model is an *ideal free distribution,*[210] in which the number of mates per male will match the resources each can offer, and female fitness will be equal across mateships.

Despite its simplifying assumptions, tests of the polygyny threshold model have generally supported its applicability to human mating systems.[73,211–218] The male-controlled resources may be political rather than economic.[219] Male coercion (especially by agnatic kin groups) may severely constrain female choice.[220] Females mated polygynously may face reduced reproductive success due to competition with co-wives.[221,222] The effects of co-wife competition may be compensated, however, if the sons of polygynously married women have in-

creased chances of inheriting wealth and mating polygynously themselves.[223]

Polygyny has been the preferred marriage form for the great majority of societies in the ethnographic record.[208] Even in putatively monogamous societies, extramarital mating and remarriage biased towards wealthier or more powerful males creates a situation of effective polygyny.[218] Human behavioral ecologists have also analyzed the rare but intriguing polyandrous case,[60,202,224–226] as well as monogamous systems,[138,227,228] especially those involving stratification and dowry.[229–232] Recent work is particularly concerned with analyzing the trade-offs between parental investment (see below) and mating effort, as noted above (Sexual Division of Labor).

Ethnoarchaeologists are just beginning to make use of HBE approaches to reproduction. For instance, the mating tactics of hunter-gatherer males may lead to mobility and ranging patterns different from those optimal for reliably securing resources.[233]

Parenting

Whatever the mating system, human offspring require extensive and extended parental care. This parental investment[234] begins with the mother's resource allocations during gestation. HBE analyses ask how the timing and amount of such investment might vary according to social and environmental constraints. Most research falls into three categories: birth-spacing, differential investment in offspring (by sex or expected reproductive value), and interactions between mating and parenting.

Birth spacing

If parental time and resources are finite, a shorter interbirth interval should result in less parental investment per offspring and may eventually reduce each offspring's fitness. This is the basis of the optimal clutch-size model (Fig. 5a) of Lack.[26] It predicts that beyond a certain point, increased fertility (larger clutches, or shorter interbirth intervals) will result in lowered overall parental reproductive success. Blurton Jones and Sibly[236] use this approach and data on !Kung San work effort and demography[235] to show that 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.[236] This effect did not occur for a mother's first interval, nor when birth followed the death of the preceding offspring; in these cases, interbirth intervals were significantly shorter (as the model predicted).[237,238]

At least one careful attempt to replicate the !Kung results among Ache foragers[239] failed, possibly because offspring mortality is more sensitive to variation in interbirth interval in the !Kung setting. It has also been argued that the !Kung results are spurious, with the long interbirth intervals a result of female infertility due to sexually transmitted disease,[240,241] an argument rebutted by Blurton Jones.[242] Finally, it may be that in the Ache case (and likely many others), the relationship between fertility and offspring survival is confounded by *phenotypic correlation*, which generally will mask the predicted functional relationship of the Lack model,[206,239,243] as illustrated in Figure 5b.

Phenotypic correlation occurs when hidden heterogeneity in uncontrolled variables confounds the effect of the causal variable under investigation. For example, wealthy individuals might tend to have more expensive houses *and* more expensive cars (a phenotypic correlation), even though we have good reason to expect a *negative* correlation between investment in houses and investment in cars due to the fact that the same dollars cannot be spent on both.[244] While the logic of phenotypic correlation is straightforward, uncovering hidden heterogeneity and controlling for its effects in nonexperimental studies like those undertaken by HBE (and other fields studying human behavior in naturalistic settings) are difficult. If selection has designed the reproductive system to adjust facultatively to situational constraints, then interbirth intervals will be short when the parent's resources are relatively abundant and long when their condition is poor. The modal measures typically available to us obscure this intrasample variability. There is abundant evidence for such adaptive variability in human reproductive ecology.[203,204] One possible solution, multivariate analysis, requires larger samples than anthropologists are usually able to generate. Another is to use historical data on individual families within the sample to track functional links between birth spacing and resources, but this is obviously not an option if the requisite time series is lacking.

Differential investment

Parental investment throughout a child's development affects that 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. Set (1) is indirectly subject to ecological variation (e.g., patterns of coresidence will affect the likelihood that a social parent or other caregiver is a close genetic relative), while sets (2) and (3) are more directly affected by ecological variables, and hence at the center of HBE analyses.

Postpartum parental investment decisions range chronologically from whether or not to keep the child—the alternatives being infanticide, abandonment, and adopting out—to delegation of care to others, generally either relatives or hired laborers such as wet nurses, to the legacy the child may receive prior to or upon death of the parents. Fitness payoffs for nearly all of these decisions may differ according to sex of offspring. The Trivers-Willard[245] prediction that parents in poor condition or with limited resources will invest more heavily in offspring with the lowest expected variance in reproductive success (usually daughters) has received HBE attention, as have a variety of other hypotheses (Box 3).

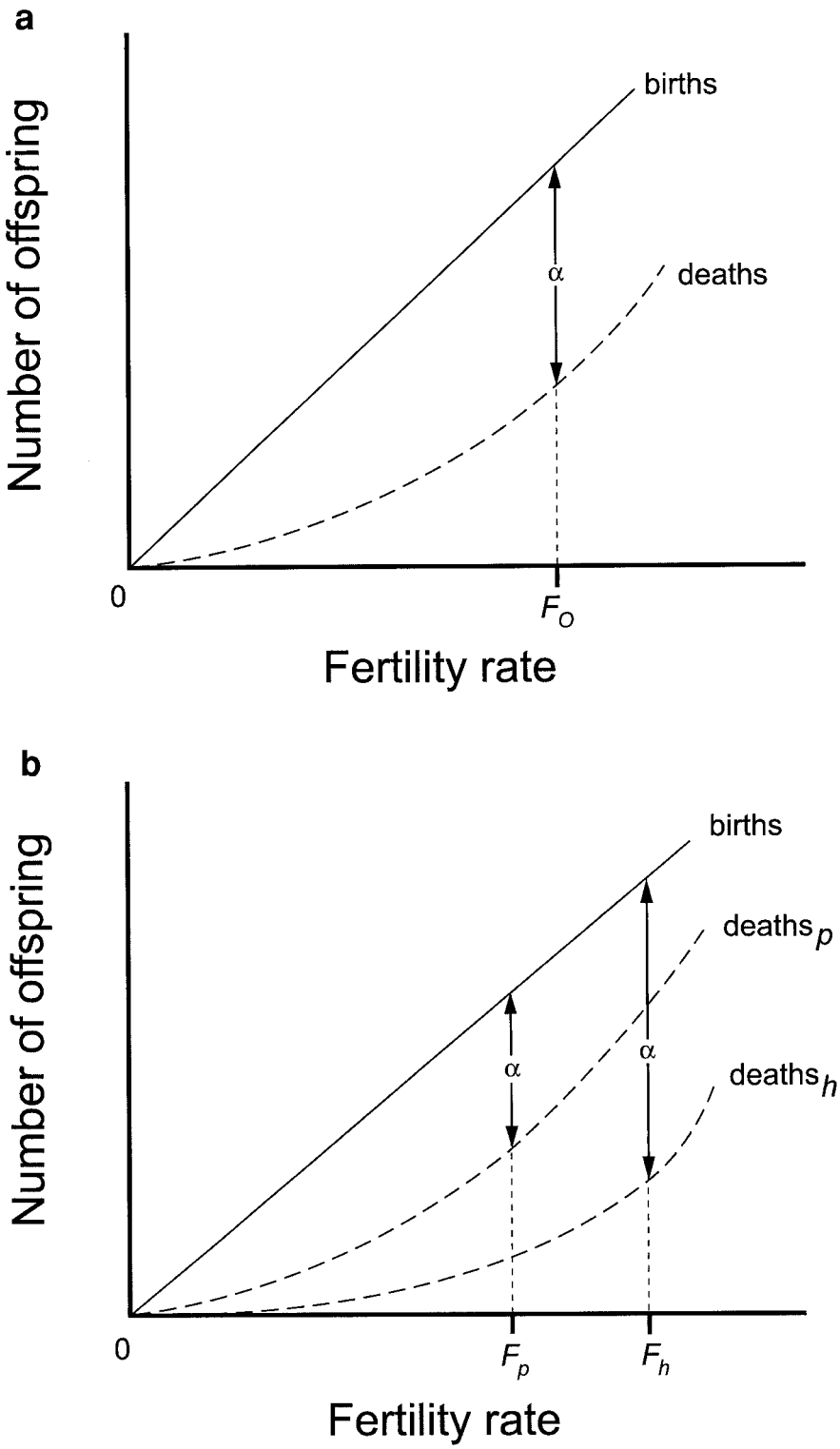

Figure 5. A graphical model of optimal fertility rate, based on Lack.[26] Solid diagonal lines represent births per unit time, while dashed curves represent mortality as an increasing function of fertility rate. The net difference between fertility and mortality is the number of surviving offspring, with α representing the maximum value this can take for a given pair of fertility/mortality curves. The graph assumes that selection favors maximum values of α, given the constraints a parent faces, and hence an optimal fertility rate F_o. **a**: A single parent is considered. **b**: Parents with different resource or phenotypic endowments have distinct offspring mortality curves as a function of fertility rate. Thus a "poor" parent faces higher offspring mortality at a given level of fertility, and hence a lower optimal fertility rate F_p than a higher-quality parent with optimal fertility rate F_h. If analyses of fertility and mortality do not control for this heterogeneity, the lumped data may make it seem that fertility rate and offspring mortality are *negatively* correlated. The result is that the pattern of fertility optimization may be masked by *phenotypic correlation* (see text), and the prediction of positive correlation will be rejected even though correct.

Parenting-mating strategy interactions

Following the lead of primate and avian behavioral ecology, HBE researchers have begun to consider if paternal care and resource provisioning, rather than simply being forms of parental investment, may be designed to attract or maintain a relationship with a mate (Fig. 6).[21,138,276–278] For example, Albuquerque men as well as Xhosa men in South Africa invest more time and resources in stepchildren who are offspring of their current mates than they do in stepchildren from former relationships (though less than they invest in ge-

Box 3. Selected HBE Tests of Parental Investment Theory

The evolutionary analysis of parental investment need not include a direct focus on ecological factors. However, HBE studies generally examine the ways in which ecological constraints shape the fitness-related costs and benefits of various alternative patterns of parental care, which in turn leads to predictions concerning variation in parental investment decisions. These constraints can include a variety of economic, demographic, political, and mating prospects for offspring that may vary by their sex or phenotypic condition, as well as by the social status and relationships of the parents. Some of the primary HBE predictions about parental investment are listed below, along with a representative sample of empirical studies that attempt to test these predictions. *Not all studies listed below necessarily support the prediction under test.*

Prediction[a]	Representative studies
Reduced genetic relatedness or reproductive conflicts of interest lead to lower PI	Daly and Wilson;[246] Anderson et al.;[247,248] Strassman[249]
Offspring with reduced prospects of survival receive lower PI	Daly and Wilson[250]
Parents reduce PI per offspring as number of offspring increases	Borgerhoff Mulder;[251] Hill and Hurtado[239]
PI per child is increased when marginal benefit of PI is higher	Bereczkei;[252] Kaplan et al.[253]
Adoption and fostering are adaptively modulated according to parental circumstances	Silk;[254] Pennington[255]
Mothers able to delegate nursing and infant care gain increased reproductive success	Bereczkei;[256] Blaffer Hrdy;[257] Turke[258]
Postmenopausal women allocate resources and care to grandchildren or other close relatives	Hill and Hurtado;[191,239] Hawkes et al.[194,259]
Parents with fewer resources preferentially invest in offspring (usually daughters) with lower variance in expected RS	Boone;[260] Borgerhoff Mulder;[251,261] Gaulin and Robbins;[262] Judge and Blaffer Hrdy;[263] Mealey and Mackey[264]
Offspring of the sex that faces better adult economic opportunities receive higher PI	Hewlett;[265] Low;[266] Low and Clarke;[267] Voland et al.[268]
Offspring of the sex that has greater probability of contributing to future support of siblings receive higher PI	Borgerhoff Mulder;[251] Hewlett;[265] Hill and Hurtado;[239] Smith and Smith[269]
Offspring of the sex that has greater probability of competing with siblings for resources or mates receive lower PI	Borgerhoff Mulder;[251] Mace;[270] Voland et al.[271]
If daughters (or sons) have greater future mating opportunities, they receive higher PI	Dickemann;[217] Boone;[260] Bereczkei and Dunbar;[272] Cronk[273,274]
If daughters (or sons) are better able to claim and hold political power, they receive higher PI (especially inheritances)	Blaffer Hrdy and Judge;[275] Boone;[260] Hewlett[265]
Parental resources with increasing marginal benefits to offspring are characterized by unigeniture (single heirs)	Boone;[260] Voland et al.[268]
Increasing marginal benefit of biparental care leads to increased pair-bond stability	Hurtado and Hill;[138] Blurton Jones et al.[104]

[a] PI, parental investment; RS, reproductive success.

netic offspring under comparable circumstances).[247,248] This pattern is not adaptive as parental investment per se, but does make adaptive sense if one views it as investment in maintaining a current mating relationship (i.e., as mating effort). Unraveling interactions such as these is a promising area for future HBE research, but will require a great deal more theoretical and empirical effort.

Life History Strategies

Life history theory is concerned with the evolution of maturation rates, reproductive rates and timing, dispersal patterns, mortality patterns, and senescence. Most HBE work on life history thus far has focused on three topics: 1) links between production and reproduction, 2) reproductive effort and maturation, and 3) evolutionary explanation of the so-called demographic transition.

The grandmother hypothesis (described above) and related proposals take up the issue of reproductive effort and maturation, particularly the possible evolutionary causes and consequences of menopause. Perhaps the most impressive work to date is that by Hill and Hurtado,[239] who developed a model of reproductive timing based on Charnov[279] that successfully predicts variation in age of reproductive maturation of women in three different populations: Ache, !Kung, and North America. Analyzing data from contemporary Chicago broken down by residential neighborhoods, Wilson and Daly[280] show how life history variables such as life expectancy and reproductive timing respond to variation in social and ecological factors such as economic opportunity and homicide rates (Box 4).

Demographic transition

"Demographic transition" can refer to any dramatic and sustained change

in patterns of fertility and mortality, but conventionally it is used to label the rapid decline in completed family size observed throughout Western Europe in the late 18th and early 19th centuries.[281] This decline was due to a combination (not generally simultaneous) of reduced mortality and an even greater reduction in fertility; elsewhere in the world, populations have shown various degrees and combinations of these two trends, with resultant levels of population growth or equilibrium. While demographic transition is primarily viewed as a matter of demographic rates, it is also characterized by greatly increased levels of material investment (including inherited wealth) in each child; to the extent that this material investment reduces the number of additional children that can be reared, demographic transition also involves an increase in parental investment as defined in evolutionary theory.[234]

Historical and economic demography has revealed several socioeconomic factors correlated with modern low-fertility regimes, but has failed to develop a robust explanation of demographic transition that can account for its varied occurrence in time and space. The conjunction of increased wealth and decreased fertility characteristic of post-transition populations presents an apparent paradox for evolutionary models of fertility and parental investment. Indeed, it stands in stark contrast to a growing body of data showing that in pretransition (preindustrial) societies, wealth and fertility (as well as survivorship, and hence reproductive success) are positively correlated.[282,283]

A number of HBE researchers have recently tackled this issue with a combination of analytical models, simulations based on dynamic modeling techniques, and empirical studies, with some novel and promising results.[282,284] The key theoretical idea explored in this work is that rather than maximizing the number of offspring raised, under at least some circumstances humans might adjust fertility behavior in a way that maximizes longer-term fitness. In the simplest formulation, this might be measured as number of grandchildren.[253,285] In more complex versions, it might be a weighted product of (heritable) wealth times children,[286] a fertility function weighted by risk,[287] or asymptotic (long-term expected) fitness.[288]

Figure 6. A Tanzanian Datoga pastoralist and his child. The extent of male parental effort and its relationship to mating tactics in subsistence societies are a complex and hotly debated issue in human behavioral ecology. In pastoralist societies like this, even though men engage in mating effort throughout their lives by accumulating polygynously married wives, deep affection is observed between fathers and their children. Photograph courtesy of Monique Borgerhoff Mulder.

Kaplan et al.[253,289] and Kaplan and Lancaster[290] have developed an explanation of fertility reduction that focuses on parental investment to prepare offspring for successfully competing in labor markets where "human capital" (education and acquired skills) is a prime determinant of success. In their formulation, reduced fertility and demographic transition result from high levels of parental investment *per child* coupled with maladaptive levels of fertility reduction aimed at reducing these costs across a parent's set of offspring. Support for the model includes the finding that parents respond to increased skills-based labor market opportunities with reduced fertility, despite the fact that larger family sizes still yield larger numbers of grandchildren.

The dynamic optimization model developed by Mace[285] is meant to apply to subsistence-based societies rather than economically modern ones, but nevertheless has implications for understanding demographic transition. The model predicts that increased productivity and reliability of subsistence lead to increased fertility (as observed in traditional societies): "when living conditions are easier, parents can afford more children, and do not need to be so generous to each child" in order to maximize the number of surviving grandchildren (p. 395). It also predicts that an increase in the cost of raising children leads to a marked reduction in the optimal fertility rate, as well as an increase in average inheritance and average wealth, all features associated with post-transition societies. Interestingly, reduced mortality also lowers fertility, but not by a large amount.

. . . rather than maximizing the number of offspring raised, under at least some circumstances humans might adjust fertility behavior in a way that maximizes longer-term fitness.

In another original approach to the issue, Winterhalder and Leslie[287] use a risk-sensitive model of fertility optimization to predict that reduced fertility will result from any socioeconomic or environmental factors that reduce the degree of unpredictable variance in completed family size, decrease the costs of unusually low fertility (such as reduced reliance on household labor by offspring), or increase the costs of unusually high fertility. From the perspective of this model, the lowering of mortality due to stochastic events like epidemics or

Box 4. The Wilson-Daly Study of Mortality and Reproductive Timing in Chicago

In an innovative application of life-history analysis, Wilson and Daly[280] examine the relationship between risk-taking (measured by homicide rates as well as other risk-based causes of mortality), life expectancy (with homicide effects statistically removed), reproductive timing, and economic inequality. Wilson and Daly propose that poor economic opportunities and lowered life expectancy from extrinsic factors lead to elevated risk-taking behavior, including status contests that sometimes escalate into homicides. This steep discounting of future prospects should in turn favor early onset of reproduction.

Analyzing data by neighborhood units (n = 77), Wilson and Daly show that these measures do covary across neighborhoods in precisely the manner predicted: 1) Homicide rates vary 100-fold, and are highly correlated with both male and female life expectancy, even after homicide mortality is removed (see table, below). 2) A stepwise regression shows that the "Robin Hood index" (a measure of income variance within neighborhoods) is an independent predictor of homicide rates as well—local income inequality encourages lethal competition. 3) Women respond to low life expectancy with earlier onset of reproduction, and high fertility rates in the early childbearing years (see figure). The detailed results of this study provide compelling evidence that humans respond to perceived variation in life chances with major shifts in life history variables, even in environments far different than those experienced during most of human evolution.

VARIATION IN LIFE HISTORY ACROSS CHICAGO NEIGHBORHOODS[a]

Variable	Lowest L_x	Highest L_x
Male life expectancy (L_x)	57.1	74.5
Homicide rate	85.2	7.0
Birth rate (women aged 15–24)	414.0	135.0
Age of women giving birth	22.6	27.3

Notes: [a] Data from Wilson and Daly.[280] L_x, mean life expectancy at birth. The "lowest" column contains data on the 10 neighborhoods with the lowest L_x values, and "highest" column is for the 10 with the highest L_x. Homicide rates are neighborhood averages for males and females combined, per 100,000 per year; birth rates are neighborhood averages per 1,000 women aged 15–24 per year; and the last row provides the median age of women giving birth in each set of neighborhoods.

subsistence failures seen in the transition to modern economies would favor reduced fertility simply by dampening the stochastic variation in realized family size. Whether these effects of risk-sensitive fertility optimization are large enough to account for a substantial portion of the fertility reduction observed in historic transitions is as yet unknown.

HBE AS A PROGRESSIVE RESEARCH TRADITION

Although it may seem a brash claim given the current anthropological fashion for relativism, the 25-year history of HBE is one of clear scientific progress. To make this point, we summarize the accomplishments of HBE in terms of *epistemic values*.[291,292] These are six characteristics that guide pragmatic assessment of scientific progress. In the contemporary ambience of anthropology, even cautious partisans of scientific knowledge aid themselves and the discipline by an occasional and reflective defense of its possibilities.

Predictive Accuracy

Theory development often begins without the data or even the operational methods needed to make testing feasible and convincing. Nonetheless, given the premium on predictive accuracy in science, empirical confirmations must be forthcoming. Taken individually, HBE research projects generally use more rigorous, quantitative methods than their ethnographic counterparts, with good predictive success. However, the number of compelling, data-rich HBE studies is still quite small. The reasons are several. Relatively few anthropologists work with behavioral ecology theory, and its data demands are extensive and exacting. Concepts and methods are advancing rapidly, and hence early studies look primitive by comparison to current standards. The use of confidence-inspiring tools such as independent estimate of parameters, null hypotheses, and significance measures have lagged behind the development and interpretive use of HBE models. On this most important of desiderata—superior agreement

with observation—the HBE record is positive but altogether too thin.

This qualified assessment does not detract from solid and important empirical gains. For instance, optimal foraging theory has stimulated the gathering of extensive data on the profitability of various classes of resources. These data now are at the heart of recent analyses of prehistoric resource intensification and plant domestication. Likewise, quantitative HBE data on time allocation to food production and net yield of foraging, both as a function of sex and age, are central to debates about the show-off and grandmother hypotheses,[12,193] with their extensive implications for hominid life history and socioecological evolution.

Internal Coherence

The parts of a theory should cohere in a logically consistent manner, without gaps or ad hoc elements. Relative to sociocultural anthropology generally, HBE is strong on coherence, benefiting from its close association with two relatively mature fields: economics and evolutionary theory. Although HBE is in the early stages of devising "families"[293] of subject-specific models, there is every reason to project cumulative and coordinated development. Because of the ambitious reach of the topics it addresses, maintenance of internal coherence is an especially important accomplishment of HBE.

Changing ways of valuing resources provide an example. Originally, resource value was appraised in terms of the nutritional yield (e.g., calories) of the prey, an absolute and resource-specific measure. Scrounging models highlighted the importance of assessing marginal value, with its emphasis on the state and needs of the forager relative to others in the group. Hypotheses concerned with trade-offs between parental investment and mating effort suggest that value (and currency) may be sex- and age-specific. Each of these refinements gives us new, coordinated insights into the diversity possible in optimal patterns of resource selection. Another example is the grandmother hypothesis, which links together subsistence, mating and parenting behavior, and life history theory, in a theoretically coherent manner.

External Consistency

A theory should be consistent with related theories that have a general, background claim of applicability to the subject matter. HBE's congruence with neo-Darwinism and microeconomic theory is primary here. HBE benefits by distancing itself from claims of human exceptionalism and the historical attempt to isolate anthropological from collateral theory in the natural and some social sciences. Red-winged blackbirds, hunter-gatherers, and search engines on the world wide web face some of the same resource selection trade-offs. General models of scrounging apply to house wrens and hunter-gatherers; those of risk-sensitive adaptive tactics are equally at home in biology, anthropology, and economics.[294] Life history compromises affect all primates, be they chimpanzees, early hominids in Africa, or the contemporary residents of Albuquerque.

Simplicity is valued for analytical and aesthetic reasons but may be the most troublesome quality of a research tradition to define and assess.

Fertility

Does the theory, over the long term, continue to generate novel predictions, extensions, and modifications not anticipated in its original formulation? Those of us who set out in the 1970s to test diet breadth and related OFT models had no inkling of the extent and diversity of the HBE applications that would be forthcoming. Because its early critics so tightly and confidently circumscribed the "narrowly defined domain"[295] of HBE theory, present advocates can more securely claim that its topical expansion represents genuine and unexpected explanatory fertility.

Unifying Power

Unifying power is the cumulative result of a coherent and fertile theory. Does the theory succeed in establishing relationships among previously disparate subjects? Does it achieve broad scope by uniting these subjects within a common explanatory framework? For HBE, the initial signs look good. Central place foraging models have been adapted to generate insights about field processing and hominid transport. Diet selection models have generated new insights into population ecology and have given new purchase to long-standing archaeological concepts such as the broad spectrum revolution. Cost-benefit methods that were developed to study patch choice are now being used to examine life-history trade-offs and possible causes of demographic transitions. How far this trend will go, and how well it withstands competing theoretical developments, are issues for the future.

Simplicity

Simplicity is valued for analytical and aesthetic reasons but may be the most troublesome quality of a research tradition to define and assess. If we focus on its fundamental theoretical premises, and view them relative to potential explanatory reach, then HBE is extraordinarily simple. If we focus on the dozens of models and myriad of hypotheses that make these basic premises operational, then the situation can appear quite complex. An evaluation of simplicity depends where, along this axis of premises-to-empirical research, one wishes to place the assessment.

AUGURY

Early work in behavioral ecology by biologists, including papers now among the most cited in the field, were routinely rejected by the major ecological journals.[76] By contrast, the anthropologists who took up HBE typically fared well at the hands of

referees and editors. In subsequent influence on their respective disciplines, these roles have reversed. Behavioral ecology in biology has become a thriving subfield. Although readily published, HBE work has not yet achieved comparable scale or impact, and HBE remains a modest and marginalized enterprise in contemporary anthropology. Some archaeologists and the occasional cultural anthropologist follow the field, but it has had little impact, for instance, on general textbooks or broader theoretical discussions. Given the expansion of HBE from foraging to take up traditional problems in archaeology and anthropology, this seems likely to change. By generating sound empirical results on topics of broad interest, HBE surely will pique the curiosity of a broader array of anthropologists.

We see several fruitful directions for HBE. First, old models are being revisited in light of new discoveries and applications. The original diet breadth model is being applied with new appreciation that resource valuation may be differentiated by sex, and it is being used on new problems such as the broad spectrum revolution. Second, old models also are being revised in light of new methods such as evolutionary game theory and risk-sensitive or dynamic programming approaches. Third, the theory is being extended from its base in ethnographic, hunter-gatherer studies to paleoanthropological and archaeological applications and to other production systems, efforts sometimes requiring new or modified models. Fourth, we expect to see new efforts that address gaps in existing studies. For instance, most HBE work to date has neglected proximate analysis of the mechanisms guiding the adaptive behavior of individuals, be these rules of thumb, evolved psychological dispositions, or sociocultural inheritance. Likewise, it has neglected the actual histories by which such traits develop in populations.[296] Fifth, we foresee an elaboration of HBE theory to help explain how complex social institutions and processes (such as social stratification) can emerge from adaptively directed individual decisions interacting with historical constraints. This will require that HBE be integrated with more traditional forms of social science theory and research.[297] What HBE can offer in this partnership is such tools as evolutionary game theory[133] and costly signaling theory.[174] Finally, there are outstanding questions of synthesis. Explicitly reductionist in its methods, as HBE matures it will have to demonstrate that it can successfully reintegrate topically isolated models into a compelling and more holistic understanding of human adaptive behavior.

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