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Perspective

Behavioral Ecology of the Family: Harnessing Theory to Better Understand Variation in Human Families

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Abstract: Researchers across the social sciences have long been interested in families. How people make decisions such as who to marry, when to have a baby, how big or small a family to have, or whether to stay with a partner or stray are questions that continue to interest economists, sociologists, demographers, and anthropologists. Human families vary across the globe; different cultures have different marriage practices, different ideas about who raises children, and even different notions of what a family is. Human behavioral ecology is a branch of anthropology that is particularly interested in cultural variation of family systems and how these differences impact upon the people that inhabit them; the children, parents, grandparents. It draws on evolutionary theory to direct research and generate testable hypotheses to uncover how different ecologies, including social contexts, can explain diversity in families. In this Special Issue on the behavioral ecology of the family, we have collated a selection of papers that showcase just how useful this framework is for understanding cultural variation in families, which we hope will convince other social scientists interested in family research to draw upon evolutionary and ecological insight in their own work.



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1. Introduction

In this Special Issue, we showcase how using the evolutionary framework of human behavioral ecology (HBE) can provide deeper insight on human families. Human behavioral ecologists are interested in how human behavior can be understood from an adaptive standpoint. In the context of this Special Issue, we are interested in how families vary across time and space and how by understanding this variation we can shed light on human sociality more broadly. Moreover, this issue seeks to investigate contemporary policy-relevant problems (e.g., [Lawson et al. 2015](#)). Family is a cornerstone of social science research and a building block of human sociality, and here we argue that by utilizing the theoretical framework of HBE, we can develop new and empirically-testable predictions for human family research.

HBE recognizes human social behavior as the result of interactions between evolution and ecology. Originally developed in mainstream biology as a way to examine how an animal's behavior is adapted to the environment in which it lives ([Simmons 2014](#)), human behavioral ecology uses this ecological framework to investigate human behavioral diversity ([Borgerhoff Mulder 1991](#); [Cronk 1991](#); [Winterhalder and Smith 2000](#)). Behavioral ecology begins with the assumption that over time, behaviors that increase fitness become more common in the population. Fitness refers (in somewhat simplified terms) to the differential ability of alleles, strategies, or traits to replicate themselves ([Coulson et al. 2006](#)). Human behavioral ecology, therefore, is concerned with how different behaviors (and other traits) are associated with reproductive success. Over time, the characteristics that lead to more surviving offspring will become more frequent in the population. Human behavioral ecologists assume that individuals will generally act in an optimal way to maximize their

fitness for a given ecology; an assumption that allows us to generate and test hypotheses to understand human behavior (Nettle et al. 2013).

What do we mean by ‘ecology’? Along with the theoretical framework, HBE has also borrowed this terminology from mainstream biology, although human ecologies are more complex. An ecology traditionally includes environmental factors, such as rainfall, temperature, and altitude, but it also is comprised of social factors such as interactions with predators or conspecifics. This is the ecology that all organisms navigate and adapt to. Of course, any examination of humans is incomplete without incorporating culture as part of the environment. Culture has many definitions, but given our focus on studying humans, we may view it colloquially as ‘the knowledge and behavior that characterizes a particular group of people’ or ‘information that is learned socially’ (Heyes 2020). Cultural institutions, defined as socially created and culturally inherited rules on behavior that set expectations about social interactions (Currie et al. 2021), such as marriage systems, inheritance rules, educational institutions, and socioeconomic deprivation, all influence which behaviors or traits are successful (Gibson and Gurmu 2011; Henrich et al. 2012; Mattison et al. 2016; Moya et al. 2021). We can say that humans inhabit *socioecologies*. This approach leads to iterative questions regarding why particular cultural traditions or institutions developed, with human behavioral ecologists hypothesizing that ecological variables can provide insights into these cultural traditions too (Ember et al. 2007; Holden and Mace 2003; Mace 2014; Mattison et al. 2016; Nettle et al. 2013), although there are limitations to this approach as other factors, like subjugation may also play a role (Borgerhoff Mulder 1992). Originally, human behavioral ecologists studied cultural and behavioral variation using data from small-scale societies as these are the study sites of most anthropologists, however now the focus has been expanded to include data from large, industrialized societies to gain a more balanced understanding of human behavior.

While behavior is not genetically determined, we do assume that there are genetic bases for a range of behavioral responses and that individuals are able to respond flexibly given their current environment or situation. Furthermore, human genotypes are similar across human populations and as genes interact with the environment, humans exhibit immense phenotypic plasticity—the facultative ability of one genotype to be expressed differently depending on the environment (Cronk 1991). Humans are known for their ability to live in diverse environments, create eclectic cultures, and exhibit many varying behaviors, suggesting that human plasticity has been selected for over evolutionary time.

One of the main strengths of HBE is that researchers can focus their areas of inquiry on those that are predicted by theory, which may lead to unexpected insights and reduce data-driven trial-and-error. For instance, HBE predicts that people will produce children even though children are immensely costly (Mace 2014), that people are willing to engage in dangerous or risky behavior if it is needed to attract a mate (Wang 2002), and that mental health will suffer if parents are isolated without help to raise children during a global pandemic (Myers and Emmott 2021). All of these can be empirically tested.

Some have argued that the dramatic decline in family size that has been observed in most parts of the world provides evidence against an evolutionary understanding of human behavior (e.g., Vining 1986), but HBE sees this as an opportunity to better understand which environmental factors lead to this unique behavioral response. Indeed, many HBE researchers examine reproductive decision-making to understand the demographic transition (e.g., Borgerhoff Mulder 1998).

Another strength of adopting ecological theory is to think about behaviors as adaptive choices for a given ecology. For instance, in this issue, Schaffnit and Lawson (2021) examine “child” marriage. While global health campaigns have called for the eradication of child marriage, Schaffnit and Lawson use HBE to consider why this behavior is so widespread. An understanding of how this may be an optimal choice for a given environment can remove the stigma of behavior that may be viewed by outsiders as ‘problematic’. We argue that by understanding *why* certain behaviors persist, instead of casting them as social ills, we can understand them as the result of costs and benefits, which in turn, depend on the

environment. This approach has yielded success in thinking about other social issues such as obesity, crime, polygyny, and teenage pregnancy (Abbots et al. 2020; De Courson and Nettle 2021; Lawson et al. 2015; Nettle 2010; Nettle and Bateson 2019). This is not to say that where behaviors can be understood as adaptive under given conditions that as a society, we condone them. This is known as the naturalistic fallacy and thinking that what happens is 'natural' and thus must be morally right, is a misguided (and even damaging) use of evolutionary theory in understanding human behavior. In this special issue we hope to convince researchers across the social sciences that the HBE approach can bear rich fruit for those studying human social behavior, by showcasing here its value in family research.

2. Family Research in HBE

Family is a key area of focus in HBE, including family formation (or breakdown), investment in children, conflict/cooperation among family members, and how cultural institutions influence all parts of family life. Family is difficult to define (see this issue, Kramer 2021), but human behavioral ecologists typically follow the anthropological tradition of using the term 'kin' to refer to one's family. Across cultures, kin include people related biologically, through marriage, or via other processes (e.g., "fictive kin"; the family we choose). While human behavioral ecologists focus on genetic kin because genetic ties contribute to fitness and thus shared interests, a lot of work is also done on allegiances between classificatory kin and affinal kin (through marriage) as these are important relationships that build cooperation and reciprocity. Human behavioral ecologists who focus on family research generally examine variation in mating and partnering strategies, who, besides the mother, cares for children (alloparenting), and reproductive outcomes such as family size, birth spacing, and parental investment in children, all as a function of local socioecologies.

2.1. Mating, Marriage, and Divorce

A key feature of all human societies is the institution of marriage¹, although the specific rules are cross-culturally variable (for more details, see this issue: Kramer 2021). Some societies permit polygynous marriage (one man with multiple wives), others require that marriage only occurs between two individuals, and a few cultures have polyandrous marriage (one wife with multiple husbands). An HBE framework provides insights into how ecological factors, such as pathogen stress or levels of paternal investment, may be associated with marriage systems, where a greater load of pathogen stress and lower male contribution to children's welfare tend to be associated with higher levels of polygyny (Low 1990; Marlowe 2003). A cross-cultural examination of marriage demonstrates that the belief that marriages should be based on love between spouses is far from universal (for an example see this issue: Winking and Koster 2021). In many societies across the world, families exert at least some control over the selection of a person's spouse (Apostolou 2007; van den Berg et al. 2013). Recognizing the role of families in marital decision-making combined with a methodological framework that emphasizes optimal choices given socioecological constraints, Schaffnit and Lawson (2021, this issue) identify four hypotheses for why women may marry young, despite a worldwide campaign to eradicate child marriage. The authors argue that early marriage may be a product of economic deprivation, which overrides the potentially poor health consequences to early marriage (Schaffnit and Lawson 2021).

Beyond marriage, men and women sometimes engage in extra-pair partnerships². In some societies, particularly those with patrilineal descent systems, female sexual behavior is highly controlled, resulting in cultural institutions that restrict women's autonomy, such as veils, foot binding, and domestic violence (King 2008; Mackie 1996; Pazhoohi et al. 2017; Smuts 1995). What are the conditions that lead to different cultural rules regarding female autonomy and extra-pair partnerships? In this issue, Scelza and colleagues (2021) describe how the distribution of key resources influences the temporary residence locations of men and women, and among the Namibian Himba, where pastoralism (animal herding) often

leads to spouses spending long periods apart. This coupled with unusual social norms such as double descent, where individuals maintain clan membership with both the matrilineal and patrilineal lineages, with a likely history of matrilineality, promotes loosening restrictions on female sexuality, resulting in many women having long-term partnerships in addition to their marriage partner. In this context, extra-pair partnerships may be a strategy for women to gain additional resources (Scelza et al. 2021). This case study provides insight into the particular socioecological costs and benefits that influence the likelihood of women seeking sex beyond the marital union.

Researchers are also interested in factors associated with divorce, as negative child outcomes have been associated with parental divorce in many post-industrial societies (Amato 2000). An historical and cross-cultural perspective provides evidence that divorce rates vary across time and space (Apostolou 2007; Heaton et al. 2001) and a variety of factors may be associated with divorce rates, such as adult sex ratio (Schacht and Mulder 2015; Schacht and Kramer 2016), the availability of alloparents (Quinlan and Quinlan 2007), or women's financial autonomy (Snopkowski 2016). In this issue, Winking and Koster (2021) examine the causes of divorce among a Mayangna/Miskito community in Nicaragua to identify the costs and benefits of marriage and divorce, and determine whether divorce trends mirror those in post-industrial societies. The authors find that women are more likely to initiate divorce even though divorced life is harder for them than their male partners and that early marriage itself does not constitute a risk factor for divorce in this context.

Using a HBE perspective, with an emphasis on identifying costs and benefits of alternative behaviors, and examining mating behaviors cross-culturally, provides a fuller picture of human partnering behavior than simply drawing on insights from a single (often WEIRD³) context.

2.2. Reproductive Outcomes: Timing of Births, Family Size, and Parental Investment in Children

Another key area of HBE research focuses on reproductive outcomes and the associated investment in children. Given the global decline in fertility over the past centuries, researchers from a variety of disciplines seek to understand human reproductive decision-making. As mentioned above, HBE assumes that people want to maximize fitness by having children, despite their cost, in contrast to some others which assume the goal is to maximize some other utility, such as wealth or education. To understand human fertility, HBE examines fertility outcomes cross-culturally to understand how the role of physiology (Kaplan 1996) and psychology (McAllister et al. 2016) along with active decision-making and random chance (Hruschka and Burger 2016), combine to influence fertility outcomes including age at first birth, length of birth intervals, age at last birth, and childlessness (Sear et al. 2016). The field of reproductive ecology examines how women's reproductive physiology is regulated through a system of hormonal mechanisms that respond to socioecological factors, such as the energetic status of women (Ellison 2003; Panter-Brick 2000), although the physiological determinants of fertility are likely more relevant in energetically stressed populations. Recent work has attempted to integrate the role of economic costs and benefits with the insights of cultural evolution⁴ (Bentley et al. 2016; Colleran 2016).

HBE uses a theoretical framework known as *life history theory* (more details can be found in Kramer 2021, this issue) to explain how organisms allocate energy, where any investment made for one purpose cannot be used for another (Hill 1993; Stearns 1992). When considering reproductive decisions, parents face a tradeoff between investing in current offspring or shifting investment towards future children. As parents choose to invest more in their current offspring's education, status, or wealth, they may opt to reduce the number of future offspring they have (Sear et al. 2016). Researchers have long recognized the role of women's education in predicting fertility outcomes, but HBE seeks to understand *why* education matters and whether the mediating pathways vary across time or place (Colleran and Snopkowski 2018; Snopkowski et al. 2016). HBE has also examined the role of childhood experiences on reproductive outcomes, using a framework which predicts that stressful childhoods (including parental absence) may result in earlier age at

pubertal maturity and age at first birth (Coall et al. 2016; Sear et al. 2019; Sheppard et al. 2014), at least in high-income contexts. The theoretical premise is that poor conditions indicate higher mortality and so the optimal fitness-enhancing response is to reproduce sooner rather than later, when it might be too late (Chisholm 1993).

A prominent topic of research in HBE is how father absence is associated with children's, especially daughters', own reproductive trajectories. While there is fairly consistent evidence for earlier timing of puberty and family formation in WEIRD contexts (Belsky et al. 1991; Boothroyd et al. 2013; Ellis 2004; Quinlan 2003) a cross-cultural approach reveals much more variation indicating that father absence means different things depending on local ecologies (Sear et al. 2019). In this issue, Moya et al. (2021) use a longitudinal and intergenerational dataset from Sweden to examine how parental absence associates with timing of first birth, whether this is mediated by educational achievement, and if these relationships hold across two adjacent generations. Results show that all outcomes vary by parent sex, child sex, and generation. Overall, parental absence tends to expedite first births and these associations are partially mediated by university attendance, where parental absence reduces the likelihood that their child pursues higher education. One key takeaway of this article is the amount of variability that exists in these relationships, suggesting a complex web of interacting factors.

Socioecological factors likely influence not only when children are born, but which sex is produced. Prior research has found that environmental harshness is associated with sex ratio at birth (Schacht et al. 2019) as males may experience elevated frailty in utero when conditions are difficult, although evidence from industrialized societies is mixed. In this issue, Schacht et al. (2021) examine how rapid industrialization in Utah may influence this relationship, hypothesizing that the role of environmental harshness may be dampened once a population undergoes industrialization. Utilizing a natural experiment brought about by the completion of a railroad in 1869, the authors find that in years of arid conditions (likely associated with drought and increased mortality), the proportion of males born decreases, as hypothesized. This research demonstrates the important role urbanization can play in the relationship between ecology and reproductive outcomes.

As countries transition to low infant mortality rates and reduced family size, social networks change. The labor market economy means that people spend much more time with co-workers rather than family members, and children spend time at school. In contexts where people migrate long distances for work, they may no longer live near their kin. People may have fewer offspring because they have less help available (Turke 1989) or because of the information they receive (Newson et al. 2007). If kin networks are weakened along with these mortality and fertility transitions, then there is likely to be less opportunity for kin to support or help one another. Indeed, this is what Hackman and Kramer (2021, this issue) find in Mexico where some of the indigenous Mayan villages are shifting their mode of production from a subsistence agricultural economy to wage-labor earnings. Those who have moved to a market economy tend to have less kin support than those who continue to rely on subsistence agriculture. Observing what contemporary transitioning societies such as the Maya do provides clues to the processes that may have led to the demographic transition in other parts of the world.

Another avenue to explore these changing networks and their implications is to examine reports of kin and non-kin communications. In this issue, Stulp and Barrett (2021) found that Dutch women were more able to discuss their reproductive decisions with their friends than their parents, even though close family exerted more pressure to have babies. Dutch women also feel they can call upon both blood relatives and affinal (through marriage) relatives for help with childcare, but less so their friends and other members of their social networks. Like many social scientists, Stulp and Barrett are curious to understand why in higher income countries such as the Netherlands, women have fewer children than they can afford.

Using a HBE perspective lends many insights into reproductive decision-making, including how socioecologies influence the tradeoff of offspring quality and quantity.

In this issue, we explore the role of parental absence and environmental harshness on reproductive outcomes and investigate how changing socioecologies alter social networks which, in turn, influence how people make reproductive decisions.

2.3. Alloparenting

Using a comparative approach to examine differences between humans and other great ape species, anthropologists have identified unique attributes of the human family life. Human young are born much more helpless than those of other species, and have an extended period of dependence (childhood and adolescence), typically not having their first births until late teens or later (Bogin and Smith 1996). But even though human offspring have a long period of dependence, the rate at which human females can reproduce is faster than other great apes (Blurton Jones 1986; Galdikas and Wood 1990). This combination of long child dependence and short birth intervals means that human mothers typically have multiple dependent offspring of varying ages. This is in contrast to other primate species where mothers typically care for one offspring until they are independent food producers and then mothers can progress to their next pregnancy, shifting investment from one offspring to the next. It is through this comparative perspective that anthropologists recognized that a human mother cannot possibly care for her multiple dependent offspring, and herself, without help. This has led some to refer to humans as “cooperative breeders”, where individuals other than mothers help raise offspring (Hrdy 2009; Kramer 2010). This phenomenon is common among birds but rare among mammals although it has evolved in several primate species, including marmosets and tamarins (Hrdy 2007).

The recognition that mothers need help to raise offspring has become the focus of a lot of HBE research that investigates alloparents and how they influence reproductive outcomes. If mothers need help from others, then who helps? Research from HBE and the broader social sciences, has documented that while fathers provide care in many societies, their investment varies across and within societies (Geary 2000; Gray and Anderson 2010; Hewlett 2017; Hewlett and Macfarlan 2010), and men are not the only helpers of mothers. Cross-cultural evidence has found that grandparents (especially grandmothers) may be particularly important for improving child survivorship (Sear and Mace 2008) and that older siblings frequently act as ‘helpers at the nest’ (Kramer 2010).

Cross-cultural and historical research also demonstrates that the nuclear family—two parents and their children (particularly where men engage in the labor market and women care for children) is a relatively recent cultural invention (Creighton 1996; Raybould and Sear 2020; Sear 2021). For most of human history, people were integrated into larger social networks of kin. This may have been based on a descent group, where people lived near others from either their patriline (father’s kin) or matriline (mothers’ kin). And while men and women may have engaged in somewhat different productive tasks, both men and women were critical to the acquisition of resources (Sear 2021). Nevertheless, differing ecological conditions can lead to interesting flexibilities in these cultural customs. For instance, men and women’s social networks are expected to differ depending on the kinship system they live in. In this issue, Mattison et al. (2021) test this hypothesis using data from the Southwestern Chinese Mosuo, a population that has both matrilineal and patrilineal groups inhabiting neighboring regions making it ideal to test competing hypotheses for how lineages affect social ties. Overall, they found evidence for flexibility in gender roles within marriage and question the prevailing ideology that Western gender norms have been adopted globally.

Alloparenting is more than simply providing help to mothers; it can also involve the replacement of support if a parent dies or is absent due to divorce. In this issue, Perry (2021) demonstrates that among patrilineal families in rural Bangladesh, maternal kin frequently provide support to children who are left without a parent, even if that parent is the mother. However, alloparents are only partly able to mitigate the cost of losing a mother in this context; maternal orphans moved between numerous kin-carers and were more likely to have never attended school. Similarly, in rural Timor-Leste, Spencer and Judge (2021), this

issue) found that children living with grandparents, or those fostered into other homes, had higher body mass indices (denoting better nutrition) than those who lived with only biological parents. This might be because many of these grandparents had access to more household resources through veteran pensions.

Alloparenting is not only found in societies where extended families are available, as there is plenty of evidence of mothers relying on help from others in contemporary, WEIRD societies where nuclear families are the norm. In this issue, [Spake et al. \(2021\)](#) show that British women rely heavily on their partners for help with childcare but if they are unpartnered then they rely on their mothers and a select few other maternal kin. Compared with partnered women, single mothers also rely more heavily on paid childcare. This was also seen in the US, although single American women can rely on their previous partner (i.e., the father of the child) for help too, much more so than British women can. This difference may partly be explained by the more generous state social support in the UK compared to the US ([Brown 2016](#)).

Studies of alloparenting are tightly linked to other research areas in HBE. Knowing that alloparents are willing to help raise children may affect a person's decisions regarding reproduction, but also mating and even divorce. Because people integrate decisions about mates, social networks, production, sharing, conflict, and reproduction, all of which depend on one's socioecology, it is impossible to research these topics independently. Utilizing HBE, which provides a unified theoretical framework of optimizing fitness using costs and benefits, may provide insights into the integrated set of features that is the human family.

3. Conclusions

In this Special Issue, we illustrate the benefits of applying a theoretical framework to create directed research that can complement data-driven methods so commonly used in other social sciences such as demography and quantitative sociology. Human Behavioral Ecology recognizes that the currency that people are trying to maximize is fitness⁵, not wealth or status, or even health, even though those things are often quite strongly associated with fitness. This insight is the grounding of all HBE hypothesis-testing and can be harnessed to explain the immense variation in human social behavior. It can also explain how apparently illogical behavior, such as life-threatening risk-taking, or not pursuing a high-education pathway, may be a logical choice for some people given their current circumstances.

Human behavioral ecology is not only useful for understanding why people do the things they do but it has policy-relevant applications too. For instance, if we recognize that teenage pregnancy is often the product of limited choices and an unknown future that young women have in high-mortality neighborhoods ([Geronimus et al. 1999](#)) policymakers can focus attention on providing ways to improve young women's health. Similarly, policy focused on reducing poverty, such as Universal Basic Income ([Nettle 2018](#)) can remove the insecurity of the future enabling people to prioritize long-term goals over short-term risks.

Here we have gathered an array of articles that demonstrate how the rich ecologies we inhabit as a diverse species can explain the myriad different family structures, reproductive outcomes, and social networks that we see across the world. We have also demonstrated the value of conducting cross-cultural research, not only because those cultures are intrinsically interesting but also because a global perspective can provide insights about societies and behavior in the global North.

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Notes

- 1 More accurately described as ‘long-term pair bonding’ since marriage is cross-culturally variable.
- 2 Intimate relationships with people other than their marriage partner.
- 3 Western Educated Industrialized Rich and Democratic (Henrich et al. 2010)
- 4 Cultural evolutionists emphasize the role of group social norms, culturally transmitted traits (in contrast to genetically transmitted traits), and social influences at multiple interacting levels such as social networks, families, and social class to understand the evolution of human behavior. There are many similarities between the fields of HBE and cultural evolution with many researchers integrating these fields.
- 5 Fitness maximizing is not a conscious aim. Many decisions around mating, reproducing, and parenting are responses and reactions, and not necessarily done consciously.

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