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Dear Emilia,

I would like to apply for the open position in animal behavior. Enclosed is a CV and a research statement. I understand letters of recommendation can be delayed for now. My husband, David Queller, will also be applying for a position in your department. Please let me know if you need any further information.

Sincerely,

A handwritten signature in black ink, appearing to read "Joan".

Joan Strassmann, Ph.D.

Joan Strassmann – Research interests

My research interests center on social evolution. Cooperative alliances have occurred at several important transitions in the evolution of life and have proven evolutionarily and ecologically very successful. My research addresses how these alliances came to be, how conflicts are resolved, what conflicts remain, and how they influence sociality. I first used social insects - *Polistes* wasps, swarm-founding wasps, and stingless bees - for these questions, but in the last few years have moved to a new system. In the social amoebae of the Dictyostelidae social behavior can be tied to its underlying genes, and the evolution of acts and genes can be studied in a phylogenetic context.

Social amoebae

Kin selection, game theory, and mutualism theory have developed powerful predictive models for cooperation and conflict, but the theories have been developed hand in hand with work on the organisms where the theories have been tested, social insects, birds and mammals. Furthermore, none of these organisms has proved to be an ideal model system for social evolution, most notably because of long generation times, and because we have not identified the genes underlying social acts. Recently we have proposed a compelling model system for social evolution, the social amoeba *Dictyostelium discoideum*. This cellular slime mold in the Amoebozoa, sister kingdom to animals plus fungi, has a social stage with sterile castes and a solitary stage without them. Most of the time amoebae of *D. discoideum* move around the forest floor preying on bacteria. When bacteria grow scarce, and there is a sufficient number of amoebae nearby, they respond to cAMP signals and aggregate into a slug which ultimately forms a fruiting body in which about 20% of cells die to form a rigid stalk that the remaining cells flow up where they sporulate.

Since the multicellular body is formed from an aggregation of amoebae that were free-living on the forest floor, it can be chimeric, making evolutionary conflicts likely. We have shown that the population of *D. discoideum* in small, 0.2g samples is genetically diverse, making it possible for aggregations to contain more than one clone. We have further shown that genetically distinct clones readily aggregate together, and that when they do so one clone often exploits the other, contributing less than its fair share to the stalk. These chimeras exhibit within-organism conflict since they migrate less far than do slugs of pure clones. Thus *D. discoideum* meets the first requirements for a model system for social evolution. It shows both reproductive altruism, and within-group conflict. There is within-group variation in genetic relatedness. Also, it is easily manipulated in both laboratory and field. It has a short generation time for mitotic cell division and for the social stage, making experimental evolution and selection experiments feasible.

D. discoideum is in a family that varies in a number of key social traits, making efforts at tracing the phylogenetic history of social genes promising. Within the family are species that have stalks made from cellular secretions, not dead cells. Other species have an escape from the social stage: they can form spores called microcysts without going through the social stage, something *D. discoideum* and its closest relatives cannot do. In some species cells in the slug specialize into stalk much earlier than is the case for *D. discoideum*, thus reducing the time window for conflict. Other species have slugs that do not migrate, also reducing the time window for conflict. This social variation has its basis in social genes, whose history should tell us much about the evolution of sociality.

These advantages to *D. discoideum* as a model system are important, and are considerably enhanced by another type of advantage. It has been used for many decades as a model system for development. There is a sequenced genome, and techniques for knocking out and modifying genes. Hundreds of mutants of specific genes have been characterized with respect to their impact on development, on motility, on phagocytosis, and on signal transduction pathways. We have investigated three of these genes. One, *csaA*, proved to be a green beard gene, that both recognized and favored bearers. Another, *dimA*, showed that a gene that apparently favored cheating in its absence, did not by the end of spore formation,

because of the loss of another important function of the gene. This indicates that pleiotropy can have a positive function, limiting social exploitation. The third *chtA*, is favored in chimeras but loses in natural conditions because of its disadvantages when clonal.

Current research has shown that in another species, *D. purpureum*, non-clonemates are recognized and largely excluded from social aggregations when amoebae are dense, but not when they are sparse. This occurs after chemoattraction, as slugs segregate by genotype. This is in contrast to *D. discoideum* which does not exclude non-clonemates. We are looking for similar patterns in other species. We have looked at the costs and benefits of a cheater mutant and found that though it exploits others in chimeras it does poorly enough on its own and suppresses the success of the chimera as a whole sufficiently that it will not spread in nature. We have identified about 30 genes that when knocked out cause their bearer to be a cheater, overrepresented in a chimera with wildtype. We are currently characterizing the action of these genes, and identifying more cheater and victim genes. We are investigating known knockouts likely to affect cheating at different levels of relatedness to determine their action. We have conducted a 1000 generation mutation accumulation experiment, and are currently finding a decrease in social function in some of the 100 lines. We are testing the hypothesis that weaker cells will be forced to become stalk, whether or not they are less able to become spore, because of social competition. We have amassed a frozen spore library of hundreds of clones of about 8 species which is useful in many ways. We are sequencing clones of several species and placing them in the *Dictyostelium* phylogeny based on SSU rDNA to determine the best outgroup for *D. discoideum* and to evaluate species identity of other clones. Ultimately we expect to identify genes with natural variation that impacts their social behavior, trace the evolutionary history of these genes, and with homologous recombination put ancestral forms back in modern cells and see how they impact social behavior. This has not been done for any social gene in any organism.

Social insects

Here are a few highlights from 25 years of work on social insects.

Tests of kin selection theory in *Polistes* wasps: In the mid 1970s, the importance of Hamilton's theory of kin selection was just becoming known. According to this theory, altruistic acts should be performed by individuals towards relatives if the altruist passes on more genes this way. I conducted some of the first tests of this theory using social wasps. *Polistes* wasps were ideal for testing kin selection because of their behavioral and reproductive plasticity in small, easily followed groups. I used a novel behavior, the formation of satellite nests by workers or queens of *P. exclamans* colonies, to demonstrate that other workers made different decisions based on relatedness, in accord with kin selection theory. They were less likely to join a satellite nest when their relatedness to its queen was lower than their relatedness to the queen on the original nest. I also found that relatedness was essential for cooperation, that there was a convention for who became queen (the first to arrive at the nest site), and that larger groups of nest foundresses out-reproduced smaller ones, and were better at recovering from losing their nests to predation. Nine years into my work on *Polistes* I began a collaboration with David Queller which continues to this day.

Within-colony conflicts of interest and queen cycles in tropical swarming wasps: We began to study multiple queen wasps because multiple queens present a potential problem for kin selection theory. Many egg laying queens in a colony will cause low relatedness and this could be a serious challenge for kin selection. Neotropical swarm-founding wasps also have genetic conflicts of interest between workers and queens over male and female production. We found that the more numerous party, the workers, wins this conflict. The result is that new queens are produced only when there is only a single queen remaining, and males are produced when there are multiple queens. This work solved the low relatedness problem since it means that queens are the highly related daughters of a single, once-mated queen. This pattern also holds for an independent group of multiple-queen

wasps from Africa, indicating the generality of worker control and the resultant high relatedness in multiple-queen wasp species.

DNA microsatellite loci for relatedness: Any study of social evolution is dependent on accurate estimates of how interacting parties are related to each other. We were early in realizing that highly variable DNA microsatellite loci were ideal for estimating genetic relatedness and so I spent a sabbatical learning recombinant DNA techniques. I developed clear techniques, found hundreds of microsatellite loci in a variety of taxa, shared them freely before publication with other researchers, and showed how to use them for determining relatedness, parentage, mate number, and sex of brood.

Single mating and worker-queen conflict over male production in stingless bees: Behavioral conflict can be an indicator of unresolved genetic conflicts of interest. We realized that a promising arena for investigating ongoing conflict is the stingless bees of the tropics. In contrast to honeybees, where multiple mating causes both queen and workers to pass on more genes when the queen produces all males, in stingless bees workers and the singly mated queen are in conflict over male production. Does one party win this conflict and does it vary across the many stingless bee species? For this study we first established that queens mate only once, something long suspected but not demonstrated with robust molecular markers. Then we tested whether workers or queens win the conflict of interest over producing males, and found that, depending on the species, sometimes workers win, sometimes queens win, and sometimes both parties lay eggs, the workers sneaking in after the queen to replace her eggs. The observed behavioral conflict is thus explained by genetic conflicts of interest in this group.

Recent and future research: We have looked at control of activity in social insects and found that the queen plays less of a role than previously thought, even in small colonies. We have investigated the role of cuticular hydrocarbons in recognition of various sorts.

Future research on social insects will be geared towards looking for genomic imprinting to test Queller's predictions as to where and how it should appear. Kin selection predicts that imprinting will cause genes expressed in a mother's progeny to limit her investment, and those expressed in the father's progeny to do the opposite, assuming more maternal than paternal investment, and a lack of monogamy. The predictions have held up well in mammals.

DNA Microsatellites

Since we use DNA microsatellites (variable regions of short repeats like AAT) as markers for relatedness estimates, it was natural that we became interested in them in their own right. Microsatellites are thought to mutate particularly rapidly because of slippage during replication that would add or take away a repeat unit, for example taking a series of 10 AAT repeats up to 11 AAT repeats. We did a study of microsatellite evolution in a large wasp clade, then turned our attention to the origin of microsatellites using a human mutation database. We found that insertions are often repeats of pre-existing neighboring sequence, even in the absence of repeats, and so this can be the origin of short repeats.

Current research: *D. discoideum* has a higher density of repeats than any other organism, comprising about 10% of the genome. We have found that many microsatellites within genes are highly variable, contrary to the usual situation of invariable coding sequences on this species involves studying microsatellite evolution inside and outside genes (60 pairs of microsatellites; 10 on each chromosome) across a geographic sample to test whether those in genes are under stronger selection. We are also looking at microsatellite mutation in 60 genes in a 1000 generation mutation accumulation experiment. Ultimately we expect to tie microsatellite variation in genes to gene function, and are most interested in looking at genes important for social behavior.