Thomas Rachman, Class of 2020

Biology

Developing a Generalized Tug of War Model

Biographical Sketch:

Thomas is a junior majoring in biology and minoring in music. He got his start in the life sciences in sixth grade volunteering in the Entomology department at Michigan State University, around five minutes from his home in East Lansing, Michigan. In high school he continued his work there studying chemical signaling in honey bees under Dr. Zachary Huang. In the Summer of 2018, he worked in the Hajek Lab on a variety of projects centered on invasive pest management via fungal pathogens. The most entertaining project involved a test of Asian Longhorn Beetle flight capacity, which required fastening the beetles to a spinning contraption that measured flight speed and duration. Always interested in mathematics as well as biology, Thomas decided to concentrate in computational biology, which led to his current work with Dr. Hudson Kern Reeve on modeling the evolution of cooperative behavior.

Outside of the sciences, Thomas is a musician and composer, playing violin with the Cornell Chamber Orchestra and leading the Cornell Ukulele Club. He also wrote an original composition for the Cornell Symphony Orchestra, which was performed in the Spring of 2018. Additionally, he competes as a member of the Cornell Club Swim team in an attempt to hold onto his previous life as a dedicated high school swimmer.

Abstract:

At the heart of evolutionary modeling is the study of cooperation, which has played a tremendous role in bringing about the diversity and complexity of form today. However, the exact mechanisms by which organisms cooperate and how cooperative behavior has been selected remain elusive and even the most widely accepted models are contentious at best. A model applying inclusive fitness to a "tug of war" game interlocked between individuals and groups of individuals has shown how genetic relatedness can describe the dynamics of a "super-organism." However, this model only considers two levels of organization, and does not explain cooperation at the genetic level, as classic measurements of relatedness are not equipped to do this. The goal of this research, which will be conducted at Cornell University's Ithaca campus during the summer of 2019, is to outline a tug of war game for *n* levels of competition centered on genes as the initial source of cooperativity through an alternative measure of relatedness. This would have consequences for resolving disputes on the effectiveness of kin selection, multilevel selection, and inclusive fitness.

Statement of Purpose:

Among the most central questions in social evolution is how and why so many organisms have evolved cooperation. In addition to its immediate relevance in studying human evolution, cooperation is an essential component of survival for many species ranging across all spatial scales. The emergence of complex life owes itself to organization at the unicellular level, which depends on the ability for those individual cells to devote effort to an entity larger than themselves. This tradeoff of selfish and group-level investment has plagued the field of evolutionary biology since Darwin, as it requires a mathematical explanation not only for why altruistic behavior increases net reproductive success, but also why such a state would be stable, i.e. not invadable by some selfish actor (Hamilton 1963).

In 1964, William Hamilton introduced kin selection as an explanation, suggesting that the success of relatives to a focal individual provided an inclusive fitness benefit, and that if $r*b > c$, meaning the relatedness (r) times an altruistic benefit (b) to a recipient outweighs the cost (c) to the donor, then such a gene expressing the altruistic trait will spread in the population (Hamilton 1964). Although widely accepted, "Hamilton's Rule" has been a source of enormous controversy. Mathematician Martin Nowak in collaboration with E.O. Wilson, perhaps the most famous sociobiologist in history, have claimed the rule makes critical assumptions that render it irrelevant in most scenarios (Nowak et al. 2010). Their argument stems from the idea that the success of one member of a group is not independent of others, especially when competition exists such that success of the recipients of an altruistic act by one member do not add synergistically. Though these criticisms received severe backlash, the rift between kin selection and other explanations for cooperation has yet to be mended (Lehmann et al. 2013, Allen et al. 2013, Allen 2015).

An important assumption for many genetic models, either implied or by design, is that genetic relatedness is a valid predictor of shared phenotypic expression. As relatedness is measured in terms of shared genes, many models tend to assume traits can be attributed to a single locus. This concept is best outlined by Alan Grafen's "phenotypic gambit," which states that a single locus or pair of loci is enough to approximately account for expression of a trait and its heritability. While empirical data has challenged the assumptions of kin selection and the phenotypic gambit, most models of cooperation do not extend past comparison of two or three levels of biological organization, namely genes, individuals, and groups of individuals, which makes it difficult to capture all potential interactions which may influence a gene and its selection according to one phenotype (Grafen 1984, Nowak et al. 2010, Hadfield et al. 2007).

To go beyond these first few hierarchies in a meaningful way, there must be some general description of competition and cooperation applicable to multiple levels. A promising approach is an evolutionary game known as the "tug of war" in which multiple actors invest in competition over a common resource. If this game were expanded across several levels of organization, one could imagine loci influencing the allocation of expression in a genome, which then leads to changes in cell cooperation, influencing the organization of a multicellular organism, which could then cooperate in groups, groups of groups, and so on. This concept is heavily influenced by the idea of a "super-organism," which likens the coordinated effort of a eusocial colony to a single entity equipped with internal organization and decision-making ability through division of labor and is a product of intense cooperation. The first attempt and basis for this work comes from a paper published by Reeve and Hölldobler, which describes an interlocked tug of war occurring at two levels, where the inclusive fitness benefit allows group investment to vary according to relatedness among actors, and each actor chooses to invest some amount of its personal energy store to the competition occurring between actors or between groups of actors (Reeve et al. 2007).

A simple first step at generalization has been to define interlocking tug of war games for 'n' levels of competition. Instead of a single degree of freedom, competitive investment would now have n-1 degrees, and represent a vector of different fractions of investment. However, this is not flexible enough to capture the structural variation in each biological level. In particular, accurately describing competition on sub-organismal levels warrants a more precise definition of relatedness. Redefining relatedness in a manner suitable to competition and cooperation among genes would then influence the model at every level, as relatedness among organisms could then be reduced to the relatedness of gene function.

The goal of this model is therefore to describe an accounting system for relatedness on the molecular level, in terms of gene expression, regulation, and most importantly and contribution to heritable variation in phenotype, which could translate to higher levels of biological organization allowing for a general solution to competitive investment across each level. Implications for a successful redefining of relatedness would have consequences well beyond an interlocked tug of war, as it could potentially help explain cooperation among non-kin, and help to resolve some disputes over the mechanisms of multi-level selection, potentially appealing to both the proponents and critics of classic inclusive fitness models.

This research will take place at Cornell University's Ithaca campus under the guidance of Professor Hudson Kern Reeve.

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