

# Understanding cooperation through fitness interdependence

Some acts of human cooperation are not easily explained by traditional models of kinship or reciprocity. Fitness interdependence may provide a unifying conceptual framework, in which cooperation arises from the mutual dependence for survival or reproduction, as occurs among mates, risk-pooling partnerships and brothers-in-arms.

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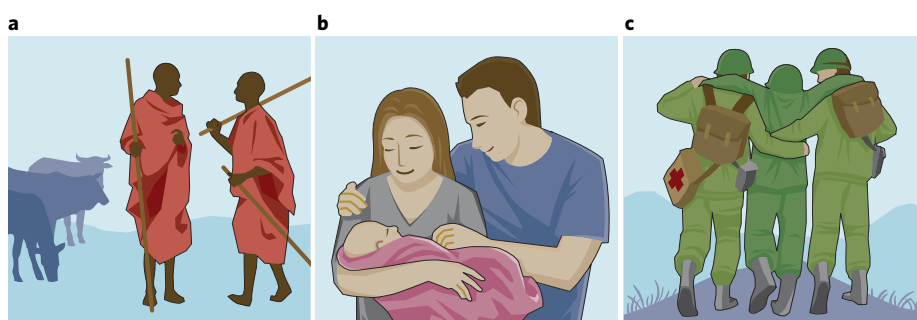
Interdependence — our mutual reliance on one another for our welfare — permeates our lives and our social relationships. Interdependence is a feature of social life across human societies, from need-based transfer systems in small-scale societies to shared interests in offspring in mating relationships to mutual dependence for survival among soldiers during times of war (Fig. 1). Fitness interdependence refers to interdependence with regard to our evolutionary fitness, that is, survival and reproduction<sup>1</sup>.

Despite decades of progress in psychology, anthropology and evolutionary biology, many questions remain about human sociality. Why do people often help others without expecting to get anything in return? When is cooperation an evolutionarily viable strategy? Do our emotions in close relationships track how entwined our evolutionary interests are? Here we propose that fitness interdependence may be an important first step towards unifying disparate literatures on cooperation, identifying exciting new avenues for research across many disciplines, and, thus, solving many of the remaining puzzles of human sociality. We provide a definition of fitness interdependence, explain how it applies to the evolution of cooperation and describe how the study of fitness interdependence can advance interdisciplinary work on human cooperation.

## Fitness interdependence

Drawing from the work of Brown<sup>1</sup>, Kelley and Thibaut<sup>2</sup> and Roberts<sup>3</sup>, we propose the following definition of fitness interdependence: the degree to which two or more organisms influence each other's success in replicating their genes.

Fitness interdependence can arise from close interactions between two or more individuals, as in symbiosis, mutualism and



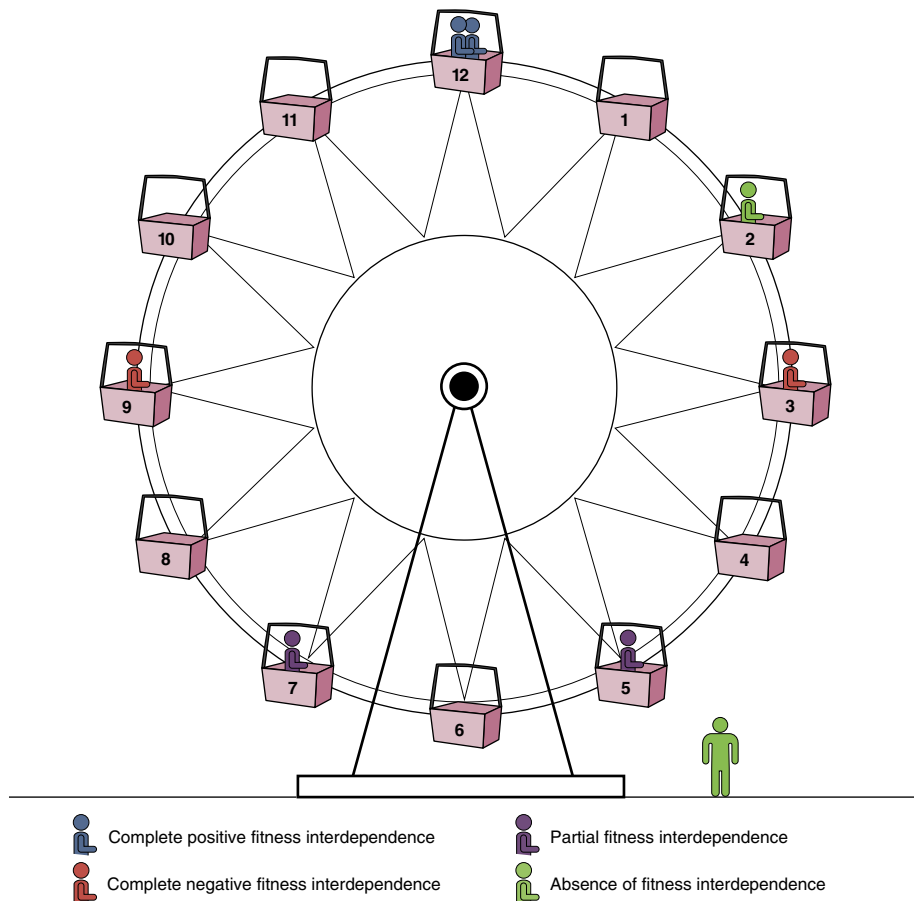
**Fig. 1 | Interdependence is pervasive in human societies and it often includes mutual dependence for survival and/or reproduction. a**, In the Maasai *osotua* system, herders share livestock with their partners in times of need; this need-based transfer system makes it more likely that both partner's herds will survive and support the herder's family. **b**, In human mating relationships, partners are often interdependent in terms of their welfare as well as their reproductive success if they have offspring together. **c**, In times of war, soldiers in the same unit are highly interdependent, relying on one another for protection and survival.

other potentially cooperative situations. These terms often apply in situations of fitness interdependence. However, the concept of fitness interdependence is distinct from symbiosis, mutualism and cooperation because these terms are a label for a type of interaction while fitness interdependence refers to the degree of influence on fitness; it is a property of the interaction that can — at least in principle — be quantified. When individuals have positive effects on one another's survival and reproduction, as with mutualism, this situation is characterized by positive fitness interdependence (positive fitness interdependence can also arise when parties can damage one another at a cost to self, as in spite; see Roberts<sup>3</sup> for a more detailed analysis). In host–pathogen, predator–prey and other zero-sum, competitive situations, individuals' payoffs are negatively correlated, and so are characterized by negative fitness interdependence (Fig. 2). When fitness interdependence is positive, we refer to it simply as 'fitness interdependence' rather than explicitly noting that it is

'positive.' This is similar to numbers, which we assume are positive unless they are explicitly described as negative.

## How does it arise?

Fitness interdependence can be examined both at the ultimate level of causation in terms of the evolutionary selection pressures that give rise to it and also at the proximate level of causation in terms of how it is represented psychologically and culturally. In ultimate evolutionary terms, because an organism can get its genes into the next generation by facilitating the survival and reproduction of its kin, genetic relatedness is an important contributor to fitness interdependence. Fitness interdependence can also arise among individuals who are not genetically related if their outcomes influence each other's fitness. This happens in mating relationships (Fig. 1b) and in challenging conditions such as natural disasters and war, which sometimes give rise to the 'band of brothers' phenomenon among co-combatants<sup>4</sup> (Fig. 1c).



**Fig. 2 | Fitness interdependence can be conceptualized as ‘rising and falling together’ in terms of success in replicating genes.** This can be represented with a Ferris wheel where individuals can be seated with others in the same car (complete positive fitness interdependence, as with the two blue figures in car number 12). Partial positive fitness interdependence is when individuals mostly ‘rise and fall together’ but not completely, as with individuals seated in nearby cars (purple figures in cars 5 and 7). Negative fitness interdependence occurs when positive outcomes for one individual mean negative outcomes for the other, as with individuals in opposite cars on the Ferris wheel (red figures in cars 3 and 9). The absence of fitness interdependence can be represented by individuals who are not on the same Ferris wheel (green figures in car 2 and on the platform).

Fitness interdependence can be established and enhanced by institutions, from military units to marriage to informal cultural institutions that create special relationships. One example of this is the livestock sharing system used by Maasai pastoralists called *osotua*, meaning ‘umbilical cord’. Following a process of cooperative partner choice that in many ways resembles courtship, Maasai willingly enter into *osotua* partnerships. Once established, *osotua* partners are obligated to help each other in times of need without any expectation of repayment, creating interdependence through the pooling of risk (Fig. 1a). Similar risk-pooling systems are commonplace around the world, especially where commercial insurance is unavailable or impractical<sup>5</sup>.

More generally, mechanisms of partner choice allow individuals to preferentially

interact with cooperators, which promotes the evolution of cooperation<sup>6,7</sup>. Preferential interactions like this may lead to the cultivation of close relationships characterized by fitness interdependence. Sometimes — as with *osotua* — these partner-choice mechanisms are culturally instantiated. At other times, partner choice may simply be a result of individual decision-making about forming friendships and other relationships. Presumably, those of our ancestors who had the ability to identify and cultivate relationships characterized by high positive fitness interdependence would have, on average, left more descendants than those that did not have that ability<sup>1,8</sup>.

Our subjective experiences of fitness interdependence are likely shaped by proximate mechanisms that evolved to assess and represent our evolutionarily entwined fates with others. Some of these proximate

mechanisms may involve the upregulation of oxytocin in the brain, which can give rise to feelings of affection that facilitate helping. In close relationships such as those with kin and mates, interdependence can arise as a result of and be reinforced by physical processes. For example, the physical acts of sexual intercourse and lactation affect our nervous and hormonal systems, enhancing feelings of closeness we have towards mates and offspring. Even when interdependence involves no physical contact, it may manifest through intense sentiments such as love, warmth, empathy, and feelings of friendship and kinship. In addition, the feeling of identity fusion, where individuals have a visceral feeling of oneness and family-like bonds with a group, may be a proximate mechanism for aligning human behaviour with the underlying fitness interdependence in the relationship or group. Identity fusion is associated with extreme self-sacrifice among ‘brothers-in-arms’ and perceived shared interests among combatants also has been associated with being more ‘fused’ with co-combatants than with family<sup>4</sup>. More generally, the common use of kin terms to refer to non-relatives with whom one has a shared fate may be an example of a cultural and linguistic manifestation of fitness interdependence.

Measuring fitness interdependence is a challenge because it can be difficult to measure the impacts of individual behaviours on fitness. Measuring the proximate mechanisms underlying it — in the form of perceived fitness interdependence — may be easier. For example, individuals can be asked about the extent to which they believe their outcomes are entwined with those of others, as studied by Brown<sup>1</sup> and as measured with a new ‘perceived fitness interdependence scale’ that has been developed by several of the authors of this Comment. Another approach is to survey individuals about the nature of the situations they are in with regard to interdependence<sup>9</sup>. Investigating the underlying evolutionary fitness interdependence in real-world situations may be a challenge, and so analytical and computational modelling can provide tools for work in this area. For example, Robert’s stakeholder model<sup>3</sup> and various game-theoretic tools<sup>2,10</sup> can facilitate future work on the evolutionary and ultimate aspects of fitness interdependence.

### Future work

Because individuals can have stakes in each other’s wellbeing and fitness that are not captured by models based on genetic relatedness or reciprocity, a broader perspective, such as that provided by

the fitness interdependence framework, is clearly needed. For example, fitness interdependence might help to explain anomalies in the predictions of kin altruism and reciprocity: for example, the lack of correspondence between kin terms and genetic relatedness in small-scale societies and the limited ability of tit-for-tat reciprocity to accurately describe real-world patterns of resource transfer. If individuals have a stake in each other's wellbeing and fitness, then many instances of seemingly puzzling cooperation become less puzzling from an evolutionary perspective.

Inclusive fitness theory triggered the development of a whole new area of research on cooperation in animal behaviour: If animals are indeed altruistic towards kin, how are they able to recognize them? The concept of fitness interdependence should facilitate the development of an analogous but ultimately broader research programme in human behaviour: How do humans represent, recognize and respond to fitness interdependence? How do humans cultivate and maintain relationships characterized by fitness interdependence? What emotions and cognitive architecture underlie perceptions of interdependence? How do representations of interdependence influence helping decisions? What role do partner-choice mechanisms play in these processes? This research programme should include the study of the cognitive, emotional and behavioural aspects, as well as the game-theoretic sources, of interdependence and its ultimate effect on the evolutionary pressures shaping human nature.

Future work should also be sensitive to the possibility that perceptions of fitness interdependence may be wrong. Further, the mismatch between ancestral and current environments may create situations in which modern humans are led to engage in self-sacrificial behaviours such as celibacy or suicide bombing by false indicators of fitness interdependence, such as the manipulative use of kin terms or participation in shared experiences such as extreme rituals<sup>4</sup>.

Another important issue to consider is how constraining partner choice can affect the evolution of mechanisms for estimating and cultivating fitness interdependence. If individuals have no choice about who they are interdependent with (for example, in certain family contexts, in arranged marriages and in some sociocultural

groups where individuals' autonomy is constrained), then the ability to cultivate long-term positive fitness interdependence may be compromised. Future work on partner choice could investigate the impact that autonomy about 'walking away'<sup>6</sup> has on the perception and cultivation of fitness interdependence. Also, future models could investigate the effect of constraining autonomy on the evolutionary viability of cooperation (that is, does limiting the ability of partners to leave increase the payoffs of exploitation enough to destabilize cooperation?).

In principle, fitness interdependence can be used to study not only human cooperation but also the evolution of sociality in non-humans (for example, among blood-sharing vampire bats) and even among cells during the transition to multicellularity. Nevertheless, there may be some unique things about fitness interdependence as it applies to humans. Throughout our evolutionary history, we have been highly dependent on one another for survival and reproduction and we appear to be well-equipped to represent and reason about fitness interdependence, even in complex social environments where individuals have varying levels of shared interests. Perhaps one of the things that makes humans unique in the biological world is our ability to represent and cultivate fitness interdependence in complex and dynamic groups filled with both shared interests and conflicting interests. By formalizing fitness interdependence and our tools for studying it, we may be able to address many remaining puzzles of human cooperation and sociality, from humans helping one another without expecting anything in return to calling non-relatives by kin terms such as 'brother' or 'sister'. The construct of fitness interdependence may also help us to understand and analyse the complexities of many human relationships — from mating to friendships to family interactions — where the outcomes for one individual are often highly interdependent with the outcome for others, for better or worse. □

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#### Competing interests

The authors declare no competing interests.