INCLUSIVE FITNESS THEORY: IS IT STILL RELEVANT IN DISCUSSIONS OF ALTRUISM?

by

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and approved by

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ABSTRACT OF THE DISSERTATION

Inclusive Fitness Theory: Is it still relevant in discussions of altruism?

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For nearly 50 years, Inclusive Fitness Theory has provided researchers an avenue to understand altruistic interactions among individuals in a colony. It has recently come under fire by prominent academics suggesting it is unsatisfactory in describing altruism. This thesis aims to provide a history of inclusive fitness theory and dissect the arguments against the theory and in favor of it. Using scientific research articles from such publications as Nature and Science, I have collected information on the history of Inclusive Fitness Theory and the development of the theory over time. Furthermore, this thesis will also delve into the methods of testing Inclusive Fitness Theory as well as fields that have arisen due to the theory. Ultimately, using arguments made by opponents and proponents to the theory, conclusions will be drawn about the validity of the theory. While the arguments against the theory seem sound, they ultimately fail to provide alternative insights into the development of altruism in colonies, and moreover these arguments are successfully refuted by leaders in the field.
Preface
Dedication

I dedicate this thesis to my wife, Iman Osman. Without her love, patience, and strength, none of this would have been possible.
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Introduction

Social insects pose an interesting conundrum for evolutionary biologists. They have societies that span the gamut of defined social constructs. How did these organisms evolve such intricate and complicated societies? Furthermore, what was the catalyst that pushed these organisms into aggregating to begin with? The theory of evolution provides a framework for understanding the millions of species that have existed beginning with the first single-celled organisms billions of years ago. Organisms undergo variations from one generation to the next, producing changes that either allows advantages to develop that allow species to flourish, or disadvantages that result in extinction. These changes are incremental can lead to immense changes further down the evolutionary ladder.

However, Darwin himself felt social insects were the “one special difficulty” fatal to the theory of evolution, in that if individuals are interested in mating in order to produce offspring, why then do some sacrifice their own fitness in order to raise the young of others (Darwin, 1859)? Darwin posited sterility and morphological differences provided an advantage to the nest, and through subsequent generations, this production of fertile and infertile offspring led to modern day social insect colonies (Darwin, 1859). It took decades of debate in addition to a greater understanding of genetics in order for a hypothesis and eventually a theory to develop.

This theory - inclusive fitness theory – aims to explain how individuals willingly sacrifice their own reproductive success in order to increase the fitness of others in the colony. It reveals that individuals will express altruistic behaviors provided the benefit of altruism increases the number of potential copies of the altruistic gene throughout the colony (Charnov, 1977; Bourke, 2011). Further, individuals are more inclined to help kin
rather than non-kin. For example, research had shown within social bees, female workers will select nest mate eggs over non-nest mate eggs for removal from the hive, indicating a preference for raising kin over non-kin (Pirk et. al, 2007).

The cornerstone of inclusive fitness theory is Hamilton’s rule. The equation itself is expressed as $rb > c$, where $r$ is the relatedness between individuals, $c$ is the cost to the individual in terms of reduced fitness, and $b$ is the benefit the altruistic gene experiences (Hamilton, 1964; Charnov, 1977). Relatedness refers to the distribution of gametes in subsequent generations. As an example, diploid organisms - or organisms that receive one set of chromosomes from both parents - provide one-half their genome to their children, leading to relatedness values between parents and offspring as $r = \frac{1}{2}$ or .5; relatedness values between siblings in diploid organisms are also one half as the siblings are related to one another through sharing $\frac{1}{4}$ the genes from the mother and $\frac{1}{4}$ the genes from the father which sum to $r = \frac{1}{2}$ (Charnov, 1977).

Relatedness varies dependent upon the species being discussed as well as when inbreeding occurs. Hymenoptera, for example, are not diploid but rather haplodiploid; that is, males are haploid and have one set of chromosomes while females are diploid and have two sets of chromosomes. Males then provide the entirety of the genome to the subsequent female generation while females provide half (Hamilton, 1964; Figure 1). Males contribute nothing to the subsequent male generation and females then contribute half of their chromosomes. This causes sisters to have relatedness values of $r = \frac{3}{4}$ with one another and relatedness values of $\frac{1}{4}$ with their brothers (Hamilton, 1964; Table 1). Hamilton’s rule uses relatedness values to describe the relationship between the relatedness among individuals and the cost to benefit ratio of their diminished fitness.
That is, altruism will spread in a colony provided the altruistic gene has a high probability of existing within the individual given aid and the drop in fitness of the altruist does not prevent the spread of the gene.

**Table 1 - Relatedness Values of Female Hymenopteran and Various Nest mates**

<table>
<thead>
<tr>
<th>Nest mate</th>
<th>Relatedness Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mother</td>
<td>0.5</td>
</tr>
<tr>
<td>Father</td>
<td>0.5</td>
</tr>
<tr>
<td>Full Sister</td>
<td>0.75</td>
</tr>
<tr>
<td>Full Brother</td>
<td>0.25</td>
</tr>
<tr>
<td>Daughter</td>
<td>0.5</td>
</tr>
<tr>
<td>Son</td>
<td>0.5</td>
</tr>
</tbody>
</table>

Table 1: Female Hymenopterans are diploid and have two sets of chromosomes. They receive one set from the father (0.5) and mother (0.5), giving them relatedness values of 0.5 to each. Full Sisters have in common the full set of chromosomes from the father (0.5) and half the half set of chromosomes (0.25) from the mother, giving them relatedness values of \((0.5 + 0.25) = 0.75\). Sisters and brothers have in common only half the half set of chromosomes provided by the mother, yielding related values of \((0.5 \times 0.5) = 0.25\). They pass only one half their set of chromosomes (0.5) to their progeny be them male or female.
Social organisms can be organized into different paradigms of sociality. That is, different organizational classifications exist based on how the colony interacts with one another. Eusociality can be described as the organization of a colony using a social hierarchy based upon reproductive castes that experience unequal reproductive success; that is, there are reproductive and non-reproductive castes (Nowak et al, 2010). Moreover, in addition to reproductive castes, there is also cooperative breeding and generational overlap (Wilson, 1971). Independent development of these traits can create different social paradigms that develop in organismal colonies (Table 2).

Within insects, commonly discussed eusocial colonies are diploid species such as termites and haplodiploid species such as bees, wasps, and ants. The reproductive castes are responsible for producing individuals, while non-reproductive castes maintain the hive, nurse larvae, and search for food. Each caste has a responsibility to the hive, and for many individuals this responsibility hinges on the sacrifice of their reproductive abilities.
Eusociality can also be considered a pure altruistic society wherein entire castes of the colony diminish their own fecundity in order to raise the fecundity of the queen. When examining eusocial behavior through this lens, we can then imagine it as the progression of altruism within colonies. In addition to eusocial colonies, other less socially hierarchical colonies that still exhibit altruism have been studied such as prairie dogs and social birds.

Table 2 - Social Paradigms in Organismal Colonies

<table>
<thead>
<tr>
<th>Social Construct</th>
<th>Qualities that Exist in the Construct</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solitary</td>
<td>No social traits exist in the colony</td>
</tr>
<tr>
<td>Subsocial</td>
<td>Adults remain with offspring for an indeterminate period of time, in order to protect or raise offspring</td>
</tr>
<tr>
<td>Communal</td>
<td>Individuals utilize the same colony, however no cooperative breeding or reproductive castes exist</td>
</tr>
<tr>
<td>Quasisocial</td>
<td>Individuals cooperatively breed within the colony, however there is no generational overlap or reproductive castes</td>
</tr>
<tr>
<td>Semisocial</td>
<td>Individuals in the colony exhibit cooperative breeding behavior and there also exists reproductive castes, however there is no generational overlap</td>
</tr>
<tr>
<td>Eusocial</td>
<td>The colony experiences all three social traits; there is cooperative breeding, reproductive division of labor, and generational overlap existing within the colony</td>
</tr>
</tbody>
</table>

Source: The Insect Societies by E.O. Wilson

Inclusive fitness theory does not have universal support among all biologists, however. In their paper published in 2010, Nowak and Wilson argue against the validity of inclusive fitness theory and present an alternative hypothesis for the development of altruism in colonies. This publication created a firestorm among evolutionary biologists and led to a heated debate between supporters and detractors of inclusive fitness theory.
A slew of papers were published in defense of inclusive fitness, as was a letter refuting the Nowak and Wilson paper signed by hundreds of biologists. In response, Nowak and Wilson themselves wrote a refutation of the refutation, and this debate is not, as of this paper, settled.

The spread of altruism through different fauna has been historically been attributed to inclusive fitness theory. The goal of this paper is to analyze inclusive fitness theory and the many hypotheses that provide its framework. Further, it aims to discuss inclusive fitness theory in light of the recent Nowak and Wilson paper, and to find if it is indeed still relevant to the discussions of altruism.

**Methods to Test Inclusive Fitness Theory**

Much research has been done in order to test this theory, oftentimes in social insects. Research methods are typically genetic in nature, analyzing genes of interest and determining relatedness among individuals in the brood (Korb et al., 2007). Traditional molecular methods confirmed the distant relationship of Isoptera and Hymenoptera, two of the most studied social insect taxa—thus social behavior evolved more than once in Insecta. Genetic research on inclusive fitness occurs most commonly through analysis of microsatellite markers in DNA, which are amplified through PCR (Hastings et al., 1998; Korb et al., 2007; Strassman et al., 1998, Kronauer et al., 2007) and analyzed for genetic structure using Fst and PhiPT values via AMOVA (Peakall and Smouse, 2006). These markers are useful for determining the degree of gene flow among colonies, colonies and geographic regions for a given species; they can be used to detect the number of matings a queen used to fertilize her brood, inbreeding, and other measures relevant to a
discussion of inclusive fitness. For example, studies performed on the dispersal of *Pogonomyrmex barbatus* found dispersal distance led to isolation and restriction of gene flow (Suni & Gordon, 2010).

Other analyses include dissections of individuals to determine age through darkening of the sternite (Strassman et. al, 1998) and paternity through analyzing the release or storage of sperm (Kronauer et. al, 2007) as well as dissections of colonies to find individual workers, drones, and queens (Husseneder et. al, 1999). Novel genomic and transcriptomic analyses seek to uncover genes associated with social behavior. Currently, there are six social insect genomes published including *Apis mellifera* and various ant species, with more currently being sequenced and compared (Fischman et. al, 2011). Ultimately, these data may help determine for example (1) when and how many times social behavior has arisen, (2) what genes are associated with social behavior, (3) how much gene flow there is among related and unrelated colonies, and so forth. Some laboratories are currently researching genes involved in the development of eusociality in order to identify what role genetics plays in eusocial development (Woodard et.al, 2011).

**The Monogamy and Haplodiploidy Hypotheses**

Because inclusive fitness theory hinges on the increased relatedness among individuals as the mechanism through which altruism spreads through a colony, hypotheses have arose that attempt to explain how colonies increase relatedness among individuals. One of these hypotheses, the monogamy hypothesis, proposes eusocial colonies develop on the basis of the rate of promiscuity of females in the group (Cornwallis et.al, 2010). Another of these hypotheses is the haplodiploidy hypothesis.
These two hypotheses are not necessarily mutually exclusive; indeed some (Fromhage et.al, 2011) believe they can often work together to develop eusociality as will be seen later. The monogamy hypothesis suggests increasing the relatedness of individuals in a group provides an incentive for cooperative breeding and altruistic behaviors to emerge. Consider if females in a group were monogamous, this means offspring share half of their genes with their siblings just as they share half with their own offspring. Cooperation may provide some benefit through decreased time spent foraging and wasted energy searching for a mate, and thus the balance would shift towards raising siblings as opposed to one’s own children (Cornwallis et.al, 2010).

Importantly, this is the trend seen in colonies of termites, where – theoretically – the relatedness of workers to one another is equivalent to the relatedness among workers and their potential offspring ($r = \frac{1}{2}$). The reproductive female, the queen, is exclusively monogamous and mates with a single male when founding a colony. For offspring born of this mating, the fitness gains of founding their own colony versus raising their mother’s offspring are equivalent. However, the risks associated with founding colonies - such as an increased probability of dying through lack of food or predation - are significant while the benefits of raising their siblings are even greater. There are significant advantages to sacrificing their own reproductive abilities in order to ensure the success of the nest and these advantages allow the queen to produce more offspring and thus increase the indirect fitness gains made by the workers (Thorne, 1997).

Sibling mating - or inbreeding - however, is often seen in termite colonies leading to relatedness values greater than the expected. As siblings share chromosomes from both parents, the have relatedness values of 0.5. Sibling mating causes these shared
chromosomes to be passed to their offspring, leading to not only increased relatedness to their parents, but among those in their generation as well (Husseneder et al., 1999). The genes they inherit from the father are also the genes they inherit from the mother, leading to the increased relatedness one sees. Sib-mating can raise the relatedness of siblings to values nearer 0.70 rather than the values of 0.5 expected from random mating (Korb et al., 2007; Figure 2). Also, it is important to note that helpers in some termite colonies retain their sexual organs or the ability to differentiate into reproductive while workers in hymenopteran colonies oftentimes lose their reproductive capabilities. Termites, therefore, have the ability to leave the hive and find their own nests. However, termite helpers choose to remain in the parental nest and raise their nest mates despite retaining the ability to reproduce (Thorne, 1997).

Eusocial colonies with unequal relatedness among individuals also see lifetime monogamy among queens and reproductive males. Colonies of ants, wasps, and bees oftentimes have the queen store male sperm and utilize it as the only mating she will experience (Boomsma, 2007). Indeed, experimental evidence suggests the queens of army ants refuse to copulate with new males and will reject copulation attempts to re-mate (Kronauer et al., 2007). The importance of monogamous mating in eusocial insects cannot be overstated. It appears as though monogamy is essential to the successful founding of eusocial colonies where altruistic, cooperative breeding behavior is seen. There are indeed colonies of eusocial insects that do have non-monogamous mating, however recent phylogenetic analyses have shown these colonies all arise from previously monogamous ancestors (Boomsma, 2009). When colonies have strict reproductive and non-reproductive castes established, the threat of multiple mating
disrupting the colony diminishes. Clearly evident is the necessity monogamous mating has on the development of eusociality – and therefore altruism – in a colony.

Another hypothesis proposed for the development of eusociality in colonies is termed the haplodiploidy hypothesis. In haplodiploid colonies – typically Hymenopterans – fertilized or diploid eggs develop into females while unfertilized or haploid eggs develop into males. This creates a colony where sisters have relatedness values of \( r = \frac{3}{4} \) with one another and relatedness values of \( r = \frac{1}{2} \) with their own daughters, creating a colony where sisters are more related to one another than with their own offspring (Gardner et.al, 2012). Presumably, this increased relatedness among sisters allows eusociality – and therefore altruism - to evolve easier, due to the importance of relatedness in Hamilton’s Rule (Ratnieks et.al, 2009).

**Figure 2 - Inbreeding raises relatedness in subsequent generations**

Breeding causes chromosomes to pass on into subsequent generations. In inbreeding, genetic lineages are shared causing relatedness to increase in later generations. F1 generation males and females have relatedness values of 0.5 while the F2 generation has relatedness values of greater than 0.5.
In models of haplodiploid colonies, it appears that haplodiploidy increases the likelihood of altruistic genes invading the colony. In models of with single-mating queens, invasion of a gene that produces altruistic female workers is three times more likely to occur in haplodiploids than diplodiploids (Johnstone et.al, 2011). Moreover, even as the number of mating queens increases, haplodiploids still obtain a 50% increase over diplodiploids in the invasion of an altruistic allele (Johnstone et.al, 2011). However, there is an important caveat associated with this increase; sex-biased dispersal must favor males leaving the nest. It appears there is support of haplodiploidy favoring the evolution of helping behavior provided specific sex-biased dispersal in the hive. The importance of sex-biases in haplodiploid organisms can be understood more easily through comparing relative genetic distribution in the hive. It can be easily understood why workers will stay and raise their sisters, it is in their best interests as they share significantly more genes with them than their own offspring. However, having to raise their brothers is non-advantageous due to decreased relatedness to brothers than their own offspring, male and female (Gardner et.al, 2012). Therefore, there must be biases in the allocation and dispersal of sexes in nests in order for haplodiploidy to have an effect on the development of altruistic behavior.

There is still debate as to the effect haplodiploidy and monogamy has on the evolution of eusociality and helping behavior. Some (Fromhage et.al, 2011) believe the two work in concert to produce eusocial colonies. Models have shown haplodiploidy can
strengthen positive assortment of cooperators allowing for the easier evolution of
eusociality as well as protecting the hive from invasive, selfish genes (Fromhage et al.,
2011). Cooperators are more like to mate with one another, preventing opportunists from
taking advantage of cooperative behavior while providing nothing. Both monogamy and
haplodiploidy appear to have a role in the evolution of eusociality.

**The Importance of Kin Recognition**

Another important aspect of inclusive fitness theory is the importance of kin
recognition and the role it plays in altruistic behavior. From parasitic insects to
vertebrates, recognition of kin plays a role in altruistic acts. Cooperative breeders often
are unable to breed on their own, and thus improve the reproductive success of others,
oftimes close kin. Kin recognition allows individuals of a colony to selectively assist
others in a way to maximize a kin’s reproductive successes and therefore their own
indirect fitness gains (Lize et al., 2006).

Kin recognition has been shown in many different taxa and provides the ability to
test altruistic behaviors in laboratory settings. In hymenoptera, for example, honeybees
have been shown to be able to discriminate between nest mate eggs and non-nest mate
eggs, and preferentially select nest mate eggs for rearing (Pirk et al., 2007). Ultimately,
energy and effort is going to be provided to those who would provide the most benefit to
the altruistic individual. Because inclusive fitness theory relies on the relatedness among
individuals, kin recognition and discrimination is essential in determining which
individuals one is altruistic to.
Cannibalistic tiger salamanders also have the ability to discriminate between kin and non-kin, and this discrimination allows more relatives to survive to metamorphosis (Pfennig et.al, 1999). For a cannibalistic species, sparing siblings from becoming a meal leaves an individual at a distinct disadvantage. However, it also allows the spared sibling to have a greater chance at developing into an adult and thus reproducing. Cannibalistic tiger salamanders avoid cannibalizing siblings even when there may be greater costs associated with this altruistic action, and in fact twice as many siblings reach metamorphosis (Pfennig et.al, 1999). In order to satisfy Hamilton’s Rule, there must be some way to determine who is a relative, and who is not. Without the ability to discriminate between kin and non-kin, there is no way to maximize the indirect fitness gains the altruist experiences.

Even in solitary insects kin recognition can reveal insights in altruistic behaviors. Parasitic larvae of *Aleochara bilineata* invade hosts in the area surrounding their birthplace, avoiding already parasitized hosts (Fournet et.al, 2001). Superparasitizing – or parasitizing an already parasitized host – leads to a fight to the death between the two parasitic larvae (Fournet et.al, 2001). Females lay egg in clutches, and due to this fact siblings hatch and search for hosts in the company of their siblings, and often find hosts already parasitized by siblings. However, siblings are capable of recognizing one another, and avoiding hosts already parasitized by a sibling; furthermore, a higher rate of death is observed in individuals that avoid superparasitization of hosts parasitized by siblings (Lize et.al, 2006). Individual parasites choose to continue foraging for hosts and avoid hosts parasitized by siblings, and risk death by doing so. While the cost to the altruist is high, the benefit the sibling experience is as well. Provided the benefit continues to be
greater than the cost, altruism will be expressed. Thus, recognition in these organisms leads to altruistic behaviors being exhibited.

**Criticism and Support of Inclusive Fitness Theory**

Inclusive fitness theory is not without its detractors, however. A few prominent researchers have begun to suggest inclusive fitness theory is not the primary reason for eusocial and altruistic behavior. Chiefly among them are Edward O. Wilson, Martin Nowak, and Corina Tarnita. These researchers contend ultimately inclusive fitness theory is flawed and no longer supported by empirical evidence. The first contention cited that arises with inclusive fitness theory is the decreasing significance of the haplodiploidy hypothesis. Many species have been found to be eusocial despite having diplodiploid sex allocation (Nowak et.al, 2010). This distribution of genetic material effectively renders the $r$ value equivalent with regard to offspring and siblings, relinquishing any gains due to unequal sex determination in haplodiploids ineffective in diplodiploids. Furthermore, these diplodiploid colonies can create castes of non-reproductives that raise young or defend hives, indicating these groups do not exist solely in haplodiploid colonies as previous assumptions maintained. It is even suggested that high relatedness among individuals of a colony arise as the by-product of the formation and development of a colony, and is the not cause through which a colony forms (Wilson et.al, 2005).

Another issue Nowak and colleagues address is the failure of inclusive fitness theory to explain the lack of development of eusociality in colonies of haplodiploids or clonal reproductives. As clonal reproductive have relatedness values of the highest possible, they therefore are expected to develop eusocial colonies, yet only one group of
these has achieved it (Nowak et.al, 2010). This limitation of inclusive fitness theory to accurately predict behaviors in colonies leads to an inability on the parts of Nowak, Wilson, and Tarnita to support the theory. Moreover, this failure arises in discussions of haplodiploid colonies as well. Parasitoid hymenopterans of which there are tens of thousands of species that have no known eusocial colonies, as do not cooperative larval hymenopterans (Nowak et.al, 2010). The haplodiploid hypothesis, and ultimately inclusive fitness theory, purports increased relatedness will lead to altruistic – and in this discussion eusocial – behaviors, scores of species fail to achieve this behavior, indicating an inability of inclusive fitness theory to accurately predict colony behaviors.

This reasoning fails to provide insight, in that the examples provided are handpicked and do not provide any explanations as the why this is the case; it can be equally stated that there are thousands of diploid species across many taxa that also fail to achieve eusociality (Herre and Wcislo, 2010). Is the inability of these vast numbers of diploid organisms to achieve eusociality indicative of the unlikelihood of diploids becoming eusocial? It is not ploidy or the ability of organisms to form communal nests driving eusociality to evolve, but rather maintaining high relatedness that is the essential key for its evolution (Herre and Wcislo, 2010). All hymenopteran species that are eusocial developed from ancestral species that maintained monogamous breeding, which as aforementioned leads to high relatedness within the brood; high relatedness is not as Wilson describes a by-product but rather a source or at the very least coincident with the evolution of eusociality (Boomsma et. al, 2010). Moreover, monogamy and high relatedness affect diploid organisms in addition to haplodiploids. Cooperative breeding in birds overwhelmingly is seen in monogamous species, and when individuals develop
promiscuity the cooperative behavior can vanish; in addition, these differences can be seen in ancestral species leading to findings that high relatedness leads to cooperation and when relatedness drops we also see a drop in cooperative behavior (Boomsma et. al. 2010). High relatedness is not all that is required to evolve eusociality, the importance of the benefits of eusociality to altruistic individuals cannot be understated in leading to its evolution as well. Species with monogamous mating do not necessarily evolve eusociality, as the benefits of eusociality do not overcome the costs the individuals experience with losing their own reproductive abilities (Boomsma et. al., 2010).

However, once that threshold is surpassed, we can expect to see species that express eusocial behavior.

Nowak and colleagues begin by making the assumption that inclusive fitness theory is correct, and express the following: if both natural selection and inclusive fitness theory describe identical outcomes, but natural selection theory can describe all scenarios while inclusive fitness theory is limited to specific interactions, why continue to use the less applicable theory (Nowak et.al, 2010)? Their assertion makes it appear that inclusive fitness theory is being embraced for reasons other than its own merits. Moreover, they contend inclusive fitness theory can only work when assumptions taken by the theory remain constant, and if these assumptions are violated the theory fails to provide insight (Nowak et.al, 2010). Ultimately, they insist in a world with competing theories for description of natural phenomena, the one capable of providing explanations to all cases is preferable to the theory describing fewer and more specific cases (Nowak et.al, 2010).

Many have charged this criticism is baseless, as it creates a false dichotomy in which natural selection and inclusive fitness act independently of one another. Instead,
natural selection describes the phenotype of organisms while inclusive fitness theory describes how the phenotype is used; that is, natural selection maximizes the effect of inclusive fitness (Abbot et.al, 2010). Inclusive fitness theory is an aspect of natural selection; it explores and provides predictions beyond just eusociality (Herre & Wcislo, 2010). Indeed, inclusive fitness theory provides the ability to explain how natural selection produces phenotypic variation, and these explanations are both predictive and falsifiable, and this fact would lead to the identical outcomes Nowak and colleagues describe (Abbot et. al, 2010).

The assumptions Nowak, Wilson, and Tarnita contend exist within inclusive fitness theory are not found in Hamilton’s original description of inclusive fitness theory, and more importantly, these assumptions are not required in order for inclusive fitness theory to accurately describe predicted outcomes (Abbot et. al, 2010). These assumptions arise when describing models of specific cases and are not relevant to the generalized theory of inclusive fitness; moreover, these models allow inclusive fitness theory to provide testable predictions and explanations of many natural phenomena from sex allocation to cooperation, and even spiteful behavior (Abbot et. al, 2010). Inclusive fitness theory provides insights on why individuals direct costly altruistic acts and behaviors towards kin over non-kin a significant majority of the time, as well as the importance of benefits arising due to altruism leading to helping behavior over reproductive behavior; further, an entire field of study - kin recognition - that did not exist prior was developed due to inclusive fitness theory (Strassman et. al, 2010). In addition, Nowak and his colleagues contention that the theory of inclusive fitness cannot explain all scenarios is pointless; the theory had never sought to explain and define all
social behaviors in organisms, instead the theory sought to explain true altruism, and it remains the only theory that can (Strassman et al., 2010).

Another contention arises from Hamilton’s Rule itself. In a previous publication, E.O. Wilson described an inherent flaw in Hamilton’s Rule as he saw it: it fails to include altruism that arises between those individuals who are unrelated (Wilson et al., 2005). This can be observed in the primitive termite species *Zootermopsis nevadensis*. Unrelated colonies occupy the same decaying log and typically war with one another leading to the death of reproductives; following this, the survivors form a merged colony leading to workers raising nest mates they are unrelated to (Johns et al., 2009). Wilson uses examples such as these to suggest a modified equation \((rb_k + b_c) > c\) wherein \(b_k\) is the benefit resulting from kin selection and \(b_c\) is the benefit arising from selection on the colony without regard to relatedness (Wilson et al., 2005). As \(b_c\) increases and becomes significantly greater than \(b_k\), \(b_k\) begins to become insignificant and incapable of being measured, which Wilson suggests occurs in the natural world (Wilson et al., 2005).

Moreover, the issues with Hamilton’s Rule are expounded on in the Wilson, Nowak, and Tarnita paper. They contend in spatial models, relatedness is often seen as not the factor that is greater than the cost to benefit ratio, but rather some undefined other unidentified factor (Nowak et al., 2010).

An aspect Nowak and colleagues fail to address is that inclusive fitness theory does not aim to describe altruism outside of related species. It is true that unrelated individuals in a colony, community, or ecosystem may be altruistic to one another, however defining and determining the reasons why this occurs is not the goal of inclusive fitness theory. Instead, inclusive fitness theory seeks to explain why related individuals
choose to raise the offspring of kin over their own offspring. In the example used by Nowak and colleagues of *Zootermopsis*, it has been found that wars erupt between neighboring nests with the losing colony being absorbed into the winning colony, leading to the formation of a typically unrelated megacolony (Johns et. al, 2009). In these wars, the kings and queens of the two colonies can die, leading to the development of new reproductives. The reproductive roles can be filled by the helpers of either of the colonies that created the newly formed megacolony, leading to a selective advantage to remaining with the megacolony; moreover the individuals who differentiate into the new reproductives are siblings of the workers already in the two colonies increasing the relatedness and inclusive fitness gains to the workers who remain with the megacolony (Johns et.al, 2009). Unrelated individuals also experience fitness gains from maintaining a guaranteed food source, habitat, and survivability, resources that may not exist should they leave and find their own colony, provided kin become reproductives. Most importantly, increased colony size increases the likelihood of winning future wars with other colonies, where workers can potentially become reproductives (Johns et.al, 2009). The benefit arising on the colony is in the end due to relatedness, as helpers become related through the ascension of new reproductives, and thus inclusive fitness most definitely plays a role in this example.

Wilson, Nowak, and Tarnita suggest an alternative to inclusive fitness theory, one which proceeds stepwise through several stages leading to full eusocial behavior. To begin, they claim the first step in the development of eusociality is the formation of groups within a colony (Nowak et.al, 2010). These groups can form in a multitude of ways, from cooperative breeding between parents and offspring to even randomly; what
is essential is these groups are persistent and lasting (Nowak et.al, 2010). These persistent groups can even form between unrelated groups, such as the colonies that develop in *Zootermopsis*; the important aspect of group formation is the advantage of a defensible nest (Nowak et.al, 2010).

Next is the aggregation of traits that allow the transition into eusociality to become more probable. These pre-adaptations arise through selection pressures on an individual level from adaptive radiation, leading some species to develop more effective traits than others (Nowak et.al, 2010). Pre-adaptations for eusociality can be seen in some species of solitary bees wherein there appears to be a eusocial ground plan that arises when these species are force to interact; they create divisions of labor and develop leadership roles (Nowak et.al, 2010). These pre-adaptations allow groups to develop that become increasingly more likely to develop social hierarchies, especially with increasing numbers.

The third stage in the Nowak, Wilson, and Tarnita model is the evolution of eusocial alleles (Nowak et.al, 2010). These alleles can arise through presently known methods - mutations or recombination - and these alleles do not need to create new behaviors but instead needs to erase previous behaviors - that is, removing the behavior for individuals to go find a nest will make an individual remain in the group nest (Nowak et.al, 2010). Nowak and colleagues observe there are no known genes designating eusocial behavior, however there are genes discovered that can alter social behavior through silencing already acquired traits - such as the mutation in which diet could alter wing development in ants, leading to the evolution of the worker caste (Nowak et.al,
At this point, if selective pressures are strong enough, the group can make the switch to eusociality.

The fourth stage of eusocial development is the development of defenses, while the fifth is the emergence of intracolony selection (Nowak et al., 2010). Defensive mechanisms against predation and rivals appears to have great import in the evolution of primitive eusocial species, however due to the lack of research done on this topic there remains much to be seen (Nowak et al., 2010). Intracolony selection provides the evolution of reproductive castes as well as influencing the lifecycles and development of individuals in the group, leading to the formation of specific and specialized social behaviors (Nowak et al., 2010).

Nowak, Wilson, and Tarnita have identified troubles and problems they feel arise in inclusive fitness theory and seek to address these problems through the development of their own hypotheses regarding the evolution of eusociality and social structure. Their criticisms of inclusive fitness theory stem from issues with its inability to accurately predict the development of eusocial behaviors in many clades as well as the apparent dichotomy and thus conflict between natural selection and inclusive fitness theory (Nowak et al., 2010). Their hypotheses on the formation of eusociality are in depth and appear logically consistent. They provide not only a theoretical framework but also provide empirical evidence in support of their hypothesis.

However, the paradigm Nowak and colleagues discuss hinges on the ability of persistent groups to form - related or unrelated. They argue these groups form first and following their formation the species develop eusocial traits. These traits spread due to selective pressure on the individual. We have seen earlier that ancestral species of current
eusocial organisms experienced monogamous mating, and infer groups formed due to the increased relatedness of the siblings to one another (Boomsma et.al, 2010). The monogamy yields increased related among the siblings. At this point, there is no group or nest, merely related individuals. However, as the relatedness among individuals remains static, or potentially increase due to sibling mating and inbreeding (Korb et. al, 2007), group dynamics begin to emerge. These dynamics yield increase survivability for the related individuals. There is yet to be reproductive caste development, however individuals cooperatively breed. The guarantee of safety and nourishment provides an incentive for reproductively capable offspring to remain with the group and raise siblings; the benefits of cooperation outweigh the drop in fitness experienced by the individual (Cornwallis et. al, 2010; Thorne, 1997).

Nowak and colleagues hypothesis hinges on the premise that group formation must be the first step in a series that leads to eusociality. However, should group formation not occur first their hypothesis falls apart. Phylogenetic evidence suggests monogamy yields the development of groups in species, as the colony requires some incentive to develop these groups contrary to Nowak and colleague’s assertion groups form independently of relatedness (Herre and Wcislo, 2010). While they provide some choice examples of unrelated altruism, these examples are unhelpful in the supporting their hypothesis. The example provided by Nowak and Wilson of *Zootermopsis* as a species that expresses unrelated altruism is irrelevant in these discussions. The megacolony forms through the combination of two colonies that maintain interrelated workers; moreover, the megacolony offers workers the opportunity to develop into reproductives, thus increasing the interrelatedness of the megacolony (Johns, et. al,
One can see that relatedness is required to develop the two original colonies that form the megacolony.

**Conclusions**

The empirical evidence in support of Inclusive Fitness Theory cannot be denied. There is without a doubt an influence on the altruistic nature of organisms based on the interrelatedness among individuals in a colony as seen in experimental data (Lize et.al, 2006; Pirk et.al, 2007; Pfennig et.al, 1999). Species exhibiting cooperative breeding cease cooperation when the relatedness of siblings is reduced through polygamy (Boomsma et.al, 2010); clearly relatedness among siblings and kin plays a role in the expression of altruism.

More importantly are the foundations of altruism and how it developed throughout the animal kingdom. Nowak and colleagues argue it arose due to the development of aggregates of individuals who may or may not be related; they do acknowledge these groups may arise due to cooperative breeding but maintain it can arise among unrelated groups (Nowak et.al, 2010). This is difficult to ascertain however, as we cannot empirically prove groups developed due to increased relatedness. However, a phylogenetic analysis of current species posits the groups that develop did so through ancestral monogamy, providing evidence contrary to this hypothesis Herre and Wcislo, 2010). Monogamy led to increased relatedness among individuals, leading to cooperative breeding among individuals and thus to the development of groups. Altruistic interactions among the individuals in a nest or colony arise first due to the increased relatedness among those individuals, not through random interactions among the individuals.
Nowak and colleagues attempt to provide an alternative that disregards the evidence in support of the theory to postulate their own; however their attempt is unsatisfactory. They create an avenue in which natural selection and inclusive fitness theory exist as mutually exclusive processes (Nowak et al., 2010), when in fact inclusive fitness is a pathway through which natural selection acts. The evidence in support of inclusive fitness combined with the fallacies perpetuated by Nowak and colleagues leads one to reject their hypothesis.
References


Curriculum Vitae

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