Life History Theory and Evolutionary Psychology

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The evolution of life is the result of a process in which variant forms compete to harvest energy from the environment and convert it into replicates of those forms. Individuals "capture" energy from the environment (through foraging, hunting, or cultivating) and "allocate" it to reproduction and survival-enhancing activities. Selection favors individuals who efficiently capture energy and effectively allocate it to enhance fitness within their ecological niche.

Energy does not come for free. Were individuals able to expend unlimited energy at no cost, in principle they could evolve to grow and develop so rapidly they could begin reproducing immediately after birth, massively produce offspring, and preserve themselves such that they never age. In biological reality, however, individuals must live within finite energy "budgets" (themselves earned through energy and time expenditures), never spending more than they have available. Allocation of a finite budget entails trade-offs and hence forces decisions about the relative value of possible ways to spend. Acquiring one expensive item means giving up others; consumption today may entails less tomorrow.

In the face of trade-offs, how should a budget be spent? People managing their personal expenses presumably spend it based on what they value (even if sometimes only fleetingly and later regrettably). Moreover, their decisions are often based on individual circumstances that, over time, change: Wealthy individuals can afford to spend more on luxury items than can the middle-class or poor; college students often see little value to saving for retirement until, through education, they gain better employment; people with steady, good incomes can afford to keep less as a buffer against bad times than those whose future incomes are uncertain.

Selection favors organisms' strategies for allocating energy budgets on the basis of one criterion: The strategy that leads to the allocation of energy that, on average, results in the greatest fitness is the one that wins out over others. In this sense, selection is expected to result in "fitness-maximizing" or "optimal" strategies. (Of course, those strategies are "optimal" only in a restricted sense: They are optimal *under the constraints* imposed by trade-offs between allocations of energy; see Parker & Maynard Smith, 1991[1]). Just as strategies of how to spend money depend on individual circumstances, so too do optimal energy allocations: Newborns optimally allocate energy differently from adults; healthy individuals optimally allocate differently from those with infectious disease; the best allocation strategy for individuals in stable circumstances differs from that of individuals whose future circumstances are unpredictable.

Fundamentally, Life History Theory (LHT) provides a framework that addresses how, in the face of trade-offs, organisms should allocate time and energy to tasks and traits in a way that maximizes their fitness. Optimal allocations vary across the lifecourse and, hence, LHT generally concerns the evolutionary forces that shape the timing of life events involved in development, growth, reproduction, and aging.

A major goal of evolutionary psychology is to understand the nature of psychological adaptations. Evolutionary psychology intimately connects with LHT for two reasons. First, psychological adaptations are some of what humans have been selected to invest in, at an expense; obviously, the development, maintenance, operation, and utilization of psychological adaptations require allocations of energy and time. Because their evolution has been subject to the fundamental forces of selection that LHT concerns, LHT can effectively guide inquiry into their development, nature, and operation.

Second, optimal decisions about how to invest time and energy into various life tasks themselves often require processing of specific information about the environment (current features as well as cues about what the future holds) upon which allocation decisions ought to be based. Some psychological adaptations, presumably, are designed to provide and act upon that information. LHT can once again guide thinking about the nature of these adaptations.

We first provide an overview of LHT. We then consider specific applications of LHT to an

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[1] Other constraints may also exist: e.g., genetic constraints that don't allow for some phenotypes in light of an organism's developmental system. "Optimal" strategies evolve under these constraints as well (Parker & Maynard Smith, 1991). In addition, of course, evolved strategies need not be optimal, even under constraints, in environments other than those in which they evolve.

understanding of the human lifecourse. Finally, we argue for ways in which LHT can and should be infused into evolutionary psychology.

Life History Theory: An Overview

Fundamental Tradeoffs in Life History Theory

Individuals can enhance fitness in two primary ways: They can invest in traits that affect the age-schedule of mortality; or they can invest in traits that affect the age-schedule of fertility.[2] Ultimately, the influence of traits on inclusive fitness must be mediated through changes in mortality or fertility or both (though they may do so by enhancing the mortality and/or fertility of kin—e.g., offspring—as well as self; Hamilton, 1964). Because of allocation trade-offs, many if not most traits have opposing effects on mortality and fertility, opposing effects on the same fitness component at two different points in time, or opposing effects of a fitness component of self (e.g., own fertility) and that of a related individual (e.g., offspring survival and/or fertility). Examples include: (a) a trait that increases fertility by increasing mating frequency (e.g., a mating display) may simultaneously reduce survival by compromising immune function; (b) energetic allocations to growth reduce fertility at younger ages, but increase fertility at older ages; (c) allocations to offspring viability (e.g., feeding) reduce one's own survival or fertility. LHT conceptualizes specific allocation trade-offs in terms of three broad, fundamental trade-offs: the present-future reproduction trade-off, the quantity-quality of offspring trade-off, and the trade-off between mating effort and parenting effort.

The trade-off between present and future reproduction

At any point in time, an organism faces a decision. Its energy can be converted into offspring or into life sustaining activities (e.g., additional energy harvesting, growth, predator reduction, repair, etc.), in any proportion. Allocation of energy to future reproduction entails the

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[2] Biologists and demographers use the terms fertility and fecundity differently. For biologists, fertility refers to the ability to conceive, whereas fecundity refers to quantity of actual offspring. For demographers, fecundity (or fecundability) refers to ability to conceive, whereas fertility refers to quantity of actual offspring. We adopt the usage of demographers for this chapter.

opportunity cost of not reproducing now. Reproducing now typically entails the cost of increasing the chance of not reproducing in the future.

Cole's paradox (Cole 1954), an early inquiry into life history evolution, illustrates this trade-off. Imagine an asexual perennial plant that reserves energy at the end of each growing season to survive the winter and live to reproduce the next year. If it produced just one more progeny with the reserve energy and die rather than overwinter, its fitness would be unchanged, as it would have replaced itself. In principle, seeds are cheap and, if the plant could produce many with the energy it takes to overwinter, it would seem better to do so and die. In fact, however, seeds may be much less likely to survive the winter than its adult parent so that it may cost less to overwinter than to produce just one single surviving progeny (Charnov & Schaffer 1973). The best strategy depends on which allocation results in greatest inclusive fitness.

The problem of senescence. In the 1950s and 1960s, the issue of current vs. future reproduction was primarily applied to an understanding of why organisms senesce. Medawar (1952; see also Fisher, 1958) argued that selection is stronger on traits expressed at younger ages because a greater proportion of the population is alive to experience its effects. An organism's viability should therefore tend to decrease with age, as deleterious mutations whose effects are only expressed late in life should accumulate due to weaker selection against them. Williams (1957) extended this reasoning to genes that exhibit *antagonistic pleiotropy*—ones with opposing effects on fitness at two different ages (e.g., a positive effect on fertility at a younger age and a negative effect on survival at an older age). Such genes with beneficial effects early in life but deleterious effects later in life should accumulate in populations. Aging (defined as an increasing risk of mortality with age) results. Williams furthermore proposed that selection on age-specific mortality rates should be a function of *reproductive value* (RV; expected future reproduction at a given age, conditional on having reached that age), which increases until age of first reproduction and decreases thereafter. Hamilton (1966) developed a mathematical model generally supporting Williams's proposals, though it showed that selection should track expected future reproduction at a given age *not conditional* on surviving to that age. Hence, the mortality rate should be constant prior to reproduction and increase thereafter.

Life history formulations. Williams and Hamilton assumed tradeoffs but were not concerned with their cause. Gadgil and Bossert (1970) developed the first modern LHT framework—one conceptualizing tradeoffs as necessarily entailed by finite energy budgets. Organisms capture energy (*resources*) from the environment. Their capture rate (or *income*) determines their energy budget. At any point in time, they can “spend” income on three different activities. Through *growth*, organisms can increase their energy capture rates in the future, thus increasing their future fertility. For this reason, organisms typically have a juvenile phase in which fertility is zero until they reach a size at which some allocation to reproduction increases fitness more than growth. Through *maintainance*, organisms repair somatic tissue, allocate energy to immune function, engage in further energy production, and so on. Through *reproduction*, organisms replicate genes. How organisms solve this energetic tradeoff shapes their life histories. Because maintenance and growth affect fitness through impacts on *future* reproduction, the tripartite tradeoff collapses into a *tradeoff between current and future reproduction* (Bell & Koufopanou, 1986; Hill, 1993; Lessells, 1991; Roff, 1992; Stearns, 1992) The loss of future survival, energy capture, and reproduction because of energy allocation to current reproduction is referred to as the cost of reproduction (Williams, 1966).

The present-future tradeoff can be analyzed by decomposing RV into two components: reproduction during the current time interval and total reproduction at all future time intervals after the current one until death (see Lessells, 1991; Hill, 1993, for reviews). In general, one of three outcomes can be expected: (1) no current reproduction, all energy allocated to the future, which occurs during the juvenile period and during unfavorable circumstances, when even a small allocation to reproduction increases fitness less than an additional allocation to growth or maintenance; (2) a mixed allocation of effort to present reproduction and to future reproduction, where, at optimum, the fitness benefits derived from an extra unit of effort to current and future reproduction are equal; (3) full allocation to reproduction followed by death (semelparity), which occurs when even a small allocation to the future is worth less than an additional allocation to current reproduction (e.g., in spectacular fashion, salmon, whose soma decomposes as they spawn). In general, optimal life history programs maximize total allocations of energy to reproduction over the lifecourse (Charnov, 1993).

Senescence appears to be an inevitable byproduct of optimal allocation design (Kirkwood, 1990). If maintenance were perfect and therefore senescence did not occur, a small additional investment in further maintenance would have no effect, as the upper limit would have been reached. At this point, then, some reallocation of effort to reproduction would positively affect fitness. Hence, the disposable soma theory states, it is always optimal for organisms to allow the body to decay at a non-zero rate.

As risk of death due to difficult-to-avoid causes such as predation, accidents, and so on increases, the benefit of allocating energy and resources to the future diminishes (Kirkwood & Rose, 1991), as that energy is more likely to be “wasted.” Accordingly, greater “extrinsic” mortality risks (death due to unavoidable causes) leads to faster senescence. Accordingly, much of LHT (e.g., Charnov, 1993) models life history outcomes as a function of age-specific rates of extrinsic mortality (although see below on “Embodied capital”).

The trade-off between quantity and quality of offspring

A second major life history trade-off, first discussed by Lack (1954, 1968), concerns a division within the resources allocated to current reproduction: allocation to increase offspring *quantity* vs. allocation to increase offspring *quality*. This trade-off, typically operationalized as number vs. survival of offspring (e.g. Harpending, Draper, & Pennington, 1990; Lack, 1954, 1968; Lloyd, 1987; Smith & Fretwell, 1974), arises because parents have limited resources to invest in reproduction and, hence, additional offspring must reduce average investment per offspring. In a simple model, selection is expected to shape investment per offspring to maximize offspring number times rate of survival. When, as typically assumed, the benefits of investment decrease as level of investment increases (i.e., the return curve is diminishing), the optimum is reached when the proportional decrease in number of offspring produced equals the proportional increase in survival of offspring to adulthood (Harpending et al., 1990). Hence, the optimal investment is less than that required for maximal survival (as the proportional increase from investment is ~0 at maximum survival). In addition, the optimal amount of investment per offspring is independent of parental income (Smith & Fretwell, 1974), such that lifetime fertility is merely total resources divided by resources expended per offspring. More complex multi-generational models consider not only offspring survival but also the adult fitness of offspring, which can vary due to body, health, skills, etc., accrued as a result of parental investment (Kaplan, 1996).

Sexual reproduction, LHT and the trade-off between mating and parenting effort

Sexual reproduction complicates the quantity-quality trade-off. Whereas offspring share roughly equal amounts of their parents' genetic material, parents may contribute unequally to their viability. Offspring are, in effect, 'public goods', with each parent profiting from the investments of the other parent and having an incentive to divert resources to the production of additional offspring. Conflicts of interests between the sexes result.

A near-universal outcome of sexual reproduction is the divergent evolution of the two sexes. Sex is defined by gamete size, the sex with the larger gametes being female. Larger gametes represent greater initial energetic investment in offspring. The difference in initial investment is often exaggerated with investment beyond energy in gametes, but it may also disappear or even reverse. Females provide all investment to offspring in ~95% of mammalian species, but males provide similar amounts or more total investments in most altricial birds, male brooding fish, and some insects (Clutton Brock & Parker, 1992).

The sex difference in investment into parenting (increasing offspring quality) and mating (increasing offspring number) that typically arises should be due to a difference in the payoffs to each. When females are highly selective about mates due to greater initial investment in offspring (Trivers, 1972), those males who are eligible for mating (by virtue of female preferences, often based on genetic quality) can expect a relatively high future reproductive rate, leading them to engage in mating rather than parental effort. Males who might benefit by parenting (because of a low expected future reproductive rate derived from mating effort) don't get the chance because females don't select them (Kokko & Jennions, 2003).[3] Of course, in some circumstances—presumably ones in which the value of biparental care is substantial—females partly select males for their willingness to invest in parenting, leading to a smaller sex difference in allocation toward mating and parenting.

Competition for mates and sexual conflicts of interest lead to inefficiencies in offspring production due to what economists refer to as negative externalities. One sex (typically males) will "waste" resources on costly displays (Grafen, 1991) or fighting rather than offspring production. The sexes may furthermore interfere with one another's reproductive strategies (Rice, 1996).

Ecology and Life History Evolution

Variations in ecological factors (e.g., food supply, mortality hazards) imply different optimal energy allocation strategies (e.g., Charnov, 1993; Kozlowski & Weigert, 1987), which leads to across- and within-species differences in life histories. Some organisms, such as bivalve mollusks, tortoises, and porcupines, apparently benefit significantly from allocations to predator defense and live long lives. Birds, bats and primates appear to lower predation rates by spending less time in terrestrial habitats and by being able to escape to aerial strata. Primates may reduce predation through grouping and social behavior. Species that eat more variable or difficult-to-capture foods probably benefit more from investments in learning than do more simple feeders, such as grazing animals.

Species-level adaptive specializations result in bundles of life history characteristics,

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[3] The lack of certain paternity also leads males to devalue parental effort.

which can generally be arrayed on a fast-slow continuum (Promislow & Harvey, 1990). For example, mammalian species on the fast end exhibit short gestation times, early reproduction, small body size, large litters, and high mortality rates, whereas species on the slow end have the opposite features.[4]

In response to ecological variability, many, if not most, organisms are selected to be capable of slowing down or speeding up their life histories depending upon conditions (e.g., food availability, density of conspecifics, mortality hazards) over several different time scales: over the short term in relation to food supply and energetic output (Hurtado & Hill, 1990, Lack, 1968); over longer time intervals through developmental effects (e.g., short adult stature in rats resulting from food shortages during youth; Shanley & Kirkwood, 2000); through differential selection on genetic variants in different habitats (e.g., grasshoppers at different elevations; Tatar et al., 1997).

Similarly, male and female parental investments vary with local ecology (Clutton Brock & Parker, 1992). A classic example is katydids. Males provide females with “nuptial gifts” (boluses of condensed food energy) to support offspring production. Manipulations of food density, which affect the foraging time necessary for males to produce gifts, shift male and female mating effort. When food is sparse, male provisioning requires more time than female provisioning, males are in short supply, and females actively compete for males; as food density increases, this trend is reversed and males compete for females (Gwyne, 1991).

A mix of specialization and flexibility is fundamental to understanding human life histories and mating systems. It is generally agreed that the large human brain supports the ability to respond *flexibly* to environmental variation and to learn culturally.[5] At the same time,

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[4] A related distinction was once referred to as r-selected (fast) vs. K-selected (slow) life histories (MacArthur & Wilson, 1967). The idea was that species differed in the extent to which they evolved in expanding populations or populations near carrying capacities. As slow and fast life histories are controlled by additional factors, this particular conceptualization is now seldom used in LHT.

[5] Naturally, learning and flexible responsiveness themselves require specialized psychological adaptations. The point here is merely that learning and flexibility entail costs in currencies of acquisition time and brain tissue.

the commitment to a large brain, a long period of development, and sensitivity to environmental information necessary to make it fully functional require *specializations* for a specific slow life history. In fact, consideration of the learning-intensive nature of human adaptation reveals shortcomings in traditional LHT and inspires a more general approach to life history evolution, the focus of the next section.

Embodied Capital and the Brain

Embodied capital

Growth and development can be viewed as investments in stocks of embodied capital: Investments in self that can be translated into future reproduction. In a physical sense, embodied capital is organized somatic tissue (muscles, digestive organs, brains, and so on). In a functional sense, embodied capital includes strength, speed, immune function, skill, knowledge and other abilities. Because allocations to maintenance counteract the depreciation of stocks of embodied capital with time, they too can be treated as investments in embodied capital. In this language, the present-future reproductive trade-off is that between investments in own embodied capital vs. reproduction, and the quantity-quality trade-off is that between investments in the embodied capital of offspring vs. their number.

When translated and extended into an embodied capital framework, LHT allows one to entertain possibilities not explicitly conceptualized by standard treatments. Standard models tend to treat investment in the future as physical growth. But growth is only one form of such investment, as illustrated by brain development. The brain has the capacity to transform present experiences into future performance. Brain expansion among higher primates represents an increased investment in this capacity (Armstrong & Falk, 1982; Fleagle, 1999; Parker & McKinney, 1999). But this investment is realized not only in growth of neural tissue; substantial energy and time may be allocated to encountering experiences that, through changes in neural tissue, yield benefits realized over time—investments in the future.

How selection affects these investments depends on costs and benefits realized over an organism's lifetime. Growing and maintaining neural tissue entails substantial energetic costs (e.g., Holliday, 1978) and, by curtailing "pre-programmed" behavioral routines, compromise performance early in life (e.g., consider the motoric incompetence of human infants). Hence, the *net* benefits of learning are only fully realized as the organism ages (see Figure 1). In a niche where there is little to learn, benefits never offset early costs and smaller brains are favored. In a more challenging niche, small brains might be better early in life but much worse later, such that large brains are favored.

Other systems may similarly become more functional through time—e.g., the immune system, which requires exposure to antigens to become fully functional (presumably a reason mortality decreases from birth to the end of childhood). Embodied capital theory can address the evolution of any form of investment in a stock of capital that pays off over time.

Co-evolutionary processes and their modeling

Because the returns gained from large brains lie in the future, ecological conditions favoring them also favor greater expenditure on survival. Conversely, exogenous ecological conditions that lower mortality favor increased expenditure on survival and hence also greater investment in brain capital (Kaplan & Robson, 2002; Robson & Kaplan, 2003); cf. Carey and Judge, 2001). As expected, lifespan and brain size (controlling for body size) positively covary in mammals (Sacher, 1959) and primates (e.g., Allman, McLaughlin, & Hakeem, 1993; Judge & Carey, 2000; Kaplan & Robson, 2002; Kaplan et al., in press).

Standard LHT treatments are not fully adequate to model this coevolution. They assume an "extrinsic" component of mortality not subject to selection (Charnov, 1993, Kozlowski & Wiegert, 1986), which provides leverage for understanding other life history traits, such as age of first reproduction and rates of aging. But this approach is theoretically unsatisfying, as organisms exert control over virtually all causes of mortality (e.g., by altering patterns of travel to avoid predators, by investing in immune function). It is also analytically limited, in that it prevents a full understanding of how mortality rates evolve. A more useful approach is to assume that what varies as a function of ecological factors are not set mortality rates, but rather *functional relationships* between mortality and efforts allocated to reducing it (see Figure 2). Exogenous variation can be thought of in terms of varying "assault" types and rates. For example, warm, humid climates favor the evolution of disease organisms and therefore increase the assault rate and diversity of diseases affecting organisms. These climates also entail relationships between efforts allocated to reducing them and mortality reduction.

This alternative treatment of mortality requires dynamic programming techniques, analytical tools that are well-developed in economics (e.g., formal analysis of capital investments). Robson and Kaplan (2003) used this approach to show that, indeed, allocation of effort into growing brains and reducing mortality should coevolve. (See that paper for an illustration of its analytical methods.)

Cost-Benefit Analysis and Life History Theory in Behavioral Ecology

Cost-benefit modeling and its relation to life history theory

LHT is part of a more general approach within behavioral ecology and theoretical biology: The optimality approach, which attempts to specify the strategy that would result from natural selection in the absence of genetic or developmental constraints by analyzing costs and benefits of possible strategies within a particular domain (see Parker & Maynard Smith, 1991). This approach revolutionized theoretical biology in the 1960s and 1970s (e.g., Cronin, 1991). Before then, biologists did not systematically think about selection in explicitly economic terms (maximization of benefits minus costs in the currency of fitness). Doing so led to an explosion of new theories, notably many of the "middle-level evolutionary theories" (Buss, 1995) that evolutionary psychologists rely upon: e.g., parental investment theory (Trivers, 1972), parent-offspring conflict (Trivers, 1974), sex allocation theory (e.g., Charnov, 1982), sperm competition theory (e.g., Parker, 1970), optimal foraging theory (Charnov, 1976), in addition to life history theory. Today, cost-benefit modeling is a core approach within evolutionary biology and the dominant one in behavioral ecology (see Grafen, 1991).

Cost-benefit analysis does not require LHT. For example, one can model foraging strategies in terms of the benefits of energy capture and the costs of expending energy, with the optimal strategy being the one that maximizes immediate net caloric intake. Such modeling is not LHT because it doesn't explicitly consider the effects of strategy choice over time. Modeling adopts a life history approach when it explicitly considers the effects of potential strategies on fitness outcomes at all subsequent ages to which the organism might live.

As originally conceived, LHT concerned the timing of life events. Increasingly, however, biologists have found that the understanding of phenomena not traditionally thought of as "life history" events in fact requires an explicit life history approach. Hence, LHT has increasingly subsumed costs-benefit analysis in many areas. Rather than being defined by the phenomena it explains, LHT is a general analytical approach to understanding selection.

An example: Honest signaling theory

Recent developments in signaling theory illustrate this point. "Honest" signals of quality are those that individuals of higher quality ("big signalers") can afford but those of lower quality cannot. Traditionally, these signals have been thought of as "viability-indicators" (Andersson, 1994)—big signalers presumably being better able to survive than others. In theory, they can "waste" more of their survival ability on a signal than other, thereby increasing fitness through fertility enhancement. A prominent instance of this model is the immunocompetence signaling model. Individuals are presumed to vary in parasite resistance (Hamilton & Zuk, 1982), and high quality individuals signal their parasite resistance to potential mates with an immunosuppressant (e.g., testosterone-dependent signal; Folstad & Karter, 1992). Viability-indicators have been contrasted with arbitrary signals (see Cronin, 1991; Fisher, 1958). The latter are presumably not honest signal of quality and hence correlated with ability to survive; rather, they presumably evolved simply because they enhanced "attractiveness" (e.g., by drawing attention from females due to its brightness or extravagance).

Grafen (1990) first modeled selection for viability-indicators. He assumed that all individuals, regardless of quality, obtain the same fitness *benefits* from a particular level of a signal (i.e., which derive from mating advantages advertised through the signal to others, who have no basis for discriminating individuals' fitness except via the signal). The signal can evolve to display quality when the fitness *costs* (in the currency of mortality) associated with developing and maintaining a particular level of the signal are less for individuals of higher quality than for those of lower quality (i.e., it evolves because of differential costs as a function of quality, not differential benefits). The signal "honestly" conveys quality because it is not in the interest of individuals of lower quality for them to "cheat" and develop a larger signal; the mortality costs they would suffer exceed the fertility benefits they could derive from the increased signal size.

Recently, limitations of Grafen's model have been noted—ones due to its not taking a life history approach (e.g., Getty, 1998, 2002). At each moment, an individual is faced with a decision of how much effort to allocate to a signal. The incremental fitness gain garnered (or loss suffered) from additional investment into the signal accrues over time, due to its effects on repeated reproductive bouts. (Indeed, a signal may be thought of as a form of embodied capital.) At the current age and all subsequent ages, fitness is the probability of living to that age times the fertility at that age. Because benefits accrue over time, the larger marginal gains from investment in a trait enjoyed by big signalers can derive from larger *benefits* (e.g., summed over several time periods) rather than lesser costs, contrary to a key assumption in Grafen's model. Although the *momentary* gains two individuals derive from a signal of a particular size should not vary as a function of their quality, one individual may derive greater benefit from investing in the trait than the other because of differences in expected mortality.

The implications of a life history approach are dramatic (see Getty, 2002; Kokko et al., 2002)—indeed, LHT transforms the foundations of honest signaling theory. In a stable honest signaling system, big signalers (i.e., those of higher quality) need not have greater survivorship than small signalers, contrary to previous thought. The relationship between age-specific mortality and signal size depends on the precise details of the signal size-fertility function and quality-dependent trade-offs between signal size and mortality. Under some conditions (e.g., when fertility gradually increases as a function of signal size; Getty, 2002), there is no reason to expect individuals of higher quality to actually have greater survivorship than those of lower quality. (In such cases, higher quality individuals end up signaling much more than lower quality individuals, giving them a fertility benefit but no survival advantage.) In extreme instances, individuals of higher quality may actually have *lower* survivorship than individuals of lower quality (Kokko et al., 2002). (Quality here, of course, cannot be defined by ability to survive per se, but rather by the ability to convert energy into replicate forms.) The same holds true of the association between immunocompetence, parasite loads, and quality: Depending on the quality-dependent marginal effects of allocating additional effort to immunocompetence, individuals of higher quality may be more or less immunocompetent than individuals of lower quality and hence have higher or lower pathogen loads (Getty, 2002). (See also Kokko et al., 2003).

In this view, the distinction between viability-indicator signal models and arbitrary signal models breaks down. “Arbitrary” signal models refer to situations in which a signal is not associated with survival but big signalers enjoy greater fertility benefits. But from a life history perspective, they may still be associated with quality. Indeed, from a life history standpoint, in all stable signaling situations in which a signal yields fitness benefits, signal size *will* relate to quality. In some situations, it will also relate to survival. In others, it will relate to fertility alone (and may even relate to survival negatively). In these latter situations, big signalers do not survive less because they *couldn’t* survive more; rather, their optimal allocation strategy leads them to allocate effort into a signal at a cost to survival. Rather than define two qualitatively different signaling models, viability indicator and arbitrary models anchor two ends of a continuum of honest signaling-of-quality (Kokko et al., 2002). This fundamental insight was made possible when a life history approach to signaling was taken.[6]

Based on the distinction between viability-indicator models and arbitrary models of

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[6] These outcomes are in fact not inconsistent with Grafen’s (1990) model; at the same time, however, they were not at all apparent from that model. Only a model that fully takes into account effects on fitness throughout the lifecourse—a life history model—makes these implications clear.

signaling, recent research has attempted to test whether facial masculinity, facial attractiveness, or symmetry are honest signals of quality by correlating them with health outcomes or longevity, with mixed results (e.g., Kalick, Zebrowitz, Langlois, & Johnson, 1998). LHT tells us that these tests cannot reveal whether these traits are honest signals of quality.

Enactment of Allocation Decisions

Thus far, we have considered the *selection pressures* that forge life histories; LHT describes these pressures. Full understanding of life histories requires analysis of all of Tinbergen's (1963) four questions, regarding proximate mechanisms, selective advantage, ontogeny and phylogeny. An understanding of proximate mechanisms and their development is of particular importance. What are the mechanisms whereby life history decisions are made and executed? And how do these mechanisms develop?

LHT speaks of allocation "decisions" made by an organism, shorthand for saying that organisms differentially use energy and time for various life tasks. It does not imply a "decision-maker"; LHT neither requires nor implies a "fitness-maximizer" or homunculus that calculates costs and benefits. Rather, selection has presumably shaped specific psychological and physiological mechanisms to be sensitive to environmental factors that moderate optimal allocation of effort in a way that would have yielded (near-)maximal fitness (relative to alternative ways of allocating effort, given trade-offs) ancestrally under the varying circumstances and life stages it experiences.

Energy allocation decisions often require coordinated tuning of a variety of systems. Increased allocation to reproduction, for instance, should be coordinated with less allocation to growth. Increased effort to immune function in response to infection may best be synchronized with lower overall expenditure. Adaptive coordination often requires systems of communication and control distributed across a variety of somatic systems. Endocrine systems have, in part, been designed to fulfill this role.

Endocrine systems are internal communication devices. Hormones released at one site (e.g., the gonads, the adrenal cortex) are “picked up” by receptors at other sites (e.g., brain structures) and thereby affect those sites. Endocrine systems can thereby simultaneously regulate a great number of different functions and modulate allocation of energy. Naturally, the precise ways that they do so depends on the distribution of receptors and their actions in response to hormone-binding. Presumably, the system has been tuned by selection (where the relevant selection pressures are, once again, described by LHT) such that endocrine action optimally modulates allocation of effort in ways.

Consider an example: reproductive hormones. During puberty, adrenarche initiates cascades of developmental changes in both sexes taking place over almost a decade. In females, mechanisms regulating energy balance lead to fat storage and regular menstrual cycling. As mediated by estrogen and other hormones, increased energy is allocated to reproductive traits and functions, including secondary sexual characteristics, while growth ultimately subsides. Males begin producing androgens in substantial quantities, which lead to greater musculature and investments in forms of mating effort, including social competition and physical performance. At the same time, some investments in immune function are withdrawn. For both sexes, modulation of psychological processes (e.g., desires, motives, situation-specific responses) is as integral to the matrix of coordinated responses as modulation of energy utilization. (For an overview, see Ellison, 2001).

Reproductive hormones also regulate differential investments on shorter time scales. Pregnancy requires maternal allocation of energy to the developing fetus, which occurs through chemical communication (e.g., involving gonadotrophins) between fetal tissue, uterine tissue, the ovaries, and the brain. Indeed, fetuses that do not “reveal” their worthiness through this process may be aborted (e.g., Ellison, 2001; Haig, 1993). Male testosterone levels subside when men become fathers, facilitating reallocation of reproductive effort from mating to parenting (e.g., Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002).

A host of other endocrine and other communication systems modulate energy release, tissue-specific uptake, and psychological processes in the face of other events that signaled, ancestrally, immediate changes in optimal allocation: e.g., glucocorticoid modulation of the stress response; the effects of epinephrine on energy release and utilization in fight-or-flight circumstances; modulation of immune function and energy utilization by other tissues achieved through the action of a variety of interleukins in the face of risk of actual pathogen attack.

None of these systems demands a “central command post” directing activity of the multitude of receptor sites and, through their action, other sites ultimately affected. Rather, the coordinated efforts are akin to that of a football team running an offensive play, where each player has a pre-planned assignment, which, in concert with others’ execution of their assignment, has been designed to achieve an adaptive outcome. The “design” of the “play” (assignments of individual “players”) has been shaped through selection.

Reallocations of effort typically involve both physiological and psychological processes; events that initiate reallocation must be perceived and acted upon for reallocation to occur. In most instances, the psychological processes involved are only vaguely understood, a theme to which we return later.

Human Life History

We now turn to topics concerning human life histories: the evolution of large brains, development and childhood, and aging.

Brain and Lifespan Evolution in Humans

Relative to close ancestors, humans have several distinct life history features (Kaplan, Hill, Lancaster, & Hurtado, 2000): late onset of reproduction; and extended period of childhood vulnerability; long lifespan. In addition, we have very large brains. Even Australiopithecus had a brain only about 2/3 the size of early Homo’s (controlling for body size; Martin, 1981). A key question concerns the nature of the changes that caused selection to shape human life histories and forms of embodied capital to differ from our ancestors.

Differences between the diets of chimpanzees and human hunter-gatherers may be key. In one comparison, vertebrate meat contributed, on average, 60% of the calories in ten human foraging societies (range = 30-80%), whereas five chimpanzee communities obtained about 2% of their energy from hunted foods (Kaplan et al., 2000).[7] Extracted foods (non-mobile resources embedded in a protective context such as underground, in hard shells, or bearing toxins: roots, nuts, seeds, most invertebrate products, and difficult to extract plant parts such as palm fiber) accounted for about 32% of the forager diet and just 3% of the chimpanzee diet. Collected resources (fruits, leaves, flowers, and other easily accessible plant parts) formed the bulk of the chimpanzee diet: 95% vs. only 8% of the forager diet.

Relative to humans, then, chimpanzees consume relatively low quality foods easy to gather.[8] Humans generally consume nutrient-dense plant and animal resources. If chimpanzees could easily consume these foods, they would have evolved to do so, as a diet of nutrient-dense foods is obviously superior to one of low quality foods, all else equal. It makes sense to think, then, that humans possess special abilities to acquire nutrient-dense foods, including creative, skill-intensive techniques supported by a large brain. Possibly, large brains and long lives in humans are coevolved responses to an extreme commitment to learning-intensive foraging strategies and a dietary shift towards nutrient-dense but difficult-to-acquire foods, allowing them to exploit a wide variety of foods and thereby colonize all terrestrial and coastal ecosystems (Kaplan et al., 2000, Kaplan, 1997).

Age-specific acquisition rates of foods lend support to this theory. In most environments, people most easily acquire fruits. In Ache foragers, peak daily fruit production is reached by the mid to late teens; even 2-3 year-olds can pick fruits from the ground at 30% the maximum adult

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[7] The hunter-gatherer data come from studies on populations during periods when they were almost completely dependent on wild foods, with little modern technology (and no firearms), no significant outside interference in interpersonal violence or fertility rates, and no significant access to modern medicine.

[8] Chimpanzees actually consume high density foods relative to many other primates, as they do hunt to obtain some meat and perform some extractive foraging such as termite extraction and nut-cracking. Within the primate order, chimpanzees also have relatively large brains. Relative to humans, however, the quantitative difference is great.

rate. By contrast, the rate of acquiring extracted resources often increases well into adulthood. For instance, Hiwi women do not reach peak root acquisition rates until 35-45 (Kaplan et al., 2000); the rate of 10 year old girls is only 15% of the adult maximum. In the Hambukushu, nut cracking rates peak at about 35 (see also Blurton Jones et al., 1994b). Presumably, people get better at these tasks in adulthood because they involve skills refined over time.

Human hunting may be particularly skill-based. It differs qualitatively from hunting by other animals. Rather than ambush prey or use stealth and pursuit techniques, human hunters draw on and integrate a wealth of information (e.g., of ecology, seasonality, current weather, expected animal behavior, fresh animal signs) both during search and after prey are encountered (Leibenberg, 1990), tend to select prey in prime condition rather than prey made vulnerable by youth, old age or disease (Alvard, 1995, Stiner, 1991), and regularly consider alternative courses of action in reference to spatial and temporal mental maps of resource availability, which cover areas much larger than those covered by chimpanzees (in a lifetime, perhaps, on average, 1000 times larger; e.g., Wrangham & Smuts 1980). Among the Hiwi, Ache, and Hadza, peak rates are reached in the mid 30s; rates of 20-year olds are, remarkably, only 25-50% of the adult maximum (Kaplan et al., 2000; Marlowe, unpublished data).

Because human production heavily involves activities that require skills to perform effectively, young humans do not pay their own way. Figure 3 presents net production (i.e. food acquired minus food consumed) by age for chimpanzees and human foragers (Kaplan et al 2000). Chimpanzees have net negative production until about age 5, zero production during a period of juvenile growth, and, for females but not males, a net surplus during the reproductive phase, which is allocated to nursing. By contrast, humans produce less than they consume for about twenty years, with the trough reaching its nadir at about 14. Net production peaks much later relative to chimpanzees—but the peak is also much higher (a 1750 vs. 250 cal/day), presumably the payoff of long dependency.

Brains and skills can be thought of as forms of embodied capital. To acquire them, humans pay a substantial cost: They allocate energy and time to their acquisition and the hardware (specific brain tissue) that support their acquisition—which could have been used other ways (e.g., direct reproduction, continued foraging for fruits). These upfront costs ultimately pay off over time, as individuals put them to use to produce nutrient-dense foods not otherwise accessible. As emphasized earlier, however, investment in embodied capital can only be selected if, on average, individuals live long enough to pay off and, indeed, exceed, initial investment costs. Figure 3 also presents probabilities of survival by age for chimpanzees and human foragers (Kaplan et al., 2000), which reveal why the human age-profile of productivity requires a long adult lifespan. Only about 30% of chimpanzees ever born reach 20, the age when humans finally produce as much as they consume. Less than 5% of chimpanzees reach 45, when human net production peaks. By age 15, chimpanzees have consumed 43% and produced 40% of their expected lifetime calories; by contrast, humans have consumed 22% and produced only 4% of their expected lifetime calories.

Figure 4 illustrates why the human age-profile of production is incompatible with chimpanzee survival rates. The thin solid line plots cumulative net production by age for chimpanzees. The bold line plots expected net production for foragers (net production times the probability of being alive) at each age. The area of the 'deficit' period, prior to age 20, approximately equals the surplus gained after 20. The dashed line shows a hypothetical expected net production profile of a human forager with a chimpanzee survival function; here, the area of the deficit is much larger than the area of the surplus, as few individuals survive to highly productive ages. An organism with a mortality curve like that of a chimpanzee clearly could not afford to have a production curve like that of humans; a species that has lifetime negative net production can't possible evolve.

Quite possibly within humans, then, large brain size coevolved with a dependent juvenile period allowing skill acquisition; allocations of energy to large brain size also coevolved with allocations of energy to mortality reduction (e.g., large allocations to immune function, behavioral strategies designed to reduce mortality through predation such as formation of larger social groups and lower risk-taking), resulting in long life spans.

Development and Aging

Characteristic features of the human growth and brain development curve

During childhood, humans allocate energy and time to growth of soma and development of embodied stocks of capital. Understanding the timing and rate of growth of different parts of the soma as well as learning requires a life history approach.

Humans are generally considered extremely altricial—relatively undeveloped and non-functional at birth. But in some respects human babies are well-developed relative to close ancestors. Compared to gorilla and chimpanzee infants, human neonates are large (3000 grams [Kuzawa 1998] vs. 2327 and 1766 for gorillas and chimpanzees, respectively [Leigh & Shea 1996]). (Female adult gorillas, by contrast, weigh about 60% more than adult women.) The differences are only partly accounted for by gestation times; human fetuses gain more weight per day. Human brains are particularly large at birth—about twice the size of chimpanzees' (indeed, the human infant brain weighs about that of an adult chimpanzee). Body composition also differs. Human neonates have 3.75 times the fat stores of infant mammals of comparable weight (Kuzawa 1998), probably used to support rapid post-natal neural growth.

By contrast, humans grow proportionally much more slowly than chimpanzees during middle and late childhood. Ten year-old humans are actually smaller than same-age chimpanzees, have low appetite, and are relatively non-productive; indeed, parents often insist that children remain in safe places and encourage them to produce only easily and safely acquired food (Blurton Jones et al., 1994a). In adolescence, however, humans develop a voracious appetite and experience a growth spurt not seen in chimpanzees, whose size they then surpass.

This pattern can be understood in the context of human life history outlined above. Infants grow fast until they comfortably support large brains. Young children do little work and do not need large bodies. Their time is dedicated to intensive learning through observation and play, as well as a large energetic allocation to the immune system (McDade, 2003; Worthman, 1999), which serves to reduce pathogen-caused mortality throughout the lifespan. They grow slowly. At the beginning of adolescence, when children's brains are almost ready for reproduction and higher rates of productivity, they grow and reach adult body size rapidly.

Humans stretch out intellectual development at every stage. The production of cortical neurons in mammals is limited to early fetal development within which, compared to monkeys and apes, human embryos spend an additional 25 days (Deacon, 1997; Parker & McKinney, 1999). Proliferation of neurons in early fetal development extends other phases of brain development, resulting in a larger, more complex, and more effective brain. Whereas myelination of the brain is largely complete in 3.5 years in macaques, in humans it continues to at least age 12 (Gibson, 1986). Formal abstract logical reasoning, which appears to facilitate the growth in knowledge that results in peak productivity in the mid 30s, does not emerge until age 16 to 18 (Parker & McKinney, 1999).

Timing of developmental achievements

A life history perspective generally expects that processes of development will be coordinated and synchronous, as whole organisms live or die. It doesn't pay to fully develop a heart without also investing in liver function and, similarly, it doesn't pay to fully invest in a brain without also investing in a body that can support it (Hill, 1993). At the same time, the relative value of some investments may shift across time, and these shifts may be key to understanding developmental sequences. Language, for instance, is arguably one of the most computationally complex and difficult cognitive processes in which humans engage, but the ability to understand and produce a near-infinite number of utterances is largely intact by the time children finish the toddler stage and before they are competent at running. Language acquisition is presumably front-loaded (by adaptations specialized for language acquisition in early childhood), even at the expense of delaying the acquisition of other capabilities, because language greatly increases the rate at which children learn about the world; the earlier its acquisition, the longer the period of its benefits. LHT offers a principled framework within which to investigate the sequencing of developmental milestones in different domains. It focuses attention on both present and future costs and benefits of different investments in specific abilities at each point in time, within the context of an overall life history strategy and a set of co-adapted traits.

The growth/reproduction trade-off

A major event in the lifecourse of an organism is its transition from a pre-reproductive period to a reproductive period, a transition during which, in many species, major skeletal growth ceases. In the framework of embodied capital theory, stocks of somatic capital accumulate during the pre-reproductive period. The enhanced future rate of reproduction that results trades off against the time not spent reproducing. The onset of reproductive capability (in human females, menarche) has been selected, in theory, to maximize the total expected reproductive output (rate at which reproduction is expected to occur times age-specific probability of survival integrated over reproductive years) under the constraints of this trade-off.

The onset of menarche may depend on individual or culture-wide conditions. Draper and Harpending (1982) proposed that the trade-off between development and reproduction should depend on the expected parental effort in a population, an idea subsequently extended and revised by Belsky, Draper, and Steinberg (1990). Increased stress, this theory argues, predicts low levels of parental effort in the population when the child reaches adulthood, which favors quantity over quality and an earlier onset of reproduction. Chisholm (1999) offered an alternative life history perspective that explains the shift through the current vs. future reproduction trade-off rather than a quantity-quality trade-off. He argued that the age of female menarche should be sensitive to cues that predict mortality risk: With increased risk of mortality, women should experience menarche earlier.

A variety of environmental factors do indeed influence menarche. Poor nutritional status leads to delayed menarche (e.g., Aw & Tye, 1970), presumably due to slow growth and accumulation of fat deposition, such that the benefits of continuing to grow outweigh the cost of waiting to reproduce despite the accelerated mortality schedule associated with poor diet. By contrast, earlier menarche is associated with psychosocial stressors: family conflict (Moffitt et al., 1992); absence of positive harmonious relations with parents (particularly fathers; Ellis et al., 1999) in middle childhood (e.g., Ellis & Garber, 2000; Graber et al., 1995; Steinberg, 1988); divorce and father absence (Ellis & Garber, 2000; Jones et al., 1972; Mekos et al., 1992; Moffitt et al., 1992; Surbey, 1990).

Interestingly, father absence and familial discord or lack of closeness appear to independently predict menarche (Ellis & Garber, 2000). Moreover, the former's relation may be driven by the presence of a stepfather or other adult male figure rather than father absence per se. Girls in stepfather-present homes reach puberty earlier than ones in single-mother homes (Mekos et al., 1992). And the earlier a new male figure enters a girl's life, the earlier she reaches puberty (an association not accounted for by timing of divorce per se; Ellis & Garber, 2000). These findings suggest alternative life history explanations. Rather than being driven by a focus on quantity over quality or increased mortality, the effect of exposure to alternative father figures may lead to earlier onset of the reproductive period because their presence signals a conflict of interest between mothers and others over degree of investment in their offspring. (In addition, stepfathers may be a risk for sexual or physical abuse.) If daughters can expect to receive less investment, a shortened prereproductive period may optimize net benefits. In addition, it could particularly pay daughters in such situations to seek support from romantic partners. Consistent with this interpretation, Ellis and Garber (2000) report hints that the accelerating effect of a significant mother-boyfriend relationship is enhanced when characterized by dyadic conflict.

Aging and differential decline across domains

As discussed earlier, trade-offs between current and future reproduction purportedly entail aging. Individuals cannot simultaneous maximize fitness and perfectly maintain somatic tissue.

Both male physical strength and fluid intelligence peak early in the reproductive period (as a life history perspective expects of investments that deteriorate through somatic decline; e.g., Kirkwood, 1990). Knowledge-based embodied capital (crystallized intelligence) and productivity, however, continue to increase through the first 4-5 decades of life (Horn, 1968; Kaplan et al., 2000). Mortality rates remain low and virtually constant. Offspring dependency loads on parents in foragers peak about age 40, just before grandparenthood begins. Through middle age, dependency loads diminish, as does productivity. After age 60, physical and psychological deterioration is rapid and mortality rates rise dramatically. Older adults attempt to be productive, reallocating their time to skill-intensive but less energy-intensive activities. In addition, they may effectively instruct youth, drawing on their knowledge of the habitat and sociopolitical skills. The human lifecourse has almost certainly been positively shaped by selection through middle age but questions remain about age 60+. These years may be a non-functional period of collapse that takes time. Alternatively, aspects of this phase may have been shaped by important inclusive fitness benefits produced during it.

These alternatives may offer unique predictions. If old age is merely a period of collapse, near-synchronous aging of different abilities might be expected (Hill, 1993). An evolved strategy that allocates resources across different somatic components in a way that keeps decline in step is expected, for a healthy heart or brain are of little value if the liver can no longer eliminate toxins. If, however, individuals contribute to inclusive fitness in old age through knowledge transfer, we might expect that crystallized intelligence and language ability were selected to senesce at rates slower than other physiological systems.

It appears that, indeed, humans are designed to experience slow aging of the brain compared to other physiological systems. Macaques exhibit Alzheimer-like neuropathology (senile plaques, neurocytoskeletal abnormalities) and cerebral atrophy by age 22-25; In contrast, humans rarely show such changes before age 60 (<1%); they are common (>30%)

only in the 80s (Finch & Sapolsky, 1999). An understanding of the differential allocation to somatic repair during the human lifecourse is only now taking shape.

Psychological Adaptations Within a Life History Framework

We have discussed human life history phenomena—the timing of developmental events, reproduction, and aging—within the framework of modern LHT. As noted earlier, however, LHT has come to be an approach within theoretical biology that offers insights into the selection on just about any evolved outcome. (We specifically discussed life history approaches to signaling.) We now turn to consider examples of how a life history approach can be applied to the understanding of psychological adaptations.

Life History Perspectives on Psychological Adaptations

The framework of evolutionary psychology

Evolutionary psychology attempts to understand psychological adaptations. The mainstream approach has several core elements (see, e.g, Buss, 1995, 2004; Tooby & Cosmides, 1992):

1. Psychological adaptations are assumed to be domain-specific—information-processing specializations designed to accept specific input and act in particular ways on that input. In this sense, psychological adaptations are modular and many in number.

2. Each psychological adaptation is assumed to represent a solution to an ancestral adaptive problem (e.g., detection of cheaters in reciprocal exchange, cuckoldry-avoidance, kin detection, avoidance of toxic foods). Psychological adaptations tend to be special purpose and numerous because each adaptive problem demands specific mappings of information to outcomes that cannot be handled proficiently by general purpose information processing algorithms.

3. Generally, human psychological adaptations are universal.

Evolutionary psychology research programs generally seek to identify specific psychological adaptations (i.e., specify ways in which information is specially processed within specific problem domains). In general, research strategies either begin with a specific adaptive problem and ask what sort of psychological adaptations would have solved it, or begin with a psychological phenomenon and ask how it might reflect a solution to an adaptive problem. As evidenced by this volume, this perspective has yielded many successes.

Psychological adaptations and a life history framework

The core elements of this perspective within evolutionary psychology are perfectly compatible with LHT. Nonetheless, several additional observations about psychological adaptations follow from LHT:

1. All features or activities require allocation of resources: energy, time, neural resources, and so on. Individuals should have evolved to allocate resources optimally under the constraints of tradeoffs (in ancestral environments). But individuals should not have evolved *perfect* solutions to adaptive problems. As noted earlier, individuals cannot optimize fitness by perfectly repairing their soma. Repair of soma in the face of factors that damage it (e.g., free radicals) is clearly an adaptive problem. And individuals have evolved specialized adaptations to repair soma. But optimally, in the face of tradeoffs, individuals will not perfectly repair it (even though, in principle, they may be able to do so) and hence will deteriorate. Similarly, tradeoffs force compromises in the solutions of every life task.[9]

This need not imply that the structures of information processing algorithms themselves are compromised (though they may be). All information processing requires allocation of time and effort from limited shared resources (energy, attention, etc.) and a life history perspective implies that tradeoffs in the allocation of these resources to the *utilization and operation* of specialized psychological adaptations compromise solutions in domains of adaptive problems.

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[9] The marginal value theorem implies that, at maximal fitness, the marginal value of allocation to all possible allocations are identical. The only way in which one could perfectly solve a particular problem at this optimum (i.e., the marginal gain be zero at optimum for that domain) is if the solution were cost-free. But solutions are never cost-free.

Example. Sexual jealousy is purportedly a specialized evolved response to threats to a romantic relationship (e.g., Buss, 2000). In both sexes, a partner suspected of having sex with another person (or suspected of being interested in sex with another person) may signal that a mate may abandon the relationship for another partner (or divert resources into another relationship). In men, a partner's infidelity may also threaten cuckoldry, as men could potentially invest in offspring not their own. In men, then, sexual jealousy may be a particularly powerful motive designed to prevent cuckoldry (see Buss, 2000).

From a life history perspective, we should not expect that men will prevent cuckoldry *at all costs*. Cuckoldry prevention requires allocation of time and energy to monitoring mates and potential rivals. Furthermore, deserting a mate because cuckoldry is possible imposes costs of needing to find a new mate. Just as optimal allocation of effort cannot possibly prevent aging, despite the tremendous benefits of survival, optimal allocation cannot possibly perfectly solve the problem of cuckoldry.

2. Ancestrally, conditions probably affected optimal allocation of effort into particular adaptive domains, leading selection to favor adjustments in allocations based on these conditions. To the extent that, within or across populations or at different points across the lifespan, individuals are exposed to different conditions, they may differentially allocate resources to solving adaptive problems. This is not to deny the universal nature of design but rather is to emphasize the conditional nature of (potentially universal) allocation rules.

Example. How much men will invest in anti-cuckoldry tactics should depend on cues of their marginal benefits and costs. For example, in cultures he has studied (e.g., the Ache), Kim Hill (personal communication) observes that some lower status men tolerate their wives bearing other men's children early in marriage (and even care for those children), as such a strategy appears to offer their best chance to reproduce (see also Marlowe, 2000). Brown and Moore (2003) reasoned that women with partners of low fitness are more likely to be unfaithful to them. Consistent with this expectation, he found that men with high fluctuating asymmetry (a marker of developmental instability and, possibly, fitness) are more jealous than men with low fluctuating asymmetry. Perhaps, even though men of low mate value may be tolerant of infidelity *certeris paribus*, they may be at sufficiently greater risk of infidelity that the net effect is that they tend to be more jealous overall.

3. Although information processing specializations themselves may be modular, allocation of resources into their development and/or utilization cannot be independent. Rather, tradeoffs mean that decisions about allocation of effort into particular domains will have implications for allocation of effort into other domains.

Example. How much men allocate effort to avoiding cuckoldry should depend not only on the costs and benefits of cuckoldry avoidance but also on the costs and benefits of competing activities.

4. In addressing the question of the extent to which individuals will invest in particular adaptations in the face of trade-offs, LHT considers the inter-temporal implications of decisions. The fitness effects of these decisions depend on how they aggregate throughout the lifecourse, from the time the decisions are made until death.[10] Individuals are expected to allocate effort to those adaptations that they would most benefit (through time) from doing so (in ancestral conditions).

Example. Mauck, Marschall, and Parker (1999) modeled the effect of mortality rate on male willingness to invest in an offspring not one's own. Deserting a mate entails costs to reproduction, particularly if one need find and attract a new mate following desertion. As the mortality rate increases, search time for mates is particularly costly, as it represents current allocation of effort for future benefits, which become more uncertain as the mortality rate increases. Hence, the model predicts that mortality rate decreases the net benefits of deserting

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[10] Indeed, fitness effects can reverberate after the death of the actor through the reproductive success of kin.

a mate when paternity is uncertain, rendering investment in other males' offspring more likely. Possibly partly for this reason, rates of extra-pair paternity appear to be higher in societies living in traditional conditions and relatively high mortality rates (e.g., Cerda-Flores et al., 1999) than in modern societies with high quality sanitation and low rates of pathogens (e.g., Sasse et al., 1993).

5. LHT expects that allocations of effort to various tasks will have coevolved with one another such that, for instance, mating and parenting strategies consist of coadapted bundles of characteristics. Hence, individual adaptations cannot be considered fully separate from others not only because allocations compete with one another; each will be most beneficial in the context of other characteristics, which themselves demand allocation of effort.

Example. As the benefit of paternal investment (or exposure to cues that would have signaled benefits of paternal investment ancestrally) increases, not only should paternal investment increase; investment in seeking multiple mates should generally decrease. As individual men see increased opportunities to have multiple mates, they may invest in offspring less (e.g., Gangestad & Simpson, 2000). Less investment in offspring may entail lower benefits from mate guarding and cuckoldry prevention. Conversely, as men pay high costs to ensuring paternity (for instance, because mate guarding severely interferes with production activities [e.g., long-term hunting forays] in light of the ecology), they may also invest less in offspring.

6. The *variations* across and within populations may hold keys to understanding mating and parenting strategies and adaptations, for they reveal how individuals are designed to make trade-offs. This need not imply that the variations are of particular importance, in and of themselves. Rather, the variations may be useful for addressing basic questions about the selection pressures that forged the adaptations by revealing the ecological factors that moderate investment in them.

Example. Some have argued that emotional and sexual jealousy have evolved in response to different selection pressures: desertion and loss of resources vs. cuckoldry (see

Busss, 2000). If so, then variations in them should be sensitive to different ecological factors and be parts of different bundles of allocations within broader mating and parenting strategies. Examination of variations in emotional and sexual jealousy across and within populations can provide key information about the conditional nature of allocations to them and, hence, the forces of selection that led to them.

How Psychological Adaptations Solve Life History Trade-Offs

Execution of the decisions regarding fundamental life history trade-offs is distributed across the soma. Hormonal systems governing the transition to reproduction, mating effort, fertility status, reproductive rate, maternal-fetal exchange of resources, parental investment, responses to stressors, and disease defenses are just a few examples. These systems do not require centralized “decision-makers.” Information processing is not restricted to neural tissue; information is processed throughout the somatic components involved.

This is not to say, of course, that cognitive processes are not critical to allocation decisions. The stress response, for instance, requires the perception of a stressor. Reallocation of effort to parenting with birth of a child involves responding to new circumstances. Differential effort based on health of the child or paternity certainty requires perception of relevant cues. Differential male mating effort as a function of attractiveness entails assessment of own attractiveness. Decisions about whether and how much to invest in particular social relationships depend upon perceptions of that relationship and its benefits. In general, allocations of effort themselves depend on psychological adaptations.

Throughout this chapter, we have emphasized how allocation decisions should be dependent upon the shape and nature of return curves. In some instances, simple cues may effectively signal changes in the return curves (e.g., detection of foreign antigens signals greater marginal gains from investment in immune defenses). In many interesting cases, however, the relevant cues will be multiple and in need of integration. Consider an example, the trade-off between nutritional payoffs to increased food consumption with predation avoidance. At each point in time, an organism receives visual, auditory and olfactory information about the potential presence of predators as well as its foraging success. It decides whether to continue foraging, to engage in vigilance or to invoke a predator-avoidance routine. A variety of factors are important: e.g., the time of last eating, the organism's reproductive state, its more general nutritional state, the density of predators, the return rate of foraging. The impact and weighting of these factors may depend importantly on individual difference factors (e.g., the foraging of subordinate baboons, compared to dominant ones, is less deterred by lion vocalizations, as they have less access to food and hence take greater mortality risks to obtain food; S. Johnson, personal communication). To make optimal decisions, the organism must assess relevant cues and integrate them.

Other examples abound. For instance, parents in traditional societies appear to make decisions about their children's activities (most notably, simple foraging with immediate benefits vs. complex foraging with future benefits via training) adaptively based on returns and costs of those activities (e.g., Bock, 1995). They appear to assess, in some way, the payoffs and risks to various activities to children and make decisions about children's activities accordingly. With modernization and the importance of education to adult productivity, parents the world over reduce their number of children, enhance allocation of investment in each child, and delay their own reproduction to achieve better outcomes for their children. These phenomena raise questions of how individuals come to decide that quality is important not only after they have had children but before they have had a first child, and how these assessment processes were shaped ancestrally (i.e., the nature of the evolved psychological processes involved).

Very little is now known about the precise nature of the adaptations by which organisms solve most trade-off problems. A primary task of evolutionary psychology, in our view, should be to address the psychological processes involved in these solutions.

Summary

This chapter has developed several themes:

1. Life histories are composed of specialized, co-adapted bundles of features that regulate age schedules of fertility and mortality, and respond flexibly in response to local ecology;

2. LHT directs attention to three fundamental trade-offs in the allocation of time and energy: a) present vs. future reproduction; b) quantity vs. quality of offspring, and c) mating vs. parenting effort;

3. Humans exhibit a specialized life history involving learning- and brain- intensive, prolonged, costly development, and extremely productive adulthood, and a long lifespan;

4. LHT offers a new perspective for organizing research in developmental/lifespan psychology, modeling the growth and decline of abilities in terms of present and future costs and benefits and it terms of co-adapted life history strategies;

5. LHT suggests new approaches to standard problems investigated by evolutionary psychologists by explicitly modeling cost-benefit trade-offs as they change over the life course and in response to individual condition;

6. Human psychology and its physical substrates can be thought of as a distributed processing system, utilizing multiple modalities, that both serves to allocate time and energy efficiently among alternative and competing functions, and is itself subject to selection, based on its immediate and long term costs and benefits.

Over the past 40 years, evolutionary biology has witnessed a tremendous explosion in understanding of adaptations, particularly as they relate to behavior. A key foundation of these developments is economic cost-benefit analysis of selection pressures. LHT is not a particular domain of cost-benefit analysis; rather, it is a broad, overarching perspective within which understanding of adaptation must ultimately be situated. The past 15 years have seen rapid and exciting developments of LHT and its applications. Its application to an understanding of human evolved psychology is in its infancy. We hope that the next 15 years will see equally exciting developments in the integration of life history theory and evolutionary psychology.

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Figure Captions

Figure 1. Age-specific effects of brains on net production in easy and difficult foraging niches.

Figure 2. Mortality as a function of investments

Figure 3. Survival and Net Food Production: Human Foragers and Chimpanzees

Figure 4. Net Production and Expected Net Production among Foragers