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Human Behavioral Ecology

Intermediate article

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CONTENTS

Human behavioral ecology applies theory and method developed in evolutionary biology, anthropology and economics to elucidate adaptive variation in human behavior, particularly social behavior. Hypotheses about resource use, mating and parenting strategies, cooperation and competition, and life history are derived from models using a selectionist logic, and empirically tested to increase our understanding of how humans adapt to their natural and social environments.

INTRODUCTION

Human behavioral ecology (HBE) is one of several approaches in the evolutionary social sciences (Smith *et al.*, 2001), other prominent ones being evolutionary psychology and cultural evolution (or meme) theory. Like these other approaches, HBE combines theory and methods from a number of different academic disciplines. From evolutionary biology it draws mathematical or graphical models anchored in basic principles of evolution by neo-Darwinian natural selection. From neoclassical economics it adopts concepts and analytical techniques such as optimization, marginal value analysis, and game theory. From anthropology, it borrows ethnographic research methods: the extended recording of behavioral observations in their immediate socioenvironmental context, often in small communities, supplemented with data collected by survey, interview or archival research.

Human behavioral ecology emphasizes quantitative methods such as those characteristic of ethology (naturalistic observation of animal populations): focal follows, scan sampling, and the like.

The topics analyzed in HBE research can be grouped into three main categories (Winterhalder and Smith, 2000): production (resource acquisition and related topics), reproduction (mating and parenting), and distribution (exchange, sharing, and coercive transfers).

Behavioral ecology has developed as the behavioral 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. Behavioral analyses have been an integral element of evolutionary ecology from the beginning, treating topics such as foraging strategies, mating systems, spatial organization, and competition. The first textbooks on behavioural ecology appeared in the late 1970s and early 1980s, and there is now a voluminous literature, including monograph series, dedicated journals (e.g. *Behavioural Ecology* and *Behavioural Ecology and Sociobiology*) and a widely read series of books edited by Krebs and Davies.

ECOLOGICAL SELECTIONISM

The adaptationist program in contemporary evolutionary biology assumes that natural selection has designed organisms to respond to local socioenvironmental conditions in fitness-enhancing ways. With this as a starting point, behavioral ecologists formulate and test formal models incorporating specific optimization goals, currencies, and constraints. Because their subject is 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, skeletal morphology or even avian courtship behavior.

Human behavioral ecology generally attempts to explain such complex patterns of cultural and behavioral variation as forms of phenotypic adaptation to varying social and ecological conditions. The field is less concerned with genetic variation on evolutionary time scales than with variation in behavior that occurs within an individual's lifetime (often in minutes or hours), or that accumulates over a few generations through cultural change. The link between such phenotypic or cultural adaptation and genetic evolution is provided by positing that the former is guided by 'decision rules' – cognitive or problem-solving propensities that themselves evolved genetically through natural selection. However, the genetic basis of these phenotypic capacities is not addressed directly in HBE, which takes an agnostic view of the underlying causal mechanisms that might shape adaptive variation in behavior. Rather, the focus is on testing predictions about the match between environmental conditions or payoffs and behavioral variation, without worrying too much about developmental or learning mechanisms that create or maintain this match.

MODELS AND DECISION RULES

In common with many scientific fields, including general behavioral ecology, HBE research is strongly theory-driven. The research strategy is built around mathematical models of particular phenomena. Any given model is designed to answer a particular set of questions: for example, 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 capture correctly 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 (e.g. optimal foraging theory, or parental investment theory) covering a relatively broad empirical domain.

A complete HBE explanation combines models of 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. 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 have a significant role in evolutionary processes (for example, ruling out strategies that increase longevity without increasing number of surviving descendants or other genetic kin).

All HBE models incorporate a goal (which the strategy under consideration is designed to optimize), a currency (for measuring the relevant costs and benefits), a set of constraints (characterizing the social and environmental context in simplified form) and a decision set (the range of behavioral options considered). Different evolutionary goals may require different optimization methods: deterministic, stochastic, or dynamic optimization, as well as game-theoretic analysis.

Human behavioral ecology usually frames the study of adaptive design in terms of decision rules, which are presumed to be panhuman adaptations that have evolved by natural selection in order to generate behavioral variation that is sensitive to environmental context. These decision rules are often conditional strategies that take the general form 'In context *X*, adopt one behavioral tactic; in context *Y*, switch to the other tactic' (and more complex variants for strategies with more than two tactics). For example, the polygyny threshold model (Figure 1) assumes 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 current socioecological settings.

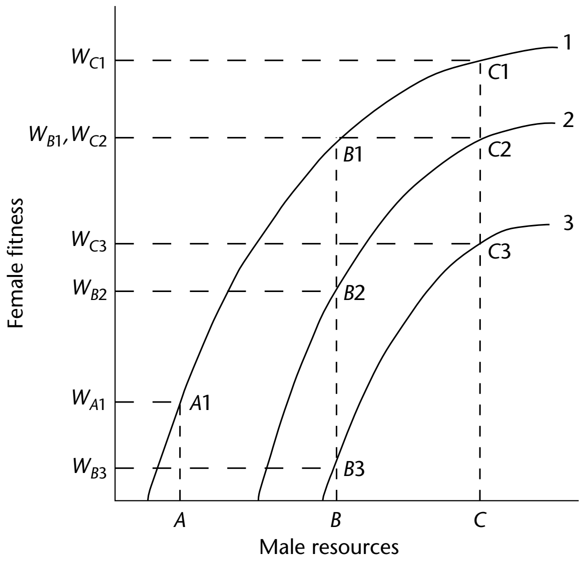

Figure 1. The polygyny threshold model. When female fitness is at least partially a function of the resources controlled by her mate, females may benefit reproductively by mating polygynously with males controlling higher amounts of resources. In this example, a female who became the third wife of a male controlling *C* amount of resources would obtain higher fitness (W_{C3}) than if she were to be married monogamously to a male controlling *A* resources, or the second wife of a male controlling *B* resources. She would have higher fitness if married monogamously to a poor male controlling *A* (W_{A1}) than being the third wife of a male controlling *B*.

THE PHENOTYPIC GAMBIT

Emphasizing generality, most HBE models strive to be as simple as possible. They seek to capture the essential features of an adaptive problem, and thus analyze complex socioecological phenomena in a relatively reductionistic fashion. Such 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 compensating benefits (increased generality and analytical tractability).

More generally, 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 short cut, known as the 'phenotypic gambit', is taken because it makes it much easier to build and test general (widely applicable) models, focused on ultimate adaptive design. The phenotypic gambit may of course be wrong in any particular case: humans may, as some evolutionary psychologists claim, be easily addicted to sugar and fats because in our ancestral environments these nutrients were rare and of high adaptive value. Ignoring such an evolved bias might lead to erroneous predictions about the adaptive value of diets in modern populations. On the other hand, humans seem to have the cognitive and cultural machinery needed to produce adaptive responses quickly to novel environmental conditions (including, in the present example, dieting regimens, gymnasiums filled with exercise equipment, and nutritional and medical knowledge for dealing with the threats posed by overeating). Hence, it is probably premature to draw any firm conclusions about the overall validity of the phenotypic gambit.

EMPIRICAL RESEARCH

Production

Research into HBE can be grouped into three broad topical areas: production, reproduction, and distribution. Analyses of production – resource acquisition behavior – draws on optimal foraging theory (OFT), a family of models initially developed by biologists borrowing heavily from neoclassical economics. These models address resource choice, time allocation, and movement between different habitat sectors or 'patches'. By far the most popular has been the prey choice model (sometimes termed the diet breadth model). It is used here to exemplify the HBE research strategy.

As with all HBE models, the prey choice model (PCM) incorporates a goal, a currency, a set of constraints, and a decision set. The PCM predictions test our assumption that foragers have the goal of choosing the set of available prey types that, under given environmental conditions, yield the maximum value per unit foraging time. Because it can be readily measured and is quite general, the currency used in the PCM is usually the net energy acquisition rate (e.g. kilojoules per 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 energy is not strictly limiting.

The constraints of the PCM include those endogenous to the forager, such as available information, cognitive capacities, and technology, as well as exogenous factors such as the availability, behavior and nutritional value of the potential prey resources. In any given application all constraints but one are considered to be relatively fixed, and the remaining constraint becomes the independent variable that predicts choices among the decision set. For example, the independent variable might be the encounter rate with various resource types, the foraging technology for pursuing them, or information processing capabilities, depending on the researcher's interest. The decision set specific to the PCM consists of all the possible combinations achieved by stepwise addition of resources which have been ranked by their pursuit and handling profitability.

The model predicts that diet breadth will shrink as high-ranking prey become more abundant, and that increased abundance of a resource outside of the optimal set will not cause it to be harvested. These and other predictions, as well as ones derived from other OFT models, have been tested among a variety of hunter-gatherer populations (Kaplan and Hill, 1992). The theory is relatively successful in explaining observed patterns of prey choice and patch use, as well as shifts in subsistence patterns in response to such factors as changes in technology, climatic fluctuations, anthropogenic prey depletion, and human population growth. The OFT framework has illuminated why children harvest different resources from adults in the same society, why hunters often fail to conserve prey species, why some resources are processed at the harvest or kill site and others transported whole back to camp (of great significance for interpreting archaeological data), and even why foragers in various parts of the world have independently engaged in a process of plant and animal domestication leading to agricultural production systems (Winterhalder and Smith, 2000).

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 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, application of the PCM has been used to examine the circumstances under which sexual selection might favor different currencies for males and females (Bliege Bird, 1999).

Distribution

Foraging models concern themselves with the short-term production decisions of individuals. However, for humans and their hominid ancestors, the harvesting and consumption of resources generally occur in a social group, a context that adds 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 and predator detection. However, group foraging can also increase resource depletion and competition; and even where cooperation is beneficial, modeling has shown that optimal group size itself may be unstable owing to conflicts of interest between existing members and potential joiners (Figure 2). Once groups form they provide the context for complex social dynamics, including competition and conflict.

The conditions favoring different kinds of resource transfers (sharing, scrounging, and so on)

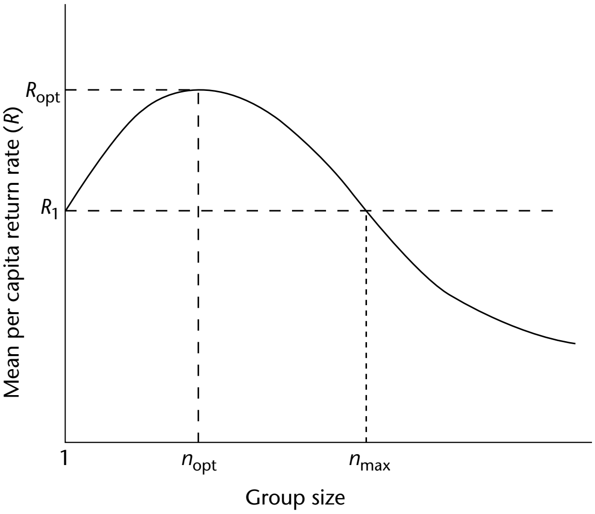

Figure 2. Optimal group size and member–joiner conflict. When the per capita return rate R (e.g. kilo joules per forager per hour) reaches a maximum (R_{opt}) at a group size of $n_{\text{opt}} > 1$, then members of a group will suffer a decline in their share of group production if additional individuals join, but potential joiners have an incentive to join as long as their share will be greater than what they can obtain through solitary production (R_1), up to the equilibrium group size $n_{\max}$.

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 or storage for later use is likely. There are a variety of models to study this, each making somewhat different assumptions about the socio-ecological circumstances and the evolutionary mechanisms that may shape resource transfers.

All resource transfer models address a common circumstance, the unsynchronized acquisition of valuable resource packets by individuals within a group. The models differ primarily in the additional circumstances specified (e.g. group size, information flow, frequency of interactions among the individuals involved, the nature of the resource) and in the evolutionary mechanism they invoke (e.g. individual, kin, sexual, group or cultural selection) (Winterhalder, 1997). 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 unsynchronized, harvesters might benefit by pooling the catch and thereby minimizing subsistence risk (variance in resource consumption).

In by-product mutualism the individual discovering or possessing a resource obtains a net gain as a result of encouraging others to participate in its capture, defense or consumption. In this case short-term cooperation is mutually beneficial, so defection or cheating, a potential threat to reciprocal altruism, is not an issue. One form of by-product mutualism is costly signaling: by successfully harvesting and then distributing difficult-to-capture resources, individuals reliably signal their prowess, benefiting themselves as well as potential allies, mates or competitors, who gain both food and useful information about the provider (Smith and Bliege Bird, 2000). In trade, individuals swap unlike resources or services because both will gain by doing so. Finally, inclusive fitness selection should lead to transfers through kin-provisioning that balance costs and benefits against degrees of relatedness.

There are several empirical studies assessing the relative importance of one or more of the proposed 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.

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. In contrast to evolutionary psychology, HBE posits that this variation involves phenotypic tracking of current circumstances, rather than the playback of relatively fixed behavioral routines specific to species, sex or age that were adaptive in our remote evolutionary history. Nevertheless, HBE approaches overlap considerably with these other two evolutionary traditions and with certain versions of cultural evolution, as well as with less explicitly neo-Darwinian fields such as demography and reproductive ecology.

In HBE, analyses of reproductive behavior can be divided into three topics: life history, mating, and parenting (Borgerhoff Mulder, 1992). Life history is the broadest category, subsuming in principle the entire range of activities involved in survival and reproduction (Figure 3). The central concept in life history theory is the principle of allocation (Hill and Hurtado, 1996): any effort (time, energy, resources) allocated to one domain (for example, enhancing one's own 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 trade-offs that are amenable to optimization models.

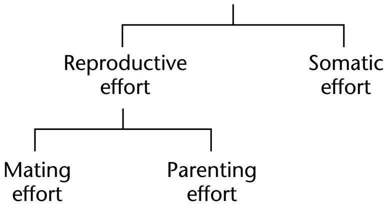

Figure 3. The domains of adaptive effort defining major life history trade-offs.

Mating strategies

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. 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 mentioned earlier (see 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 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). For instance, the male-controlled resources may be political rather than economic. Male coercion (especially by agnatic kin groups) may severely constrain female choice. Females mated polygynously may face reduced reproductive success due to competition with co-wives, though this may be compensated for in the next generation if the sons of polygynously married women have increased chances of inheriting wealth and mating polygynously themselves.

Polygyny has been the preferred marriage form for the great majority of societies in the ethnographic record. Even in putatively monogamous societies, 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 (though serial polyandry, in which women remarry to find better mates, is presumably much more common, but has only recently begun to be studied).

Parenting

Whatever form the mating system takes, human offspring require extensive and extended parental care. This parental investment begins with gestation and, among humans, can continue beyond the parent's death (through the bestowing of land, wealth, and other forms of property inheritance). Human behavioral ecology analyses ask how the amount and timing of such investment might vary according to social and environmental constraints. Most research falls into one of 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, 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 avian reproduction, but easily generalized to apply to any species with parental investment, including humans (Figure 4(a)). This model predicts that beyond a certain point, increased fertility (larger clutches, or shorter interbirth intervals) will result in lowered overall parental reproductive success.

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. At least one careful attempt to replicate the !Kung results among Ache foragers of Paraguay failed, possibly because Ache offspring mortality is less sensitive to

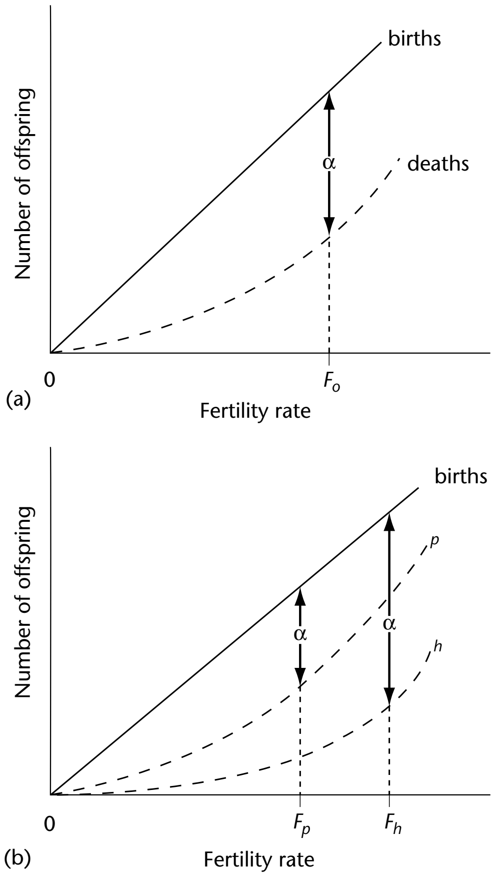

Figure 4. A graphical model of optimal fertility rate. Solid lines represent fertility rate (births per unit time), while dashed lines represent mortality as a function of fertility rate, the latter curving upwards to reflect the effect of reduced parental investment per offspring. The net difference between these is the number of surviving offspring, with a local maximum of α. The model assumes that selection favors maximizing α given the constraints that a parent faces, and hence favors an optimal fertility rate F_o. (a) Fertility rate of a single parent. (b) Comparison of 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 (P) at a given fertility rate, and hence a lower optimal fertility rate F_o than a higher-quality parent (h) with optimal fertility rate F_o.

variation in interbirth interval (Hill and Hurtado, 1996). Alternatively, it may be that in many cases the relationship between fertility and offspring survival is confounded by phenotypic correlation, which generally will mask the predicted functional relationship of the optimal clutch-size model (Figure 4(b)).

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. 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; there is abundant evidence for such adaptive variability in human reproductive ecology. Solutions to this problem include multivariate analysis, use of historical data to track functional links between birth spacing and resources, and experimental manipulation (the latter being unlikely in the human case).

Differential investment

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 analyses.

Postpartum parental investment decisions range chronologically from whether or not to keep the child – the alternatives being infanticide, abandonment, or adopting out – to delegation of care to others, to investments in nurturing and education, to wealth transfers that often accompany marriage (bride price or dowry), to any legacy the child may receive upon death of the parents. Fitness payoffs for nearly all of these decisions may differ according to the sex of the offspring. A variety of parental investment hypotheses have been the subject of ethnographic and historical research in HBE (Table 1).

Parenting-mating interactions

Following the lead of primate and avian behavioral ecologists, HBE researchers have begun to consider when 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. For example, men in Albuquerque, New Mexico, as well as Xhosa men in South Africa, invest more time and resources in

Table 1. Human behavioral ecology analyses of parental investment (PI)

Predictions tested	*Representative studies (locales and authors)*[a]
Reduced genetic relatedness or reproductive conflicts of interest lead to lower PI	Cross-cultural (Daly and Wilson); USA and South Africa (Anderson *et al.*); Mali (Strassman)
Offspring with reduced prospects of survival receive lower PI	Cross-cultural (Daly and Wilson)
Parents reduce PI per offspring as number of offspring increases	Tanzania (Borgerhoff Mulder); Paraguay (Hill and Hurtado)
Parental investment per child is increased when marginal benefit of PI is higher	Hungary (Bereczkei); USA (Kaplan *et al.*)
Adoption and fostering are adaptively modulated according to parental circumstances	Cross-cultural (Silk); Botswana (Pennington)
Mothers able to delegate nursing and infant care gain increased reproductive success	Hungary (Bereczkei); Europe (Hrdy); Ifaluk, Micronesia (Turke)
Postmenopausal women allocate resources and care to grandchildren or other close relatives	Paraguay (Hill and Hurtado); Tanzania (Hawkes *et al.*)
Parents with less resources preferentially invest in offspring (usually daughters) with lower variance in expected RS	Historic Portugal (Boone); Tanzania (Borgerhoff Mulder); North America (Gaulin and Robbins); USA (Judge and Hrdy); North America (Mealey and Mackey)
Offspring of the sex that faces better adult economic opportunities receive higher PI	Cross-cultural (Hewlett); historic Sweden (Low *et al.*); historic Germany (Voland *et al.*)
Offspring of the sex that has greater probability of contributing to future support of siblings receive higher PI	Tanzania (Borgerhoff Mulder); cross-cultural (Hewlett); Paraguay (Hill and Hurtado); Canada (Smith and Smith)
Offspring of the sex that has greater probability of competing with siblings for resources or mates receive lower PI	Tanzania (Borgerhoff Mulder); East Africa (Mace); historic Germany (Voland *et al.*)
If daughters (or sons) have greater future mating opportunities, they receive higher PI	Historic Asia (Dickemann); historic Portugal (Boone); Hungary (Bereczkei and Dunbar); Kenya (Cronk)
If daughters (or sons) are better able to claim and hold political power, they receive higher PI (especially inheritances)	North America (Hrdy and Judge); historic Portugal (Boone); cross-cultural (Hewlett)
Parental resources with increasing marginal benefits to offspring characterized by unigeniture (single heirs)	Historic Portugal (Boone); historic Germany (Voland *et al.*)
Increasing marginal benefit of biparental care leads to increased pair-bond stability	Paraguay and Venezuela (Hurtado and Hill); Tanzania (Blurton Jones *et al.*)

[a] Full references provided in Winterhalder and Smith (2000). PI, parental investment; RS, reproductive success.

stepchildren who are offspring of their current mates than they do in stepchildren from former relationships (though less than they invest in genetic offspring under comparable circumstances). This pattern does not match predictions from parental investment theory, but it does make adaptive sense if viewed as investment in maintaining a current mating relationship (i.e. as mating effort). Unravelling interactions such as these is a promising area for future HBE research.

Life History Strategies

Life history is a broad topic, subsuming in principle the entire range of activities involved in survival and reproduction. In practice, life history analyses center on a few key decision categories: the timing of growth and maturation, subadult and adult dispersal strategies, the onset of reproduction, the timing of reproductive events (e.g. birth spacing, weaning, menopause), mortality patterns, and senescence. Most HBE work on life history thus far has focused on four topics: links between production and reproduction; reproductive effort and maturation; menopause and extended human life span; and 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), while the fourth is reviewed by Borgerhoff Mulder (1998).

CONCLUSION

Human behavioral ecology applies neo-Darwinian theory and ethnographic and ethological methods to elucidate adaptive variation in human behavior, particularly social behavior. It combines elements from a number of different academic disciplines, including anthropology, economics, ethology, and evolutionary biology. Mathematical or graphical models anchored in basic principles of evolution by natural selection are used to derive hypotheses concerning how humans adapt to their natural and social environments. Predictions are then tested with ethnographic, historical, and archeological data. Human behavioral ecology assumes that human decision-making is guided by evolved 'decision rules' or conditional strategies, but focuses on facultative behavioral outcomes and adaptive consequences rather than on the underlying cognitive mechanisms or ontogenetic processes. The topics analyzed in HBE research fall into three main categories: production (resource acquisition and related topics), reproduction (mating and parenting), and distribution (exchange, sharing, and coercive transfers).

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