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Ants and Prisoners

1. Kin Selection Theory

One of the major challenges that has arisen to Darwin's theory of Natural Selection is the role of altruism in social insect societies. Altruism can be defined as occurring "when an individual behaves in such a way that the result is an increase in the survival or offspring production of another individual and decrease in its own survival or offspring production" (1). Altruism is common in eusocial populations which are characterized by individuals that care for their young, a reproductive division of labor, and a caste of normally sterile workers that assist their mother in raising their sisters and brothers. Ants and the larger class of Hymenoptera including bees and wasps have are eusocial insects. They are characterized by a small number of reproductives within the larger colony and are often haplodiploid, which means that diploid females are produced from fertilized eggs while haploid males are produced from unfertilized eggs (5,7).

The issue of altruism and social insects was a problem that Darwin recognized within his lifetime and attempted to explain by extending his idea of the 'unit of self-interest' beyond the individual to include the family, or colony of relatives (1). Darwin's idea was that an individual can act in a way that is detrimental to its own survival or reproductive success as long as the sacrifice is outweighed by the benefit to the family as a whole. This idea was further developed and formalized by William D. Hamilton (1963) as inclusive fitness theory and was termed kin selection by Maynard Smith (1964).

Kin selection theory assumes that the gene is the unit of self-interest and recognizes that genes can be passed to successive generations either by increasing the fitness of their vehicle (measured by classical fitness), or by increasing the fitness of relatives who share copies of the gene. Measures of inclusive fitness incorporate into classical fitness the effect on the reproduction of all collateral relatives, and the probability those relatives share the allele of interest (3).

* Classical Fitness = E(RS)/Average RS for population

* Inclusive Fitness = E(RS) + ∑[bjE(RS)]/Average IF for population

E(RS) is the average direct reproductive success of individuals possessing the genotype of interest. bj is the coefficient of relatedness, the probability relative j possesses the allele of interest (3). This means that if a certain allele promotes altruistic behavior in its vehicle, since it is inherently selfish, it will spread through the population via the collateral relatives of the altruistic actor. In other words, altruism is associated with a specific allele, and an individual which is dominant for this allele acts altruistically towards its kin because its kin have an above-average probability of also bearing this allele and will therefore propagate it through reproduction. Formalized, the allele for altruism will spread if $C/B < gBA$, where C is the cost of the altruism in terms of loss of fitness of the altruist, B is the fitness gain to the beneficiary, and gBA is the relatedness between altruist and beneficiary (3, 1).[1]

[1] This is alternatively written as $rb-c > 0$, where r= relatedness, b = benefit, and c= cost (1), and $rbb > rcc$ where rb= actor's relatedness to beneficiary, b= fitness gain to beneficiary, rc= actor's relatedness to individual, and c= fitness loss to relative experiencing cost(5), but all three inequalities amount to the same result.

Kin selection theory allows analysis of tradeoffs in animal behavior between reproductive gains and losses in the short term and long term, and explains how altruistic behavior is consistent with natural selection. An essential prediction of kin selection theory is that altruism should be directed toward kin, the validity of which has been shown through numerous studies showing that social insect colonies are extended families and unrelated individuals are customarily recognized and excluded.(5) We will return to this validation later in regard to unicolonialism.

2. Kin Recognition

Kin selection depends on kin recognition, or more generally nestmate recognition. If an ant cannot distinguish its colony from outsiders, obviously it cannot selectively act altruistically towards its kin. Ants inspect one another by sweeping their antennae, acutely sensitive chemical sensors analogous to the human nose, across each other's bodies. If the ants recognize each other, there is little behavioral response. If they do not recognize each other they attack with a degree of violence somewhere across a spectrum of aggression with interspecific interactions as the most aggressive and intraspecific interactions with non-colony members ranging across a gradient of less aggressive response (8).

Each ant has a set of recognition cues, chemical odors that are particular to that ant and its nest. There is little evidence to support the idea that ants actually recognize other individual ants, or even that they recognize their kin specifically. The evidence shows rather that ants recognize their nestmates and the generally accepted explanation is that recognition cues are a combination of genetics, environment and diet, and that they change subtly over an ants lifetime due to the latter factors (7, 3). The idea behind the genetic portion of the recognition cue explanation is a simple complement of kin selection theory. There is a specific gene that forms the basis of each ants particular recognition cue and this is expressed in the phenotype as a chemical odor. Since colonies of ants tend to be strongly related it is likely they share the same allele for a particular recognition cue. In addition, it is advantageous to the ants to increase the fitness of their kin, therefore through natural selection colonies of ants evolve to share the same gene for recognition if they do not already. (The ants that share the same allele have greater fitness).

In addition to a label, each ant has a template with which to interpret the cues of other ants through comparison. If an ant is encountered that does not match the template, it is assumed to be an outsider. There is little evidence to support the idea of a genetic template, rather it appears the template is learned through normal social interaction between colony workers such that each worker shares the same profile. This is referred to as the single mean template, or the colony "gestalt" model (7). It is assumed that as the colony recognition cue changes subtly over time due to environmental and dietary factors, the template changes respectively.

The exact nature of the cue and template is of hot debate. One of the major questions is whether the queen influences worker ants' recognition cues, or whether it is mainly passed between workers. Another question is what influence environmental factors and diet have on a colony gestalt cue. Other questions involve how the cue is learned, how many templates each ant might store, whether enemies are recognized specifically or just noticed as different, and so forth. My opinion on the matter is a variation on Carlin and Holldobler (8). In my opinion, the queen's odor is important in monogynous colonies, but polygynous colonies have evolved to factor it out. Also, I believe the environment is important only in its possibility to confuse. This would mean that most of an ants competitors are located within a relatively small vicinity of the ants nest, and therefore most of the competitors an individual ant will be exposed to will share a similar environmental cue. This factor is then learned to be ignored from the nestmate or colony recognition cue.

I believe that when scientists expose ants in the lab to other ants they would never have any chance of meeting in the world, this experimental process is responsible for the intraspecific gradient of aggression observed in lab experiments on ant behavior. If the tested ants were exposed to these potential competitors while they were learning their recognition template they would act as aggressively as they do to other ants. This problem is enhanced by experiments in which ants eclose in the laboratory and are exposed only to their own 'nest' for the duration of their template learning time. Ants generally act at extremes of the aggression continuum, but when removed from their normal habitat and learning environment confusion can arise leading to a gradient of aggressive responses.

3. The Threat of Unicolonialism

There are many types of ant colonies which vary depending on the number of queens (monogyne or polygyny), males (monoandrous or polyandry), and nests the colony inhabits (monodomous or polydomy). The most common structure is multicoloniality, in which a "population consists of many distinct colonies whose members are mutually hostile and do not mix" (1). At the opposite end of the spectrum, the most curious of ant colony situations is unicolonialism, a situation in which the colony encompasses a huge number of individuals, is highly polygynous, and non-aggressively inhabits a large network of interconnected nests, presumably created by budding (3, 5). A unicolonial population is called a supercolony. Relatedness between individuals in the supercolony varies tremendously and may even approach zero, yet somehow altruism is maintained. This raises a problem for kin selection theory, because without relatedness as an incentive for altruism, non-reproductive workers lose all chance at propagating their genes through successive generations and worker traits can no longer evolve adaptively (5). So what is going on?

4. The Case of Linepithema Humile

Native to Argentina, Linepithema humile has been inadvertently introduced into all other continents with a Mediterranean climate, and has competitively displaced native species wherever it has been introduced (2, 9). Once established, Linepithema humile colonies reproduce by budding, which is a diffusion-like process (9) that Wilson points out as "an evolutionary step that parallels the adoption of apomixus and vegetative reproduction in nonsocial organisms" (3). This permits the rapid growth of population in sparsely distributed habitats, or in the case of invasives like Linepithema humile, systems that are relatively free from competition (3). In contrast, typical ant colony reproduction involves a queen undergoing a mating flight and founding a colony independent of and often far away from her natal nest (9).

In its native home Linepithema humile inhabits a species-rich environment with many competitors, reproduces via mating flights, and behaves in a multicolonial fashion. When the Argentine ants are introduced to foreign soil however, they form giant supercolonies and dominate the region. It is well known that a lack of competitors in foreign ecosystems allow invasive species to reproduce with such abundance, the question is how does natural selection allow for intraspecific cooperation in these situations? Tsutsui, et al. examined this question in regard to the Linepithema humile supercolony in California, and Giraud, et al. in regard to the supercolony in Southern Europe, each with different results.

a) California

Tsutsui, et al. examined the relationship between genetic similarity and intraspecific aggression among nest from sites along 1,000 km transects through California (introduced range) and Northern Argentina (native range). They compared data between and within supercolonies from both areas and found that the number of alleles in the introduced range was half that found in the native range. Intraspecific aggression was absent from the California population, whereas it was pronounced in the Argentine population. In Argentine ants there was a direct relationship between the physical distance of nests, aggression level, and genetic similarity, whereas in the Californian ants equally distant nests were genetically similar and non-aggressive. This leads to the conclusion that the lack of intraspecific aggression in introduced populations is the result of a genetic bottleneck, in other words, the supercolony is in fact one big extended family and they are more related than was originally thought. The reduced intraspecific competition due to relatedness between the ants allows for the high nest density associated with budding and the resulting dominance of Linepithema humile. This hypothesis is consistent with kin selection theory and natural selection, but it does not answer the question of how supercolonies are possible when the individuals are *not* highly related.

b) Southern Europe

Giraud, et al. investigated the largest known supercolony on earth, a colony of Linepithema humile that reaches at least 6,004 km from the North western coast of Spain, across Portugal, the southeastern coast of Spain, Southern France, and into Italy. They collected approximately 5,000 workers from 33 nests distributed along the Atlantic and Mediterranean coast, conducted genetic analyses and aggression tests, and compared the results to those obtained for native Argentine populations. The experiment revealed the existence of two supercolonies, one smaller catalonian one with three populations in eastern Spain, and the main colony. Members of the same colony never showed signs of aggression, whereas between members of the different colonies aggression was always severe leading to the death of both workers in 98% of cases. Although European Populations of Linepithema humile did have significantly fewer alleles than Argentine populations indicating a genetic bottleneck the reduction was only 28%, as opposed to 50% in California, indicating the bottleneck was not very severe and that bat least 18-39 random haploid geneomes were introduced to Europe to account for the genetic diversity. In addition to the genetic analyses, their aggression tests showed no correlation between genetic dissimilarity and aggression, or geographic distance within the colony and aggression, indicating that loss of nestmate recognition could not be merely due to a genetic bottleneck.

Their explanation, the selective genetic cleansing hypothesis, is simple and elegant. Linepithema humile arrives on foreign soil as invader, inhabits an open niche and lacks competitors allowing it to expand unchecked in a dense budding network of nests. It has been shown that cooperation is actually more beneficial than territorial aggression, allowing higher birth rates and lower death rates (4). In areas of such dense population the benefit of aggression is clearly outweighed by the benefit of cooperation, and individuals sharing a recognition cue allele are naturally selected; the most fit ants are the most cooperative ones because they fight less often with neighbors and are more productive. This allows unicoloniality without a bottleneck and without high relatedness between individuals in the colony.

5. Stability

Many believe that the unicolonial structure is transient and doomed to failure. The expectation is that genetic mutation will cause certain individuals to act selfishly, disrupting the balance of the system. Two examples commonly given are mutations making female larvae more likely to become queens than workers, leading to the loss of a worker caste and eventual extinction, and favored mutations for nepotistic brood care, leading to a reversion to multicoloniality. On the other hand, as E.O. Wilson has pointed out, unicoloniality arises when lineages the ecological conditions are just right. Supercolonies tend to inhabit new, empty, or disturbed habitats, and are fantastic interspecific competitors, their evolution is often compared to vegetative propagation in plants. This may confer short term advantages for unicoloniality that outweigh its long term instability and allow it to evolve, perhaps similar to the evolution of asexual reproduction in some animals (1,3).

I disagree with this prediction for the supercolony's future. Most approaches to analyzing animal behavior take the approach of the prisoner's dilemma. This examines long term results of an individual's short term actions in terms of that individual's gain or loss in fitness. As we have seen, Hamilton's rule extends this take to encompass relatives, but it is still a fundamentally individualistic approach. The gain and loss are measured by the probability an individual's genes will be propagated to the next generation, and that is the bottom line. This view of the situation for interaction between two unrelated ants can be mapped out as follows:

Individual 2

Cooperative Aggressive

Individual 1	Cooperative	3,3	0,5
	Aggressive	5,0	1,1

Where benefit is measured on a scale of 0-5, 5 being the highest. The dynamic of this situation is known as a Nash equilibrium, and it is a paradox because both individuals will always act aggressively, but when both act aggressively both individuals end up the worst off. The key element of this situation is that no matter how an individual starts off acting, they will always wind up acting aggressively because they have no incentive to do otherwise. This model assumes that when the two individuals cooperate there is a mutual loss in benefit from if only one acted aggressively, and this in turn assumes that the benefit is measured in terms of the success of one's genes in a situation where resources are limited. Yet what about invasive species which occupy new niches and have little or no interspecific competition for resources? This allows a re-evaluation of the situation, because it is no longer *necessarily* advantageous to defend territory. If we evaluate gain and loss in terms of reproductive success for the individual this does not make sense, but if we evaluate it by success of the entire colony in terms of growth rate (#births-#deaths) it can, if the situation looks as follows:

		Individual 2	
		Cooperative	Aggressive
Individual 1	Cooperative	5,5	1,5
	Aggressive	5,1	1,1

The fundamental change here is that regardless of how Individual 1 and 2 behave, they have an incentive to cooperate rather than to attack. This is only possible in situations such as the supercolony in Southern Europe, where the nests of different families are located very close to one another and territorial defense carries a high price due to frequent interaction between nests. This allows for natural selection of cooperative ants over aggressive ants because the cooperative ants are better fit to their specific situation. In other words, the ants which survive to reproduce are the cooperative ants rather than the aggressive ants, so the genes responsible for cooperation are propagated to future generations.

This idea involves a fundamental shift in attitude from looking at genes as the unit of self interest to looking at a population as self-interested. From this point of view cooperative unicolonial behavior does not involve a short term success at the cost of long term stability, rather it is the most stable situation possible and is not doomed to failure.

The success of the population, or superorganism, depends on the behavior of its parts, but from very simple interactions complex behaviors can arise. Each ant follows a fundamental rule: if you recognize the other ant, act friendly, otherwise act aggressively. This allows for simple mutations in the genetic component of each ants recognition cue to have dramatic effects. When an ant is recognized by other ants and treated as a nestmate it learns to associate the cues of those ants with friendly behavior. This gives an ant with a mutation allowing it to be recognized by two nests a considerable advantage in terms of the probability it will survive to reproductive age. As the mutation propagates through the population, more and more ants will be recognized by both nests until, theoretically, both nests could be composed of mutated, dually recognizable ants. In order for this to be possible it is necessary for the recognition cues to be primarily genetically determined, and for the recognition template to be learned through experience.

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