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Modeling the evolution and formation of animal friendship

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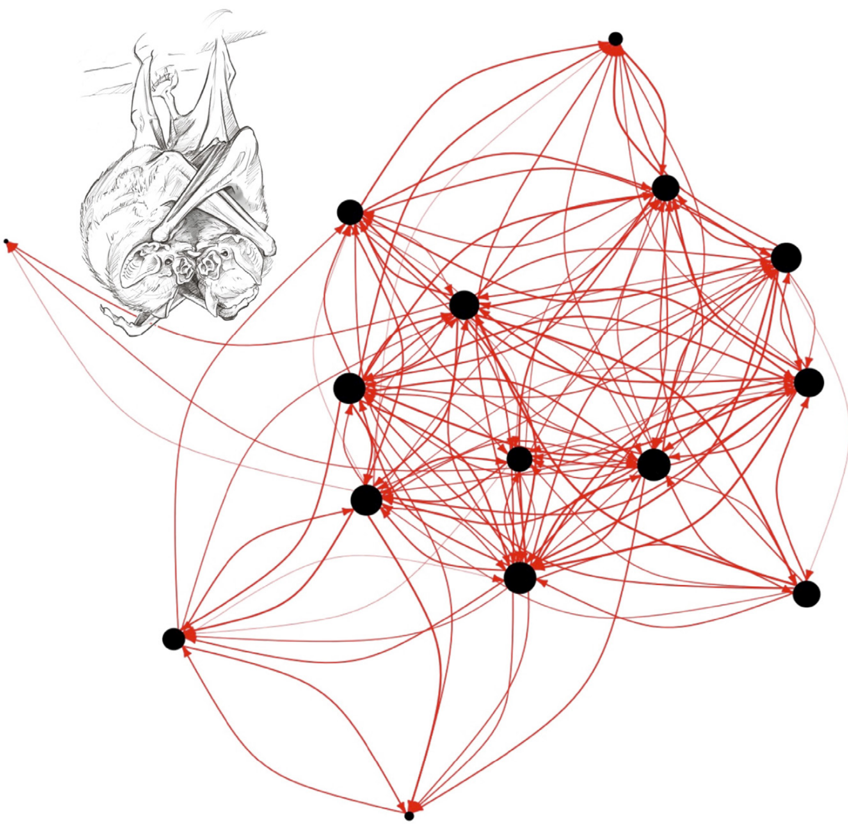

Fig. 1. A network showing food-sharing rates among female vampire bats. Thickness of network arrows (red links) indicates food-sharing rates between bats (black nodes) fasted during experimental trials (19). Node size indicates the number of partners fed. Illustration of food sharing by Javier Lazaro.

Friendship is fundamental to our health and well-being. The human capacity to form cooperative social bonds outside family has undoubtedly been a key to our survival and reproductive success over evolutionary time. Increasing evidence shows that many other animals—from chimpanzees to dolphins to crows—also build long-lasting cooperative relationships that seem analogous in form and function to human friendships (1, 2). Yet understanding friendship and social bonding from an evolutionary perspective has long been a challenge. Navigating the subtle cooperation and conflict of friendships is a cognitively complex process that violates assumptions of classic game-theory models of cooperation. Empiricists (like myself) need theories and models that incorporate more realistic decision-making into traditional game theory. A recent model by Leimar and Bshary (3) is one of the first and best attempts to address this gap. Their agent-based model combines evolutionary game theory, flexible decision-making, and learning to simulate how helping and social bonding change over evolutionary and developmental time.

To understand why helping among friends does not fit well into traditional evolutionary models of nonkin cooperation, it is helpful to review some key conceptual advances (4–13). Since Darwin, reciprocal helping has been considered a crucial evolutionary advantage to friendship, as described by Williams, who wrote in his 1966 book on adaptation (4):

"It is necessary that help provided to others be occasionally reciprocated if it is to be favored by natural selection. It is not necessary that either the giver or the receiver be aware of this. Simply stated, an individual who maximizes his friendships and minimizes his antagonisms will have an evolutionary

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advantage, and selection should favor those characters that promote the optimization of personal relationships… It would involve only such immediate self-sacrifice for which the probability of later repayment would be sufficient justification."

By providing testable predictions of how cooperative relationships form, the model promises to enhance the integration of experiments and theory, bringing game theory closer to real social life.

Largely inspired by human friendship, Trivers (5) published a model for reciprocity or "reciprocal altruism" in 1971. His paper explained why a proclivity to help nonkin would be favored by natural selection and offered explanations for many psychological features of human friendship. Ten years later, Axelrod and Hamilton's (6) published a game theory model showing that the strategy "Tit-for-Tat" (i.e., help those that helped you) was evolutionarily stable in a repeated Prisoner's Dilemma Game. The Prisoner's Dilemma Game is defined by the assumption that each player is more incentivized to exploit their partner rather than to have a cooperative outcome, so this reciprocity model assumed a high level of conflict. Because each player is tempted to exploit the other, helping is a risky investment.

A "risky investment" is of course not what it feels like to help a friend. Friends trust that each has some stake in the other's welfare, which makes cooperation among friends feel less like business and more like family. Despite the popularity of the classic reciprocity model, many behavioral ecologists grew increasingly skeptical of the Prisoner's Dilemma as an appropriate model for cooperative relationships.

Connor (7) described an alternative model of cooperation, called "pseudoreciprocity," which removed the assumption of high conflict and the possibility of cheating. In the pseudoreciprocity model, helping simply enables greater return benefits that are a reliable by-product of the recipient's existence. For example, Alice feeds Bella because Bella's mere survival automatically helps Alice stay warm or avoid predators. Unlike the reciprocity model, there is no reason for Alice not to help Bella, as Bella cannot "cheat" Alice.

The pseudoreciprocity model does not fully capture helping among friends either. Although helping in a friendship is not a strict Tit-for-Tat exchange of risky investments (like Tit-for-Tat in the Prisoner's Dilemma), it is also not a mere "by-product" of self-serving behavior (as in pseudoreciprocity). Friends often do invest in helping even at a cost to themselves, sometimes leaving them vulnerable to exploitation. Most friendships exist in the gray area of intermediate conflict between the extremes of the high-risk reciprocity model and the no-risk pseudoreciprocity model (11, 12).

Friendships are built up from many small favors, rather than grand acts of self-sacrifice. In earlier game theory models, cooperative investments were all or nothing, but Connor's model of "parceling" allowed individuals to break up cooperative investments into smaller bits, reducing the risk of nonreciprocation (8). In 1998, Roberts and Sherratt (9) modified the reciprocity model by making cooperative investments continuously variable in magnitude. This change allowed for "short-changing" as a subtle form of cheating and for a "raising-the-stakes" strategy where individuals start with small helping acts but increase their investments in cooperative partners. In 2005, Roberts (10) similarly translated the pseudoreciprocity model into a continuous variable of "fitness interdependence"—a measure of how much "stake" a helper has in the recipient's welfare. These advances paved the way for friendships to be modeled as dynamic relationships where the degree of interdependence and responsiveness can change as friendships form (11, 12). As strangers or competitors become friends or allies, their conflict declines and can ultimately flip into interdependence (11, 12).

Interdependence also depends on outside options for partners. Friendships emerge not only from a history of past interactions with one partner but also against the backdrop of a network of alternative partners. Yet most classic strategies in game theory consisted of simple heuristics (e.g., "match partner's last move" or "always cooperate") for how to respond to a single player. During the 1990s and beyond, it became increasingly clear that models of cooperative relationships should include market effects of partner choice. Noë and Hammerstein (13) developed biological market models, which yielded many predictions that were empirically confirmed across many species. For instance, grooming networks in vervet monkeys were shaped by experimental manipulations of the supply and demand of helpful partners (14). Studies on human friendship showed similar market effects: People choose and compete to be chosen as friends (15).

Over the last two decades, behavioral ecologists have increasingly viewed social integration through the analysis of social networks (2). Yet, it remains unclear whether and how animals actively form and manage their social relationships One complication is that friendship dynamics occur over multiple timescales. Over evolutionary time, the heritable traits that underlie friendship evolve. Over an individual's lifetime, their cooperative behavior changes with learning. And over the course of a friendship, the benefits of helping can vary with changing circumstances. Any model hoping to capture this kind of complexity cannot be as elegant and simple as Tit-for-Tat in the repeated Prisoner's Dilemma (a strategy with four lines of code and four possible outcomes per round). However, a more complex model has the huge advantage of bringing models closer to actual animal behavior.

An innovative new model by Leimar and Bshary (3) is a next step forward. This agent-based model yields general insights into friendship-like cooperative relationships that are applicable to many species, but it was inspired by food-sharing relationships in vampire bats (Fig. 1). Female vampire bats help each other by regurgitating portions of their blood meals to unsuccessful foragers (16). Reciprocal food sharing occurs among socially bonded bats that build up relationships through social grooming (16–18). In the Leimar and Bshary model, virtual bats develop social bonds through a mechanism similar to associative learning, and these social bonds shape the helping decisions of the bats.

Having studied food sharing in vampire bats for over 10 y and seen many models of it, I believe that this model has the most realistic assumptions. The model includes the nonlinear relationships between the costs and benefits of sharing, as the costs of giving are less than the benefits of receiving (16). It captures the dynamic social structure of vampire bats; colonies include coroosting subgroups with compositions that change from day to day (16). The virtual bats vary in their overall tendency to help and have preferences for who and how much to help different groupmates. They have several heritable traits that evolve, including their tendency to form new social bonds, their rate of social bonding, the limits of their helping, and their responsiveness to partner helping. To highlight the process of social bond formation among nonkin, Leimar and Bshary intentionally removed the role of relatedness and nepotism. To assess the role of reciprocity (including partner choice), they compared simulations with and without individual recognition.

The results of the model recovered several factors that are well known to promote the evolution of cooperative traits in general, including social assortment, partner choice, and a low cost-to-benefit ratio of helping. More impressive is that results matched conclusions from empirical studies. Virtual bats formed reciprocal food-sharing relationships with highly associated partners, but the reciprocity was neither immediate nor strict (16–19). The bats evolved to have some fitness interdependence with socially bonded partners, and they also evolved some responsiveness to their partners' behavior. Consistent with the "social bet-hedging" hypothesis (19), the virtual bats evolved a tendency to diversify their food-sharing network by building new relationships, but this need was balanced against the need to also strengthen and focus cooperative investments in specific partners.

This model will likely inspire future lines of empirical work in this species and others. For example, the virtual vampire bats evolved to "kickstart" new relationships by donating close to their maximum amounts at the start of the relationship. This result does not support the idea that the bats follow a "raising-the-stakes" strategy, but they are consistent with observations of rapid food sharing between recently introduced bats that lack outside options (18). The value of conditionally responsive strategies like "raising the stakes" depends on the frequency of "cheating" in a population (nonhelpful bats exploiting helpful bats), which itself will coevolve with responsiveness (20).

Leimar and Bshary's model is a significant step forward. It will help push the field forward past the false dichotomy of choosing between "reciprocity" and "pseudoreciprocity" as strictly alternative hypotheses (12), toward thinking more clearly about cooperative investments, responsiveness, interdependence, as interacting dynamic factors that drive social bonding. By providing testable predictions of how cooperative relationships form, the model promises to enhance the integration of experiments and theory, bringing game theory closer to real social life.

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