

**DAVID C. QUELLER**

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Dear Search Committee:

I would like to submit my application for your open Animal Behavior position. I am applying jointly with my wife, Joan Strassmann, based on the possibility that there might be two positions available. Although we haven't been on the market, we are interested because of the outstanding behavior and evolution programs at Indiana University. I am enclosing my cv, a research statement, and a number of reprints. Joan sent in her application several days ago and did not include reprints, so these can stand for both of us. Emilia Martins told us we could wait on letters of recommendation, so let us know if and when you need them.

Sincerely,

A handwritten signature in black ink, appearing to read "D. Queller", with a long horizontal flourish extending to the right.

David Queller  
Harry C. and Olga K. Wiess Professor in Natural Sciences

**David C. Queller**  
**Research Interests**

**Past research**

*Plants.* I started out my research career as plant sociobiologist, exploring how some of the emerging insights from animal sociobiology would sometimes be relevant to plants. Two major lines of work emerged. First, I was one of several people to develop a theory of how kin selection and parent-offspring theory could explain the behavior and origin of nutritive tissues like the triploid endosperm of flowering plants. Second, in experimental studies of milkweeds, I showed that large floral displays primarily benefited the male function of these hermaphroditic plants.

*Theory.* After my Ph.D. my interests developed in two different directions. First, my work on kin selection in plants got me interested in kin selection theory in general, and I developed a number of mathematical models. I developed a new way to work with Price's covariance equation. This led to extremely simple derivations of both kin selection and group selection results that helped show (as has Michael Wade) how these two approaches are complimentary rather than antithetical. I also helped elucidate the role of population viscosity in kin selection. I developed a way to estimate genetic relatedness from allozyme and microsatellite data that has been very widely used. But I also developed a theory showing how eusociality evolved in the Hymenoptera not because of special relatedness issues, but because of special demographic factors (extended parental care under high adult mortality selects for adults to overlap their care). Finally, recently I have been working on the theory of genomic imprinting in social insects. If imprinting occurs in social insects, they may prove to not only be our best exemplars of cooperation between individuals, but also our best exemplars of conflict within individuals.

*Social insects.* When I moved to Rice in the 1980's I began working with Joan Strassmann, integrating into her social insects research program. We have worked on many topics, including kin recognition, the organization of work, phylogenetics, social parasitism, caste determination, and the advantages of sociality. But the dominant theme has perhaps been the role that genetic relatedness plays in the evolution of insect societies. Using allozymes, and then being among the first to switch to microsatellites, we estimated relatedness in dozens of species of wasps and bees. One important early conclusion was that the high  $3/4$  relatedness among females required by Hamilton's haplodiploid hypothesis was often not present, even in primitively eusocial species. However, relatedness remains important. With the exception of a few ants that may be irreversibly eusocial, relatedness within colonies is always well above zero, so that kin selection can work. We showed how reasonably high relatedness was maintained even in swarm founding wasps with many queens. We also documented the importance of relatedness in numerous within-colony conflicts: who should be queen, who should lay the male eggs, what the sex ratio should be, and when males should be produced. Studies of these conflicts allowed us to uncover a generalization within wasps that the queen tends to win conflicts in small-colony independent founders, but the workers tend to win in the large-colony swarm founders.

*Social amoebae.* Several years ago, Joan and I started working on the social amoeba, *Dictyostelium discoideum*, and it has now become our primary research focus. This species and its relatives display a degree of altruism parallel to that shown in social insects. Some cells die to create a stalk that facilitates the dispersal of other cells differentiating as spores. Because the fruiting bodies are formed by aggregation of separate cells, there seemed to be potential for cheating by avoiding the stalk. How cooperation is maintained in the face of cheating is central to understanding many of Maynard Smith's major transitions in evolution, and *D. discoideum* struck us as an ideal model system. A large community of biologists have worked on it for other reasons, and they have worked out numerous molecular tools and sequenced its genome. Its short generation time also makes it suitable for experimental evolution studies.

We first needed to establish a crucial point of behavioral ecology – whether the system involved conflict as well as cooperation. We showed that different wild clones mixed and that they sometimes cheated other clones in mixtures. We also documented some of the costs and benefits of mixing. We then moved on to exploring individual genes, and have found exciting results with each of our first three studies. The *csaA* gene turned out to be the best example of a greenbeard gene – a gene that produces a phenotypic marker, recognizes it in others, and acts altruistically to those it recognizes. In this case, all three properties emerged from the homophilic cell adhesion protein coded by this gene. Second, the *dimA* gene showed how pleiotropic effects, which normally act to constrain adaptation, can actually enhance group adaptation. Third, we combined studies of the social effects of the *fbxA* cheater mutant with field studies of relatedness to show how high relatedness limits the spread of this cheater in nature.

## **Future research**

*Social amoebae.* We are greatly expanding our studies of cheater mutants. Selections for knockout mutants that act as cheaters are identifying dozens of candidates. After we characterize the costs and benefits of these cheaters, and how they fare under different levels of genetic relatedness, we expect to have the most complete picture of cheater control for any system. We will also test the prediction that social conflict leads to more rapid adaptive evolution at these loci, using both within-species tests and phylogenetically based tests. For genes where statistical tests suggest interesting adaptive evolution, we can reconstruct ancestral sequences and insert them into *D. discoideum* background to determine how often selectively favored variants are cheaters.

We are also conducting studies of kin recognition. We have found different clones of *D. purpureum* tend to segregate out from mixed aggregations, so that they end up fruiting with their own type. This contrasts with the freely mixing *D. discoideum*, giving us a nice comparative test: we predict rapid conflict-driven evolution in *D. discoideum* but not in *D. purpureum*. We will also test whether *D. discoideum* recognizes foreign clones by using microarrays to see if consistent sets of genes get upregulated or downregulated in mixtures compared to clonal aggregations.

We will also be exploiting the system for studies of experimental evolution. We have already completed a thousand-generation mutation accumulation experiment. In addition to some of the standard questions addressed in such experiments, we are also

testing whether getting into spores (instead of stalks) acts like a fitness component, as expected if there is conflict between clones, but not if development is normally uniclonal. Other experimental evolution experiments will explore questions such as the importance of relatedness, the ease of evolving cheater lines, and the ease of evolving control of cheaters.

*Microsatellites.* In our studies of social evolution we have made considerable use of microsatellites as markers, and have also done a bit of work on the evolution of microsatellites. The recent publication of the *D. discoideum* genome revealed it to be the most microsatellite-rich genome sequenced. What is particularly intriguing is that a substantial fraction of coding sequences have long triplet repeats. These appear to code for long strings of amino acid monomers, often over 40 in row. Our early results indicate that such sequences are highly variable in length within the species, like non-coding microsatellites, but in sharp contrast to the usual low variability of coding sequences. In fact, one of the three genes we have examined closely approaches the level of variability in human MHC genes. We are interested in pursuing the evolution and possible functionality of such sequences. Mutation rates, estimated in a mutation accumulation experiment, are not unusually high for microsatellites. Comparisons with non-coding microsatellites will reveal the extent to which sequence variation is constrained by selection. If selection appears important, we will investigate the role of microsatellite length variation in some of our social genes.

*Imprinting in social insects.* David Haig has argued that genomic imprinting and uniparental gene expression are selected in the context of sexual conflict: paternally inherited genes in offspring have less interest in the health of the mother and will be selected to compete aggressively for maternal resources. This exciting theory would be more convincing if it could make successful predictions in a novel context. I wrote a theoretical paper arguing that social insects the best test case. The necessary relatedness asymmetries are created not just by multiple mating (as in the standard case), but also by multiple queens, and by the haplodiploid genetic system. Moreover, social insects interact with kin in many ways other than the maternal feeding of offspring. My paper showed that, if Haig's ideas are correct, haplodiploid social insects should be rife with imprinting conflict. In the future, we would like to test whether social insects have DNA methylation (the usual mechanism underlying imprinting), whether they have parent-specific gene expression, and whether the effects of this imprinting are as predicted by theory. Besides being our best examples of cooperation among individuals, social insects might also be outstanding examples of conflict within individuals.