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Resource Competition Amid Overlapping Territories: The Territorial Raider Model Applied to Multi-Group Interactions

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Abstract

Many organisms maintain collective territories and compete on behalf of the fitness of the overall group. Inspired by this concept, the territorial raider model is a graph-based resource competition in which populations have fixed home locations and a limited range of sites accessible for raiding. In our present extension of the model, groups control "colonies" or "armies" which can be divided across multiple locations. We present Nash equilibria for games played on both regular graphs and regular bipartite graphs, and we also examine differences that emerge when populations are composed of discrete units (pack scale) or when they are continuously divisible (colony scale). Reliance upon defense over aggressive raiding is greater here than in the original model where populations had to totally commit to a singular action. This defensive posture increases with the advantage of the local population and also varies with the degree of the graph's connectivity. When discrete units are employed, multiple strategies emerge.

Keywords: structured populations, game theory, animal groups, territory

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1. Introduction

A key focus within spatial ecology is the identification and understanding of mechanisms that regulate the distributions of differing species across the available landscape (Urban and Keitt, 2001; Fortuna and Bascompte, 2006; Fortuna et al., 2009; Bellisario et al., 2010). Various factors influence the dispersal of animal populations and limit their ranges, including the physical topography of the landscape and the social context within and external to the group in question (Jacoby et al., 2012; Farine et al., 2015; Strandburg-Peshkin et al., 2015; Jacoby and Freeman, 2016). Diamond (1975) posited that competition was one of the most important factors generating any structure within a community, with territorial overlap between rival groups potentially leading to losses of scarce resources such as food, water, or shelter to nearby rivals (Jetz et al., 2004). In this paper we focus on a model of group interactions over resources in which populations may strategically allocate their forces across multiple locations. We adopt a multiplayer game theoretic model of overlapping territories or neighborhoods on a graph network Broom and Rychtář (2012); Galanter et al. (2015) to explore territoriality among competing groups (e.g. prides, colonies, armies). Further we examine how the defensive posture or raiding aggressiveness of a population responds to variations in the potential encounter size of opposing groups and the advantages afforded to home site defenders.

Many organisms, including humans, maintain a social structure and division of labor that permits the achievement of multiple tasks simultaneously by allocating portions of total available effort to each purpose on behalf of the group as a whole. The most common example of this phenomenon involves the dispersal of individuals to retrieve food items and other resources for subsequent group consumption at a designated home site. Examples of territorial animals with communal sharing include African wild dogs and foxes (Ginsberg and Macdonald, 1990), roadrunners (Kelley et al., 2011), lynx (Schmidt et al., 1997), chestnut-crowned babblers (Sorato et al., 2015), and green woodhoopoes (Radford and du Plessis, 2004). The prevalence of prides among African li-

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ons (Heinsohn and Packer, 1995; Mosser and Packer, 2009) may result from territorial conflicts with con- and heterospecifics (Packer et al., 1990). The violence attendant to group conflict ranges considerably across taxonomic groups. At one extreme, troops of male chimpanzees vigorously defend their own ter-
³⁵ ritorial food resources and violently raid those of others (Watts and Mitani, 2001; Williams et al., 2004). Conflict resolution is less deadly, however, between colonies of the honeypot ant, *Myrmercocystus mimicus*, which perform rituals, dances, and displays in a demonstration of group strength (Hölldobler, 1981; Hölldobler and Wilson, 1990). So too, boundaries between rival groups
⁴⁰ may fluctuate temporally, or they may be sharply preserved with little territory shared.

Graph and network theory have become a valuable tool in understanding the formation of community structures and ecological movements (Lewinsohn et al., 2006; Montoya et al., 2006; Sah et al., 2014). They have been applied to many
⁴⁵ ecological and evolutionary phenomenon (Dale and Fortin, 2010), and graphs have proven useful in large scale systems such as metapopulations (Economo and Keitt, 2008), biogeographic areas (Noss, 1991), and in wildlife or fisheries management (Christensen et al., 1996). Moreover modern theoretical efforts have contextualized how games are played upon graph structures (Nowak and
⁵⁰ May, 1992; Lieberman et al., 2005; Shakarian et al., 2012; Broom and Rychtář, 2013; Antal and Scheuring, 2006; Taylor et al., 2004; Hadjichrysanthou et al., 2012; Jeong et al., 2014). These efforts resolve one of the primary drawbacks of traditional game theoretic models of biology, namely the assumption of well-mixed populations or communities, while not rising to the level of intractability
⁵⁵ characteristic of continuum models (however, see Cosner (2005); Rowell (2009, 2010)). Biological applications of this theory now include epidemiology (Keeling et al., 2010; Meyers, 2007; Shirley and Rushton, 2005) the study of the evolution of traits under synergystic effects (Taylor, 2013), cooperation among relatives (Allen and Nowak, 2015), cooperation in public goods games (Rand et al., 2010;
⁶⁰ Szolnoki and Perc, 2012), and the consequences when the underlying interaction structure changes (Broom and Cannings, 2013).

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Broom and Rychtář (2012) introduced the territorial raider model as a framework to describe interactions such as when territorial animals competed for food resources (for other attempts at multiplayer approaches see Kurokawa and
65 Ihara (2013). They alternatively considered scenarios with random movement of agents with strategic interactions using the hawk-dove game, as well as with strategic movement and deterministic outcomes. Bruni et al. (2013) further analyzed multiplayer hawk-dove territorial games, while Broom et al. (2015) incorporated birth-death processes into both hawk-dove and public goods games.
70 Galanter et al. (2015) recently explored similar models in which defensive units could pre-emptively secure a portion of a site's resources prior to the initiation of conflict (which is resolved with a proportionate division of contestable resources). Here we extend those previous results to territorial interactions between social animals living in communally held territories. Each population
75 can allocate portions of available forces to multiple raiding and defensive tasks rather than being restricted to a complete commitment to a single activity. Our main results focus on a continuous model in which a group's force can be divided into arbitrarily small units; however, we do also consider scenarios with discrete army units.

80 2. Army Territorial Raider Game

Consider an environment comprised of a set of distinct patches connected by a network of traversable corridors, with each patch serving as the home territory of a single population. We mathematically represent this arrangement by a graph $G = (V, E)$ containing n vertices in the set V which are connected
85 by the edges in E. The graph is a reflection of habitat connectivity (Fischer and Lindenmayer, 2007), and it may result from either the spatial configuration of habitat patches or larger tracts of contiguous habitats (Ferrari et al., 2007; Rayfield et al., 2011). To reflect the spatial conflict over resources during territorial raids, we define the army territorial raider game (ATR Game) played on
90 the graph G by the following rules and assumptions (see Table 1 for a complete

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list of variables). There are n populations, denoted a_i, who participate in a competition for resources scattered across the graph. Each population is associated with a unique home vertex $v_i \in V$ which has a corresponding resource value R_i. Each population manages an army whose total strength, T_i , may be allocated across the population's home vertex (defending) and any adjacent vertices (raiding). This allotment of forces on the graph is the population's strategy, represented by the vector $s_i = (m_{i1}, \ldots, m_{in})$. All allotments are non-negative, $\sum_j m_{ij} = T_i$ and $m_{ij} = 0$ if the vertices v_i and v_j are non-adjacent. The combined distribution of forces for all populations result in a payoff X_i for population a_i.

In the ATR Game, defending units have an inherent advantage over raiders, characterized by the score $H \in [0,1]$. A population using a portion of its forces $p_i = m_{ii}/T_i$ to defend its home vertex automatically protects $p_i H R_i$ resources. The remaining $(1 - p_i H) R_i$ resources are proportionately divided amongst all contesting forces, $\sum_k m_{ki}$. If no raiders are present at the vertex v_i, i.e. $\sum_{k \neq i} m_{ki} = 0$, then by default all resources are awarded to the home population a_i. The total payoff for population a_i is thus a combination of defended resources and those obtained while raiding the home vertices of other populations,

$$
X_i = \begin{cases} R_i + \sum_{j \neq i} \dfrac{(1 - p_j H) R_j m_{ij}}{\sum_k m_{kj}}, & \text{if } \sum_{k \neq i} m_{ki} = 0, \\[4mm] p_i H R_i + \dfrac{(1 - p_i H) R_i m_{ii}}{\sum_k m_{ki}} + \sum_{j \neq i} \dfrac{(1 - p_j H) R_j m_{ij}}{\sum_k m_{kj}}, & \text{if } \sum_{k \neq i} m_{ki} > 0. \end{cases} \tag{1}
$$

A Nash equilibrium to the ATR Game is a set of strategies $S = \{s_1, s_2, \ldots, s_n\}$ such that no individual population can improve its payoff by changing strategies independently of the other populations.

In this paper, we will consider the ATR Game subject to the additional constraints that the resources at all locations are equal $(R_i = 1)$ and that the size of the army available to each population is likewise the same $(T_i = T)$. In the results below, we consider separately whether each army is infinitely divisible or if they are composed of discrete units that cannot be further decomposed

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(e.g. platoons or squads). In the first scenario, the army size managed by each

110 population is set to $T = 1$ and the allocation of forces are drawn from $m_{ij} \in [0,1]$. In the second case, each army is composed of $T = U \in \mathbf{Z}^+$ discrete units, and force allocations are $m_{ij} \in \{0, 1, \ldots, U\}$.

Symbol	Meaning
G	Graph representing a configuration of populations and territories
V	Set of all vertices in G
E	Set of all edges in G
v_i	Vertex in V
R_i	Total available resources at vertex v_i (always 1)
a_i	Population with home vertex v_i
T_i	Size of army a_i
U	Units in an army in the discrete game
m_{ij}	Amount of population a_i's forces present at vertex v_j
s_i	Strategy distribution of population a_i's forces over the vertices in G
S	Set of each population's strategies in a round
p_i	Portion of army a_i defending
H	Conversion from portion of army defending to resources protected
X_i	Total payoff obtained by population a_i
d	Degree of a regular graph
A	Independent set of a regular bipartite graph
B	Independent set of a regular bipartite graph
d_A	Degree of the vertex sets A in a regular bipartite graph
d_B	Degree of the vertex sets B in a regular bipartite graph

Table 1: Notation symbols and meanings

3. Results

We considered the ATR Game played on different types of graph structures.

115 For armies with continuously divisible strength (scaled to 1), we demonstrated

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that symmetric uniformity in raiding forces is a self-reinforcing strategic feature. Furthermore under symmetric raiding, there is a single defensive posture which is the strategic equilibrium.

3.1. Regular Graphs

A d-regular graph is a graph $G = (V, E)$ such that every vertex $v_i \in V$ has d neighbors. Regular graphs encompass several different graph families including cycles and complete graphs.

Our primary result is that if a population's field of opponents a_j employs equal defensive postures, $p_j = p$, and that their raiding forces are uniformly allocated to all targets, represented by

$$
m_{jk} = \begin{cases} \frac{1-p}{d}, & \text{if } j \neq k \text{ are connected,} \\ p, & \text{if } j = k, \\ 0, & \text{otherwise,} \end{cases} \tag{2}
$$

then for any given defensive posture p_i and for any p, the optimal strategy for population a_i is also to adopt a uniform raiding allocation over all potential targets. Secondly, there is a unique defensive posture $p^* \in [0, 1]$ such that if all populations defend with p^* forces and send $m_{ij} = (1 - p^*)/d$ forces to all neighboring sites v_j, then the game is at a Nash equilibrium state.

3.1.1. Proof of Uniform Raiding as an Equilibrium

To prove this, let a_i be a population on a regular graph with d vertices. For all opposing populations a_j with $j \neq i$, let their strategy be a defensive posture of $p_j = p$ with their remaining forces split equally between all adjacent vertices. If population a_i sends no raiders and only defends, $p_i = 1$. Then the uniform distribution of population a_i's raiding forces is trivially true in that $m_{ij} = 0$ for all $j \neq i$. Now assume that $p_i \in [0, 1)$ and that the home-site advantage is $H \in [0, 1)$. The reward to population a_i for raiding site v_j simplifies to

$$
\frac{(1 - Hp)m_{ij}}{m_{ij} + 1 - \frac{1-p}{d}}, \tag{3}
$$

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and the total payoff for all raiding activity is

$$f = (1 - Hp) \sum_{j=1}^{d} \frac{m_{ij}}{m_{ij} + 1 - \frac{(1-p)}{d}}. \tag{4}$$

The function f is continuous, differentiable and strictly concave down on the closed set defined by $m_{ij} \geq 0$ and $\sum_{j \neq i} m_{ij} = 1 - p_i$. There is thus a unique maximum to the function, namely the symmetric raiding strategy

$$m_{ij} = \begin{cases} \frac{1-p_i}{d}, & \text{if } i \neq j \text{ are connected,} \\ p_i, & \text{if } j = i, \\ 0, & \text{otherwise.} \end{cases} \tag{5}$$

Within the domain, the closed set defined by $m_{ij} \geq 0$ and $\sum_{j \neq i} m_{ij} = 1 - p_i$, langrangian optimization using the constraint $\sum_{j \neq i} m_{ij} = 1 - p_i$ and the raiding payoff function f verifies that this strategy is an equilibrium, and the bordered Hessian confirms this strategy is a maximum.

3.1.2. Proof of Defensive Posture p^* as an Equilibrium

Assume that population a_i therefore adopts symmetric raiding. With some algebraic simplification, the total payoff for population a_i (Eq. 1) from both defense and raiding becomes

$$X_i = \frac{[H(1-p) + 1]p_i}{p_i + (1-p)} + \frac{d(1-p_i)(1-Hp)}{p - p_i + d}. \tag{6}$$

A purely defensive strategy ($p_i = 1$) yields $X_i = (1 + H(1-p))/(2-p)$. For some parameter combinations $\frac{\delta X_i}{\delta p_i}|_{p_i=1} > 0$ and the payoff for this strategy is a local minimum and should not be adopted. At the other extreme, a pure raider strategy, $p_i = 0$, earns $X_i = d(1-Hp)/(p+d)$. This strategy is typically another local minimum for the population's payoff; however this is not uniformly true for all parameter combinations.

The symmetric strategic equilibrium occurs when $\frac{\partial X_i}{\partial p_i} = 0$ subject to the constraint $p_i = p$. Thus we have the quadratic equation of p

$$[H(1-p) + 1](1-p) - \frac{1}{d}(1 - Hp)(p + d - 1) = 0. \tag{7}$$

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The symmetric strategic defense posture is

$$p^* = \frac{(1+H) - \sqrt{(1+H)^2 - 4H\left(\frac{1+dH}{1+d}\right)}}{2H}.\tag{8}$$

¹⁴⁰ The upper solution of the quadratic formula has been discarded as it always exceeds 1 under the conditions on H, whereas the lower solution $p^* \in [0,1]$. The solution is at least a local maximum for population a_i $(\partial^2 X_i/\partial^2 p_i < 0)$, and the population cannot increase its payoff by independently deviating from this strategy, nor can any other population, by symmetry. Figure 1 presents the

¹⁴⁵ defensive posture of each population at the strategic equilibrium p^* as a function of H for different degrees of connectivity within the regular graph. The defensive posture p^* strictly increases with the home-site advantage H, and as H goes to 0, p^* approaches $1/(1+d)$. This value is the uniform allocation of forces over all targets and the home vertex. At the other extreme, populations adopt a

¹⁵⁰ purely defensive strategy $p^* = 1$ when $H = 1$ without regard to the degree of the graph. In this particular case, however, the solution is a weak equilibrium as ineffective raids neither gain nor cost anything to the deviating population. Analysis of the discrete game supports the contention that a defense of p^* with equal raiding is the only Nash equilibrium for the game.

¹⁵⁵ *3.2. Regular Bipartite Graphs*

A bipartite graph is a graph $G = (V, E)$ such that there exist two disjoint subsets A and B that partition V, i.e. $A \cap B = \varnothing$ and $A \cup B = V$, and where every edge in E connects a vertex in A to a vertex in B. The graph is said to be regular if every vertex $v_y \in A$ has degree d_A and every vertex $v_z \in B$ has degree

¹⁶⁰ d_B.

Let G be a regular bipartite graph with sets A and B defined above. Let $v_y \in A$ be the home vertex of population a_y, with $v_z \in B$ an adjacent location. Assume that all other populations associated with set A have defensive posture p and equally divide raiders among all potential targets. Assume all populations

¹⁶⁵ associated with B do likewise with defensive posture q.

As with regular graphs, population a_y with defense p_y will respond to the symmetry of its peers and raid each target with $m_{yz} = (1-p_y)/d_A$. Let $\rho = d_A/d_B$
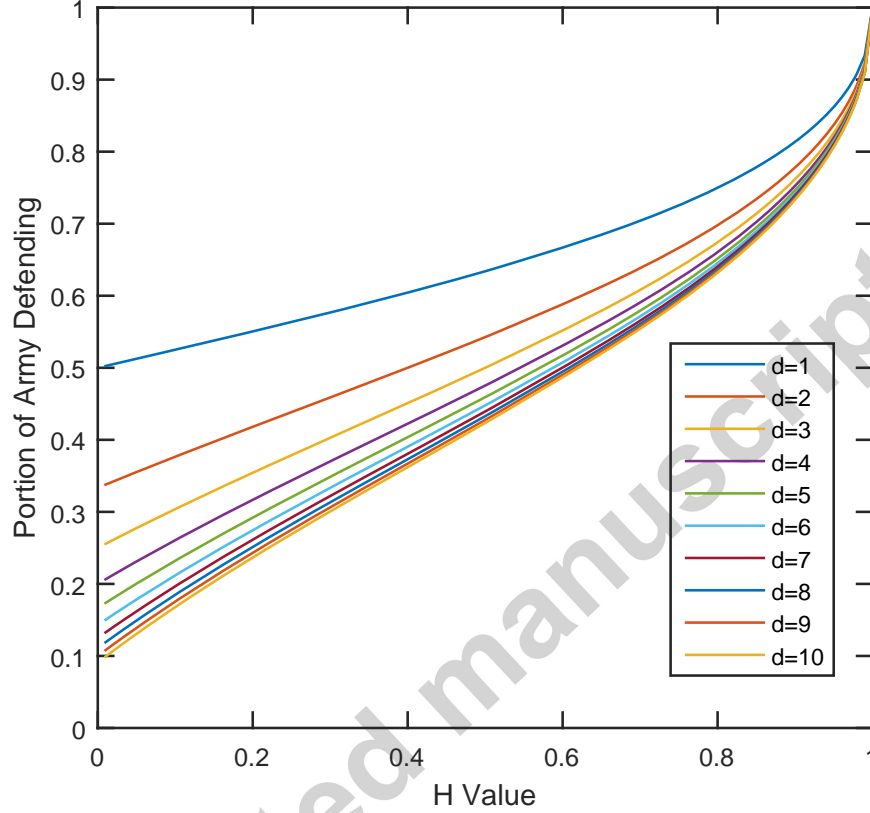
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Figure 1: Equilibrium strategies represented by portion of army remaining at home vertex for all populations. Strategies are graphed by H value and d, the degree of the graph.

be the ratio of degrees for each set. The payoff to population a_y from both defending and raiding is

$$X_y = \frac{p_y(1 + \rho(1-q)H)}{p_y + \rho(1-q)} + \frac{d_A(1 - Hq)(1 - p_y)}{(1 - p_y) + [d_A q + (d_B - 1)(1-p)]}. \tag{9}$$

Maximization involves a pair of third-order polynomials, so equilibrium solutions to the optimal defense postures for populations in each set were obtained numerically using the vpasolve function in Matlab. For low values of H, the set of populations characterized by the larger degree abandoned all defense and

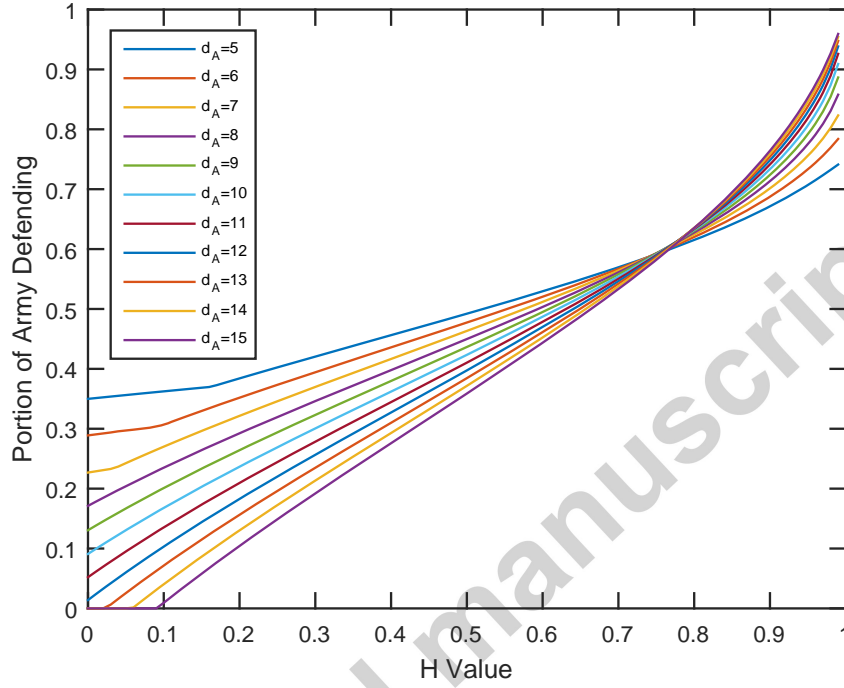170 adopted a pure raider strategy (see Figures 2 and 3). As observed with regular

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Figure 2: Equilibrium strategy represented by portion of army remaining at home vertex for populations in A. Strategies are graphed by H value and d_A, with d_B constant at 5. As a note, the lines for each d_A intersect over a small range of H values, not a single point.

graphs, defensive postures still increase with the advantage H; however p^* does not always decrease with the number of neighbors. Rather, that relationship is seen only at low and intermediate values of H, however, between H values of approximately 6.5 to 7.5 , the solution curves for different degrees cross, switch-
175 ing their order. Additionally, the relationship between p^* and the degree of the other set is reversed.

3.3. Games with Discrete Units

The continuous game is a sensible model approximation for groups with vast numbers of individuals, e.g. ant colonies; however the concept of infinitely
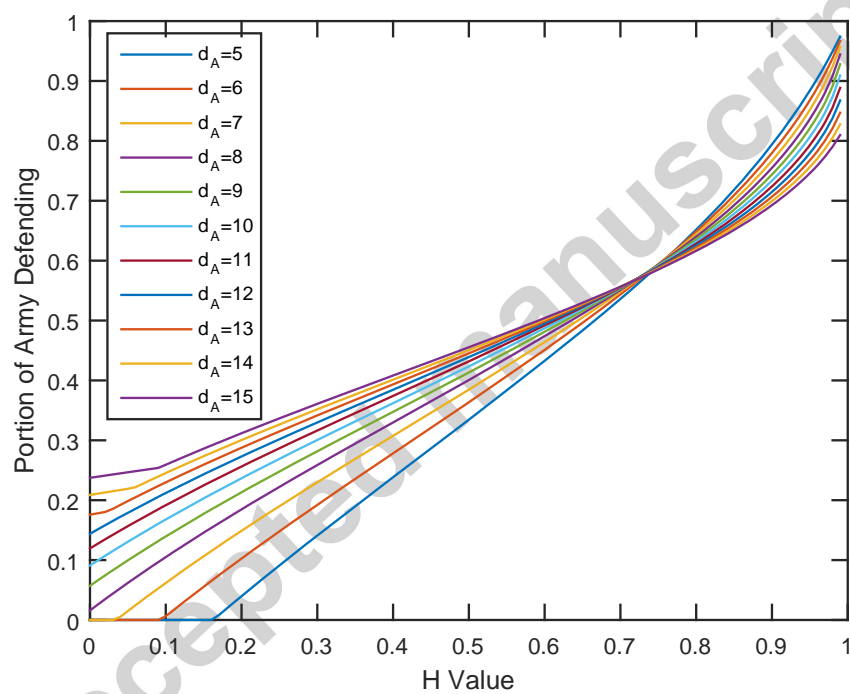
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Figure 3: Equilibrium strategy represented by portion of army remaining at home vertex for populations in B. Strategies are graphed by H value and d_A, with d_B constant at 5.As a note, the lines for each d_A intersect over a small range of H values, not a single point.

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180 divisible forces breaks down when groups have few members (e.g. lion prides, canine packs) or there is an organizational hierarchy such as armies composed of companies or platoons. In the discrete ATR game, each population controls an army with U units, and every deployment m_{ij} must be an integer between 0 and U. We conducted studies for three different structures, comparing them 185 to continuous games with the same graph structures.

The first game analyzed consisted of a single pair of connected vertices, a 1-regular graph. Populations were alloted between 5 and 30 units for their armies. Figure 4 compares the equilibrium results for defensive postures here with those found with a 1-regular graph with continuously divisible units. As the number 190 of units increased, the observed portions of an army devoted to defense drew closer to the solution curve for the game with continuously divisible armies.

The second game we analyzed was played on a hl3-cycle, a 2-regular graph. We compared this with our continuous solution for 2-regular graphs. (Figure 6). As with the 1-regular game, the average portion of units defending home 195 vertices follows the prediction from the continuous case, especially as army size increased. More importantly, multiple equilibria were demonstrated to exist for a given game (Figure 5), and they were not always symmetric.

The final graph studied was the three-leaf star (Figure 7). This structure is a bipartite graph with $|A| = 1$ and $|B| = 3$. While there are pure Nash 200 equilibria to the game for specific combinations of units U and advantage H, not all combinations of these parameters supported the existence of a pure Nash equilibrium. For instance, there is no equilibrium when $H = 0.5$ and $U = 15$ or when $H = 0.75$ and $U = 5$.

4. Discussion

205 In this paper, we extended the territorial raider model (Broom and Rychtář, 2012; Galanter et al., 2015) to encapsulate the behavior of multi-tasking, group-oriented collectives, e.g. armies or colonies, engaged in a spatial resource competition with similar groups. Both natural defensive advantages and the com-
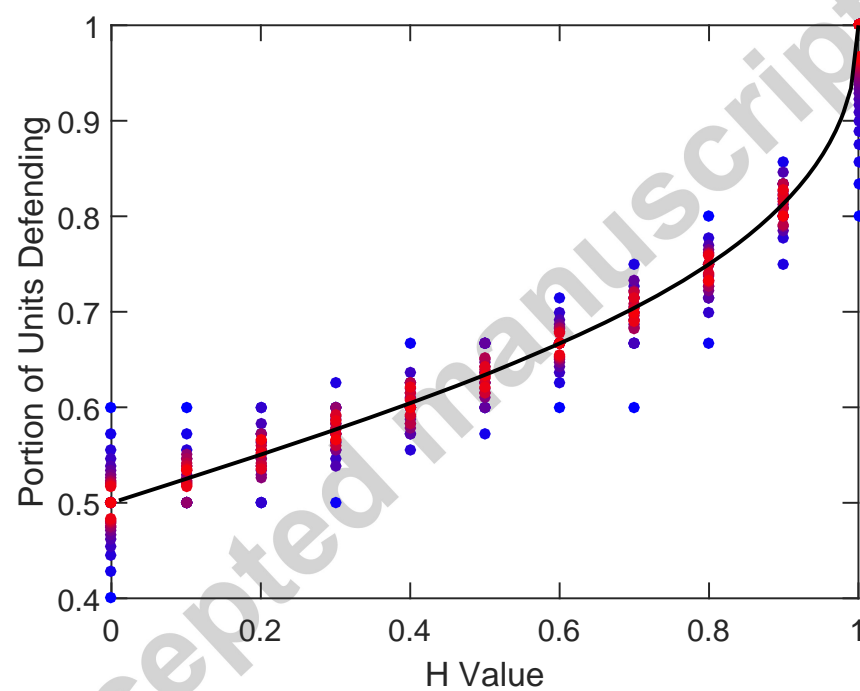
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Figure 4: Two population discrete and continuous game equilibria. Completely blue points are equilibria for the 5 unit game, completely red points are equilibria for the 30 unit game, and as units increase points become more red.
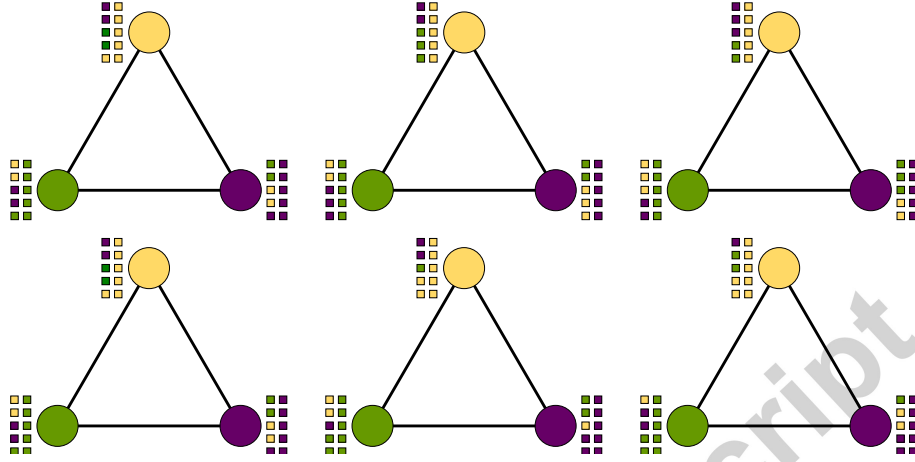
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Figure 5: Representation of the three possible equilibria for a K_3 graph with $U = 10$. The first row of strategies correspond to when $H = 0.5$. The second row corresponds to when $H = 0.75$. Unit colors and vertex colors correspond. The portion of units kept home is nondecreasing relative to H.

munity structure defined by overlapping territories affect the aggressiveness ob-
₂₁₀ served within the community. As the inherent advantage afforded to defenders (H) increases, the equilibrium level of defense (p^*) also increases. Thrips, for example, illustrate this advantage as some resident individuals bearing large heads form plugs that physically block access into nest galls (Bono, 2007). This advantage has a dual effect of increasing the immediate reward for defenders ₂₁₅ while simultaneously reducing the potential share available to raiding groups. This combination naturally selects for a more defensive behavioral phenotype. The discretization of sub-units within the population leads to similar, if not identical, equilibria as in the continuously divisible case. The extent to which any asymmetries are present among the populations diminishes as the divisibil-₂₂₀ ity improves to finer levels. Furthermore, multiple solutions are documented to exist for these games.

Naturally connected networks, such as those constrained by topographical features like rivers or ridge lines, are ideally represented by graph networks (Urban and Keitt, 2001). The complexity of the habitat structure often relates
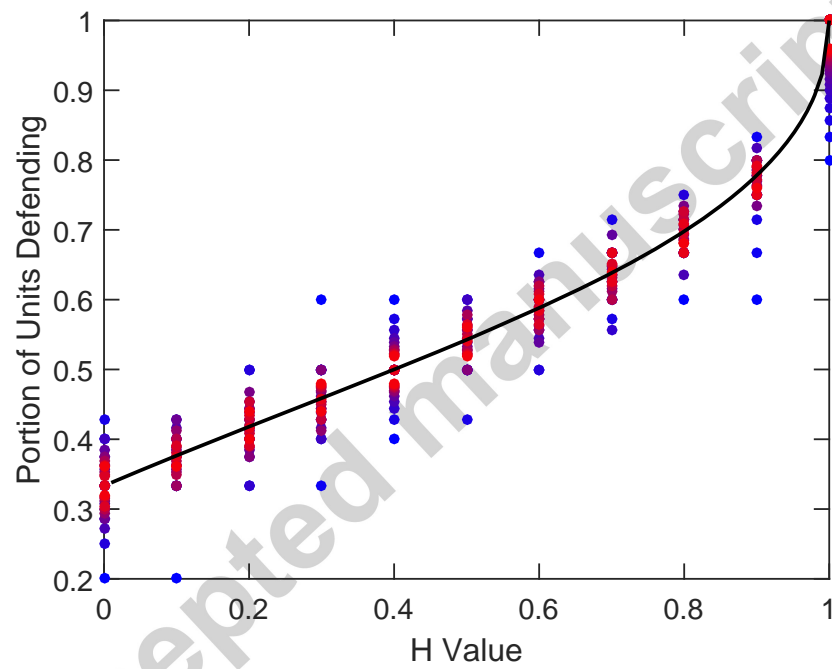
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Figure 6: Three population discrete and continuous game equilibria. Completely blue points are equilibria for the 5 unit game, completely red points are equilibria for the 25 unit game, and as units increase points become more red.
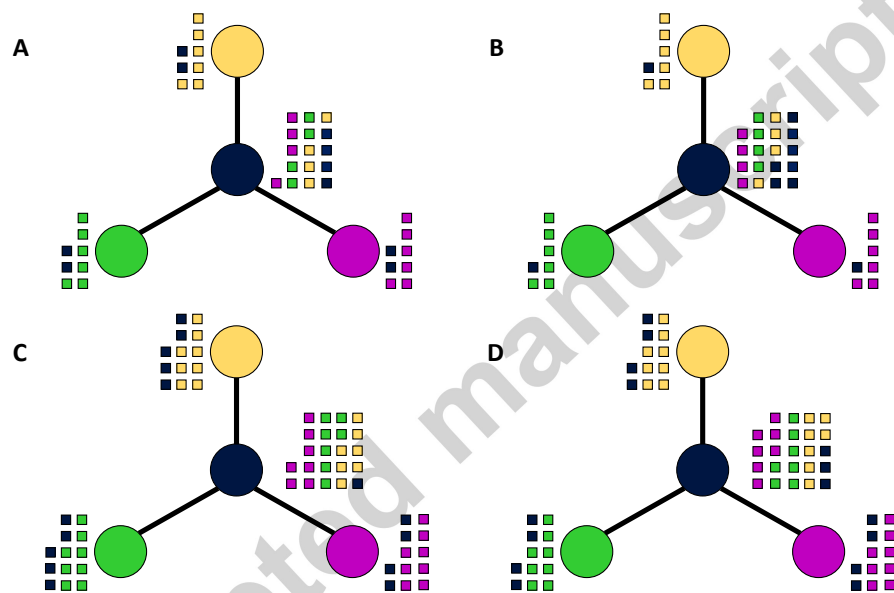
Figure 7: Representation of the four possible equilibria for a three leaf star graph. Chart A is the equilibrium for $U = 10$ and $H = 0.5$. Chart B is the equilibrium for $U = 10$ and $H = 0.75$. Chart C is the equilibrium for $U = 15$ and $H = 0.1$. Both rotations of the picture shown are also equilibria. Chart D is the equilibrium for $U = 15$ and $H = 0.25$. Unit colors and vertex colors correspond.

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₂₂₅ to the both population size and the structure within the community, and this can be seen in many animals including fish (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984) and macro-invertebrates (Barthélemy, 2003). In our model, the defensive posture decreases with the degree of connectivity in the graph as raiders overwhelm the host population's share of resources that could

₂₃₀ not be sequestered prior to conflict. This provides a testable hypothesis that behavioral aggression should increase as additional out-groups are added to the community via the manipulation of travel corridors between group sites.

For the purposes of this initial study, we limited our consideration to symmetric games on regular or regular bipartite graphs, with the former as the base

₂₃₅ case stated above. Bipartite graphs have now been used for many plant-related interactions including plant-animal mutualisms (Bascompte et al., 2003; Jordano et al., 2003; Lázaro et al., 2005), pollinator webs (Memmott et al., 2004), herbivory (Higashi et al., 1991), plant-pathogen models (Brooks et al., 2008), and frugivory and seed dispersal (Carlo and Yang, 2011). As these examples

₂₄₀ attest, bipartite graphs typically contain two distinct classes of nodes or populations. One could similarly characterize our bipartite model as a coalition game with non-aggression among populations of the same alliance (e.g. kinship systems or conflicts that are primarily heterospecific in nature). Even without that characterization, however, many standard systems are actually bipartite, such

₂₄₅ as lattice grids, linear patch networks, and simple gradient webs. These stencils are useful in breaking up larger landscapes into smaller, internally homogeneous patches (Urban and Keitt, 2001).

Bipartite graphs affect the results in conflicting ways, and their structure may impose a minimum threshold on H before defense commences ($p^* > 0$).

₂₅₀ Defensive postures respond to the degree of connectivity of a population's home site differently than that of its target sites. As in the base case, the former weakens the defensive value of home sites, reducing contestable shares of resources as the number of invaders increases. Meanwhile, the latter dilutes the population's projected strength as there are more rivals with which to contend at target lo-

₂₅₅ cations. Additionally, the ordering of solution curves by degree inverts at higher

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higher defensive advantages, — something not observed in regular graphs. It is uncertain why this should be so and merits further investigation. Finally not all regular bipartite graphs admit a pure strategy equilibrium for discrete games, while others permit multiple solutions.

₂₆₀ Although there is a presumption of an actual physical domain underlying the graph structure of these games, our model is also applicable to the study of niche generalization and specialization. Broadly speaking, two species interact if they have matching traits along some phenotypic dimension (Eklöf et al., 2013). Nodes are interpreted as specific ecological niches, with the resident pop-₂₆₅ ulation its corresponding primary specialist and the parameter H understood as the advantage conferred by specialization. The degree of a population's home site represents its niche breadth (sensu Pielou, 1972), and the distribution is effectively a phenotypic assortment Farine (2014); Farine et al. (2015). In this interpretation, a population should be a facultative generalist until such time ₂₇₀ as specialization advantage allows for the exclusion of other populations.

The current model is distinguished from the previous territorial raider model (Galanter et al., 2015) in that, as a result of the divisibility of the group, defense is more readily incorporated into equilibrium strategies. When the group was a singular cohort in the earlier model, every strict equilibrium that ex-₂₇₅ isted occurred when all populations raided another's territory in a one-to-one permutation of positions regardless of graph structure and H value. With the army territorial raider model, however, strict equilibrium strategies do involve a non-trivial level of defense (or reluctance to raid) for sufficiently large H. In comparison, continuous models of individual-focused spatial competition (e.g. ₂₈₀ Rowell, 2010) demonstrated that increased costs from heterospecific conflicts (similar but not fully analogous to the homesite advantage here) led to spatial instability and patchiness in the distribution of rival populations with no attempts to further expand ranges (termed the "Armed Camp" scenario).

This pilot study has assumed a degree of homogeneity over the graph net-₂₈₅ work including the degree of connection and structural symmetry; however, most ecological networks are heterogeneous in the distribution of their edges

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(Bansal et al., 2009; Sah et al., 2014). With current concerns over possible environmental disruptions (Agrawal et al., 2007), one promising application of this work is investigating how increasing disconnectedness among animal popula-

²⁹⁰ tions and heterogeneity alter the structure of communities as edges are created or destroyed due to either the landscape effects of human activity (Crooks and Sanjayan, 2006), e.g. by erecting new barriers or removing previously existing ones, or its general effects on territorial quality (Fischer and Lindenmayer, 2007), e.g. modulation of resource availability at different sites.

²⁹⁵ Additionally, further analyses could relax existing conditions on resource availability, the size of fighting forces, and defensive advantages by allowing these parameters to vary across populations. Moreover, although proportional allocation of resources may be appropriate when there is no direct fighting or when conflict is resolved at the individual level (Johnson and MacKay, 2015),

³⁰⁰ something like Lanchester's squared law of conflict (Lanchester, 1916) might be more appropriate for conflicts involving ant colonies (Franks and Partridge, 1994), chimpanzees (Wilson et al., 2002), and hominids and early humans (Johnson and MacKay, 2015). Also, one can expand our model by allowing within population conflict or situations where actions are not perfectly coordinated. Fi-

³⁰⁵ nally, variant models could also feature costs of fighting in the payoff functions, expanding the model's scope to encompass all encounters from the ritualistic to the violent and costly. These costs could either be equal for raiders and site owners or variable, as in the original territorial raider model.

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