

1 Human Behavioral Ecology

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The study of human behavior has been at the core of scientific research since its inception, and theories to describe its emergence, transformation, and diversity continue to engage scholars across the natural and social sciences. For many social scientists, evolutionary theory has been a useful framework for understanding what motivates and constrains human behavior and also why it varies both among individuals in the same society and across cultures. Within the diversity of perspectives studying the nexus of evolution and human behavior, the field of human behavioral ecology (HBE) emerged as the study of the adaptive nature of behavior as a function of socioecological context. In this volume, we explore the history and diversification of HBE, a field which has grown considerably in the decades since its emergence in the 1970s. At its core, the principles of HBE have remained a clear and cogent way to derive predictions about the adaptive function of behavior, even as the questions and methods of the discipline have evolved to be more interdisciplinary and more synergistic with other fields in the evolutionary social sciences.

Any study of human behavior is helped by first highlighting the myriad ways in which we are unique as a species. As primates, we share many important traits with our closest relatives, the great apes, including a slow life history, a large brain-to-body size ratio, group living with kin-based alliances, and complex patterns of social behavior. However, among apes, humans are also distinct. For instance, humans exhibit less sexual dimorphism than other great apes, not only in overall body size but also in the size of canine teeth that can serve as weaponry among primate males. The slow life history of apes is even more extended in humans, with a long period of childhood and a delayed age at first birth. Yet, compared to other primates, humans have a relatively high fertility rate, resulting from shorter interbirth intervals. In addition, humans routinely live for an extended time beyond the birth of their last children, and this long postreproductive life span is common even in settings without modern health care technologies. The intersecting features of delayed maturity, short interbirth intervals, and long life span contribute to our designation as a species of cooperative breeders, as it is common for multiple individuals to contribute to the care and provisioning of human children, including care from grandparents and elder siblings.

Other facets of human behavior also distinguish us from our primate relatives. In general, collaborative subsistence strategies and food sharing are ubiquitous features of human societies, as opposed to the more solitary foraging habits of other primates. Our social organization is relatively flexible, and kinship systems, rules of descent, and postmarital residence rules exhibit remarkable cross-cultural diversity.

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This variation partly relates to local ecological constraints, paralleling the heterogeneous social organization of nonhuman primates. However, the diversity of social structures among humans displays variety and combinations not seen within other species. These structures are further elaborated by cultural practices, which add additional complexity. For example, marriage is a cultural universal with deep evolutionary roots, and it involves social connections and obligations that go far beyond mating. Kinship likewise extends beyond biological bonds through cultural processes such as fictive kinship, affinal relationships, and adoption.

Our system of communication, including symbolic language, is also unrivaled in the animal world. In particular, humans exhibit a pronounced reliance on language for cultural transmission and social learning. Cumulative cultural transmission facilitates the use of tools and other technological adaptations to local environments. Language and other adaptations also allow humans to cooperate on unparalleled scales, not only with kin and other local group members but also with out-group members – an unusual trait for any primate. Together, the capacity for human culture has allowed us to inhabit and thrive on the most remote parts of the planet, create complex institutions, and develop cumulative technologies that transform both our own ways of life and the ecosystems we inhabit.

Human behavioral ecologists maintain a long-standing interest in both the evolution of these distinctive traits and the ways in which they vary within our species. To pursue research questions along these lines, projects typically occur at the level of individuals. This methodological individualism (Udehn 2002) reflects several key assumptions of the HBE approach. First, long-term evolutionary processes are the result of variation in fitness-related outcomes among individuals throughout their lives (Williams 1966b). Accordingly, studies of behavioral variation in human populations can elucidate key trade-offs that underlie the long-term evolution of adaptive traits. Relatedly, humans are assumed to respond flexibly to socio-environmental variation in ways that promote fitness-enhancing outcomes.

This assumption of behavioral flexibility is central and implicit in theoretical models, meaning that behavior is expected to vary across individuals based on their respective socioecological circumstances. The resulting view of behavioral flexibility departs from alternative views of behavior as instinctive, rote, or culturally determined. That is not to claim, however, that all human behaviors are unambiguously adaptive. Humans also exhibit maladaptive behaviors, and these behaviors potentially reflect important constraints on human evolution, therefore meriting attention from researchers, too. In general, though, the HBE approach posits that humans evolved to respond effectively to diverse evolutionary challenges, and the resulting natural history of our species is what motivates human behavioral ecologists to pursue their research.

1.1 The Intellectual History of Human Behavioral Ecology

Human behavioral ecology has its roots in two fields, both of which emerged in the middle of the twentieth century. The first, cultural ecology, sought to understand the

role of the natural environment in effecting culture change. Cultural ecology was a response to two opposing worldviews of the time, each of which propagated an iteration of the nature versus culture dichotomy. First, emphasizing nature as primary, environmental determinists proposed that human behavior was dictated by local environmental conditions, relegating culture to a response rather than a primary force. On the other hand, the possibilists, led by Franz Boas and Alfred Kroeber, posited that human response to environmental conditions was extremely mutable and that culture could take a variety of possible forms in the same environment, with cultural history and the diffusion of ideas and technologies playing key roles. The cultural ecology movement, led by Julian Steward, proposed that the environment influenced the ways that people adapted to their environment but did not *determine* it, offering a middle ground between determinism and possibilism. This middle ground was a critical contribution of cultural ecology. However, it did not offer an explanation for *why* such patterns of adaptation would occur. To fill this gap, early human behavioral ecologists turned to evolutionary theory.

Like cultural ecology, the field of ethology focused on human–environment interactions, but it grew out of biology and comparative psychology. It can be traced back to Darwin, but the works of scholars such as Konrad Lorenz and Niko Tinbergen focused evolutionary theory on the study of behavior in natural settings, which would become a hallmark of behavioral ecology. The 1960s and 1970s saw the emergence of many of the models and theories that would form the backbone of behavioral ecology, including kin selection theory (Hamilton 1964), optimal foraging theory (MacArthur and Pianka 1966), parental investment theory (Trivers 1972), and life history theory (Stearns 1976). These models continue to be at the core of behavioral ecology and are the foundation of much of the work in this volume.

In the mid-1970s, a number of anthropologists and archaeologists began to apply evolutionary theory and the aforementioned models within particular human populations through ethnographic fieldwork. These early studies tackled basic questions about the roles of kin selection, sexual selection, and fitness optimization in humans (Chagnon 1979; Hames 1979; Strassmann 1981; Turke and Betzig 1985). Around the same time, the first applications of optimal foraging theory were applied to hunter-gatherers (Winterhalder and Smith 1981; O’Connell and Hawkes 1981; Smith 1985). In general, the results of these studies frequently upheld the predictions of HBE models, which helped to launch additional theorizing and applications to increasingly diverse research questions.

1.2 Basic Principles of HBE

The evolutionary study of behavior is traditionally organized around four complementary approaches: causation, development, function, and phylogeny (Tinbergen 1963). The first two focus on *proximate* (i.e., more temporally direct or immediate) explanations: understanding the mechanism of the behavior (causation) and its ontogeny (development). The second two questions address *ultimate* (i.e., more distal or evolutionary) explanations: studies of phylogeny and studies of adaptation or

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function. Of these, behavioral ecologists have almost exclusively focused on function, aiming to understand how natural selection has produced organisms that respond to environmental conditions in ways that increase their chances of surviving and passing on genes to the next generation. This focus on adaptation means that HBE uses, as a starting point, the hypothesis that behavior will be close to optimal in terms of maximizing fitness.

Human behavioral ecology's conventional agnosticism about development and mechanism has been exemplified through its acceptance of the "phenotypic gambit," an assumption that systems of inheritance do not meaningfully constrain adaptive responses to local variation. In practice, this approach allows a researcher to study the fit between ecology and behavior without needing to uncover or specify the exact proximate mechanisms (developmental, physiological, or behavioral) through which this fit is achieved.

While HBE research continues to focus on function, the field has become more integrative of other approaches to the study of behavior. In so doing, the methodological agnosticism that initially characterized HBE is being replaced by the notion that "mechanisms matter" (Borgerhoff Mulder 2013). For example, researchers in genomics have made important discoveries about feedbacks between genes and behavior that highlight the need for a deeper consideration of genetic mechanisms (Adkins et al. 2018; Kuzawa and Thayer 2011). In addition, the role of transmitted culture is increasingly being recognized by human behavioral ecologists as important not only to understanding why maladaptive outcomes occur but also in illuminating how behavioral strategies arise and thrive (Mesoudi 2021; Newson et al. 2007), which again highlights a need for greater integration of proximate and ultimate approaches in research. Throughout this volume, readers will see evidence of this integration of the four basic approaches, though generally still with an overarching emphasis on adaptation and function.

Another central tenet of behavioral ecology involves conceptualizing behavior in terms of conditional strategies to understand variation in phenotypes, often organized around a strategy set that represents possible variations of a behavior in a particular context. In simple form, conditional strategies involve logic such as: "When conditions are *X*, use strategy *i*, but when conditions are *Y*, switch to strategy *j*." For example, males in a population who want to find a mate could either fight to control a territory and the females on it or try to sneak matings from within other males' territories. Which strategy any individual male chooses is predicted to be contingent on factors such as his physical condition, his relative status, and the density of females in the area.

More complex decisions require much larger strategy sets. When a forager decides what resources to pursue, for example, she has a variety of possible combinations to choose from. Strategies can also cross domains, including decisions about how to meet both childcare and food production goals (Scelza and Bliege Bird 2008; Starkweather et al. 2023), or assessing both the social and productive aspects of foraging alone versus in a group (Smith 1985; Alvard and Nolin 2002). Behavioral responses are expected to vary according to local conditions; thus, what is optimal in

one context is likely to differ from what is optimal in another circumstance or for another person. Early HBE studies focused on how ecological variation in the physical environment helps to explain the diverse behavioral repertoire that characterizes modern humans despite a lack of noteworthy genetic differences across populations. As the field has grown, ecology has begun to be construed more broadly to include social and institutional contexts such as socially enforced norms and government policies.

The goal of HBE continues to be understanding variation in phenotypes and predicting what characteristics of the local environment lead to the uptake of one strategy over another. At their core, these decisions are believed to be about optimizing fitness. This approach might include predictions that foragers will pursue only resources that increase their return rate, that optimal family size will reflect local mortality risks, or that the likelihood of cooperation between individuals depends on their biological relatedness and level of need.

Human behavioral ecology's reliance on the logic of optimization does not presuppose that humans are perfectly adapted to their environments (though this is a common misconception).¹ Instead, optimization models follow from the principles of natural selection, which is expected to favor locally advantageous adaptations over time, leading to an increasingly better fit of behavior with local environments. Yet, behavioral ecologists are also keenly aware of the potential for mismatch between fitness and local behavioral adaptations when environments change very quickly, as they have been in many regions of the world in the era of globalization (Gurven et al. 2017). In these contexts, behavioral ecologists aim to understand how traditional behavior may have been adaptive given the past environment and also how changing patterns of behavior may be understood from an evolutionary perspective.

In order to assess the costs and benefits of alternative strategies, behavioral ecologists need a standardized “currency” for comparison. The ideal currency for evolutionary models is fitness, but fitness is a probabilistic rather than an absolute measure, representing the likelihood that an individual will survive and pass on genes to the next generation. This makes it very difficult to measure directly. Instead, behavioral ecologists use fitness proxies, traits that are widely accepted to be positively correlated with survival and reproduction. Within human behavioral ecology, commonly used proxies include calories, body composition, mating frequency, number of children born, and number of children who survive early childhood.

¹ Another common misconception about behavioral ecology involves the individuals' conscious awareness of their decision-making processes. One might imagine, for instance, that advanced mathematics might be necessary for individuals to identify the optimum strategy amid a large set of possible alternatives. On the contrary, behavioral ecologists expect that natural selection will equip individuals with the cognitive architecture needed to make adaptive decisions, often relying on informal heuristics. By analogy, consider the challenge of catching a fly ball in the game of baseball. When fielding the ball, players are not consciously using trigonometry and calculus to calculate where the ball will fall. Instead, it is sufficient for them to adjust their running speed so that the angle of the ball relative to the ground remains constant (McLeod and Dienes 1996). Simple heuristics are often adequate solutions to complex adaptive problems.

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The final factors that behavioral ecologists must consider are the constraints to the system, namely the aspects of the environment that are not under the control of the actors whose decisions are being modeled. Most systems have both extrinsic and intrinsic constraints. Extrinsic constraints include ecological characteristics, such as the distribution of prey in the landscape, the number of competing hunters in the group, or the level of risk from infectious disease. Intrinsic constraints can include diverse perceptual and sensory factors, cognitive constraints, and physiological limitations and other morphological considerations.

1.3 What We Work On

Human behavioral ecology focuses on behavioral responses to variation in the environment, which opens up a wide variety of topics for its practitioners. However, the majority of HBE studies have focused on production, cooperation, distribution of resources, and reproduction. Here we provide a brief history of work on these topics, and then we shift to describe what we perceive as the major trends that are guiding current and future research in HBE.

Human behavioral ecology largely originated with applications of optimal foraging models, borrowed from behavioral ecology and applied to contemporary foraging societies. These models address trade-offs and strategies of subsistence-based production, including whether to pursue a prey type when it is encountered, how long to stay in a particular location or “patch,” and how to account for stochasticity in the resource base to avoid shortfalls. Over time, this part of the field expanded further to consider the motivations behind foraging activities (e.g., do men hunt to provision families or to attract mates?), how foraging strategies vary across the life span, and the sexual division of labor. Market integration has also resulted in changing modes of production and increased the likelihood of mixed modes of production within communities, meaning researchers need to pay careful attention to complicated aspects of the household economy, including the practice of traditional livelihood strategies (e.g., agriculture, fishing, herding) alongside new ones (running a local shop, migrating to cities for work) – several of which may be simultaneously evident among members of the same family, household, compound, or village (Tucker et al. 2010; Ready and Power 2018; Starkweather 2017). The first part of this volume addresses these topics with chapters on foraging strategies (Chapter 3), modes of subsistence (Chapter 4), and the division of labor (Chapter 6).

Another recurrent theme within HBE research has been a focus on the unprecedented scale of cooperation that humans exhibit. At first, much of this work examined the question of altruism and the conundrum of how natural selection could favor behaviors that benefit others at a cost to the actor. Kin selection and reciprocal altruism, both also widely discussed in other species, were early models that HBE practitioners considered in depth. Much of the empirical work on this front focused on food sharing and cooperative production, providing interesting addenda to tests

of optimal foraging models. These extensions include the ways in which biological markets have affected cooperation and food sharing (Jaeggi et al. 2016b). Beyond food production and distribution, HBE has devoted attention to myriad other aspects of cooperation, including political alliances, warfare, and childcare. This volume addresses these topics in chapters on cooperation (Chapter 5), status and hierarchy (Chapter 7), and political organization (Chapter 8).

Studies of reproduction represent the broadest and fastest-growing area of research within HBE (Nettle et al. 2013). This literature encompasses studies of mating and marriage, the role of parents and alloparents, and broader demographic patterns of fertility and mortality. Much of this work relies on principles from life history theory, which outlines how natural selection can shape patterns of growth, survival, and reproduction in a given species. Classic research in this area focused on variation in mating and marriage strategies, often extrapolating from models like the polygyny threshold model (Borgerhoff Mulder 1990), as well as tackling variation in marriage payments across societies (Dickemann 1991; Gaulin and Boster 1990). Early work on fertility and parental investment investigated the optimality of birth spacing (Blurton Jones 1987) and differential investment (Mace 1996; Daly and Wilson 1983; Borgerhoff Mulder 1998a), and researchers also took on the challenge of explaining the demographic transition (Borgerhoff Mulder 1998b; Mace 1998).

As with studies of production, changes brought about by urbanization, market integration, and globalization have also spurred strong interest in shifting patterns of mating, marriage, and parental and alloparental investment. Recent studies of mating and marriage have considered how an HBE perspective can be useful for understanding issues such as dowry inflation (Shenk 2007), the relationship between wealth inequality and polygyny (Ross et al. 2018), and how labor migration affects mating market dynamics (Schacht and Smith 2017). Industrialization is also often implicated in the shift toward more intensive investment in a smaller number of children who can compete for opportunities in the emerging wage labor economy (Kaplan 1996). This shift has prompted novel forms of parental investment, notably including formal education, which was traditionally nonexistent but is often the primary form of investment in children in market-integrated societies. These changes have motivated researchers to consider how investment in children changes with subsistence patterns (Hassan et al. 2021) and also how to conceptualize such new forms of investment from a theoretical perspective. Moreover, education leads to novel forms of social learning and cultural transmission (Kline et al. 2013), which may accelerate the effects of cultural change in market-integrated societies (Richerson and Boyd 2005); it is thus unsurprising that the study of social learning has become a very active field of study in the past few years. Finally, new iterations of sexual selection theory have triggered reevaluations of some classic evolutionary models, as seen in studies of the adult sex ratio and mating market dynamics (Schacht and Borgerhoff Mulder 2015) and the role of multiple mating for women (Scelza 2013). Often drawing upon life history theory (Chapter 2), the second half of this volume addresses these topics, including chapters on mating (Chapter 9),

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marriage (Chapter 10), parental investment (Chapter 11), cooperative breeding (Chapter 12), and evolutionary demography (Chapter 13).

As HBE has developed, not only have the questions changed, but so have the ways in which researchers have addressed them. With an increasing number of researchers working alongside NGOs and in areas of the world where economic development policies are being implemented, the field has also taken a turn toward applied approaches, leading to the emergence of a subfield of applied evolutionary anthropology (Gibson and Lawson 2015; Pisor and Jones 2021; Tucker and Rende Taylor 2007). The goals of this approach are to apply the logic and models of HBE to address practical challenges faced by communities and to engage with the international development community to understand the consequences of development projects, ideally steering programs in a more locally appropriate direction. Human behavioral ecologists taking this approach have studied numerous topics, including health (Lawson and Uggla 2014; Pepper and Nettle 2017), the green revolution (Tucker 2014), microfinance (Lamba 2014), family planning decisions (Leonetti et al. 2007), the nutrition transition (Neill 2007), sex ratio bias (Shenk et al. 2014), and climate change (Bliege Bird and Bird 2021). As in other subfields of anthropology, these approaches sometimes constitute a critique of policies promoted by development agencies that ignore important ethnographic context or take unrealistic or ethnocentric approaches to problems where evolutionary theory provides key insights, such as work on “child” marriage (Schaffnit and Lawson 2021), dowry (Shenk 2007), and domestic violence (Stieglitz et al. 2018).

To address these issues and generally add depth to the study of HBE, causal mechanisms have become an area of greater interest. There has also been a shift from studies focused largely on individual-level decision-making to ones that encompass institutions and cultural processes. Whereas HBE has historically been set in tension with other disciplines studying evolution and human behavior, increasingly researchers are finding fruitful areas of overlap. Accordingly, this volume includes chapters on human biology (Chapter 14), cultural evolution (Chapter 15), and evolutionary psychology (Chapter 16), which showcase the ways in which HBE fits within the larger field of evolutionary social science.

1.4 How We Work

Like most basic science research, HBE relies on a hypothetico-deductive research strategy, which involves the use of models to derive specific, testable predictions. HBE strategically relies on simple models that capture the basic elements of a situation, sacrificing detail and nuance for clarity and generalizability. Simple models are useful because they can be applied across many contexts. This means that general theoretical concepts can be applied across diverse settings to identify the kinds of conditional strategies that are at the core of the field. But the fact that HBE models are generalizable rather than context-specific has sparked intermittent criticism from cultural anthropologists, who assert that such reductionism is unrealistic. In one sense, this criticism is justified; simple models cannot provide a holistic replication

of real-world dynamics. Yet, rather than trying to replicate reality, HBE models aim to highlight the central role of particular variables and trade-offs that underlie behavioral strategies in multiple contexts. This approach requires simplifying assumptions, including assumptions that are unlikely to capture all relevant variation.

For example, when human behavioral ecologists first adapted the polygyny threshold model from biology (Orians 1969), it was assumed that co-wives did not offer benefits to one another, such as increased production efficiency or help with childcare (Figure 1.1). The models focused only on the relative benefits that women could gain from partnering with either an unmarried or an already married man. This allowed for the derivation of clear predictions (e.g., women should choose to marry a married man only when the share of resources that she would receive are greater than those she would have upon marrying an unmarried man). The goal was to identify the effect of male resources on women's decisions about whom to marry.

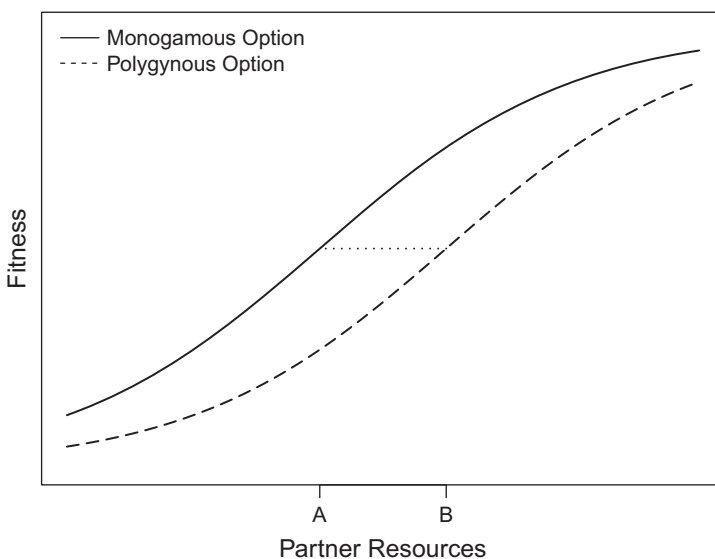


Figure 1.1 A graphical depiction of the polygyny threshold model (Orians 1969). The two sigmoidal curves show the respective fitness functions of a woman who either partners monogamously (solid line) or as a second mate (dashed line). The curves vary as a function of the male partner's resources, and assuming an unconstrained choice, women are expected to choose the option that maximizes their fitness. The optimal choice depends on the potential partners' respective resources. Consider the choice between the monogamous option in which the partner's resources are represented by point A and the polygynous option with a partner's resources at point B. The horizontal dotted line represents the threshold at which the choices are equivalent. If point B were to shift downward, then monogamy would be favored. Conversely, if point B were to shift upward, the polygynous option would be advantageous. Note that the fitness functions depicted here are hypothetical and could vary substantially in different contexts, particularly when integrating additional considerations such as those described in the text (e.g., potentially beneficial cooperation among co-wives).

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Empirically, however, researchers found mixed support for the basic polygyny threshold model. Among Kipsigis of Kenya, female choice based on relative resource access appeared to be a key factor in the decision to marry polygynously, supporting the conceptual model (Borgerhoff Mulder 1990). In other settings, however, polygynous women fared worse than their monogamous counterparts, indicating that the female choice model advanced by Orians does not necessarily fit well in human populations and that men may be coercing women into polygynous marriages that benefit their own fitness interests (Chisholm and Burbank 1991). This led researchers to follow up with studies that focused on the importance of co-wife cooperation and conflict as motivators or detractors for choosing polygyny (Jankowiak et al. 2005; Scelza 2015), the interaction of polygyny with other socioecological factors (Lawson et al. 2015), and the role of parental marriage arrangements in curtailing female choice (Apostolou 2007). Other work incorporated richer demographic data to assess the links between polygyny and fertility and to assess whether a choice or coercion model is a better fit (Winking et al. 2013). That is, researchers started with a simple model, and then, as they accrued data, they were able to use previous results to develop refined models that better predicted men's and women's decisions.

To test their models, human behavioral ecologists employ diverse methods from biology, anthropology, economics, and psychology, often integrating quantitative and qualitative data. Typically, quantitative data are used in direct tests of predictions, while qualitative data help researchers to design methodological tools and contextualize their results. Quantitative methods frequently include surveys or questionnaires for demographic data, direct observation for behavioral data, weighing and measuring of items (e.g., gathered foods or household goods) to understand return rates or wealth, and health measurements (e.g., height, weight, blood pressure). Traditional qualitative methods from cultural anthropology are also widely used, including open-ended interviews, focus groups, and participant observation. These are central to gaining local ethnographic knowledge, developing nuanced questions for more structured data collection, and interpreting the results of those data during analysis (Box 1.1).

One set of methods, borrowed from behavioral ecology studies of other species and advantageous for providing both reliable observations of behavior and deeply contextualized data, is the systematic recording of time allocation (Hames 1992). Common sampling designs include focal follows, which allow for longer periods of observation focused on a single individual, or instantaneous scans, which are designed to gather information on many individuals over a short period of time. In humans, time allocation data have been used to test optimal foraging models (Hill et al. 1987; Koster 2008), to assess the role of parents and alloparents in studies of investment (Ivey 2000; Scelza 2009), and to examine behavioral specialization and trade-offs in subsistence strategies (Koster and McElreath 2017). The methods have also been used to address questions about human life histories, including how time allocation changes across the life span (Gurven and Kaplan 2006) and how children's labor can help to offset their costs, allowing for larger family sizes (Kramer 2004).