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Exceptions to the Kin Selection Model in Ants and Wasps

The complex social structures and reproductive hierarchies found in eusocial insects have long been put into evolutionary context by the scientific community with Hamilton's theory of kin selection. Haplodiploid genetic systems that can lead to greater than 50 percent relatedness between siblings are found in some species of these insects. These levels of relatedness combined with Hamilton's mathematical representation of how costs, benefits, and relatedness come together to produce a "pretty," clear picture of how eusociality works and succeeds in nature. However, researchers have realized that within the many variations of eusocial colony organization there are exceptions to the behaviors and social groups predicted by a simple model of kin selection. In some cases, supercolonies of distantly related individuals manage to survive and thrive. Hamilton's model would predict the opposite, since unrelated individuals would receive no indirect fitness benefits from helping each other. There are also instances of elevated, high cost aggression between closely related individuals. Hamilton's model would predict cooperation or at least decreased aggression with close relatives. A study of each of these exceptional systems, presumably derived from the more conventional type of eusociality, is very relevant to the comprehension of the genetic and behavioral traits that lead to and maintain general social structure in insects. The uniqueness of these systems is also of great importance ecologically when taken in the larger context of contact with individuals outside the colony level. From an evolutionary perspective, it is necessary to distinguish between subsets of species that may behave differently due to different ecological circumstances. To maximize the benefit of learning from such configurations, integration of the evolutionary, behavioral, ecological, and genetic aspects of supercolonies and other distinctive social groups is to be encouraged.

The history of kin selection theory

Darwin's theory of evolution by natural selection has been disparaged as "cruel" since its introduction to the general public. While the term "survival of the fittest" is not really an apt description of evolution in general, the clearly negative response of many to this type of picture of the world points to an interesting question of evolution itself. Humans, it seems, would at least like to think that they and their surroundings are inherently inclined to civilized behavior, which generally does not include the mortally competitive, entirely selfish conduct implied by "survival of the fittest." Altruism, defined loosely for the moment as unselfish behavior, is highly regarded in human culture and must be for social systems such as ours to exist. Aversion to natural selection by many could be due at least in part to its inability to explain altruism as we humans experience it. Social systems in nature are not all like our own so ideally an explanation of altruistic behavior would be general enough to explain those, as well. At the same time, one must consider that without the status the ideal of altruism holds in human communities, scientists may not have tried to find any version of it in non-human organisms. The introduction of kin selection as a theory, and Hamilton's derivation of a rule to mathematically predict when it is likely to happen were thus immediately embraced by the scientific community. Kin selection incorporates behavior and population genetics into an elegantly simple model (Queller 2000b). Eusocial insect groups are not only explained, but are used as examples of the accuracy of these theories (Queller 1998). In fact, upon its introduction kin selection was considered so satisfactory an explanation in the 1960's it managed to divert the scientific community as a whole toward research involving the ultimate causation of animal behavior (Alcock 2003). However, while kin selection as a concept has withstood the test of time, some recent studies indicate that Hamilton's rule may not apply to all cases as easily as previously thought.

Basic kin selection as defined by Hamilton

Kin selection simply says that when organisms act altruistically, their actions are more likely to be aimed at genetically related individuals (Queller 1998). The scientific definition of altruism used in

this theory refers specifically to actions that decrease the potential reproductive success of the giver, while increasing the potential reproductive success of the receiver. Eusocial insect colonies are often given as the classic example of this, since colony workers spend all of their resources increasing the reproductive success of their queen (Sundström 2001). Hamilton's rule offers a mathematical relationship to explain when these and other organisms would be best served by performing such behavior. The simplest expression of the rule is: $rb > c$. In this inequality, r is the relatedness of an actor to a receiver, b is the benefit incurred by the receiver, and c is the cost incurred by the actor. The rule can be modified to calculate costs to non-actor relatives as well, by multiplying a coefficient of relatedness (rc) of the other relatives to the cost incurred value (Queller 1998). Because related individuals carry some genes that are from common ancestors (genes that are identical by descent,) they are helping some of their own genes reproduce by helping relatives reproduce. This indirect fitness, combined with the individual's own reproductive success, is called the inclusive fitness of an organism. Hamilton's rule is actually a very simple statement summarizing the extensive derivations that gave mathematical evidence for the validity of his concept of inclusive fitness and its link to overall costs and benefits (Hamilton 1964).

Order Hymenoptera, which includes ants, bees, and wasps, is a special case in kin selection because of the unique system by which sex is determined. Males in this order are haploid; they are produced from unfertilized eggs and have only one of each chromosome. Females are diploid, with a chromosome from each parent. Since males only have one of each chromosome, they contribute identical genes to each egg that is fertilized. Queens, however, contribute 50% of their total genetic complement, since they have two of everything. This means that the sisters with half their genes from one male and half their genes from one queen share on average 75% of their genomes. This high coefficient of relatedness is often cited as a primary reason for eusociality, as the increased r in Hamilton's mathematical model means that workers gain almost as much reproductive benefit from helping their supersister queen reproduce than they would from attempting reproduction on their own.

Supercolonies as extended “family”

The Argentine ant, *Linepithema humile*, has attracted a considerable amount of attention due to its extraordinary ability as an invasive species in both North America and Europe. Argentine ant colonies in their natural habitat are large and polygynous, with more than one queen per colony (Tsutsui 2000). In their home range, these ants will aggressively attack conspecifics from different colonies if their colony's territory is breached (Tsutsui 2003) but can still coexist with them and with other species. When these ants are introduced to new areas, however, they are usually found in one large supercolony that can extend for miles. Ants within a supercolony do not attack one another, regardless of genetic relatedness or native location (Tsutsui 2003). Supercolonies such as these can be found in California (Tsutsui 2003) and in southern Europe (Giraud 2002). The supercolony system can be seen as contradictory to the expectations of kin selection, since non-relatives are treating each other as if they were in the same colony (which usually implies at least some genetic relationship). The earlier Tsutsui study (2000) used a behavioral assay where they observed aggression between conspecifics from different regions and supercolonies. They also did some microsatellite analysis on their study populations. They observed no aggression between members of the same supercolony, regardless of location of origin. Microsatellite analysis uncovered a genetic bottleneck, which lowered the populations' allele variety in comparison to the native populations in Argentina. Tsutsui (2000) concluded at the time that this genetic bottleneck led to a population of ants that were indistinguishable from one another chemically, since they all carried the same alleles. Since Argentine ants determine comradeship based on whether the individual in question is different from its own template, and they all had the same chemical template because of the bottleneck, it was assumed they did not respond aggressively to supercolony-mates. This hypothesis matches predictions from Hamilton's model and was accepted widely by other scientists (Queller 2000a). The Giraud (2002) study involved behavioral and genetic assays of southern European Argentine ants. Their behavioral results were as expected for supercolonies, with no aggression within colony but high aggression between supercolonies. They then

used microsatellite analysis to determine relatedness within and between supercolonies, using a separate sample from Argentina as a reference population. Their results showed evidence of a slight genetic bottleneck in the European ants' history, which was unsurprising since they are an invasive species. However, they drew a different conclusion about this bottleneck than did Tsutsui (2000). Giraud noted that the ants within European supercolonies showed considerable differences at 8 loci, implying that the ants are not "relatives" in a sense that would be significant to kin selection. They were not likely to be responding to phenotypic similarities based upon environmental influence, since members of the same supercolony could live in the next nest, or thousands of kilometers from each other. Tsutsui et al. (2003) showed similar results in later experiments on their southern California populations. Aggression was nonexistent between members of supercolonies, no matter where they were from, and was completely independent of genetic relatedness. The hypothesis put forth by both groups, in slightly different forms, was that although there was a slight bottleneck in the invasive populations, the potent factor in Europe and California was that supercolony ants had lost their ability to distinguish nestmates from non-nestmates. In their native habitat, aggressiveness between nestmates and non-nestmates would have a lower cost because populations were less dense than in the introduced areas. The high cost of aggression in high-density areas where the invasive species does very well (presumably due to lack of parasites and predators, a common assumption made with invasive species) would be magnified by the increased likelihood of encountering a non-nestmate. This in turn would snowball once the trait of aggression was selected against, leading to a situation where preference for kin would be essentially ignored and causing problems for Hamilton's rule.

Ecological situation and supercolonies

Fire ants and Argentine ants are not the only species that create supercolonies. Red ants (*Myrmica sulcinodis*) can also exist in this social structure. van der Hammen et al. (2002) present an example of microsatellite analysis on supercolonies of this species. These colonies are found on islands in Denmark, and like the Argentine ants, show evidence of genetic bottlenecks due to founder effect.

Ingram (2002) indicates that highly dense Argentine ant populations tend to have more closely related neighboring nests, but these nests tend to have fewer queens and less reproductive success than nests in less dense areas, demonstrating that there is an ecological factor involved in the likelihood of supercolony development. Though Tsutsui and Giraud both dismiss the possibility that founder effect bottlenecks can be the sole explanation for the initiation of supercolonies, it appears that all examples of supercolonies currently in the literature are invasive to the area in which they are found and have bottlenecks in their genetic history. At this point it is impossible to distinguish between the effects of change in allelic frequency due to founder effects, and the invasive nature of the organisms in their overall trend toward supercoloniality.

Nestmate or relative? The within-colony problem

A much simpler version of this story can be seen within colonies. Carlin and Holldobler (1983) found that recognition in ants is not based upon purely genetic signals. Eusocial hymenopterans often use chemical signals to distinguish comrades from strangers (Carlin 1983). However, these chemical signals are created by environmental exposure, not by the genetic makeup of the individual carrying the signal. Usually, this does not matter much because close relatives are often nestmates and therefore the chemical signal is an honest representation of the relatedness of the individuals. It can cause conflict in polygyny where the queens are not closely related however, giving the false impression that a nestmate is kin. Polydomy, when one colony has more than one nest independent of queen number, leads to a false negative; in this case genetic relatives are spread over multiple nests, which could have different chemical makeup and which may lead to an individual attacking kin. Argentine ants, for example, have been shown to use cuticular hydrocarbons to assess conspecifics and respond aggressively to any chemical considered “foreign” even when presented on a nestmate (Liang 2001).

Recognition methods in hymenopterans

The ability to use chemical signals for nestmate recognition does appear to be at least partly genetic, since the ants must have the ability to detect the signals. Krieger and Ross (2002) discovered a single

gene that determines whether fire ants (*Solenopsis invicta*) have monogynous (one queen) or polygynous colonies. Fire ants also show evidence of supercolony structure as invasive species (van der Hammen, 2002). The discovery of any single gene that affects complex behavior so profoundly is important to understanding eusociality; the genetic makeup of hymenopterans is so unique and single gene effects on any trait are rare. The gene identified by Krieger and Ross, *Gp-9*, is believed to control a protein used by workers to recognize queens' chemical profiles, which can influence the overall chemical profile found in a nest. Homozygotic queens collected in Georgia were monogynes, while heterozygotes were polygynes. The discovery of this association allowed the investigators to consider the evolutionary history of polygyny, which in the *Solenopsis* line they verified as the newer of the two phenotypes. More importantly, however, the existence of *Gp-9* may offer a hint about a possible proximate explanation of the mechanism behind the unparalleled success of introduced ant supercolonies. If a gene in Argentine ants similar in function to *Gp-9* exists, it is possible that it would be the only changed gene needed to create a supercolony phenotype. A mutation that overrides the recognition system in the workers would decrease costly confrontations with neighbors, and could be the difference between supercolonies and more typical colonies of the native range.

Sometimes, an inability to distinguish between nestmates and non-nestmates is simply due to physiological constraints. Astruc et al. (2001) found an example of this by testing the ant *Tetramorium bicarinatum*, a polygynous species that often is surrounded by closely related colonies. Response to conspecific and allospecific (*Myrmica rubra*) was tested and chemical content was compared. Nestmates, predictably, were not aggressive. Intraspecific contact in *T. bicarinatum* was also aggression free, which was not expected in non-nestmate encounters. However, non-nestmate *Myrmica* meetings and *T. bicarinatum/Myrmica* combinations led to aggressive response. A proximal cause for this result is that the ants do not have the physical means to distinguish the subtle differences in chemical signals of conspecifics. This could be due to the high viscosity of the species; relatives tend to be neighbors if not nestmates, so the selective pressure for distinguishing between nestmates and

neighbors is diminished. A situation such as this could be a model for how predisposition toward supercolonies arises.

A model of altruism without kin selection

Hamilton was clear in his original paper that his model, like all mathematical models, was only expected to have complete success with populations under rather strict rules, some rarely seen in reality (Hamilton 1964). In this case, the model works so well with real populations that only now are scientists complicating the rules to make more accurate models. Le Galliard et al. (2003) offer a new model of how altruism may arise in haploid organisms that incorporates some of the differences between the original kin selection model and the organization observed by scientists in the field and lab. First, they do away with the assumptions inherent to kin selection that individuals are sessile and the population in question is at its environment's carrying capacity. They also assign costs to movement and allow for changes in costs and benefits based upon variety in resource availability. Their models manage to produce obligate altruism within parameters of evolutionary expectation (Le Galliard 2003) but without invoking kin selection to augment an individual's inclusive fitness. The limit to this model appears to be in its focus on haploid organisms. While it is a testament to the strength of Hamilton's model that more models like this one are not better known and used within science, it is becoming more and more necessary to incorporate new models into Hamilton's.

Sibling rivalry: when competition with relatives unravels kin selection

Kin selection is expected to keep aggression between relatives below what would be expected in non-relatives. As mentioned above, it assumes that the organisms in question are sessile, which would allow individuals acting altruistically to ensure that their actions are directed at kin (Le Galliard 2003). In real situations, however, evidence shows that kin in limited dispersal situations do show a considerable amount of aggression toward each other. An example of this is a study by West et al. (2001) on fig wasps. By incorporating data on aggressiveness of flightless males in many species of fig wasp, they found that there was no association between relatedness of individuals and degree of

aggressiveness. However, there was an association between future mating potential and aggressiveness, leading West to conclude that totally local competition between relatives for direct fitness as seen in fig wasps can be more important to actual behavior than the possible increase in inclusive fitness Hamilton's model predicts. Local competition makes the reproduction of others a higher cost to the individual, since that individual must share resources for its own reproduction (West 2001).

Summary

Hamilton's theory and mathematical model of kin selection have played an enormous role in shaping the direction of eusocial behavior research for the last 40 years. Recent studies, especially those on supercolonies, have demonstrated that this model may not be adequate to completely explain eusocial systems and their origins. Supercolonies' low overall relatedness show evidence of "misdirected" altruism within the parameters of kin selection, but their evolutionary success in invasive populations at least for now makes them worthy of note and considerable research effort. Combining data from genetics, behavior, and ecology could offer some insight into the development and success of supercolonies. Evidence that kin selection's predictions are being broken in the opposite "direction" by closely related individuals that do not adjust aggression toward each other in times of limited resource furthers the argument that kin selection cannot be applied as widely as it has been in the past. Future research on the more detailed aspects of eusociality with cautious use of kin selection theory is likely to smooth out the inconsistencies between Hamilton's very useful rules and the reality of insect behavior.

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