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New Approaches to the Evolution of Social Behavior

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One of the most fascinating topics in evolutionary biology is how and why organisms cooperate with each other. Natural selection works through competition between alleles for representation in the next generation. Yet one sees everywhere organisms actually helping each other, from mutualisms between ants and plants to the altruistic acts of firefighters storming into burning buildings to rescue people. But how can natural selection lead to cooperation? This, of course, is not a new question, and a tremendous amount of work in evolutionary theory in the last 40 years has shown that helping others can frequently be the winning strategy in the struggle for existence. We have a sophisticated theory of social evolution, dealing not only with helping behaviors, but also other behaviors such as policing, spiteful harm-doing, and so on.

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A recurrent complaint of members who attend ESA Annual Meetings is that the large number of concurrent sessions make it impossible to attend all the ones of interest. Symposium Reports from the ESA Annual Meeting is one response to this dilemma. They provide, for those who could not attend, an overview of the symposium presentations and the resulting discussion, as well as a convenient means to identify the presenters. And attendees can review the session! The Editor hopes these Reports are useful, and encourages future Symposium organizers to write Reports for the *Bulletin* when the presentations are given. For detailed instruction for contributions see: ‹http://esapubs.org/esapubs/journals/Bulletin.htm#Typ›.

Symposium 6: New Approaches to the Evolution of Social Behavior

One of the most fascinating topics in evolutionary biology is how and why organisms cooperate with each other. Natural selection works through competition between alleles for representation in the next generation. Yet one sees everywhere organisms actually helping each other, from mutualisms between ants and plants to the altruistic acts of firefighters storming into burning buildings to rescue people. But how can natural selection lead to cooperation? This, of course, is not a new question, and a tremendous amount of work in evolutionary theory in the last 40 years has shown that helping others can frequently be the winning strategy in the struggle for existence. We have a sophisticated theory of social evolution, dealing not only with helping behaviors, but also other behaviors such as policing, spiteful harm-doing, and so on.

But we cannot say that our explanations for the evolution of social behavior are complete yet. In particular, despite its high sophistication at the evolutionary level, much of social evolution theory is based on very simplistic models of how individuals actually behave: Individual are modeled either as genetically destined for some kinds of behaviors, or as simple automatons having a few contingent strategies. Yet in reality, we know that even "simple" organisms such as lizards are capable of quite complicated behavior. And we also know that most behavior is contingent and plastic. Evolution does not act on genes prescribing particular behaviors, but on genes that prescribe the mechanisms that produce the behavior. Therefore, a more realistic view of the evolution of social behavior should model behavior as it is determined by the decision-making mechanisms in the social context, and then consider the evolution of these mechanisms according to the fitness consequences of behavior they produce.

The aim of this symposium was to bring together researchers that investigate social evolution from such a perspective, incorporating not only the evolutionary dynamics in their models, but also the mechanisms of behavior. (I use the term behavior more loosely than its customary usage, to include interactions not only between animals, but also between cells, or plants and microbes.) Each of the talks in the symposium investigated an interaction both in terms of the mechanisms making it function as well as the evolutionary pressures that act on these mechanisms. This two-tiered approach to studying is the unifying new approach to social behavior. Below, you will find a summary of the talks given by the speakers, which included established leaders of the field as well as up-and-coming researchers.

Our moderator **Laurent Lehmann** opened the session with an excellent introduction, which presented a useful overview of the different levels and timescales at which social evolution operates, and a preview of the particular timescales that would be considered in this session.

Our first speaker was **Richard Michod**, who presented an overview of his work on the evolution of multicellularity and germ cell–somatic cell specialization in Volvox colonies. His explanation for how multicellularity has been brought about centered on a life history gene, regA-like, that regulates cell growth through choloroplast expansion. In multicellular colonies, this gene is expressed in some cells to keep those cells small; as a result they do not reproduce, i.e., they stay as somatic cells. He then turned to the fitness reasons for why such regulation of growth and the resulting multicellularity can be adaptive. He showed evidence for the existence of a trade-off between mobility (which is related to survival) and multicellularity. Mobility is mediated through flagellation of the cells, which impairs cell division after five divisions. Multicellularity, however, allows specialization of soma cells to mobility by retaining their flagella and not dividing. This breaks through the mobility–reproduction trade-off, increasing both the survival and the fecundity of the colony (Michod 2007).

Lou Gross from the University of Tennessee was next, and started his talk with a survey of the various ways in which plant growth and physiology are being modeled, including systems biology, network models, agent-based simulations and cooperative game theory. He then turned his focus to the possibility of using cooperative games in a community and within individuals. Cooperative games deal with the stability of coalitions, i.e. groups of individuals that interact with each other. Therefore, Gross suggested that cooperative game theory might be helpful in the emerging field of community genetics by analyzing the fitness consequences of different community associations and predicting stable genetic associations.

Next was **Régis Ferrière,** who presented his recent work, co-authored with Dominique Carval, on the evolution of common and private interests between two interacting species, based on the "liaison dangereuse" idea, published earlier by van Baalen and Jansen (2001). This model considers an interaction with two species whose individuals had the possibility of forming symbiotic complexes with each other. The survival of such complexes introduces a common interest component to the interaction. The species have traits that affect the performance of these complexes, and their survival outside the complex. The ecological dynamics of these two species are then integrated with the evolutionary dynamics by introducing a mutant and determining whether the mutant can invade. In this adaptive dynamics framework, Ferrière and Carval explore the different evolutionary trajectories taken by the common good and the private interest during the evolution of the underlying traits. They identified six possible trajectories, the most interesting of which was that the common good can be bolstered even though at the same time the species' interests evolve to be more in conflict with each other. This counterintuitive result suggests that conflict might evolve as a side consequence of cooperation.

Joel Brown continued the theme of integrating the ecological dynamics with the evolutionary one using the adaptive dynamics framework. He described his recent work with Tom Vincent, which explores the payoff structures in a cost–benefit game (Brown and Vincent 2008). Their results show that the emergence of cooperation depends on the functional form of costs and benefits as a function of investments, e.g., whether costs accelerate or decelerate with increasing investment. The evolutionarily stable level of cooperation depends critically on the shape of these functions, which represent the ecological constraints and benefits from investing in an interaction.

Next, **Joan Roughgarden** switched gears and discussed the interactions between behavioral dynamics and ecological effects. She described two mechanistic models for deriving the functional and numerical responses in a population dynamics model. The functional response model envisions a solitary sit-and-wait predator that is maximizing energy intake per time as a function of the prey density (Roughgarden 1995). Interestingly, the functional response derived in this way does not match any of the three types of functional responses, in that it increases slower than linearly with prey density; however it does not level off as a type two functional response does. This changes the population dynamics such that instead of the damped cycles found in models with density dependence in prey, the system exhibits heteroclinic cycles. This illustrates how considering the behavioral dynamics might change the population dynamics qualitatively. The numerical response part of Roughgarden's talk was based on a simple game theory model, and drove home the point that in many predators, reproduction is a social affair, and multiple outcomes are possible depending on whether or not individuals cooperate with each other. The linkage between the social dynamics of a predator and its ecological implications remain poorly understood.

I was up next (Erol Akçay) and reported on the work we did together with Jeremy Van Cleve, also at Stanford University. Our model combined the behavioral dynamics of a social interaction that are driven by internal motivations of individuals, with the evolutionary dynamics of these motivations. The most striking result was that even when individuals' interests are conflicting, they can nonetheless evolve to "care" for each other's payoff. In other words, the evolutionary stable motivations are such that individuals will be intrinsically willing to increase their partner's payoff, despite this being costly. Furthermore, this result was obtained under direct selection on individuals, i.e., it does not rely on kin- or group-selection processes, demonstrating that adding the behavioral tier while considering the functional basis of behavior can lead to unexpected results.

The next presentation was by **Lee Worden**, from the University of California, Berkeley. He presented a generalized Lotka-Volterra model for multispecies population dynamics, but with the added twist that the entries in the interaction matrix were allowed to evolve. He showed, through simulation studies, that in the absence of any constraints, selection tends to increase the entries of a matrix on a row-by-row basis, which means that each species evolves to benefit from the presence of another, and interactions evolve from competition toward mutualism. This unconstrained scenario, however, is too optimistic, and changes when the interaction coefficients are constrained by the underlying traits of the two species. This evolution toward mutualism can then be prevented by either species, due to the available variation imposed by the underlying trait, or due to selection in one row of the matrix (which increases the coefficients in that row), causing indirect selection on coefficients in other rows, because the same trait is involved in determining those as well. Thus, the underlying trait structure of the interaction matrix can give rise to diverse patterns of evolution.

Our final speaker was **Herbert Gintis**, an economist active in many areas, including the evolution of social behavior. His talk was about the disconnect and inconsistencies among the different sciences that investigate human behavior, which include Economics, Sociology, Biology, and Psychology. All of these fields, he argued, have different models for what causes behavior, both proximately and ultimately, and these models are incompatible with each other. But at most only one of these different models can be true, and in fact, none of them might be. He then outlined how a unified model of what causes behavior can be achieved using five conceptual units, which are (1) gene–culture coevolution, (2) norms that can be social or internalized, (3) game theory, including behavioral and evolutionary game theory, (4) the rational actor model (or a model of decision-making based on beliefs, constraints, and preferences), and (5) complexity theory, which deals with emergence of system-wide properties from interactions among lower levels. Some of his thoughts on these issues can be found in his recent target review article (Gintis 2007).

The talks in the symposium thus covered a wide range of topics, yet were also unified in some deep sense in the approach they were taking. Take for example, the two talks that deal with taxa most distant from each other. Gintis' approach to behavioral sciences emphasizes the importance of the beliefs, constraints, and preferences model as describing the "mechanics" of decision making, which is not far conceptually from Michod's emphasis on a life history gene that modulates the growth and thus division of cells. Both of these proximate mechanisms set the stage for selection to act on, and evolutionary pressures seize on them to move the system in one way or another. Understanding the trajectory of evolution, be it cultural or genetic, requires understanding of both levels. Judging from the research reported in this symposium, exciting developments await in pursuing this goal.

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