The Evolution of Human Life History

Introduction

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Human life history differs from that of other primates in several initially puzzling ways. Our children depend on others for subsistence much longer than do the offspring of any other mammal, yet we wean babies earlier than most other apes do. Our age at first reproduction is much older than that of other apes, but our fertility can be higher. We have the longest lifespan of any terrestrial mammal, yet women stop bearing children in the middle of it. Some of these apparent contradictions have been attributed to our big brains and to the nuclear families and sexual division of labor that ethnographers have found in all human societies. But over the past two or three decades, findings in hunter-gatherer ethnography, Paleolithic archaeology, human paleontology, and comparative primatology have raised questions about these long-standing ideas.

Recent applications of life history theory (Stearns 1992) to distinctive features of the human life course (for example, Smith and Tompkins 1995; Hill and Hurtado 1996; Hawkes et al. 1998; Kaplan et al. 2000) have helped fuel a more sophisticated debate over the evolution of human life history. This body of theory was developed in evolutionary biology to explain the diversity of life cycles among living things. To

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address that enormous variety, life history theoreticians make use of two fundamental principles: natural selection and the trade-offs required by the inevitable limits of time and energy (reviewed in Stearns 1992). Energy is allocated in three general ways: for growth, for maintenance and repair of somatic tissues, and for current reproduction. Because the energy available to an organism is limited and energy spent for one purpose cannot be used for another, more energy for one means less for another. Organisms face additional trade-offs within each of these categories; for example, investment in reproduction can go to parenting or mating, and investment in parenting is traded off between quantity and quality of offspring. Natural selection favors tendencies to allocate available energy in ways that maximize lifetime fitness. Because the final accounting of the fitness consequences of alternative allocations is over lifetimes, mortality risks affect the net gains and losses for each trade-off. Life history theoreticians therefore take a demographic perspective, looking at rates of survival and reproduction at each age class in a population.

THE ADVANCED SEMINAR

The School of American Research sponsored an advanced seminar titled "The Evolution of Human Life History," November 2 through 8, 2002. The seminar was organized with three clear goals: to identify the distinctive features of human life history, to debate current models of life history evolution, and to critically evaluate the data available for describing the evolution of human life history and testing current hypotheses. Current descriptions of variation in life history features among living species of mammals would provide a context for identifying the derived characteristics of human life histories—those that distinguish us from common ancestors with other primates—and would help focus questions about when and why those characteristics evolved in our lineage. These rate and timing variables not only shape individual lives but also are major determinants of the age structure of populations. Therefore, both our lives and the character of our societies depend on our life histories.

The defining feature of the advanced seminar was its interdisciplinary approach. The study of human life history evolution has been dominated by paleoanthropologists, primatologists, and evolutionary

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ecologists working with foragers. These specialists have brought the inquiry to a point of general agreement about some distinctive features of human life history. However, there is still strong disagreement about the key variables that promoted the evolution of these derived human traits.

This advanced seminar brought specialists in human paleontology, primatology, and hunter-gatherer behavioral ecology together with specialists in demography and paleodemography, human growth and development, nutrition, and the genomics of aging. The range of specializations was dictated by the central problems of identifying and explaining human life histories. Ethnographic observations of modern foragers capture activity differences by age and sex, patterns of growth and development, and age-specific fertility and mortality in conditions similar in many ways to those of people in the pre-agricultural past. Combined with the patterns of growth, development, and age-specific nutritional effects in humans who depend on other modes of subsistence, these ethnographic and demographic data indicate distinctive aspects of maturation and age-specific mortality in our species. Skeletal remains of past populations provide evidence about the antiquity of these patterns. Only the fossils and archaeology place the evolutionary changes in time and space, as well as in the ecological context in which they emerged and spread. Other lines of evidence illuminate phylogenetic changes. The human lineage is a part of the larger radiation of the primates, so any regularities in life history variation across living primate species set the general framework for the inquiry into what happened in human evolution. Even more broadly, the recent explosion of work in aging genomics provides a window into the enormous diversity of life cycles in the living world and hints at some of the possible mechanisms that pace life histories, including our own.

VOLUME ORGANIZATION

As we originally envisioned it, the advanced seminar would focus on two central issues: (1) the selective factors affecting the evolution of human life history and (2) our ability to reconstruct it, especially for hominids other than modern humans. Following the current wider debate, participants focused on several issues: offspring provisioning and child needs, learning and development, and survival of postreproductive

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women. Participants quickly (if provisionally) agreed that attention should be concentrated on a short list of derived features of human life histories that characterize our species: our relatively long potential lifespans, our relatively late maturity, our relatively early weaning at ages that precede feeding independence, and the relatively large divergence between curves of declining fertility and increasing mortality risk with greater age ("midlife menopause").

Participants also agreed that processes applicable to broad mammalian and specifically primate variation are likely to be implicated in our own evolution and that the derived human features are probably linked, especially in light of the cross-species regularities in mammalian life history variation. Two of the most promising explanatory models currently available, the Grandmother and Embodied Capital hypotheses, link all or most of the four derived features. The former builds on symmetry models for explaining mammalian life history variation, nominating the trade-offs in those models and a novel role for ancestral grandmothers to propel the evolution of the derived human features. The latter argues that the developmental requirements and behavioral advantages of expanding brains in the context of increased emphasis on hunting explain our delayed maturity and increased longevity. Hillard Kaplan (Kaplan et al. 2000; Kaplan and Robson 2002; Kaplan, Lancaster, and Robson 2003) has played the leading role in elaborating the Embodied Capital model and applying it to human evolution; we had hoped that he would participate in the seminar, but his other commitments intervened. Although we missed his active presence, his model is discussed, explained, and critiqued in several chapters.

Two of the original seminar participants, Leslie Aiello and Caleb Finch, do not have chapters in this volume. Their presentations and contributions to the discussions in Santa Fe enriched the advanced seminar. Those discussions had impacts not fully realized at the time, but the chapters here have been extensively revised in light of them.

In the second chapter, Shannen Robson, Carel van Schaik, and Kristen Hawkes assemble current evidence on the life histories of the living great apes to reconstruct the likely life history of our common ancestor. By comparing the most recent empirical data on orangutans, gorillas, chimpanzees, bonobos, and modern humans, the authors identify the longer adult lifespans, later age at first parturition, earlier

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weaning, and shorter interbirth intervals that distinguish human life history from those of our closest living relatives. Reconstructions of past taxa based on living descendents must always be provisional, but the comparisons strongly suggest that the human values on these traits are derived; that is, they evolved after our lineage separated from an ancestor in common with the living great apes. The living taxa do not, however, differ in the age at which female fertility declines, suggesting that this is a life history feature conserved from our common ancestor.

Robson and colleagues also report comparative data on brain growth and dental maturation. The brain growth data show that human and chimp infant brains approach adult size at about the same age, refuting the common assumption that humans require a much longer time to grow their big brains. The comparative data on dental development—a topic discussed by Hawkes in chapter 3 and in greater detail by Skinner and Wood in chapter 11—show that different aspects of dental development do not vary together as a correlated block within the great ape clade. Among these species, neither molar eruption ages nor crown formation times vary in tandem with variation in life histories. Skinner and Wood refer to these as "life history related variables" (LHRVs) and draw a clear distinction between LHRVs and life history variables (LHVs). The important lesson, often rediscovered, is that even though growth and development are not independent of life history, they themselves are not life history variables. Genera and species face different problems within life stages, and developmental patterns can be selected accordingly, with little or no alteration in the life history variables that determine population vital rates.

In chapter 3, Kristen Hawkes provides an historical overview of research on human life history evolution. First, she introduces the field of life history evolution, reviewing key assumptions and modeling tools, especially the Euler-Lotka equation and stable population theory. She discusses r and K selection (MacArthur and Wilson 1967), noting explanatory weaknesses of this widely cited model, and Charnov's (1993) alternative approach, which focuses on life history invariants. Steven Jay Gould (1977) linked developmental heterochrony with life history, and Hawkes uses his influential ideas about slow human maturation to lead off a review of work on each of the distinctive features of human life history. The chapter underlines the important difference

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between questions about mechanisms and about adaptive effects and considers some impacts of genomics on ideas about the evolution of life histories. It concludes with a discussion of the most influential adaptive hypothesis about human evolution, the Hunting hypothesis, and a brief summary of the empirical challenges that emerged at the end of the 1970s. This sets the stage for the next chapter's discussion of subsequent modifications and alternatives that are explicitly grounded in life history theory.

In chapter 4, Hawkes focuses on the slow-fast variation in mammalian life histories and Charnov's symmetry approach to explaining it. Hawkes summarizes data and theory indicating that adult mortality rates are likely determinants of other life history variables, including varying investment in individual offspring. She speculates that increased somatic maintenance, which slows aging in adults, also lowers mortality rates in juveniles, a possibility consistent with Kirkwood's (1977, 1981) Disposable Soma model. The novel suggestion she makes here is that higher levels of somatic repair might be a physiological reason for cross-species correlations between rates of aging and rates of offspring production. Slower-aging mammalian mothers may earn higher marginal gains for additional investment in offspring equipped to build more effective mechanisms for maintenance and repair. The slow-fast mammalian regularities and Charnov's mammal model are the foundation for the hypothesis that long human childhoods and more expensive youngsters are consequences of slowed aging and the novel productive role of aging females. She concludes by comparing and contrasting this Grandmother hypothesis with the influential Embodied Capital argument, which hypothesizes that our late maturity and expensive juveniles evolved because of ancestral reliance on investment from hunting fathers.

Carel van Schaik, Nancy Barrickman, Meredith Bastian, Elissa Krakauer, and Maria van Noordwijk (chapter 5) discuss some of the consequences of slow life histories for distinctive features of primate lives. They review life history variation across the order, giving particular attention to differences in brain size. Variability among primate species provides an opportunity to test hypotheses about causes and effects of slower life histories. The authors identify two main classes of models—those using demographic tools and those based in natural

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history—that have been proposed to explain the relatively long immaturity for a given body size that distinguishes primates in general, including humans, from nonprimate mammals. Charnov's demographic model assumes an allometric growth / production function and shows that age (and therefore size) at maturity is determined by the level of adult mortality. This model successfully explains major variation in mammalian life histories, including perhaps those of humans. The other class of models addresses lineage-specific details of natural history. The Juvenile Risks model associates large brain size to slow development and therefore late maturation, and the Skill Learning hypothesis suggests that a long period of immaturity is necessary to learn the numerous skills required for success as a reproducing adult. Both natural history models have broad support, though we currently lack empirical resolution to distinguish between them.

Van Schaik and colleagues argue that Charnov's (1991, 1993) demographic model is compatible with these developmental natural history models and propose that the latter may provide some of the mechanisms underlying the particular size allometries that play important roles in Charnov's model. The authors conclude that future work should concentrate on testing the critical predictions of the two natural history models and perhaps develop an overarching model that focuses on the role of adult brain size in the development of larger-brained organisms such as primates.

Like other primates, human newborns initially depend entirely on mother's milk. But weaning marks feeding independence for other primates, whereas human children continue to depend on supplements from others long after nursing ends. In chapter 6, Daniel Sellen reviews the distinctive and common features of human and nonhuman primate lactation. Though he laments the overall lack of data on the biology of lactation in nonhuman primates, especially apes, Sellen makes a number of basic biological comparisons. He pays special attention to transitional feeding in which infants begin to consume foods in addition to breast milk.

Early exclusive breastfeeding is enormously beneficial to human infants. After about six months of age, however, breast milk is no longer sufficient to meet typical infant nutritional needs. Sellen notes that our pattern of transitional feeding, which includes highly

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processed foods with breast milk, is a unique characteristic of humans. Infants continue to benefit from breastfeeding into their third year. From there, the marginal returns on continued breastfeeding diminish rapidly. These distinctively processed foods may enable infants to survive without breast milk at a much younger age, as well as smaller size, than infant apes.

Sellen argues that the use of highly processed, nutrient-rich, complementary foods was a derived feature that co-evolved with a reduction in the costs of lactation. Together, these made lactation shorter and reduced interbirth intervals without increasing maternal or infant mortality rates. Sellen goes on to suggest that behavioral and physiological shifts toward complementary feeding and early weaning may have promoted the evolution of distinctive patterns of human foraging, parenting, and social behavior.

Barry Bogin (chapter 7) discusses the physiological aspects of "childhood," which he argues provided crucial reproductive advantages to hominin mothers, and offers hypotheses from a human development perspective. Bogin defines childhood as the period from weaning to the onset of the juvenile growth period. During this time, human children must depend on older individuals for food and protection. In contrast, weaned chimpanzees and juveniles of other primate species must forage for their own food from the time they are weaned. In terms of physical growth, human childhood comprises seven to ten years of relatively slow growth after weaning. Following this period, humans experience a few years of rapid growth (the adolescent growth spurt) in virtually all skeletal dimensions of the body. Bogin argues that childhood made it possible for hominins to replace long lactation with cooperative provisioning, shortening a mother's interbirth intervals. The extensive learning and practice that take place during childhood constitute, he concludes, a secondary benefit of the stage.

Nicholas Blurton Jones uses his work among Hadza foragers in northern Tanzania to address four questions in chapter 8: (1) whether adult mortality rates observed among contemporary hunter-gatherers indicate species-specific adult mortality, (2) whether Charnov's (1993) growth function adequately captures Hadza children's growth, (3) whether improvements in foraging effectiveness with age among Hadza children support long-standing ideas that our late maturity results from the need for long periods of learning and practice to prepare for adult-

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hood, and (4) whether Hadza women past childbearing age increase their fitness by helping descendants.

Blurton Jones summarizes results from his Hadza demography showing their low adult mortality and long average adult lifespans. The similar relationship between the length of the juvenile period and the average adult lifespan in humans and other primates challenges the long-standing assumption that our late maturity is due to a special human requirement for long periods of learning. He shows that Charnov's simple growth model can account for a large fraction of the variation in size with age among the Hadza. Using weanling size, age at first parturition, and maternal size, he shows that female chimpanzees, orangutans, and humans are on very similar growth curves. These demonstrations further underline the applicability of Charnov's (1991, 1993) model of mammalian life history variation to human evolution.

Blurton Jones also summarizes his series of experimental studies on variation with age in Hadza foraging efficiency. Sex differences in foraging activities and boarding school attendance provided a "natural experiment" for observing whether subjects of similar ages who differed in time spent learning and practicing various tests then differed in their foraging performance. Results gave no support to the proposition that long periods of learning are necessary to master these tasks. Differences in size and strength, not length of practice, account for differences in foraging efficiency.

The Grandmother hypothesis proposes that late maturity in humans results from the same trade-offs that Charnov (1991, 1993) has modeled to explain the relationship between age at first reproduction and average adult lifespans in other primates, namely, that our late maturity results from our unusual longevity. That unusual longevity evolved in our lineage when ecological circumstances allowed more vigorous peri- and postmenopausal females to increase their fitness by provisioning their grandchildren. Tests of this hypothesis include empirical measures of the effects of grandmothers' help. Blurton Jones discusses difficulties in measuring such effects and reports some results showing that older Hadza women are generally found where their help for descendants might be most valuable. The chapter concludes with a series of questions and points related especially to growth patterns, resource acquisition, and longevity.

Testing hypotheses of human life history evolution requires specific

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data for the key periods of human evolution. A central goal of the advanced seminar was to consider the direct evidence for the life histories of past populations. What was the lifespan of prehuman hominids? What was their age of reproductive maturity? What was the intensity of mortality, and how did it differ with age at each critical point? Did a significant number of individuals, particularly females, live past reproductive age (Trinkaus 1995)? Recent reevaluations of paleodemography have shown how difficult it is to reconstruct even age and sex for anatomically modern humans accurately and without bias (Bocquet-Appel and Masset 1982).

Lyle Konigsberg and Nicholas Herrmann (chapter 9) discuss the use of paleodemography to reconstruct ancient longevity, and they address the essential question of whether (anatomically modern) human aging patterns have changed during our past. They review three main sources of error that currently plague paleodemographic life tables: the assumption of demographic stationarity, which they dismiss as "fairly trivial"; misestimation of age at death from skeletal indicators; and nonrandom sampling with respect to age in death assemblages. Paleodemography is making important advances in improving age estimation methods, especially in dealing with reference sample bias (Hoppa and Vaupel 2002a). Konigsberg and Herrmann focus on this second problem, in particular, evaluating how reference sample bias (Bocquet-Appel and Masset 1982) can be eliminated from age-at-death distributions.

The authors illustrate how unbiased paleodemographic estimates of age distributions can be produced using a single age-at-death indicator, the sacroiliac joint. They use maximum likelihood methods to estimate the two Gompertz parameters in a Siler hazards model (Gage 1988), which give a mortality curve. They then apply their strategy to two southeastern skeletal series, Indian Knoll and Averbuch, and finally to Loisy-en-Brie, a French Neolithic site.

We may be able to assess whether rates of skeletal aging changed in the past with statistical approaches like those outlined in this chapter, combined with tooth cementum annulation studies as a proxy for known ages (Wittwer-Backofen and Buba 2002; Wittwer-Backofen, Gampe, and Vaupel 2004). The authors are encouraged that the life tables they generated for ancient populations, using unbiased statistics

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and uncertainty in age estimation, resemble the life tables of extant foragers and horticulturalists—unlike many paleodemographic life tables based on biased aging methods. However, they warn that we should approach current demographic reconstructions of any hominin besides anatomically modern *H. sapiens sapiens*, including recent studies of Neanderthal paleodemography (Trinkaus 1995; Bermúdez de Castro and Nicolás 1997; Bocquet-Appel and Arsuaga 1999), "with considerable caution."

The historical demographic record (Oeppen and Vaupel 2002) shows remarkable increases in life expectancy from the nineteenth century to the present. Until about 1950 these changes were due primarily to decreases in infant and juvenile mortality. The historical demographic record, though fragmentary, also suggests that there were improvements in adult life expectancy perhaps dating back to the fourteenth century (Russell 1948; Hollingsworth 1977). Richard Paine and Jesper Boldsen (chapter 10) look at paleodemographic evidence for changing selective pressures in the Holocene in an attempt to assess whether the historical observations represent a long-term trend or a more recent change. The period from the Mesolithic through the onset of historical demographic records (which become widespread in the seventeenth and eighteenth centuries) is characterized by increased population growth, urbanism, and expansion of trade networks. All of these facilitate the survival and transmission of epidemic diseases. Paine and Boldsen explore whether changes in patterns of epidemic disease during the Holocene could have raised levels of extrinsic mortality.

From the perspective of life history theory, differences in mortality rates with age are all important (Hawkes, chapter 3). Paine and Boldsen focus their attention on the mortality of subadults, between 2 years old and the onset of reproduction at about 18 years old, to estimate changes in extrinsic mortality that would have affected all ages. They chose the juvenile age span for two reasons: skeletons between these ages are well represented in excavated samples, and age estimation for these ages is relatively accurate. Paine and Boldsen model the effects of increasing epidemic frequency with a series of Leslie matrix projections and compare the age distribution of subadult death from the projections with historically reported subadult death patterns

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through the Holocene. Their modeling supports the contention that the frequency of epidemics increased throughout the period from the Mesolithic through the Middle Ages. Adult extrinsic mortality increased from the Mesolithic through about the Roman Iron Age and then began to decrease as shortened intervals transformed epidemic diseases into diseases of childhood. Elevated levels of extrinsic mortality lasted longer for children but eventually declined. A result of this pattern would be a temporary suppression of life expectancy. The model captures both widely observed paleodemographic patterns and historical trends, specifically, the historical pattern of adult life expectancy increases preceding improvements in life expectancy at birth. Paine and Boldsen suggest that historical demographic patterns may not be very good indicators of Pleistocene ones.

Matthew Skinner and Bernard Wood (chapter 11) address the deeper antiquity of human life history characteristics, this time from a paleoanthropological perspective. They discuss the hominid fossil record and what it might tell us about the sequence and timing of life history changes. They explain the methods paleoanthropologists use to organize fossil hominins into taxa, summarizing the hominin fossil record under two contrasting taxonomic schemes. The "long" taxonomy emphasizes discontinuities, a punctuated model of evolution, and a branching or cladogenetic interpretation of the fossil record and leads to a large number of species. The "short" taxonomy emphasizes morphological continuity and a more gradualistic view of evolution, leading to fewer species. They use the contrast in taxonomies to highlight the influence of taxonomic hypotheses on interpretations of the evolution of human life history.

Skinner and Wood then critically review inferences about life history characteristics from fossils and attempt to assess when and in what taxon various distinctive characteristics of human life history first appear. They distinguish between life history variables (LHVs)—such as age at weaning, age at sexual maturity, gestation length, and longevity—and life history related variables (LHRVs)—such as body mass, brain mass/endocranial volume, and patterns of dental development, which show correlations to LHVs among primates. No LHVs can be retrieved directly from the hard tissues studied by paleoanthropologists. Some morphological LHRVs, such as endocranial volume, can be estimated from hard tissues and have been used to estimate when the

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distinctive characteristics of human life history (LHVs) may have appeared. Because teeth preserve better than other skeletal tissues and their microstructure provides a precise record of the time course of their own development, these tissues are of special interest for reconstructing ontogeny. Skinner and Wood review features of dental development and compare modern humans with chimpanzees to show that aspects of dental development do not vary as a block across these taxa. Dental development provides LHRVs, not LHVs. The fact that these are distinct classes of variables (as Robson and colleagues discuss in chapter 2 and Hawkes chronicles in chapter 4) certainly complicates the process of reconstructing the life histories of past taxa, but coming to terms with the distinction is a necessary step to making that reconstruction possible.

As with living primate studies and the paleodemographic data, the picture Skinner and Wood present of the fossil record is necessarily far from complete and far from conclusive. Life history related variables—body mass, cranial volume, and dental development—present an inconsistent picture in which extinct taxa had life histories comparable to that of modern humans. The problem is most acute surrounding *H. ergaster* and *H. erectus*. Body mass estimates are similar to modern humans, but neither estimates of brain mass nor dental ontogeny conform to modern human patterns.

OUTCOMES OF THE ADVANCED SEMINAR

Participants found it surprisingly easy to agree on a short list of things that need explaining and on the contending explanations, but data necessary to more precisely characterize empirical patterns and test particular hypotheses proved surprising in another way. The limits of available data sets, as well as the precarious assumptions and extrapolations necessary for inferences about life history, emerged repeatedly in discussion. Those working on one line of evidence had assumed that experts on others had better data. Consequently, all saw that one outcome of the advanced seminar would be a relatively long wish list for comparative data on the nutrient needs and developmental patterns in nonhuman primates, as well as comparative physiological and behavioral measures of age-specific changes in performance to add to demographic measures of senescence.

The combination of data on living populations with archaeological

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and fossil evidence of past life histories resulted in bad and good news. On one hand, aspects of development do not directly index age at first parturition, an especially consequential life history variable. On the other hand, techniques for precisely aging dental events and calculating individual ages from teeth have great promise for extracting ontogenetic information from specimens dated to both the more recent and the deeper past, and the development of methods that deal probabilistically with the age estimates in skeletal samples makes possible a seriously informative paleodemography.

Other living primates are a potential source of information about life history evolution that has only begun to be tapped. Many features of growth, development, and aging are less well studied in our nearest living relatives, even though differences between humans and the other living apes are crucial for posing and testing hypotheses about human life history evolution. Overall, the advanced seminar increased the participants' appreciation of the difficulties of data collection and interpretation faced by their colleagues and the importance of the multiple lines of evidence needed for describing and explaining the evolution of human life histories.

The advanced seminar brought together scholars often separated by respective specialties in a remarkably collegial setting. This enabled us to discover that assumptions unexamined by one specialty were inconsistent with evidence well known in another and also that concepts, questions, and findings from one field could be of great use in another. Our respective research directions were clarified in unexpected ways, and our collective inquiry into the evolution of human life history much energized as a consequence. All the participants would like to thank the School of American Research once again for providing this unique opportunity.

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