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Psychological Adaptations for Fitness Interdependence Underlie Cooperation Across Human Ecologies

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Humans evolved to solve adaptive problems with kin and nonkin across fitness-relevant domains, including childcare and resource sharing, among others. Therefore, there is a great diversity in the types of interdependences humans experience across activities, relationships, and ecologies. To identify human psychological adaptations for cooperation, we argue that researchers must accurately characterize human fitness interdependence (FI). We propose a theoretical framework for assessing variation in FI that applies to the social interactions humans would have experienced across situations, relationships, and ecologies in the ancestral past and continue to experience today. According to this model, FI is characterized along four dimensions: (a) corresponding versus conflicting interests (b) mutual dependence versus independence, (c) asymmetrical versus symmetrical dependence (i.e., power), and (d) coordination. Because humans evolved to be highly mutually dependent on others to solve myriad adaptive problems, even compared to our closest living relatives, there is immense variability in the types of interdependences humans experience in daily life. Here, we describe the kinds of variation in interdependence humans experience, paying particular attention to social life in small-scale societies. In demonstrating the diversity of conflicts and coordination problems humans manage, we contend that humans evolved psychological adaptations to infer from signals, cues, and properties of the environment the four dimensions of FI under degrees of uncertainty to reduce the costs of cooperation. We conclude by discussing the theoretical implications of FI theory and emphasize that when individuals understand that others depend on them, it gives way to a new means of leverage to influence how others behave toward them.

Keywords: interdependence, cooperation, evolution, power, coordination

Humans have evolved to cooperate with each other to the degree that in providing benefits to others, individuals promote their own survival and reproductive success. A high level of need for cooperation is built-in to human life history in many ways, such as through an extended period of juvenile dependence that necessitates high-cost investment from multiple caregivers (Hrdy, 2011; K. L. Kramer, 2019). Moreover, humans depend on ingroup and outgroup members to pool resources where there is resource uncertainty and to trade for vital resources (Cronk & Aktipis, 2021). Humans across many societies follow a division of labor based on age, sex, and skill and share in the benefits of that labor (R. B. Bird, 2007; Burton & White, 1984), and coalitions form for group defensive and offensive purposes (De Dreu et al., 2016; Glowacki et al., 2016; Macfarlan et al., 2018). This biologically entrenched reliance on cooperation to solve adaptive problems with others who have diverging fitness interests; who have greater, lesser, or equal power; and who have differential access to information produces a great diversity in the types of interdependent situations humans experience across the life course and, therefore, a marked diversity in the behaviors humans deploy to promote their fitness interests. Here, we offer a theoretical framework of how fitness interdependence (FI) can vary along four dimensions: (a) corresponding/conflicting interests, (b) mutual dependence/independence, (c) asymmetrical/symmetrical dependence (i.e., power), and (d) coordination. This framework can advance our understanding of the costs individuals pay to cooperate over time and the evolved psychological mechanisms humans rely on to maintain cooperation.

Recent theoretical modeling work indicates that natural selection could promote the evolution of psychological mechanisms to infer fitness interdependence under the condition that there is sufficient variation in FI to offset the cost of inference (Colnaghi et al., 2023). This work indicates the need to study the diversity of interdependence that characterizes human social life, especially in the ancestral past which could have provided the selection pressure for the emergence of adaptations to infer fitness interdependence. Indeed, the high degree of mutualisms that occur in human relationships, as evidenced through collaborative foraging and childcare, suggests

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that the human social ecology over evolutionary time likely involved a substantial degree of variation in fitness interdependence. We contend, thus, that humans are endowed with an evolved psychology that detects variation in FI across social interactions to make strategic decisions, including whether to collaborate, negotiate, compromise, take charge, acquiesce, defect, and reveal or withhold information. We propose that this evolved psychology enables humans to maintain cooperation across diverse ecologies.

This article makes the following contributions. First, we outline how fitness interdependence can vary across four dimensions. Second, we apply the model to consider how human cooperation across multiple fitness-relevant domains has altered fitness interdependence over the course of evolution, emphasizing a shift toward a recent proliferation of the types of interdependent situations humans can experience. Third, we discuss how humans experience variation along each dimension of FI across relationships and ecologies, arguing that humans have evolved to detect variation in these dimensions to achieve cooperative outcomes. Fourth, we discuss the theoretical implication of FI theory for evolutionary models of cooperation and the cultural transmission of norms and institutions.

A Multidimensional Model of Variation in Fitness Interdependence

Interdependence is the manner in which an individual's behavior affects her own and others' outcomes (Balliet et al., 2017; Kelley & Thibaut, 1978; Roberts, 2005) and can be used to model the payoffs of any social interaction including outcomes that impact Darwinian fitness—that is, the survival and productive success of an individual (or the successful replication of genes responsible for a trait; Queller, 2011). Theoretical biologists have long recognized that the fitness outcomes of individuals are interdependent with others within a population, and this interdependence is key to understanding the evolution of social behaviors (Sigmund & Nowak, 1999; J. M. Smith, 1984); however, shifting assumptions about the structure of interdependence can affect conclusions about the evolution of social behaviors. For example, evolutionary game theory has been used to model the evolution of cooperation when humans (and other organisms) experience interdependence involving a conflict of interest, which has led to the discovery that features of the ecology,[1] broadly defined, including all aspects of the natural environment, such as genetic relatedness with others (Hamilton, 1964), repeated interactions (Van Lange et al., 2011), and sanctions (e.g., gossip), can help maintain cooperation (Nowak & Sigmund, 2005; Wu et al., 2016). These features of the ecology alter the FI of individuals within a population, such that there are greater fitness benefits associated with cooperation (Roberts, 2005). That is, an individual is likely to have greater correspondence of interests with others when they share genes (i.e., kin selection), when they are likely to be encountered in future interactions (i.e., direct reciprocity; Trivers, 1971), and when they are comembers of a social network in which helping is based on reputation (i.e., indirect reciprocity; Garfield et al., 2021; Nowak & Sigmund, 2005). Other variable aspects of the ecology include resource problems that necessitate social solutions, such as collaborative hunting and resource pooling, that might involve coordination and/or collective action problems (see Tomasello et al., 2012). Although it is widely recognized that humans share interdependence of fitness outcomes with each other and that features of the ecology create variation in fitness interdependence, there has been little effort to systematically model variation in FI within a population, across ecologies, overtime within a generation, and throughout the life course.

A. Aktipis et al. (2018) defined "fitness interdependence" as the extent to which individuals "rise and fall together" in terms of fitness outcomes. Individuals can experience varying degrees of FI with others in their social network, which can be characterized as (a) complete positive fitness interdependence, (b) complete negative fitness interdependence, (c) partial fitness interdependence, or (d) an absence of fitness interdependence (i.e., no influence on fitness outcomes). This definition of fitness interdependence is essentially a correlation between two individual's fitness, which can range from completely positive to neutral to completely negative (see Colnaghi et al., 2023). Therefore, this conceptualization of FI identifies a single dimension of variation in fitness outcomes.

This model is aligned with much prior work on evolutionary game theoretical models of cooperation, which has focused on the cost-to-benefit ratio of cooperation (Barclay et al., 2021). When an action provides a much higher benefit to others at very little cost to the self, people have relatively high corresponding interests compared to a behavior with a similar benefit to others but a greater cost to self (Kelley et al., 2003; Rapoport & Chammah, 1965). Any ecological condition that alters the benefits of cooperation so that the actor receives a subsequent benefit from cooperation (e.g., benefits to kin, direct reciprocity, reputational benefits) essentially increases the degree of corresponding interests (i.e., Roberts, 2005). Such shifts in interdependence toward more corresponding interests likely promoted cooperation over evolutionary time. Indeed, decades of behavioral experiments have found that people are more likely to cooperate in situations with more corresponding interests (e.g., Jin et al., 2024; Komorita & Parks, 1996; Spadaro et al., 2022). However, the fitness outcomes of social interactions vary for reasons beyond the degree of correspondence (Balliet & Lindström, 2023).

Interdependence theory proposes a multidimensional model of interdependence (Kelley et al., 2003). Kelley and Thibaut (1978) applied an analysis of variance approach to decomposing and analyzing the sources of variance in how each person's actions can affect the possible outcomes people can experience. This approach was used to analyze the simplest representation of interdependence, a 2 × 2 matrix in which two people have two behavioral options. Variance in the possible outcomes that each person can experience in a dyadic interdependent situation can be explained by (a) Person A's (George) behavior, (b) Person B's (Charlotte) behavior, and (c) a combination of George and Charlotte's behaviors. This analysis of variance approach has been used to identify four dimensions that characterize variation across different interdependent situations (for details, see Balliet et al., 2017; Bruns & Kimmich, 2021, Kelley et al., 2003).

Humans experience variation in FI along four dimensions, including the following: (a) correspondence–conflict, or the degree to which one's best outcomes are another's worst outcomes; (b) mutual dependence–independence, the degree to which each person's outcomes are determined by how each person behaves; (c) asymmetrical–symmetrical dependence (i.e., power), the degree to which one person affects another's outcomes more than the other person affects their own and others' outcomes; and (d) coordination,

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[1] The ecology includes all aspects of the natural environment including the social environment.

the degree to which one's behavior influences how their partner's behavior affects their own outcomes (see Table 1). This four-dimensional model of interdependence can be applied to analyze variance in interdependence across situations, activities, and the "supergames" that characterize human relationships.

FI theory offers insights about psychological mechanisms evolved to infer interdependence and functional consequences of such an ability for social behavior (Balliet et al., 2017). According to evolutionary psychologists, the human mind has evolved computational mechanisms to solve adaptive problems that occurred repeatedly over evolutionary time (Tooby & Cosmides, 1990, 2005), including an ability to infer the costs and benefits of social behaviors (e.g., Delton & Robertson, 2016; Tooby et al., 2006). Many evolutionary and social psychological theories already correspond to the dimensions of FI. For instance, kinship detection (Lieberman et al., 2007) and cheater detection (Delton et al., 2012) concern identifying degrees of correspondence–conflict that can each factor independently into assessments of how an individual decides to cooperate. Similarly, humans appear to detect prestige (Henrich & Gil-White, 2001) and dominance (Araujo et al., 2021; Durkee et al., 2018; Sell et al., 2009, 2010), which are independent, but not mutually exclusive, mechanisms of power from a FI perspective. Although power asymmetries (i.e., asymmetric dependence) have been shown to destabilize reciprocity in an iterated prisoner's dilemma (Dawkins, 2010), evolutionary models of human cooperation have largely neglected how individuals reduce the costs of cooperation when they are at a power disadvantage—a common feature of social interactions (Bernhard & Cushman, 2022).

In short, FI theory is an evolutionary psychological framework for identifying the psychological mechanisms needed for humans to resolve recurrent adaptive problems that required cooperation over evolutionary time. The four dimensions underlie game theoretic models such as signaling theory (e.g., Harbaugh, 1998; E. A. Smith & Bird, 2000), which demonstrate, for example, that high degrees of correspondence and mutual dependence increase the costs individuals are willing to pay to signal "stake" in others' outcomes (e.g., Barclay et al., 2021), whereas high degrees of conflict can lead to defection, if mutual dependence is relatively low or if mutual dependence is high, leveraging threats of defection to negotiate for better outcomes (Kennan & Wilson, 1993). Specifically, being able to infer interdependence, thus, allows individuals to adjust their behavior to reduce the costs of cooperation and achieve positive fitness outcomes. FI is, therefore, domain independent.

Human Evolution and Fitness Interdependence

Humans exhibit a high degree of dependence on others to survive and reproduce. Over the course of hominin evolution, our lineage increased cooperation in the domains of childcare (Gettler et al., 2020; Hawkes, 2003; Hawkes et al., 1998), foraging (Tomasello et al., 2012), territory acquisition and defense (Lopez, 2016, and sources therein), and learning (Flinn, 1997; Muthukrishna et al., 2018; Richerson & Boyd, 2008). Human subsistence is unique among great apes and is characterized by central-place foraging and high-intensity, high-cost extractive activities with high caloric returns that enable surplus distribution and storage that can subsidize nonproducers and periods of resource shortfalls (E. A. Cashdan, 1985; Cronk & Aktipis, 2021; Isaac, 1983; Kraft et al., 2021; Marlowe, 2005). Although our knowledge of the exact evolutionary progression of the juvenile period from our last common ancestor with chimpanzees (genus *Pan*) to modern humans is incomplete (Bolter et al., 2020), our species' protracted developmental period likely coevolved in the genus *Homo* with expanding brain size (Beynon & Dean, 1988; Dean, 2006; Dean, 1987; Dean & Lucas, 2009). Food provisioning from an extended social network of adults potentially served to offset the energetic demands of an increasingly large brain (Isler & van Schaik, 2012) that in turn supported complex social intelligence (Cosmides et al., 2010; Dunbar, 1998, 2009; Flinn et al., 2005; Garfield et al., 2019; Hagen & Garfield, 2019; N. K. Humphrey, 1976; Whiten & Byrne, 1988).

Our species' high degree of cooperation marks a departure from our great ape relatives. Whereas human mothers rely on a network of caregivers to provide both direct care (including holding and feeding) and indirect care (Gettler, 2010; Gettler et al., 2020; Hawkes & Coxworth, 2013; Helfrecht & Meehan, 2016; K. L. Kramer, 2019), great ape mothers closely guard their offspring, are wary of anyone who approaches the infant, and solely provide provision (Grueter et al., 2019; Mitani & Watts, 1997). Modern mobile human foragers engage in collaborative hunting and central-place foraging, but neither chimpanzees nor any of our other nearest relatives display the degree of cooperation and sharing required for these tasks (Tomasello et al., 2012). Human foragers live in highly fluid bands consisting of extensive social networks of genetic and affinal kin and nonkin, with individuals frequently visiting and relocating to other camps (Bird et al., 2019; Hill et al., 2014); nonhuman primates, in contrast, do not form long-term bonds between groups (Rodseth et al., 1991). For instance, when chimpanzee and bonobo groups fission, they do not maintain relationships, and although bonobo groups are tolerant (Samuni et al., 2022), chimpanzee intergroup interactions are largely hostile (Wilson & Wrangham, 2003). Humans, in contrast, maintain between-group alliances to trade, allow access to territories, exchange marriage partners, and call upon for assistance in times of need, such as warfare and environmental hazards (Chapais, 2013; Pisor & Jones, 2021; Rodseth et al., 1991; see also Spikins et al., 2021). Hill et al. (2014) estimated that hunter–gatherer males interact on average with about 300 same-sex interaction partners, whereas chimpanzee males interact on average with about 21 same-sex interaction partners.

FI is, of course, not unique to humans. Intergroup coalitional conflict, for instance, is observed in fish, birds, insects, and mammals (De Dreu & Triki, 2022). Many nonhuman primates (and other species) enjoy the benefits of group living, such as decreased predation risk and group defense, and pay the costs, such as increased competition for food and mates (Alexander & Sherman, 1977; Hamilton, 1971; Van Schaik & Janson, 1988; Wrangham, 1979). That said, a key difference between nonhuman primates and humans is that humans evolved to solve more adaptive problems with the assistance of other humans from subsistence to childcare to resource pooling, and this relatively higher degree of mutual dependence with others means that humans experience a *greater diversity of interdependence*. Furthermore, the dimensions underlying FI across activities, relationships, and ecologies are dynamic throughout the lifespan. To illustrate, human offspring maintain relationships with their parents, continue to share in provisions, provide sick care, invest in mutual kin across most societies, and even rely on parents to help find a mate (i.e., arranged marriage), and parents and offspring may live and work together in the same household or community, fulfilling different roles and responsibilities in distinct cooperative domains. Appreciating this diversity in FI,

Table 1

Four Dimensions of Fitness Interdependence, Their Definitions, Signals, and Sources of Variation in Human Societies

Dimension	Definition	Type of variation	Source, signal, and cue of variation
Corresponding versus conflicting interests	The degree to which one individual's best outcome is another's worst outcome. This can vary from completely corresponding to completely conflicting interests.	Parent–offspring conflict Mating conflict Resource competition Intrasexual competition Temptation to free-ride/cheat Division of benefits	Yelling/arguing (verbal), threats, fighting (physical), anger, depression, active avoidance and/or withholding cooperation, uneven payoffs for effort, cheater detection
Mutual dependence versus independence	The degree to which each person's outcomes are determined by how each person behaves in that situation.	Division of labor Food sharing Coparenting Warfare coalitions People who may not interact	Eye contact, head–body orientation, emotional reactions to other's behavior, frequency of interactions, kinship, proximity, joint and communal activities, sharing and exchange, prior interaction
Power symmetry versus asymmetry	The degree to which one person affects another's outcomes more than the other person's behavior affects their own and others outcomes (and vice versa).	Coalition size Physical formidability Wealth Access to information Status/prestige	Physical characteristics, weaponry, competence, prestige, dominance, position within a group/group formation, voice volume and pitch, coalition size, market value
Coordination	The degree to which one's behavior influences how their partner's behavior affects their own outcomes.	Collaborative hunting Coalition building Building shelter Moving large objects	Language/communication, eye contact, mimicry, synchrony, ethnic markers, rituals, social norms

Note. See Gerpott et al. (2018); Balliet et al. (2017); Columbus et al. (2021); Kelley et al. (2003).

across social interactions and relationships that occur within social networks, can generate insights about the evolved psychology that enables humans to identify the costs and benefits of cooperation and to act in their best interest.

Psychological Adaptations to Infer Fitness Interdependence

We contend that humans possess specialized psychological mechanisms to manage the great diversity of social situations that humans would have encountered over evolutionary time (Tooby & Cosmides, 1990, 2005), and that our ability to detect and respond to this variation maintains cooperation across ecologies, including in large-scale societies (Powers et al., 2021). To illustrate, if our ancestors faced free-riding as a consistent threat to collective action, as in food sharing and building shelters, then the human mind should have evolved cognitive mechanisms to detect and avoid or punish free-riders, which humans likely do (Fehr & Gächter, 2000; Kiyonari & Barclay, 2008; Price, 2005; Tooby et al., 2006). However, cheater detection relies on more than a simple action rule of avoiding individuals not participating in cooperation. For instance, at some point in their lives, cooperators fail to participate in collective action, because they are temporarily incapacitated, and to maintain large-scale social networks across the life course, humans must be able to distinguish free-riding from illness (Delton et al., 2012). Furthermore, given that the act of avoiding cooperation is both a sign of free-riding and a response to free-riding, an individual must distinguish between someone who is free-riding and someone who is withholding cooperation in response to free-riding (or perhaps the collective action is a volunteer's dilemma rather than a prisoner's dilemma; Archetti et al., 2020; Archetti & Scheuring, 2011). Individuals can also cooperate to gain advantage over others, such as through competing for status and prestige (Macfarlan et al., 2012, 2013) or creating dependence in others (Mayer, 2003/2018; Wutich, 2011). Finally, individuals might cooperate with others, because the costs of avoiding cooperation are too high (e.g., tolerated theft; Blurton-Jones, 1987). Using cues and evolved signals to infer how interdependence varies along each dimension enables humans to make inferences about other parties' incentives for cooperation and its social ramifications.

Evolutionary psychologists have argued that humans rely on a constellation of interpersonal and environmental indices of value that are integrated and computed into interpenetrative motivational systems that output adaptive behavior (Tooby & Cosmides, 1992; Tooby et al., 2008). For example, signals and cues of health, physical attractiveness, and cooperativeness, among other qualities, can be computed into a single index of mate attractiveness (Miller & Todd, 1998). A shared childhood coresidence and seeing one's own mother care for a newborn are cues for an index of genetic relatedness (Lieberman et al., 2007). Tooby et al. (2008) termed these as internal regulatory variables (IRVs) that estimate properties of people (and the environment) that are not directly observable, indexing their value to the self in a fitness-relevant domain and thus regulating individual motivations toward social others and to situations. IRVs can inform multiple motivational systems that act in concert to produce adaptive behavioral output. For instance, the kinship index is a cue of a type of corresponding interest and is likely to promote cooperation within certain domains, such as childcare. However, the kinship index can also discourage certain types of cooperation, as in the mating context or where nepotism is penalized. Recent theoretical modeling work suggests that higher variation in fitness interdependence produces greater benefits to being able to infer FI and then conditioning social behaviors on these inferences (Colnaghi et al., 2023). We propose that there exist four IRVs that track fitness interdependence: a correspondence index, mutual dependence index, power index, and coordination index.

Human Fitness Interdependence

Next, we break out each FI dimension to (a) define each dimension, (b) discuss how the dimensions vary across relationships and ecologies, and (c) explain how an IRV that tracks each dimension of FI can regulate fitness enhancing social behaviors.

Variability in Corresponding Versus Conflicting Interests

Interdependence can vary from individuals having completely corresponding outcomes, in which each person can mutually achieve their best outcome, to completely conflicting outcomes, in which one individual's outcome is another's worst outcome (A. Aktipis et al., 2018; Balliet et al., 2017; Kelley et al., 2003). To illustrate, relationships characterized by corresponding interests include mutualisms within and between species (e.g., obligate monogamy, plant–pollinator interaction, mycorrhizal fungal networks), sexual reproduction, and collaborative foraging. Relationships that are characterized by stronger conflicting interests (e.g., zero-sum games) can include intrasexual competition and predator–prey dynamics. However, most of the games humans play, including in competitive contexts, are "mixed games," involving both conflicting and corresponding interests (Schelling, 1980). There are no human relationships that could be characterized by completely corresponding interests over time, including close kin like parents and offspring (Gibson & Gurmu, 2011; Haig, 1997; K. L. Kramer et al., 2016; Lawson & Mace, 2009; Trivers, 1974).[2]

The central puzzle of the evolutionary literature on cooperation is the free-rider or collective action problem (Hardin, 1968). The crux of the "collective action problem" is that even though everyone benefits from the products, each individual gets the highest payoff by free-riding (Olson, 1971), which has been formalized in the Prisoner's Dilemma (Dawes, 1975). Free-riding, however, is one type of conflict, whereas battle of the sexes and game of chicken are others with different payoff structures (Bruns & Kimmich, 2021). Some situations allow for opportunities whereby all parties can mutually benefit, others can involve compromise or sacrifices, and yet others are zero-sum (i.e., a gain to one is a loss to another). Because humans cooperate with kin and nonkin in diverse fitness-relevant domains (e.g., mating, subsistence activities), humans need to recognize the degree of correspondence–conflict across relationships, over time, and across domains of cooperation. In fact, the degree of correspondence–conflict in outcomes can vary across

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[2] Here, we discuss both genetic conflict (e.g., parent–offspring conflict) and overt conflict (e.g., fighting). Genetic conflicts can achieve Nash equilibria without overt conflict, whereas overt conflict concerns the way organisms impose costs on each other to resolve conflicts and can include yelling, fighting, and more subtle behaviors, such as avoidance (see Cant & Young, 2013; Parker et al., 2002). Resolving conflict includes resolving coordination problems (see Coordination).

all human relationships, including parent–offspring, mates and coparents, and coalitional members (Columbus et al., 2021). Indeed, genetic relatedness (Hamilton, 1964), partner quality (Hammerstein & Noë, 2016; Noë & Hammerstein, 1994, 1995), and group membership (Boyd & Richerson, 1990) are types of correspondence, but some degree of conflict is inevitable.

Cooperation and Conflict in the Family

Parent–offspring conflict (Trivers, 1974) arises from genetic asymmetries between parents and offspring, because the allocation of resources that maximize a parent's biological fitness does not necessarily maximize individual offspring fitness (see also Bossan et al., 2013). Nevertheless, children across societies provide direct care for their younger siblings (K. L. Kramer, 2014; K. L. Kramer & Kramer, 2009; Turke, 1988), contribute resources, and share in labor that benefits their household (Bird & Bird, 2005; Tucker & Young, 2005; Turke, 1988). Similarly, sexual conflict arises when the optimal outcomes for each sex are not mutually achievable (Borgerhoff Mulder & Rauch, 2009; Parker, 1979, 2006). Based on sex differences in the maximum rate of reproduction and postreproductive parental investment, human males stand to benefit more from multiple, low-investment mateships, whereas females stand to benefit more from mating with fewer high-investing partners (Clutton-Brock & Parker, 1992). Where social monogamy occurs, females might further benefit from cuckoldry (Kokko, 1999). Nevertheless, humans have evolved a mating strategy characterized by long-term pair bonds (Chapais, 2009), and biparental care is widespread even though both monogamy and paternal investment are rare in mammals and not exhibited by our closest great ape relatives (Geary, 2000; Kleiman & Malcolm, 1981), suggesting that human reproductive strategies coevolved with intensive cooperation between reproducing males and females (e.g., provisioning of lactating females) that resulted in mutual benefits (Geary, 2000; Gettler, 2010; Marlowe, 2003; Quinlan & Quinlan, 2008; Ross et al., 2023).[3]

Coalitional Cooperation and Conflict

Human societies have a nested or modular structure, consisting of a collection of households within a residential group (e.g., camp, village) and a collection of residential groups that make up a larger social network through which members trade resources and information and exchange marriage partners (Bird et al., 2019; Rodseth, 2012; Roscoe, 2009). Modern mobile foraging bands are characterized by low genetic relatedness among members and bisexual dispersal wherein both sexes influence residence patterns (Dyble et al., 2015; Hill et al., 2011); they live in multifamily groups, with high between-camp mobility and extensive cooperation (Dyble et al., 2015; Migliano & Vinicius, 2022). Across all societies, individuals cooperate, sometimes preferentially, with nonkin and acquire various direct and indirect benefits from their cooperation. Research on raiding and warfare in small-scale societies shows that raiding partners are more often distant kin, affines, or friends, as opposed to close genetic kin, such as siblings (Glowacki et al., 2016; Macfarlan et al., 2014, 2018; Rodseth, 2012). Nevertheless, there are conflicts between coalition members over status, access to resources, and mates, and people can disagree over how to distribute resources, whether to go to war, or how to punish a norm violator. Thus, human relationships are embedded in complex social networks in which correspondence–conflict varies across relationships and beyond simply the degree of kin relatedness.

Corresponding Versus Conflicting Interests Across Ecologies

Humans display remarkable flexibility in managing cooperation across diverse ecologies that engender various modes of social organization and adaptive problems that create powerful constraints on behavioral strategies in fitness-relevant domains, such as subsistence and reproduction (Nettle et al., 2013), and just as correspondence–conflict within relationships can vary across situations, it can vary within relationships (e.g., kin, mates, and ingroup members) across ecologies. As we elaborate below, humans' evolved psychological capacity to detect correspondence–conflict relies not only on detection of cues of kinship (Lieberman et al., 2007), mate quality (Symons, 1995), or ingroup membership (Balliet et al., 2014) but also on combined indicators of fitness. These indicators track one's own biological and reproductive needs relative to others under local ecological conditions (e.g., resource availability, social organization).

Social organization and economy can shape the degree to which coresiding kin experience reproductive conflict. Among Gabbra pastoralists, where wealth is measured in herds that are passed down from father to son, reproductive conflict is marked between brothers (Mace, 1996). Because marriageability depends on wealth, and this wealth is transferred from father to son, males with more elder brothers face resource depletion as each elder brother subsequently marries, reducing the herd size (Mace, 1996). In other resource settings, however, coresiding reproductive-aged females experience reproductive conflict arising from resource competition (Cant & Johnstone, 2008; Ji et al., 2013; Mace, 2013). Among Mosuo, the reproductive success (RS) of females is constrained by their sisters, as older sisters have greater RS than younger sisters, whereas the RS of brothers is not affected by their sisters' RS (Mace, 2013). This is because traditional Mosuo households follow a residence pattern in which males and females live with their natal families up to three generations and men visit wives ("visiting" marriage)—a cultural adaptation to the limited population growth of these geographically constrained farming communities (Mace, 2013). Individuals, however, are responding to ecological changes in the form of an expanding tourism market that has created new economic opportunities to accumulate wealth that has been associated with individuals leaving their natal households to establish new residences (Mattison, 2010), potentially reducing reproductive conflict in households and increasing individual fitness.

Ecologies likewise alter correspondence–conflict between males and females in mating and parental investment. Whereas maternal investment is high across ecologies, paternal investment is highly variable and facultatively expressed depending on opportunity costs including mating opportunities, role specializations, economic opportunities, and the potential benefits to offspring (Gettler, 2014; Schacht et al., 2018). Fathers in pastoralist societies provide relatively little in direct care because males primarily contribute investment through indirect provisioning (i.e., maintaining wealth in

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[3] Sexual conflict is also influenced by culture (e.g., gender roles; Lawson et al., 2023).

livestock) and have high rates of polygyny and, consequently, have more to gain by diverting investment to mating effort (a source of conflict; (Hewlett & Macfarlan, 2010). Males also appear to provide less investment when their contribution to subsistence is relatively low, and offspring gain little from paternal investment (Mattison et al., 2019).[4] Thus, the degree of correspondence–conflict between males and females varies across ecologies based on the costs and benefits to each offspring investment and extrapair mating as well as other factors.

Distinct subsistence modes are associated with and likely create varying degrees of correspondence–conflict within and between communities. For example, foragers have lower frequencies of warfare and violent death compared to horticulturalists, farmers, and pastoralists (Ember & Ember, 1997; Hames, 2019; Wrangham et al., 2006). Among pastoralists, on the other hand, coalitional raiding for livestock is widespread and central to their livelihoods (Ember et al., 2014; Irons, 2003), creating collective action problems within communities to manage resource conflict from outside the community. Rice farming appears to create collective action problems that are less pronounced in wheat farming communities (Talhelm et al., 2014). Correspondence–conflict within same-sex community members might also be shaped by intrasexual competition (Maner & Ackerman, 2020). Therefore, the degree of correspondence–conflict and types of conflicts community members encounter vary according to the adaptive problems communities experience that are rooted in the material reality of subsistence and economy, features of the mating market (e.g., sex ratios), and social organization.

Detecting Variation in Corresponding Versus Conflicting Interests

The fact that different ecologies can generate distinct conflicts within families and communities is a testament to the human ability to adapt to the conflicts that arise in different resource and social organizational settings. We propose that humans have an IRV indexing correspondence–conflict that tracks its degree across situations and relationships, relying on combined environmental input: To what degree do others want what I want? To what degree do others value me, and how much do I value them? To what extent are my allies another's allies, and vice-versa?

People signal correspondence–conflict to social partners, in part, by their actions. The costs that others are willing to pay to provide benefits to others indexes their welfare trade-off ratio (WTR), wherein A should help B whenever $\text{WTR} \times b > c$ (Delton & Robertson, 2016; Delton et al., 2023). WTR measures how much one values another person relative to oneself, which, in turn, informs how B should behave toward A (Barclay, 2020); therefore, both people's WTR for their partner in a relationship may provide input to assess correspondence–conflict (see also Power). People also detect correspondence–conflict by observing the benefits others have relative to themselves and to what extent anyone else can lay claim to those benefits (e.g., resource competition; see also Power; E. A. Smith & Codding, 2021).

Sharing networks are structured by correspondence–conflict between kin and community members in particular resource settings that inform perceived WTRs (see also Mutual Dependence). Among Pimbwe villagers in Tanzania, kin relations have shown signs of strain in this changing economic system with rising inequality in which the wealthier may choose to withhold contributions to sharing networks, relying on their own privately stored wealth to manage risk rather than on reciprocal exchange even among kin (Kasper & Borgerhoff Mulder, 2015). This contrasts with data from the Sidama, agropastoralists in Southwest Ethiopia, where data show that the wealthy maintained reciprocal exchange relations with poorer individuals, which Caudell (2015) attributed to reliance on shock-resistant crops that allows the wealthy to assist the needy without depleting their stores. Indeed, environmental shocks, like natural disasters, can affect local resource supplies and create resource competition among kin and community members (Prediger et al., 2014). To manage sharing networks, individuals must anticipate how others will treat them, which can be estimated based on, among other things, local sharing norms (see also Coordination), whether an individual or household has shared with them in the past (Kasper & Borgerhoff Mulder, 2015), and distribution of need (see also Mutual Dependence next).

Paternal investment is indicative of the degree of correspondence–conflict between reproducing couples in the local ecology. Because males who invest in offspring are at risk of cuckoldry, males are predicted to experience greater sexual jealousy than females and to safeguard wives against extrapair mating. Indeed, sexual permissiveness tends to be more common in societies with lower paternal investment (Geary, 2000), and recent evidence suggests that jealous responses to sexual infidelity are higher in societies with greater levels of paternal investment and lower frequencies of extramarital sex (Scelza et al., 2020). However, in some ecologies, males tolerate or even encourage extrapair mating. In lowland South American cultures that practice "partible paternity," for example, children with secondary fathers (i.e., men who had sex with their mothers while she was pregnant) have higher survivorship than children without secondary fathers (Beckerman, 2000; Hill & Hurtado, 2017).[5] In some societies, husbands even offer other males sexual access to their wives to establish or maintain reciprocal social relationships (Elkin, 1938; Rauchholz, 2016), creating a different type of sexual conflict.

To summarize, the degree of correspondence–conflict between two or more individuals is not fixed based on genetic relatedness, ingroup membership, history of reciprocity, or whether they share children but rather varies based on the types of resource and reproductive problems humans encounter in different ecologies. Thus, human cooperation depends on more than detection of genetic relatedness, repeated interactions, and sanctions, but also depends on inferring correspondence–conflict based on combined environmental inputs including kinship and reciprocity, but also other signals and cues, including division of benefits relative to effort or need, differential benefits per investment, and resource scarcity, among others.

Variability in Mutual Dependence–Independence

Mutual dependence–independence is the degree to which actors' outcomes are determined by how others in a situation behave (Balliet et al., 2017; Columbus et al., 2021; Kelley et al., 2003). Interactions and relationships vary in the degree to which

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[4] Research suggests that paternal investment during adolescence is associated with differential reproductive outcomes (Scelza, 2010).

[5] See also Prall and Scelza (2020) for discussion of "social fatherhood" among the Himba.

individuals experience mutual dependence or independence. Mutual dependence is greater when outcomes are more heavily influenced by the actions of others and lower when outcomes are more heavily influenced by the actions of an individual. A crew of whale hunters is experiencing greater mutual dependence than a solitary small-game hunter. "Brothers-in-arms," or coalitional fighters, experience greater mutual dependence in combat compared to an individual fighting in a duel. Mutual dependence occurs both when two parties engaged in a joint activity perform the same task (e.g., sharing in the burden of carrying a heavy object) or perform specialized tasks (e.g., one person serves as the helmsman and another the harpooner). Mutual dependence also takes the form of "trade," that is, when parties exchange resources or services in different fitness currencies, or "tit-for-tat" reciprocity, that is, when parties exchange resources or services in the same fitness currency (Kaplan et al., 1985), collaboration (Tomasello et al., 2012), and risk-pooling (Cronk & Aktipis, 2021).

Human relationships have long been recognized to vary in mutual dependence—which is often assessed with measures of closeness or social distance (Berscheid et al., 1989; Hruschka et al., 2018). Groups can vary in the mutual dependence–independence experienced among ingroup members, which other researchers have labeled and measured via the concepts of cohesion, entitativity, and social capital (Cota et al., 1995; Gaertner & Schopler, 1998; Mouw, 2006). Yet the concepts of cohesion, entitativity, and social capital confound at least two dimensions of interdependence: mutual dependence and corresponding versus conflicting interests (see Balliet & Lindström, 2023). Mutual dependence does not imply a certain degree of correspondence–conflict, however, as it also characterizes situations involving zero-sum games, in which a gain to one party is a loss to the other. Where parties are totally independent, there is no possibility for correspondence–conflict, since the actors do not affect each other's outcomes. Furthermore, parties in a cooperative endeavor might experience symmetrical or asymmetrical dependence (see Power), yet when dependence is symmetrical (and so mutual), the degree of dependence can still vary in magnitude. As we discuss next, the degree of mutual dependence individuals experience with others is influenced by the types of adaptive problems they experience in different ecologies, including subsistence, resource scarcity, and relational mobility.

Mutual Dependence–Independence Across Ecologies. Subsistence modes affect variation in mutual dependence across societies. Rice farming, for instance, is more labor intensive than wheat farming and requires farmers to engage in cooperative labor exchanges with other households, including coordinating planting times so that different households can assist each other during the harvest (Bray, 1986). Additionally, much rice cultivation depends on the construction of irrigation networks that require farmers to coordinate water use, so that all farms maintain access to a sufficient supply (Talhelm et al., 2014). Other subsistence modes, however, are characterized by a greater degree of independence. Among the Turkana, traditionally highly mobile pastoralists, Gulliver observed, "… it is a lonely life," for a boy herding stock alone in the bush,

> And one in which a boy must learn a good deal of self-reliance. From a very early stage he discovers that unless he stands up for himself and makes sure of securing his own rights, no-one will do it for him and he will forfeit those rights (Gulliver, 1951, p. 191).

Mutual dependence can vary across societies as the result of natural hazards that create resource scarcity and the social institutions that culturally evolve in response to these environmental conditions. Turning again to sharing networks, need-based transfer is a risk-pooling strategy used to manage the risk of unpredictable crises, and it can be an especially important strategy in ecologies prone to unpredictable hazards and resource shortfalls (Campenni et al., 2017; Hao et al., 2015; Wutich et al., 2018). Indeed, ethnographic and historical reports show that humans must resort to extreme individualism during long periods of resource scarcity (Dirks et al., 1980; Ember et al., 2018; Townsend et al., 2020). Agent-based models show that need-based transfers outcompete debt-based transfers in keeping agents alive in volatile environments (A. Aktipis et al., 2016) when shocks are uncorrelated (Campenni et al., 2017). Many pastoralists have need-based sharing institutions (see Almagor, 1978; Bollig, 2010; Cronk et al., 2021; Flannery et al., 2016; Gulliver, 2013), which can intensify mutual dependence within specified relationships. Among Maasai pastoralists of East Africa, *osotua* (literally umbilical cord) is a cattle-sharing institution wherein partners (*isotuatin*) transfer livestock to social partners in need following unpredictable losses due to disease, drought, or theft (C. A. Aktipis et al., 2011; Hao et al., 2015). Maasai and other pastoralists will even seek out partners in different ecological zones to avoid depending on those who will experience concurrent losses (Campenni et al., 2017; Dixit et al., 2013; Gulliver, 2013). Foragers also rely on need-based transfers established through exchange relationships that are also called upon in periods of drought or food shortage, and because partners are geographically distant, the risk is spread across the network (Wiessner, 1982). In market economies, however, people tend to rely more on private insurance and storage to retain their own risk (see also Dorfman, 2007, on risk retainment).

Societies differ in relational mobility—that is, the degree to which social relations are fluid or fixed (Yuki & Schug, 2020)—which can influence mutual dependence. In small-scale societies, geography and terrain may constrain travel, and institutional norms can affect who relocates to a new group after marriage and who stays, creating variation in relational mobility. However, even large-scale, industrialized societies differ in relational mobility. Prior research shows that western societies, like the United States, tend to experience high relational mobility—that is, they can choose relationships based on their own preferences (Thomson et al., 2018). People in many other societies, like Japan and Ghana, experience low relational mobility—that is, their relationships stem more from circumstance (Oishi et al., 2015). Relational mobility can impact the degree of mutual dependence with specific others. People in high relational mobility settings can replace relationships at a lower cost, and so relationships in low relational mobility settings are more stable (Thomson et al., 2018); thus, people experience higher mutual dependence with *specific* partners in ecologies characterized by low relational mobility and may not be able to switch partners as easily.[6]

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[6] There is some evidence that relational mobility has negative association with historical threat exposure and with greater historical reliance on agriculture (as opposed to herding; Thomson et al., 2018), which is consistent with the hypothesis that exposure to ecological threats creates greater mutual dependence (Gelfand et al., 2011) and that sedentary farming makes community members more dependent (Talhelm et al., 2014).

Detecting Variation in Mutual Dependence–Independence. An IRV indexing the degree of mutual dependence in situations and relationships concerns: To what degree does my behavior impact others, and how much do others affect me? To what degree do others rely on me, and how much do I rely on them? How often do I need them, and how often do they need me? To what degree does their absence affect me, or vice versa?

Although researchers have devoted less attention to how people infer mutual dependence within social situations, there are many signals and cues that people can rely on to make such inferences. A high frequency of interactions and close residential proximity suggest a high degree of mutual dependence, whereas fewer interactions and greater distance between residence often (though again not always) suggest lower mutual dependence. An obvious exception is when family members migrate for work to send remittances back home (Le De et al., 2013). Therefore, the amount and frequency of economic transfers in addition to interactions between individuals are indicative of both mutual dependence *and* correspondence (except in situations involving coercion).

Membership status in a risk-pooling network (e.g., *osotua*) signifies a type of mutual dependence among social partners. Conversely, impersonal, private insurance networks signify a greater degree of independence of members of these networks, because members need not invest directly in each other. Because multiple risk-pooling strategies can exist in a population, and the availability of certain strategies can change over time, people must be able to track what others are doing to identify the optimal strategy. As the example of the Pimbwe showed, as market integration and wealth inequality increase, wealthier individuals tended to invest more in private storage (Kasper & Borgerhoff Mulder, 2015). Indeed, prior research has found that when individual solutions to solve collective actionproblems are possible, this reduces mutual dependence and cooperation (Gross & De Dreu, 2019). In observing the effects of the introduction of cash on the Shipibo economy, Behrens (1992) described the gradual deterioration of traditional exchange systems based on kinship and reciprocity, as cash allowed for the purchase and self-storage of nonperishable foods. Similar effects of the cash economy on traditional risk-pooling networks have been observed among the Dobe !Kung (Yellen, 1990) but not among Tsimane forager–horticulturalists (Gurven et al., 2015), possibly due to differences in resource defensibility between these populations (H. S. Kaplan et al., 2009). An actor's optimal strategy to buffer against risk is likely to be frequency-dependent such that if more individuals within a population shift to private insurance, then a social insurance network becomes less viable (Gurven et al., 2015). There are thus many indicators by which people can detect changes along the mutual dependence–independence index in social networks to determine what social strategies to pursue.

In short, the mutual dependence–independence between two or more individuals varies across interactions based on the requirements of the task at hand but also systematically across ecologies based on subsistence, economy, and norms, institutions, and local geography that affect relational mobility. Assessing mutual dependence is necessary to predict cooperative outcomes. To illustrate, if independence is high, then a high degree of conflict between parties can be resolved by partner choice mechanisms; however, if both mutual dependence and conflict are high, then individuals must use alternative strategies to reduce the costs of conflict, including asserting or resisting power.

Variability in Power Symmetry and Asymmetry

Power, or asymmetric dependence, is the degree to which one person affects another's outcomes more than the other's behavior affects their own and others' outcomes (Balliet et al., 2017; Fiske, 2010; Keltner et al., 2003; Magee & Smith, 2013). Relatedly, bargaining power is defined as the ability to exert control over others by imposing costs or withholding benefits (Parker, 1974; Sell et al., 2016; J. M. Smith & Parker, 1976; Sosis et al., 1998; see also Bernhard & Cushman, 2022; Milinski, 2022). People can experience high power, equal power, or low power relative to social partners (Columbus et al., 2021; Fiske, 2010; Keltner et al., 2003; Magee & Smith, 2013). Extrinsic goods, such as food or cash, can be sources of power or an individual herself can be a valuable resource as a social partner, mate, or kin member, and individuals can impose costs and benefits by provisioning or withholding resources or assistance to strategically influence others' behaviors (see Cheng, 2020, for discussion). As noted, one's own market value in a network of partners is a form of power (Sell et al., 2016). Leaders across societies accumulate power by bestowing benefits and imposing costs on followers (Cheng, 2020). Individuals who are formidable, intelligent, or knowledgeable or who have strong coalitional support are more likely to have positions of power and influence over others (Fessler & Holbrook, 2013; Garfield et al., 2020; Hagen & Garfield, 2019; Wrangham, 1999). Power can vary across ecologies based on the ability of individuals and groups to control resources and information. Moreover, individuals are going to experience variation in power based on age and sex across the life and across ecologies.

Power Symmetry–Asymmetry Across Ecologies. Human societies range in political complexity from small-scale predominantly egalitarian bands to large-scale state-level societies. The ability to accumulate and control surplus distribution of resources is thought to be the basis of the emergence of elite power across societies (Mattison et al., 2016), and variation in wealth inequality is tied to reliance on wealth that is heritable, a form of monopolizability, such as land and cattle (Borgerhoff Mulder et al., 2009). Among the !Kung and other modern, mobile foragers, a lack of monopolizable wealth and close-knit residential living has until recently precluded the unequal accumulation of wealth, and leveling mechanisms, such as minimizing individual achievement, curbed individual inclinations toward dominance (Draper, 1975; Wiessner, 2002).

Although nomadic, egalitarian foragers are often depicted as the prototype of human social life during the Pleistocene, many foraging societies were either sedentary or semisedentary and stratified with marked differences in status and power (Arnold et al., 2016; Singh & Glowacki, 2022). Several societies in the Americas, for instance in the Channel Islands, supported elites who had the power to control production (Arnold, 1992). Among the Kwakwaka'wakw of the Pacific Northwest, hereditary chiefs decided when lower status people could harvest salmon (Boas, 1921). Thus, the ability to control and limit resource access is a key source of power asymmetry within societies.

Coalitions can establish institutionalized power at the societal level when they have privileged access to and an ability to defend a resource patch, where patches are unevenly distributed and the costs of dispersal are high, such that group members are forced to submit to the resource holders (Carneiro, 1970; Kennett et al., 2009; Mattison et al., 2016). This creates the conditions for the emergence of patron–client relationships (Eisenstadt & Roniger, 1980).

Coalitions, more generally, can protect their position and interests by harnessing different types of power including maintaining or expanding coalitional strength, controlling information, factionalizing potential insurgents, and creating and enforcing norms that benefit the coalition and codify their power (Singh et al., 2017). For example, strategic control of the spread of information is a key tactic by which authoritarian governments maintain power (Huang et al., 2019) and is a source of variation in power asymmetry across societies. As we discuss next, because information is central to facilitating coordinated action, by controlling information, the powerful can limit the ability of competing coalitions to vie for power. Given the persistence of dominance behavior, and its advantages, humans likely used dominance to their own and their allies' fitness interests as the need for it arose over recent evolutionary time (Singh & Glowacki, 2022).

Detecting Variation in Power Symmetry–Asymmetry. An IRV indexing the degree of power symmetry–asymmetry in situations and relationships concerns: To what extent can I affect the outcomes of a conflict in my favor (e.g., imposing costs, withholding benefits) compared to others? Who should I look to make decisions, and who looks to me to make decisions? To what degree do my decisions affect another's outcomes, and their decisions my outcomes?

A variety of research suggests that humans can detect power and powerlessness. People can accurately infer men's physical formidability from facial, body, and auditory cues (Durkee et al., 2018; Sell et al., 2009, 2010). Status markers can signal certain currencies of social power, such as wealth (Harbaugh, 1998; E. A. Smith & Bird, 2000). In geographically distant societies, shamans publicly display "supernatural" power (C. Humphrey & Onon, 1996; I. M. Lewis, 1971; Singh, 2018), which from the perspective of FI theory, the attention given to the shaman in the display is a means of establishing authority (Chwe, 2013; see also Coordination). Thus, individuals must detect a combination of physical and cultural signals and cues of power to protect their interests against a person or party who could inflict costs if conflicts arise.

Detecting power symmetry–asymmetry goes beyond recognizing dominance and prestige (or lack of it), however, as people also benefit from specifically being attuned to powerlessness and vulnerability in social partners and themselves compared to others. Humans detect another's health status, a type of physical vulnerability, from biological sickness signals (Steinkopf, 2015; Tiokhin, 2016), which may trigger either approach or avoidance behaviors in others. Emotional vulnerability, such as crying, can also signal need, and so high relative dependence on others (Soltis, 2004), and the degree of correspondence and mutual dependence between individuals should inform an observer's decision to provide care. In addition to helping kin and social partners in times of need, inferring one's own and others' power relative to others can minimize the time and energy spent on costly contests (Sell et al., 2009). Thus, detecting power symmetry–asymmetry is integral to providing and receiving assistance and deterring costly conflict.

In short, the power symmetry–asymmetry between two or more individuals varies across interactions and relationships. Measures of power include wealth, knowledge, and disparities in level of need. Detecting power is necessary not only for averting harm but also for providing to group members high in correspondence based on need. When power asymmetry is high and conflict is high, high-power individuals have a distinct advantage in bargaining; however, FI theory points to a fact that has been largely overlooked in evolutionary models of cooperation—that low-power individuals throughout human evolutionary time engaged in protests, including violating agreements and norms, to impose costs on more powerful parties with whom they are mutually dependent (e.g., parents and elder kin, resource holders). Thus, variation in conflict and power symmetries across ecologies can be reflected in social upheavals, such as frequency and severity of disruptive or violent protests.

Variability in Coordination

Coordination is the degree to which one's behavior influences how their partner's behavior affects their outcomes (Balliet et al., 2017; Kelley et al., 2003). Kelley and Thibaut (1978) referred to this as the basis of interdependence. In situations requiring high levels of coordination, partners can improve their outcomes by adjusting their behavior based on what their partners are doing. For example, net hunting is carried out by a group of individuals who synchronize their behaviors wherein those individuals who capture the prey with the net adjust their behaviors to each other and to those who drive the game into the net (Noss & Hewlett, 2001). Coordination problems are situations that involve interdependent decision-making and multiple equilibria—that is, achieving mutual benefits depends on what the other actor(s) will do, as in the Stag Hunt scenario (D. K. Lewis, 1969; Schelling, 1980). For instance, it matters less which side of the road people drive on than that everyone knows and agrees to drive on one side. As such, information, obtained through observation or communication (including social norms), allows actors to anticipate what partners will do to resolve the coordination problems.[7]

Situations can vary in the extent to which actors can coordinate to impact their outcomes—that is, how much they can adjust their behavior to what their partner is doing to achieve better outcomes. In situations lacking coordination, each person's behavior may affect their partner's outcomes, but there is nothing one can do to influence how their partner's behavior affects their own outcomes. Say, Charlotte calls her brother, George, to request urgent, last minute childcare, while he is driving along a rural route to check on a sick friend and can only take the call for a moment knowing he is about to lose service. George informs her that whether he can help her with childcare depends on his friend's level of need. If the friend's level of need is low, he will be at his sister's place in an hour, but if the friend's level of need is high, then he will not. George's behavior, including his assessment of his friend's level of need compared to Charlotte's, has a major impact on her outcome, but under the constraints of the situation, specifically the inability to communicate, she can do nothing to achieve a better outcome for herself. That is, she cannot adjust her behavior to alter George's behavior, which Kelley et al. (2003) referred to as Partner Control.

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[7] Common knowledge among agents promotes coordinated action (D. K. Lewis, 1969; Schelling, 1957). Common knowledge is a belief state in which A knows X, B knows X, A knows that B knows X, B knows that A knows X, and so on recursively ad infinitum (N. Smith, 1982; K. A. Thomas et al., 2014). Citizens who are oppressed by their government, for instance, are incentivized to band together in protest. However, if only a few turn out to protest, they not only risk arrest or physical harm but also waste time on an ineffectual demonstration. Political dissidents need not only knowledge of the time and place of the protest but also knowledge of others' knowledge of others' knowledge of the protest (K. A. Thomas et al., 2014).

If neither party can adjust their behavior to achieve a better outcome for themselves yet still affect their partner's outcome, this is termed *mutual* Partner Control. As an example of mutual Partner Control, imagine a one-shot interaction in which Charlotte collects nuts for George, and George hunts rabbit for Charlotte, and they exchange the goods at the end.[8] However, the other end of the coordination dimension is characterized by Joint Control. To illustrate *mutual* Joint Control (i.e., coordination), George and Charlotte might engage in complementary behaviors, such as alternating between childcare and constructing a shelter with each person adjusting their behavior based on communication and what they observe the other doing (Balliet et al., 2017; Kelley et al., 2003).[9]

Partner Control versus Joint Control captures the variation in the degree to which coordination affects outcomes. That said, situations that allow for coordination predominate in human interactions. Although situations can involve mutual or asymmetric Partner Control, we suspect that mutual Partner Control, particularly, would not likely have been a recurring problem in the small, face-to-face human communities that characterized the Pleistocene. As humans have become increasingly mutually dependent to solve adaptive problems, these problems were experienced in social settings in which people could (potentially) communicate and adjust their behavior to their partner's behavior to affect outcomes. For example, though a human forager might eat her fill of foraged foods before returning to camp to avoid sharing, this is likely to be noticed by others in her sharing network who have the ability to withhold their own goods and services in turn. Hence, sharing and other cooperative acts in central-place human foraging communities were not one-shot events but occurred in many rounds over years, wherein individuals could adjust their behavior, such as giving or withholding benefits, in response to their partner's past behavior to influence their partner's future behavior.

In sum, coordination is vital to human interactions (see Table 2); in fact, we are not aware of work investigating *variation* in the possibility for coordination (Joint Control vs. Partner Control) across ecologies. As we discuss in the next section, humans are less adept at detecting variation in coordination across situations compared to the other dimensions (see Gerpott et al., 2018).

Coordination Index Across Ecologies. An IRV indexing coordination concerns would address the following questions: Can I coordinate with others to enhance fitness (e.g., via resource acquisition, childcare), and how can we coordinate (e.g., division of labor, taking turns, social contracts)? Resolving coordination problems comes down to information, hence the importance of communication, social norms, and focal points in establishing expectations and resolving coordination problems (see Cronk & Leech, 2013).

All human societies involve coordination problems, and all humans share species-typical information-sharing capabilities through language and symbolism (Lachmann et al., 2001; Silk et al., 2000), the use of rituals (Chwe, 2013; Durkheim, 1915; Turner, 1969), and evolved signals (Skyrms, 2010) to generate knowledge between agents to coordinate action. Psychological adaptations, such as language and gesturing, might be part of a suite of uniquely human traits that foster shared intentionality—a state in which two or more actors have a shared commitment to achieve a goal involving coordinated action (Herrmann et al., 2007; Tomasello, 2018; Tomasello et al., 2005, 2007). An enhanced ability to infer what others are intending to do may be especially important in coordination situations that involve role differentiation.

Additionally, people should infer coordination from properties of social situations and other aspects of the environment. For instance, the very necessity of coordination can only arise in a context of corresponding interests in at least one aspect. For instance, stotting in gazelles can signal to potential predators that the animal is too fast to be worth the chase (FitzGibbon & Fanshawe, 1988). Indeed, a zero-sum game, in contrast to mixed games, is characterized by strategic randomness in actors to prevent the other party from predicting one's own strategy, and even enemies in war can find common interests to, for instance, avoid mutually assured destruction (Schelling, 1980) and end war (Kecskemeti, 1970).

In summary, coordination is widespread across social interactions, from daily subsistence activities to engaging in intergroup conflict. Humans are adept at identifying means of resolving coordination problems, and across societies, humans employ a combination of social learning (e.g., public rituals, religious belief) and innovation (e.g., creative use of symbols) to resolve specific coordination problems, including maintaining cooperative norms across vast populations or communicating covertly to coalition members. Given the ubiquity of coordination problems, humans benefit from being able to detect how their interests align with others and effectively communicating (or concealing) their interests to others to coordinate behaviors. As we discuss below, however, there may be cognitive biases built-in to human psychology toward overperceiving the need for coordination. In fact, experimental work testing people's ability to infer the dimensions of FI has found that people are less adept at distinguishing how social interactions vary in the extent that coordination can affect outcomes (see Gerpott et al., 2018).

Inferences of Interdependence

Recent models have demonstrated that variation in interdependence can influence the evolution of cooperation (e.g., Hilbe et al., 2018; Salahshour, 2022) and that there can be adaptive benefits to conditioning cooperation on inferences about the interdependence that are experienced in an interaction (e.g., Bear & Rand, 2016; Colnaghi et al., 2023). For example, Colnaghi and colleagues systematically manipulated variation in fitness interdependence (i.e., the degree of corresponding and conflicting interests) across interactions and studied whether this influenced the evolution of adaptive agents that would pay a cost to infer their interdependence within an interaction, and then only cooperate when there were corresponding interests (compared to fixed behavior agents that either always cooperate or always defect). These models found that natural selection could promote the evolution of psychological adaptations to infer fitness interdependence and that this especially occurred when the ancestral environment was characterized by larger heterogeneity in fitness interdependence across interactions. Thus, initial modelling work does support the potential for evolution to select for psychological adaptations to infer interdependence.

There is indeed some evidence that humans can infer their interdependence with others. For example, Ayers et al. (2023) found that people can evaluate whether they have corresponding versus

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[8] A repeated game creates opportunities for coordination.

[9] Technology also plays a role in resolving coordination problems (Boulianne et al., 2020; Mullins et al., 2013).

Table 2

Costs of Misperceptions Across Dimensions of Fitness Interdependence

Dimension of fitness interdependence	Costs of misperception
Correspondence–conflict	
False positive = perceiving correspondence when there is conflict	• Being the victim of exploitation. • Assorting with partners who have opposing interests and incentives to harm. • Costly pursuit of unproductive or harmful relationships.
False negative = perceiving conflict when there is correspondence	• Failure to optimize benefits of collective action. • Create costly overt conflict. • Impose costs on cooperators who in turn impose costs (e.g., reputational harm). • Antisocial punishment.
Mutual dependence–independence	
False positive = perceiving mutual dependence when there is independence	• Loss of benefits due to unnecessary division of spoils. • Failure to avoid or switch partners when there is conflict or coordination problems.
False negative = perceiving independence when there is mutual dependence	• Failure to optimize benefits of collective action. • Costly delays when a project can be completed more efficiently with others. • Project failure (e.g., cannot build an irrigation system alone).
Power (a)symmetry	
False positive = perceiving symmetrical power when asymmetrical	a. Ego is actually lower on power. • Costs/sanctions imposed for undercutting power. b. Ego is actually greater on power. • Loss of benefits by failing to promote one's interests.
False negative = perceiving power asymmetry when symmetrical	a. Misperceive ego as higher power. • Overt conflict and contests. • Risk being perceived as exploitative or hawkish. • Risk to mutual dependence as alter may impose costs. b. Misperceive alter as higher power. • Overly deferential and exploitable. • Failure to promote one's interests when possible.
Coordination	
False positive = perceiving the need to coordinate when no coordination is needed	• Wasted energy expenditure. • Wasted time spent on communication.
False negative = perceiving no need for coordination when parties do need to coordinate	• Coordination failure.

conflicting interests with others. Similarly, other lines of research have found that people are able to evaluate their mutual dependence with others (i.e., closeness; Berscheid et al., 1989) and social power (Righetti et al., 2015; P. K. Smith & Hofmann, 2016). Recent evidence supports the hypothesis that people can evaluate their interdependence with others in social interactions and relationships along multiple dimensions, including the degree of corresponding and conflicting interests, mutual dependence, and (a)symmetrical dependence (Columbus et al., 2021; Gerpott et al., 2018). However, as mentioned earlier, this work did not find that people could infer the extent that an interaction involved coordination. Furthermore, this research found that people condition decisions to cooperate on these inferences of interdependence. Specifically, the multiple dimensions of interdependence that people inferred about social interactions each explained unique variation in decisions to cooperate within lab studies and in situations in daily life. Although people may be able to infer interdependence, whether these assessments are accurate or biased raises another issue.

Uncertainty and Biases

The interdependence that characterizes social situations is fraught with uncertainty, in part, due to limitations in what individuals can observe and keep track of overtime. This challenge is compounded by possible active manipulation by social partners with opposing interests (Sperber et al., 2010). When judgments are made under uncertainty and the costs of false positives and false negatives were asymmetric over evolutionary time, then selection would have favored cognitive biases toward the less costly error (Haselton & Buss, 2000; Haselton & Nettle, 2006). For instance, the cost of detecting a predator when one is not present (a false positive) is far lower than the cost of not detecting a predator that is present (a false negative); therefore, it pays to have many false (positive) alarms (i.e., the smoke detector principle) under uncertainty even if the resulting behavioral output is suboptimal (Nesse, 2001). However, a threat detection system that is biased toward downplaying threats might be more advantageous in some situations (Taylor et al., 1992; Weinstein, 1980, 1982), such as when optimism promotes investment in outcomes in which greater investment improves the likelihood of success, as in mounting a defense in a contest (De Dreu et al., 2016). Individuals joining a defensive war party might be aided in perceiving their chance of success to be much greater than it really is, because their chance of success is zero if they fail to mobilize at all. Put a different way, the cost of failing to avoid the avoidable is much higher than failing to avoid the inevitable (Haselton & Nettle, 2006).

In Table 2, we delineate the types of costs people are liable to incur due to detection errors across each dimension of interdependence. Unlike the example of predator detection in which the asymmetry between false positives and false negatives is at an extreme, both false positives and false negatives in the domains of conflict, mutual dependence, and power can be similarly costly. Perceiving high correspondence when the true underlying state is conflict can result in exploitation and assorting with partners who have opposing interests; however, the costs of perceiving conflict when the underlying state is correspondence can result in similarly disastrous effects including failing to reap the benefits of collective action and creating costly overt conflict. Detecting mutual dependence when parties are independent can result in an unnecessary division of benefits or failing to avoid or replace social partners when there are conflicts or coordination problems, whereas perceiving that one is independent when the true state requires mutual dependence would result in a failure of collective action and wasted effort working independently. Misperceiving that one is higher on power than a social partner can result in costly status competitions that end in failure, but allowing oneself to be exploited or to miss out on benefits because one does not detect her own level of power is likewise costly.

Coordination is the one dimension in which there is the greatest asymmetry in the costs associated with making false positive and false negative inferences. If a situation requires George and Charlotte to coordinate their actions, then failing to recognize the need to coordinate would result in a collective action failure, whereas attempting to coordinate under uncertainty, for instance by using language, might waste energy but is low cost. In fact, trying to coordinate when it is not necessary can often be resolved through communication. For instance, if George is carrying a large, oddly shaped object and Charlotte is trying to help direct his movement or remove objects in his way, because she thinks he cannot see around the object, George can simply verbally communicate to Charlotte. Humans may, therefore, be biased toward overperceiving the need for coordination in social interactions. Such a bias is less likely to occur when inferring the other dimensions of FI since the costs of false positives and false negatives are relatively equal.

Cognitive biases are not fixed but are subject to shifting parameters of the environment (Haselton & Nettle, 2006). For example, in social interactions in which people have less information about others' preferences and behavioral options, individuals are more likely to infer the situation has conflicting interests (Gerpott et al., 2018; R. M. Kramer, 1994). Individuals may also benefit by exercising caution in a conflict scenario with an authority figure and overperceive the authority's ability to impose costs. The priors individuals have about their interdependence with others may also vary across societies (e.g., with institutions). Indeed, research has found that societies differ in the extent to which they perceive social interactions as a zero-sum game (Różycka-Tran et al., 2015). Furthermore, the costs of false positives and false negatives should be calibrated to one's resource condition. For example, in the case of an offensive attack, those at high resource levels might be able to afford to take risks, whereas those at moderate levels are likely to be more risk-averse, and those at the poorest levels might have no choice but to attack. Those in the low and high resource conditions would be predicted to overperceive success (i.e., perceive greater relative power than they have), whereas for those in the moderate condition, the less costly error might be to overperceive failures (i.e., perceive lower relative power than they have). However, despite the potential for biases in making inferences about interdependence, we stress that biases should work to minimize the costs of cooperation under uncertainty and that the distortion of cognitive biases should tend to diminish with greater information certainty.

Taken together, modeling work supports the idea that natural selection could select for adaptations to infer interdependence, and empirical research suggests that (a) people can discriminate between social interactions and relationships in terms of different dimensions of interdependence and (b) that these inferences are associated with decisions to cooperate.

Nonetheless, in social interactions, people do not know the objective fitness interdependence they have with others, and inferences of interdependence occur under a great amount of uncertainty. If the costs of false positives and false negatives for making such inferences were asymmetric over evolutionary time, then selection is predicted to favor cognitive biases toward the less costly error. However, we propose that both false positives and false negatives with regard to inferences of correspondence–conflict, mutual dependence, and power were, on average, symmetric over human evolutionary time. An exception, however, could be that humans are likely to overperceive situations as involving coordination problems. Thus, we propose that IRVs regulating correspondence–conflict, mutual dependence–independence, and power (a)symmetry have a high degree of accuracy and are well-designed to manage social relationships under uncertainty to reduce the costs of cooperation.

Theoretical Implications and Future Directions

Fitness interdependence proposes that the "logic" of social decision-making is explained by how situations vary along the four dimensions of interdependence. From the viewpoint of FI, much of human behavior, from cooperation to violence, involves negotiating shared and diverging interests that can be modeled game theoretically (e.g., Barclay et al., 2021; De Dreu & Gross, 2019). The notion that human behavior is driven by rational choice is, of course, not new, but perhaps what is missing is a clear consensus that cooperation is rooted in the high degree of mutual dependence and corresponding interests (i.e., mutualisms) between human conspecifics, and so individuals cooperate because they gain more by investing in their partner's welfare than not doing so (Roberts, 2005). Yet, because conflicts of interest can arise in all human relationships as has long been noted, humans must be able to adjust their behaviors to reduce the costs of cooperation and avoid exploitation (Roberts, 2005; Tooby et al., 2006; Trivers, 1971). We add to this the argument that to reduce the costs of cooperation, humans must be able to detect how situations and relationships vary along not only the degree of corresponding versus conflicting interests but also mutual dependence and power, which can affect, for instance, whether one cooperates with a partner or not and whether one should punish or avoid a social partner altogether. Indeed, each dimension has been found to have unique associations with social behaviors, including decisions to cooperate (Columbus et al., 2021) and strategic responses to other's noncooperation (Molho et al., 2020, see Balliet & Lindström, 2023).

FI theory offers an alternative account of human cooperation to models that focus on the selection of trait prosociality (e.g., Nesse, 2007) or "strong reciprocity" (Gintis, 2000; Gintis et al., 2008; Hare, 2017). From the perspective of FI theory, ostensibly selfless displays of generosity (i.e., giving not better explained by mutualisms) are likely explained by status competition (Macfarlan et al., 2012, 2013), a desire to create dependence in others as in exploitative patron–client relationships (Mayer, 2003/2018), tolerated theft (Blurton-Jones, 1987), or coercion (Lankford, 2014). Some instances of cooperation might reflect subordination and exploitation, wherein the weaker party may be laying low until new opportunities emerge. Human behavior, therefore, reflects self-interest, and though those interests are often shared with others, those high in power can and do take advantage of dependent parties to extract benefits from them and likely did over human evolutionary time (Singh et al., 2017). Individuals must, therefore, be attuned to shifts in power, such as new economic strategies or removal of rivals, to take advantage of new opportunities to improve fitness outcomes. Due to the high degree of entrenched mutual dependence in humans (and variable ability to use partner choice mechanisms) across fitness-relevant cooperative domains, there is great scope for variation along the other dimensions of FI.

Our model builds on the evidence that central-place foraging, coevolving with increasing childcare assistance from fathers and other kin, facilitated more efficient energy budgets that supported an extended juvenile period, brain size expansion, and the development of complex social intelligence (Kraft et al., 2021) and collaborative behavior (Tomasello et al., 2012). We propose that humans adapted to this socially denser ecology, in which mutual dependence means that partner choice mechanisms are conditional, by attending to and adjusting to shifts in the dimensions of FI across relationships and situations. Whereas Wrangham (2019) proposed that the evolution of our species favored proactive aggression over reactive aggression through counter-dominance mechanisms, specifically covert consensus building within groups to kill domineering members, we propose that counter-dominance mechanisms to a great extent involved leveraging mutual dependence through various means, such as withholding resources and labor, building coalitional support, and even violating norms of appropriate behavior—types of bargaining strategies (Kennan & Wilson, 1993; for ethnographic examples, see (Lowe, 2003; Mohsen, 1971; Syme & Hagen, 2023; Wolf, 1964). Thus, those who could attend to the dimensions of FI across a diversity of contexts and deploy strategic behaviors against the great diversity of social situations humans encounter had better fitness outcomes over human evolutionary time.

We further contend that the high degree of mutual dependence that emerged in our lineage set the stage for a suite of communicative (or bargaining) strategies and likely played a role in the evolution of language, symbolic, and ritual culture (see also Heintz & Scott-Phillips, 2023). Religious beliefs and public rituals, for instance, are hypothesized to help resolve coordination problems across large populations (Chwe, 2013; Purzycki et al., 2016), and humor and symbols can be devised and repurposed to transfer information covertly to ingroup members (Smaldino et al., 2018; Smaldino & Turner, 2021); these cultural behaviors are the product of both imitation and creative innovation. As Schelling (1980) discussed, people even in novel experimental games produce spontaneous bargaining—that is, they “accept, reject, retaliate, and even discover ways of conveying threats and promises” (p. 104).

The current leading gene–culture coevolutionary model of cooperation posits that human cooperation is maintained by psychological mechanisms for acquiring, adhering to, and enforcing social norms, including cognitive biases such as conformity, self-similarity, and prestige bias that evolved under conditions in which cultural group selection favored cooperative norms that promoted group success (Chudek & Henrich, 2011; Henrich, 2016; Henrich & Muthukrishna, 2021; Richerson & Boyd, 2008). Behavioral ecological research, however, indicates that bargaining processes—the outcomes of which are determined by power and the value of the resource or outcome to each party (Parker, 1974; J. M. J. M. Smith & Parker, 1976)—play a role in amending and stabilizing cooperative norms and institutions (Bunce & McElreath, 2017; Chen et al., 2024; Deb et al., 2024; Syme & Hagen, 2023). For example, among Orma, the transition from bride wealth, an institution that allows wealthier men to monopolize women, to indirect dowry, an Islamic precept that more directly benefits the couple, was, in part, due to an increase in the relative bargaining power of young men and women (Ensminger & Knight, 1997). FI theory proposes that norms and institutions are transmitted by (a) their contribution to enforcement among competing parties (Singh et al., 2017; see also Cadenas, 2023) and (b) their contribution to resolving coordination problems, including establishing expectations of others’ behavior, to reduce the costs of cooperation[10] (Alvard & Nolin, 2002; Cronk & Leech, 2013; D. K. Lewis, 1969).

An evolutionary approach concerns “ultimate” explanations of our evolved psychologies—how a psychological trait resolved recurring fitness problems over evolutionary time (i.e., adaptive function), whereas “proximate” explanations concern the immediate environmental, physiological, and ontogenetic regulation of the trait (Mayr, 1961). Novel environments can create evolutionary mismatch wherein satisfying our evolved psychologies can be ultimately detrimental to fitness (Corbett et al., 2018; Lea et al., 2023). From the perspective of FI theory, this means that people might infer and act on the perception of conflict to obtain and consume novel, highly valued resources that are actually harmful to health and fitness in the long term, such as high-fat, high-sugar foods that satisfy human taste for resources that were relatively scarce in the ancestral past or novel synthetic, yet highly lethal, drugs that act on evolved systems involved in self-medication (see Hagen et al., 2023). Thus, our evolved psychologies to respond to variation in interdependence can map onto novel ecologies in ways that harm fitness. Other modern technologies, like social media, might also alter FI or create distorted perceptions of FI in ways that harm health and well-being.

Conclusion

Humans are highly dependent on each other to achieve fitness-relevant ends: collaborative subsistence, food sharing, childcare, and warfare, among others. We propose that central-place foraging coevolving with increasing childcare assistance created an increasing diversity of interdependence, which provided selection pressure for humans to detect and respond adaptively to variation in the four dimensions of fitness interdependence. We propose that human psychology is adapted to a social ecology in which fitness outcomes are dependent on how individuals manage the costs and benefits of cooperation among conditions that vary along correspondence–conflict, mutual dependence–independence, power symmetry–asymmetry, and coordination. The psychological adaptations to infer interdependence, therefore, would underlie strategies of cooperation across human ecologies and allow humans to maintain cooperation under conditions in which the distributions of conflict, power, mutual

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[10] Other norms, and symbols and beliefs pertaining to norms, might persist because they are psychologically “sticky” such as stereotyped knowledge (Kashima, 2000), cognitive/cultural attractors (Falandays & Smaldino, 2022) that can serve as focal points (Cronk & Leech, 2013), or information that is minimally counterintuitive (Norenzayan et al., 2006). There are also other coordination dynamics at play such as “tipping points” in which minority norms become dominant (Centola et al., 2018), which can also be an outcome of deliberate bargaining processes, such as persuasion.

dependence, and the ability to coordinate are structured differently due to, for instance, the reproductive constraints imposed on families by food acquisition, subsistence lifestyles, and political organization. The great diversity in the types of interdependences people experience suggests that humans are endowed with an evolved psychology to track variation along four dimensions and to use this information to promote their fitness interests. Thus, FI theory is a framework for characterizing the dynamic structure of the social ecologies humans occupy that can help make sense of the trade-offs people make to establish, maintain, and amend cooperative relationships and resolve conflicts in different domains of cooperation in diverse ecologies across time.

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