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Editorial

Hamilton's rule: Game theory meets coalescent theory

Last year, evolutionary biologists celebrated the 50th anniversary of inclusive fitness theory and the publication of Hamilton's rule (Hamilton, 1964a,b). This result provides both a condition on relatedness among interactors to allow for the evolution of altruistic behavior and a general decomposition of the selective forces acting on social behavior. With three journal special issues to mark the occasion, in *Animal Behaviour* (Strassmann and Queller, 2014), *Biology Letters* (Herbers, 2013), and *Philosophical Transactions of the Royal Society* (Gardner and West, 2014), the commemoration of Hamilton's 1964 work has been perhaps the most celebrated anniversary in evolutionary biology since the double Darwin festivities of 2009.

In this issue of *TPB*, Jeremy Van Cleve both reviews the theory for social evolution in finite populations that descends from Hamilton's initial work as well as offers new insights. The review shows how the current approach to Hamilton's rule involves a combination of ideas arising from game theory and coalescent theory. Game theory comes in as the object of study is interactive behavior, and the aim is to characterize equilibrium strategies for social interactions—such as those occurring in foraging, sex-ratio evolution, or cooperative games. Coalescent theory enters as it enables quantification of how the genetic determinants of strategies sampled in different interaction partners coalesce in different recent ancestors (such as when a population is geographically structured), and how this coalescence pattern affects selection on strategies. Indeed, Hamilton's 1964 insight can be understood as a demonstration that the shape of the genealogical tree of a population crucially affects social evolution and that this effect can be usefully, albeit not always, summarized by a single measure of genetical association among interactors: pairwise relatedness.

Van Cleve (2015) applies these ideas to study interactive behavior under both short-term evolution, where higher-order relatedness coefficients obtained via coalescence times are required to characterize the dynamics, and long-term evolution, which can be characterized by pairwise relatedness alone. Surprisingly and interestingly, the simpler long-term evolution models can replicate classical qualitative outcomes of short-term evolutionary models, suggesting that Hamilton's original model might be "robust in unexpected ways".

Hamilton's proposed solution to the biological problem of altruism, which had existed since the time of Darwin, provides an example of a work of theory that has inspired a vast empirical research agenda. At the same time, Van Cleve's paper provides a deep illustration of how Hamilton's 1964 work continues to inform and influence theoretical contributions, fostering connections between areas as seemingly different as game theory and coalescent theory.

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