



Altruism in fluctuating environments

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Do fluctuating environments change the rules for social evolution? We explore the link between social evolution and stochasticity, using theory and new data. First, we formalise the elusive connection between 'bet-hedging' and inclusive fitness: by deriving a stochastic generalisation of Hamilton's rule, we identify the conditions under which altruists should pay to reduce the fecundity variance of recipients (an altruistic form of bet-hedging). Together with simulations, we use this stochastic Hamilton's rule to explore the potential for a bet-hedging route to the evolution of insect societies. This yields surprising results: in stochastic environments, it is possible for altruism to evolve even if it reduces the average reproductive success of both actor and recipient. Instead, actors can confer cryptic benefits on recipients by shielding them from the fluctuating environment, suggesting that standard field approaches to quantifying the costs and benefits of altruism may overlook a fundamental component of fitness. Second, we road-test the stochastic approach to inclusive fitness using field experiments with the tropical wasp *Polistes canadensis*. We explore whether exposure to a severe unpredictable risk (parasitism of the colony by flesh flies) changes the rules for the evolution of social behaviour. A stochastic Hamilton's rule illuminates the fluctuations that are ubiquitous in the natural world, and pinpoints the fundamental conditions required for the evolution of sociality through bet-hedging.