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Computational Models of Intergroup Competition and Warfare

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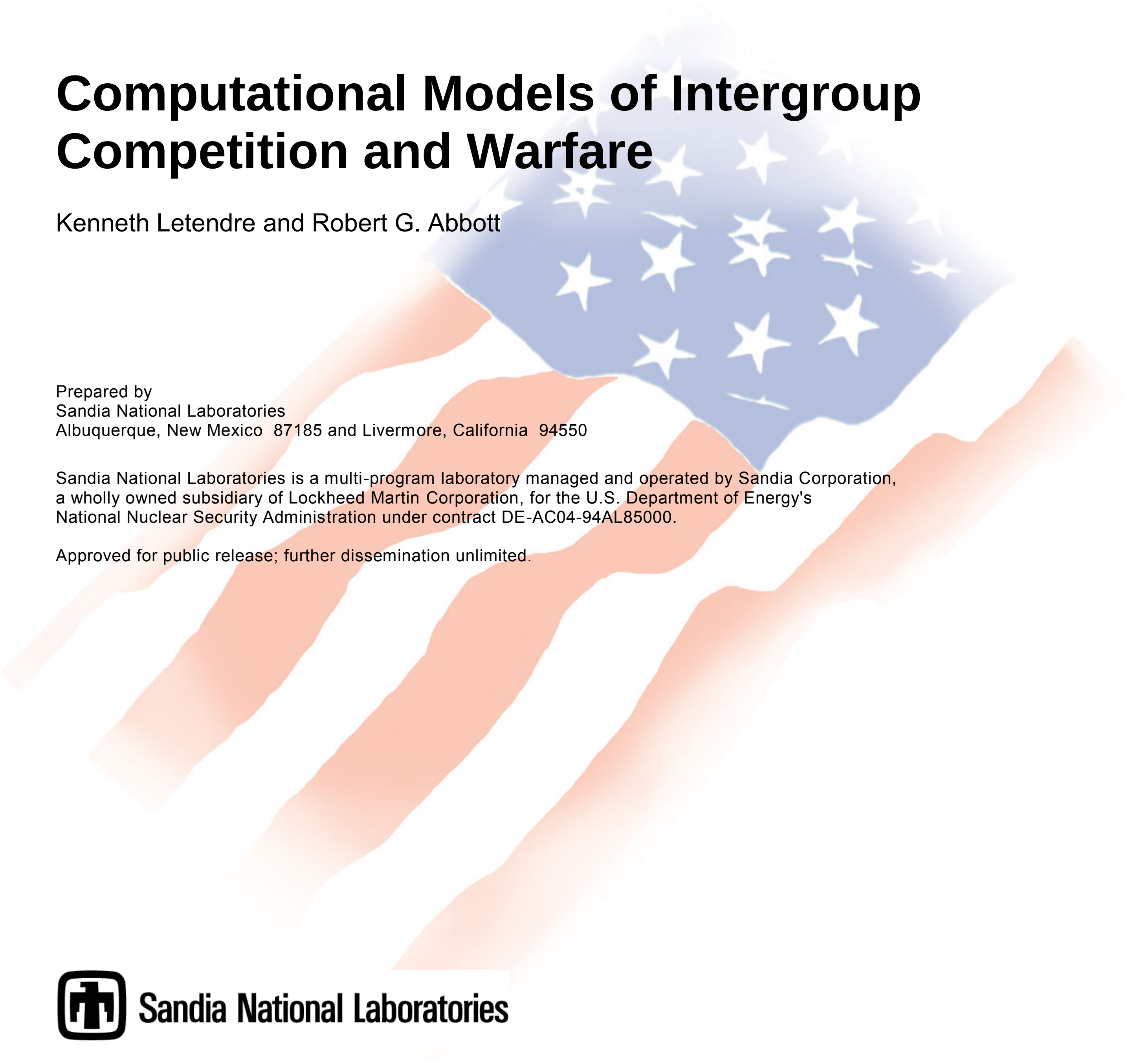

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Abstract

This document reports on the research of Kenneth Letendre, the recipient of a Sandia Graduate Research Fellowship at the University of New Mexico.

Warfare is an extreme form of intergroup competition in which individuals make extreme sacrifices for the benefit of their nation or other group to which they belong. Among animals, limited, non-lethal competition is the norm. It is not fully understood what factors lead to warfare. We studied the global variation in the frequency of civil conflict among countries of the world, and its positive association with variation in the intensity of infectious disease. We demonstrated that the burden of human infectious disease importantly predicts the frequency of civil conflict and tested a causal model for this association based on the parasite-stress theory of sociality. We also investigated the organization of social foraging by colonies of harvester ants in the genus *Pogonomyrmex*, using both field studies and computer models.

CONTENTS

INFECTIOUS DISEASE AND CIVIL CONFLICT

The first component of this project was a study of the global variation in the frequency of civil conflict among countries of the world, and its positive association with variation in the intensity of infectious disease. We demonstrated that the burden of human infectious disease importantly predicts the frequency of civil conflict (Letendre et al, 2010; Letendre et al, in press) and tested a causal model for this association based on the parasite-stress theory of sociality (Letendre et al, in press). According to the parasite-stress theory of sociality, temporal and spatial variation in parasite stresses generated past Darwinian selection that built species-typical, conditional psychological adaptations functionally designed for assessing local parasite stress. These adaptations guide the conditional adoption and use of intergroup attitudes that manage the risk and cost of exposure to infectious diseases. Host–parasite antagonistic coevolutionary races are variable and localized spatially across the range of a single human culture, yielding local co-adaptation between hosts and their local parasites. This creates a situation in which contact and interaction with non-group members (out-groups) is costly, because out-group members, relative to in-group members, carry parasites to which in-group members are not adapted immunologically. This can involve different parasite species or different variants of single parasite species. Xenophobia—the avoidance of and antagonism toward out-groups—appears to be an evolved solution to the problem of maladaptation to the infectious diseases parasitizing out-groups. Ethnocentrism is a complementary, evolved solution to the fitness challenge imposed by parasite stress: loyalty toward, assistance of, and interdependence with in-group members insures against the mortality and morbidity caused by local parasites. The greater the parasite stress in a region, the greater the ethnocentrism and xenophobia, a cultural value system which cross-cultural psychologists refer to as collectivism. Likewise, the lower the pathogen prevalence, the lower the ethnocentrism and xenophobia, a value system referred to as individualism. Out-group interactions provide benefits to individuals of broader social networks and intergroup alliances, but such benefits will exceed costs only when parasite stresses are low. Consequently, the model proposes that parasites causally influence human values/morals, a major category of human preferences, pertaining to family life and to in-group and out-group feelings, motivations and behavior in general.

Collectivism (as opposed to individualism) is a value system of out-group devaluation; in-group support; conformity to in-group norms; closed-ness to new ideas and ways; and allegiance to traditional values, hierarchy and authority. The collectivist understands self as immersed in and interdependent with the in-group, and places emphasis on distinguishing in-group from out-group members. In contrast, the ideology of individualism recognizes the validity and value of interactions with out-groups who have different norms and beliefs, and prioritizes openness to novelty, thus placing less importance on tradition and authority. The individualist understands self as relatively independent of the in-group, and in-group and out-group boundaries are dynamic and blurred.

Furthermore, parasite stress and collectivism negatively relate to democratization across the countries of the world: high parasite stress and associated high collectivism correspond to low levels of democratization, i.e., high autocracy. Compared to individualistic countries, collectivist countries exhibit greater and more widespread poverty, inequality, morbidity, and mortality as a result of the reduced investment in public welfare, health, infrastructure, education and other public goods and services by the state. This reduced investment by elites stems from the collectivist ideology of devaluing out-group members, valuing in-group members and general endorsement of human inequality.

In a cross-national study of intrastate armed conflicts, a category of within-state, civil conflict that includes civil wars (Letendre et al., 2010), we proposed that in nations with relatively high intensity of infectious disease, the combination of increased resource competition (due to widespread economic dearth and inequality) and the ethnocentrism and xenophobia characteristic of collectivist societies cause increased frequency of intrastate armed conflict. In addition to the direct, negative effect of the mortality and morbidity of infectious disease on the human capital that is necessary for the generation of wealth, xenophobic groups are less willing to invest in public goods – such as infrastructure, education, and economic development – that will be shared across many groups within a nation. In such countries, conflicts for resources are more likely to arise, and these conflicts are more likely to be resolved through armed conflict, or to escalate to civil war. In contrast, nations with relatively low intensity of infectious disease experience less severe resource competition (higher GDP *per capita* and more equitable resource distribution) and decreased ethnocentrism and xenophobia. Hence, conflicts for resources are less likely to arise in these nations; and, when they do arise, they are more likely to be reconciled through cooperative means instead of through war.

We (Letendre et al., 2010) analyzed two data sets on outbreaks of intrastate armed conflicts across nations of the world. Strand's (2006) data included small-scale intrastate armed conflict wars resulting in at least 25 battle deaths in one year, as well as large-scale civil wars. Fearon and Laitin's (2003) data, based on the Correlates of War Intrastate War data set, tallied major civil wars—those killing at least 1,000, with a minimum yearly average of 100 dead, and at least 100 killed on both sides. Hence, data were analyzed for intrastate armed conflicts across a range of magnitude in terms of mortality.

The parasite-stress model of sociality applied to civil war was supported (Letendre et al., 2010). The statistical analyses and their empirical results indicated that pathogen severity positively predicted the frequency of civil-war outbreaks across the globe, and this was found in separate analyses for small-scale conflicts with relatively low mortality, as well in large-scale civil wars with high mortality.

In addition to intrastate armed conflicts, in Letendre et al. (in press) we explored the application of the model to other categories of civil conflict: (1) non-state-government wars, hereafter non-state wars, i.e., intergroup, within-state conflicts in which the state government is not a combatant; (2) political coups and revolutions; and (3) within-state terrorist events. As does civil war, all three of these additional intrastate conflicts derive from major differences in ideological preferences among groups within a nation. We hypothesized that all three types of intrastate conflicts arise, at least in part, from elevated out-group intolerance and devaluation, and in-group alliance and cooperation, and hence will be most frequent in nations with high pathogen severity and related high collectivism.

Finally, we examined the application of the parasite-stress model to a measure of peace vs. conflict across countries, the Global Peace Index. The measure combines information about the presence or absence of internal and external conflict across many nations. This analysis allows the extension of the parasite-stress model to international warfare, as well as to internal conflict. This composite variable also allowed us to test our model with causal modeling, as this method has strict requirements for the normality of variables, and therefore other indicators of the frequency of conflict do not lend themselves to this method.

We found that the incidence of intrastate armed conflict, non-state wars, and revolutions and coups was predicted by parasite stress; the predicted relationships also were seen with a measure of peacefulness, the absence of internal and external conflict. As parasite stress and its associated collectivism increase, and GDP *per capita* decreases across countries, so does the incidence of intrastate armed conflict, non-state war, and revolutions and coups. Peacefulness increases as parasite stress and collectivism decline across countries and GDP *per capita* increases. These results are robust across a variety of categories of conflict, even when controlling for a battery of demographic, economic, and political indicators.

The one category of conflict which did not satisfy the prediction of the parasite-stress theory was terrorist incidents. We failed to find support for either a direct or indirect effect of pathogen severity on the incidence of terrorism. However the available data on terrorism may not lend itself to the analyses we performed. Terrorism, and especially modern suicide terrorism, is extremely asymmetric: attackers can inflict damage on a multitude of undefended, civilian targets, using cheap and readily available materials that are difficult to detect. Therefore, it may be that it is generally collectivist elements within a country that are responsible for terrorist events, as we hypothesize; however, if only a few collectivist individuals can carry out terrorist attacks in countries otherwise characterized by relatively individualist cultures (e.g., the Oklahoma City bombing, carried out by right-wing extremist Timothy McVeigh in the United States in 1995; Blee & Creasap, 2010), then the regression analyses performed here at the cross-national level will not reveal this relationship. Our hypothesis with respect to terrorism is suggested by other findings that terrorism is tied strongly to ethnocentric convictions about the truth of in-group religious beliefs and the falsity of out-group religious beliefs. Even secular terrorism, they suggest, is the result of strong ideological preference differences between groups. It has been posited that religion is an evolutionary adaptation for warfare in general – an adaptation likely to be implicated even in a relatively novel expression of inter-group violence such as terrorism. The positive association of parasite stress and religiosity has been described, and tested elsewhere; thus, our approach places these diverse findings in the context of a general model based fundamentally on parasite stress. We hope that given relevant data, this theory may yet shed light on the causes of terrorism.

These findings, combined with the detailed, longitudinal and cross-sectional analyses of civil wars and small-scale intrastate conflict by Letendre *et al*. (2010), support the application of the parasite-stress model of sociality to political conflict. Our analyses of the Global Peace Index across countries allow an initial examination of the parasite-stress model in relation to international political conflicts.

Our hypothesized path model did not include a direct relation between pathogen severity and the Global Peace Index, but instead linked these two indirectly via the indirect effects discussed above: ethnocentrism, resource availability (GDP *per capita*), and democratization. Analysis of our hypothesized model suggested that the model would be strongly improved by the inclusion of a direct relation of pathogen severity to peace. This addition agrees with our theory because, in order to restrict our analysis to relatively simple models, we did not include a number of other known correlates of conflict that we argue are intermediary to the relationship of infectious disease to peace (e.g., wealth disparity, political instability, etc.).

We found that removal of the relation of democratization to peace did not decrease the fit of the model. This suggests that, while democratization is a known correlate of conflict, its relationship with conflict is spurious, and is accounted for by both variables' association with infectious disease and collectivism. We also found that removal of the direct relation of ethnocentrism to peace did not decrease the fit of the model. This may be because while ethnocentrism is an important component of the cultural unidimension of collectivism-individualism, it does not correlate perfectly with the other component of collectivism, xenophobia. Thus there is the possibility that xenophobia and ethnocentrism play distinct roles in our path model. There may be a mediating role of xenophobia between pathogen severity and peace, which is not explicit in our model because we do not have a corresponding measure of xenophobia in the analysis. Alternatively, it may be, as our final model suggests, that collectivism leads to increased conflict (decreased peace) entirely through other intermediary effects, such as collectivism's negative impact on GDP *per capita*.

The results of our path analysis support the model we propose. Our revised model fit the data very well, and agrees with the overall argument that infectious disease plays an important causal role in variation in peace, via disease's indirect effects on the cultures, economies, and political structures of countries of the world. Our findings indicate that the parasite-stress model may be an important way to understand variation in the frequency and intensity of many major types of political conflicts.

THE ORGANIZATION OF SOCIAL FORAGING IN HARVESTER ANTS

The second component of this project was an investigation into the organization of social foraging by colonies of harvester ants in the genus *Pogonomyrmex*. According to optimal foraging theory, animals evolve behaviors that maximize energy gain and minimize foraging costs given the distribution of food in their environment. Group foraging can improve the efficiency of finding and exploiting food that is patchily distributed, densely concentrated, or difficult to acquire.

Ants are a model system for studying how information exchange improves foraging. They practice a range of foraging behaviors, from individual food gathering to mass recruitment of nestmates. As eusocial animals, ants have a fitness incentive to maximize food intake for the colony. Communicating the location or quality of food can direct nestmates to resource-rich areas, reducing time and energy spent searching and helping a colony out-compete neighbors for rich food sources. However, it is not clear to what extent the exchange of information among individuals, for example via pheromone trails, improves an entire colony’s foraging success.

Ant recruitment behavior is of particular interest to computer scientists and artificial life researchers because it serves as the foundation for distributed problem-solving systems like Ant Colony Optimization. However, biologically inspired computation has not yet reached its full potential, as biocomputing techniques are based on only a small sample of natural behaviors, the diversity of which is still largely unexplored. We examine how variation in food distribution affects foraging in real (Flanagan, Letendre, et al., 2010; Flanagan, Letendre, et al., in review) and simulated (Letendre & Moses, in review) ant colonies in different environments.

We investigated how the entropy of food distribution affects foraging rates in field studies and models of three sympatric species of harvester ants of the genus *Pogonomyrmex*. These well-studied central-place foragers can forage individually or use recruitment. There is a temporal and spatial heterogeneity in the distribution of seeds that make up the bulk of these ants’ diet , which affects the costs and benefits of the solitary versus social foraging. For Pogonomyrmex, time costs dominate over energetic costs in foraging. Therefore, maximizing seed collection rates maximizes net energetic intake, an important contributor to colony fitness.

In field experiments, we placed dyed bait seeds in a spatial distribution around each ant nest, varying from a random scattering of seeds, to seeds placed in 16 piles, 4 piles, or a single large pile. The seeds concentrated in a single pile formed the distribution with the lowest entropy. An ant that found the single large pile thus gained information about the location of the largest number of seeds, and the ants could exploit that information to improve foraging. We calculated a foraging rate for each distribution by monitoring the seeds of each color as they were brought into the nest. Thus, we could measure how discovering piles that conveyed different amounts of information about seed locations, affected the rate that seeds were collected from each distribution. This allowed us to test our primary hypothesis, that foraging rates increase systematically as seeds are concentrated into larger piles.

Colony size could also influence how information affects foraging success. Many colony characteristics change systematically with size. Chemical communication should increase with colony size, reflecting the increasingly complex web of information in which an individual ant is embedded. Indeed, mass recruitment is more common in species with larger colonies. Our experiments and models were conducted on colonies whose forager population sizes at maturity range from fewer than 100 for P. desertorum to hundreds in P. maricopa to over 1000 in P. rugosus.

Our experimental design controlled for two effects of colony size: larger colonies with more foragers have larger territories; and larger colonies collect seeds at greater absolute rates. After controlling for these factors, we were able to test a second hypothesis, that the relative foraging rate for clumped seeds vs. dispersed seeds would increase with colony size, as a result of larger colonies' greater ability to share information.

Previous research has shown that the distribution of food and the difficulty of finding food affect the evolution and utility of communication. A model of collective foraging by bees previously showed that agents benefitted from memory and communication when food was sparse or clustered but not when it was distributed at random. In another study, communication evolved for ant-like agents only when food was difficult to find. Together, these studies suggest that randomly distributed or easily discovered food do not justify the use of communication, but for clustered foods, communication may provide substantial benefits. We also explore the hypothesis that the benefit of communication is dependent on the distribution of food. We do this for real and simulated ants, and we describe the distribution of food in terms of the information required to specify the locations of food piles.

We were interested in understanding how specific foraging behaviors generate different foraging patterns for seeds clustered in different pile sizes. Our goal was to quantify the benefit conferred to the colony, in terms of improved foraging rates, of communicating the information of the location of these piles to other nestmates. We used Shannon information theory to quantify information and an Agent Based Model (ABM) to simulate foraging with pheromone recruitment.

In field studies, (Paz, Letendre et al., 2010; Paz, Letendre et al., in review), we experimentally manipulated the distribution of seeds available to ant colonies by supplementing the natural seed bank with a constant number of dyed seeds arranged around ant nests. We divided the seeds into piles of different sizes with distributions coded by colors in order to investigate how spatial heterogeneity in seed distribution and interspecific differences in forager population size affect foraging rates. Colony population size varies naturally across these closely related species. In populations native to the Chihuahuan Desert of New Mexico, total colony population sizes have been estimated as thousands for *P. rugosus*, a few hundred for *P. maricopa* and fewer than 100 for *P. desertorum*. Similar relative differences in forager population sizes were found by others who estimated colony forager populations of dozens in *P. desertorum* and thousands in *P. rugosus*.

In order to investigate the influence of forager number and heterogeneity in the distribution of food on foraging strategy, we developed an ABM of foraging by harvester ant colonies, based on descriptions of their behavior in the biological literature and our own observations (Letendre & Moses, in review). We used these models to test the prediction that more intense recruitment behavior will be optimal for larger colonies and for colonies foraging in environments with more heterogeneity in the distribution of food. ABMs are particularly useful for modeling systems with spatial or temporal heterogeneity and systems in which complex behavior emerges as the result of interactions among individual agents with relatively simple behaviors, just as the group behavior of an ant colony emerges as the result of actions and interactions among the individual ants.

ABM's allow us to investigate the effects of forager number and food heterogeneity on the evolution of recruitment behavior by allowing perfect control over these independent variables, while controlling for other factors that are difficult or impossible to control in the field. For example, one wants to compare species that share enough similarity in their foraging habits and environment, and that vary only in the traits of interest; but it may be that traits covary among related species in the field as a result of phylogenetic dependence. Heterogeneity in the distribution of seeds in the field has been estimated by taking soil samples, however such estimates may not provide a relevant measure of the heterogeneity of foods for a given ant species, as ants do not collect all seeds indiscriminately. Even sympatric species may vary systematically in their preference for seeds of different sizes – and thus seeds that may be found in different spatial distributions – based on the size and morphology of the workers. ABM's allow us to control all confounding factors and experimental conditions, and thus provide a perfect experimental environment so that we can study only the behaviors of interest.

We were interested in the effects of forager number and food heterogeneity on the optimal foraging behavior of ant colonies, specifically colonies' use of pheromone recruitment to food sources. Therefore we optimized our ABMs using genetic algorithms (GAs), an optimization technique that simulates the process of evolution by natural selection. In the field, the behavior of *Pogononomyrmex* species is optimized by natural selection to maximize foraging success (among other goals and constraints) given each species' particular ecology. Therefore, GAs and other evolutionary algorithms are a particularly appealing method for selecting parameters for models of biological systems.

We used GAs to determine behaviors, encoded as parameters in our ABM, that maximized seed intake. The fitness function in our GA was seed intake rate. We executed GAs over a range of forager numbers, and over a range of food distributions from fully homogeneous to fully heterogeneous, selecting for fastest rate of food collection under these varying conditions.

We replicated our field studies in simulated observations with our optimized computer models, and compared model results to field data to assess the plausibility that pheromone recruitment explains the relationships we observed between seed distribution and foraging rates. The field studies showed us how ants respond to particular food distributions in nature. The model allowed us to quantify how different behaviors of individual ants affect foraging rates of colonies under perfectly controlled conditions. The integration of models and field studies led to insights that neither could achieve in isolation.

Our field observations found no evidence that colonies with large forager populations collected clumped seeds relatively faster than smaller colonies. However, relatively more-clumped distributions were collected faster by all ant species.

The rate that ants collect seeds is a function of two processes—the time for the ants to discover seeds from a distribution and the time it takes to collect a distribution once it is found. For all species, the time to discover more dispersed seeds was faster than the time to discover more clumped seeds. However, once those piles were discovered, more clumped seeds were collected significantly faster than the dispersed seeds. By analyzing the foraging rate, we determined how much faster foraging occurs once a colony knows the location of one seed from a distribution. Our analysis focused on a normalized foraging rate—the rate that a distribution was collected once discovered by a forager divided by the rate that random seeds were collected once discovered. The normalized foraging rate accounts for differences in the number of active foragers in a given day and allowed us to make comparisons across species and conditions that varied widely.

Repeated measures analysis showed no effect of species (which vary significantly in forager population size) on normalized foraging rates. Not surprisingly, colonies with more foragers collected a larger total number of seeds. However, larger colonies can allocate a much larger number of workers and use more complex communication networks to maximize seed collection. Therefore, we expected that large colonies would be disproportionately good at collecting seeds from large piles. Our analysis indicates that large and small colonies collected seeds from large piles equally fast and seeds from smaller piles equally fast. However, these results should be interpreted in the context of our study design.

By controlling for distance in our experimental design, we controlled for colony territory size, and for the distance that foragers travel to look for food. In the case of small colonies, by giving them equal opportunity to access the seed piles, we may have provided them with what would otherwise be a rare seed availability within their territory compared to availability of seed caches in territories of larger colonies. This rare condition may trigger the activation of additional resources disproportionate to those allocated by the larger colonies.

We found a satisfying fit between the behavior of our model of density-dependent recruitment behavior and the foraging behavior of *Pogonomyrmex* harvester ants in the field. Another model of recruitment behavior based on common models of ant recruitment in the literature, in which ants leave a recruitment trail each time they complete a successful foraging trip produced a less satisfying fit, as a result of its inability to converge foraging effort on high-quality patches in environments where seeds exist in a mixture of homogeneous and heterogeneous sources. We found that when optimized by GA, the density-dependent recruitment model tended to evolve relatively selective trail-laying behavior, instead of the behavior of the simple recruitment model. This allowed the model to decrease the noise in the pheromone system that resulted from trails leading to low quality patches in the simple recruitment model, and allowed colonies to adaptively converge their foraging effort on high quality patches given any degree of heterogeneity in the distribution of food. The density-dependent recruitment model allowed the evolution of intense recruiting behavior in colonies of all sizes, and in all environments except those completely devoid of heterogeneous food sources. Density-dependent recruitment behavior allows ants to exploit heterogeneity in the distribution of food when they encounter it, even if they encounter it only rarely.

Contrary to the expectation of the simple recruitment model, in which ants leave pheromone trails each and every time they pick up food, we found that for all forager numbers and for all degrees of heterogeneity in the distribution of food, colonies always evolved a condition-dependent trail-laying behavior. The most selective trail-laying behavior tended to evolve in environments with mixed heterogeneous and homogeneous food sources, where there is greatest advantage in basing the decision to leave a pheromone trail on the presence of other nearby foods, in order to distinguish randomly scattered foods from piled foods. We found a robust effect of increasing food heterogeneity on the evolution of increasing recruitment behavior in the simple recruitment model. In the density-dependent recruitment models, recruitment behavior remained high until essentially all heterogeneity was removed from the food distribution.

Although the results of our GA runs with the simple recruitment model revealed the hypothesized positive effect of forager number on recruitment behavior, this result was supported less strongly in our density-dependent recruitment model. Like the simple recruitment model, the density-dependent recruitment model evolved increasing recruitment behavior with increasing forager number in fully homogeneous food distributions. It is in these completely homogeneous environments, however, where we least expect to see the evolution of recruitment behavior. Therefore, this result indicates colonies' use of the pheromone trails to direct foraging effort an optimal distance away from the nest, rather than toward a particular food source. This is similar to the use of foragers' use of trunk trails to travel some distance from the nest before beginning to search. It is likely, however, that individual ants have the capacity to walk a distance from the nest entrance before beginning to search, without relying on pheromone trails to do so. While it may be that ants will often drop off a pheromone trail before reaching its end in order to explore for additional, nearby food sources, we think it unlikely that pheromone trails would be used solely for directing foragers away from the nest, given that, for *Pogonomyrmex* and other ant taxa that produce trail pheromone with a specialized gland, producing pheromone presumably has some physiological cost.

In our models, we forced ants to follow pheromone trails from the nest, or else to begin searching immediately at the nest entrance, in order to force optimization on the use of the pheromone trails. The evolution of increased recruitment behavior with forager number in environments with completely homogeneously distributed foods may be an artifact of this aspect of our model. There may be other reasons that ants will use trunk trails to travel a distance from the nest before beginning to forage, e.g. avoidance of predators or management of conflict with neighboring nests; but we suspect it is unlikely that ants in nature use pheromone trails solely for the purpose of directing foraging effort away from the nest.

With the introduction of any piled foods to the environment, we found that the density-dependent recruitment model evolved relatively intense recruitment behavior even in the smallest colonies. Given some degree of heterogeneity in the environment, colonies that can exploit this heterogeneity when they encounter it are at a selective advantage over those that do not, even in species with small colonies that encounter piled foods relatively rarely. The density-dependent recruitment behavior allows colonies to exploit heterogeneity when and where they find it, even if they encounter piles of food infrequently, as for the small colonies modeled here.

We observed that the behavior of the simple recruitment model was similar to the behavior of the density-dependent recruitment model when evolved on fully heterogeneous food distributions. This is because in these environments, all available food is found in dense patches. Therefore if an ant finds a piece of food, that piece of food is necessarily coming from a dense patch and information about that location is of as much value as for that of food found anywhere else. In these environments both models tend to produce well-defined pheromone trails and converge their foraging effort on nearby piles, as predicted by common models of ant recruitment and collective decision-making. In addition, we found that the density-dependent recruitment model evolved significantly more selective use of the pheromones on fully heterogeneous food distributions than in fully homogeneous distributions. More selective trail-laying behavior allows ants to be sensitive to the depletion of dense piles, and allows the colony to more rapidly and adaptively switch to a new pile as the remaining seeds become fewer and harder to find. For example, *Solenopsis* workers at a food source may be regulated by unsuccessful foragers returning to the nest without laying a trail. Similarly, *Lasius* workers require a threshold volume of nectar in their crops in order to lay a trail. This negative feedback has a lag of several minutes, however, resulting in an ―overshoot” of the optimal number of workers arriving at a site. On the other hand, if even successful foragers are able to return from a dwindling food source without laying a trail, as we observed here, this ―overshoot” may be minimized. Thus, even for species whose foods occur only in patches too large to be collected by a single forager, e.g. army ants specializing on raiding other social insect colonies it may be adaptive to make relatively selective use of pheromone trails. Given that producing pheromone may bear some physiological cost – a cost we did not impose on the simulated colonies in our GA runs – we expect that for ants in the field, there is even greater advantage in using pheromone trails selectively.

When the simple recruitment model was evolved on increasingly homogeneous food distributions, recruitment behavior steadily fell off. We found that the addition of homogeneously distributed foods prevented the convergence of foraging effort on high quality patches. This was a surprising outcome, given the assumption that colonies will converge on high quality patches because of the increased ease of finding food in those patches. We observed that pheromone trails being drawn back to the nest by ants that picked up homogeneously distributed foods created so much noise in the system that the colonies were unable to converge; many ants that set out from the nest followed trails that led back to a site where no food was to be found, and therefore did not arrive in the high quality patches.

Instead of evolving less intense recruitment behavior with an increasing proportion of homogeneously distributed foods in the environment, the density-dependent recruitment models evolved increasingly selective use of the pheromones. By becoming increasingly selective about drawing a pheromone trail on the return trip to the nest, the information value of the pheromone trails remained high enough that colonies continued to recruit heavily even when as little as one quarter of the available food was distributed in piles.

The binary decision making process surrounding the laying of a pheromone trail is analogous to the decision-making process by scouts of the species *Leptothorax albipennis* and *Temnothorax albipennis* in nest-site selection. Scouts of these species evaluate potential nest sites and selectively recruit nestmates to preferred sites by tandem running, and a variety of nest-site properties relevant to this decision have been identified. Presumably each desired property is factored into a decision-making process such that each contributes to the probability that a scout will begin recruiting to the site. Similarly, *Pogonomyrmex* foragers may incorporate a variety of additional factors into the decision to lay a pheromone trail, including, for example, the presence of other ants which may compete for a food source if it is not collected quickly. Over time, other foragers making the same evaluation cause reinforcement of paths to high value patches and convergence on the optimal colony-level behavior, without distraction by the noise of paths leading to sites of little or no value. This model of recruitment differs from the black garden ant *Lasius niger*, in which workers modulate the weight of pheromone trails according to the concentration of sugar solutions they discover. Compared to *Lasius niger* which forages for nectars that may vary substantially in their concentration and value, there may be less variation in the quality and value of seeds returned to the nest by *Pogonomyrmex* foragers. Harvester ants select seeds within a range of sizes that are easy enough to handle given forager size and morphology of a species; within this range there may be less variation in nutrient value than that encountered by *Lasius niger* foraging on nectar. Therefore for *Pogonomyrmex* foragers, the qualities of individual seeds discovered may be less important to the colonies' foraging success than the presence of other nearby seeds, and this may be an important determinant of the optimal recruitment behavior in these taxa.

The foraging behavior of *Pogonomyrmex* species ranges from solitary foraging to recruitment using persistent trunk trails. Here we have explored via simulation the benefits of social foraging via pheromone recruitment across a range of colony sizes. Our results suggest that the behavioral components of recruitment may not differ categorically across species. Rather, the tendency for harvester ant species to engage primarily in solitary foraging vs. trunk trail recruitment may depend on the likelihood from one day to the next that a small vs. a large colony finds a high-density patch of seeds somewhere on its territory.

We wondered if differences in the ability to recruit to high quality food patches might cause the niche partitioning that allows the co-occurrence of the three sympatric *Pogonomyrmex* species. Our results suggest such a differential ability to recruit is not the answer to that question. Species with larger colony size may dominate high quality patches, however, by recruiting large numbers of foragers to these sites and overwhelming and excluding smaller colonies foraging there, while these smaller colonies are then forced to forage on randomly or less densely distributed foods. This suggests further research into interspecific competitive interactions may be fruitful in understanding how heterogeneity in the distribution of food causes niche partitioning among these ant species.

Information is a crucial currency for animals since informed individuals can adapt behavior to environmental conditions, but information is rarely measured in terms of its contributions to fitness. By quantifying how information improves foraging, we can begin to measure information in terms relevance to colony fitness or to performance metrics for artificial systems.

Our results showed that foraging rates for each piled distribution roughly doubled as the entropy of the distribution decreases from one bit (1 pile), two bits (4 piles) and four bits (16 piles). The time for ants to find the seeds increases roughly proportionally to the increase in the entropy of the distribution. So, these ants exploit the increased information available upon discovering a pile in lower-entropy distributions to improve whole colony foraging intake. Intuitively, an ant colony needs more information to exploit seeds if those seeds are distributed in more piles. A forager that finds a large pile greatly reduces the entropy of that distribution. For example, if an ant finds a seed from a 1-pile distribution, the entropy of that distribution is reduced to zero; the ant colony has information about the location of all the seeds in that pile. Additionally, the ant can convey the location of these seeds to its nest mates and attract more foragers to the pile, resulting in a faster foraging rate.

Our results can also be interpreted in the context of a recent analysis of the fitness value of information. Given an uncertain environment, the strategies that maximize fitness use effective bet hedging such that the probability of investing in any particular phenotype is proportional to the certainty that the environment will favor that phenotype. A cue that reduces uncertainty about the environment allows an organism to invest more in the appropriate phenotype. So, the cue has fitness value proportional to the amount of reduction in uncertainty, which is the information encoded in the cue. Since ant colonies do not know the distribution of the seeds, the colonies will –bet” on a strategy according to cues that reduce uncertainty about the location and availability of seeds in the environment. These cues are conveyed to the colony with the discovery of each pile of seeds, and the colony responds with a strategy appropriate to the average availability and distribution of seeds in that species' evolutionary environment.

The fitness value of information for the ants can be measured over the lifetime of an individual colony. In our ABM, the cumulative weight of pheromone leading to a food source is a signal that reduces uncertainty about the location of seeds. When seeds are clumped into larger piles, the cues encoded in the pheromone trail are more valuable, and the improvement in foraging is proportional to the information encoded in the cue. Thus, we suggest that the colony improves foraging rates in proportion to the information that an ant can convey upon finding a seed. The colony bet-hedges by allocating foragers to piles in proportion to the information about seed locations in that pile. Given that a colony faces an unknown distribution, this strategy maximizes seed intake rates over the life of the colony.

Quantifying the value of information and its communication among social foragers may help us understand how animals use information more generally. It may also help us to assess the value of information exchange between components in engineered distributed systems.

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