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-

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, *Myrmecocystus 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 synergistic 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).

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 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.

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 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.

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 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 the graph G by the following rules and assumptions (see Table 1 for a complete

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
95 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 $s_i = (m_{i1}, \dots, m_{in})$. 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
100 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,

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

A Nash equilibrium to the ATR Game is a set of strategies $S = \{s_1, s_2, \dots, s_n\}$ 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
105 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

(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 $m_{ij} \in \{0, 1, \dots, U\}$.

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

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

120 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

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

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
125 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

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

and the total payoff for all raiding activity is

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

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

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

Within the domain, the closed set defined by $m_{ij} \geq 0$ and $\sum_{j \neq i} m_{ij} = 1 - p_i$,
 130 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

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

A purely defensive strategy ($p_i = 1$) yields $X_i = (1 + H(1-p))/(2-p)$. For
 135 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

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

The symmetric strategic defense posture is

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

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. $A \cap B = \emptyset$ 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 $\rho = d_A/d_B$

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

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

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 adopted a pure raider strategy (see Figures 2 and 3). As observed with regular 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, switching 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 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 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 allotted 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 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 community structure defined by overlapping territories affect the aggressiveness observed within the community. As the inherent advantage afforded to defenders
210 (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 divisibility
220 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
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 weak-

ens 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 locations. Additionally, the ordering of solution curves by degree inverts at higher
255 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 population its corresponding primary specialist and the parameter H understood as
265 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 network including the degree of connection and structural symmetry; however, most ecological networks are heterogeneous in the distribution of their edges (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 populations 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.

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), 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. Finally, 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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References

- Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres, C., Doak, D.F., Post, E., Hudson, P.J., Maron, J., Mooney, K.A., et al., 2007. Filling key
 320 gaps in population and community ecology. *Frontiers in Ecology and the Environment* 5, 145–152.
- Allen, B., Nowak, M.A., 2015. Games among relatives revisited. *Journal of Theoretical Biology* 378, 103–116.
- Antal, T., Scheuring, I., 2006. Fixation of strategies for an evolutionary game
 325 in finite populations. *Bulletin of Mathematical Biology* 68, 1923–1944.
- Bansal, S., Khandelwal, S., Meyers, L.A., 2009. Exploring biological network structure with clustered random networks. *BMC bioinformatics* 10, 1.
- Barthélemy, M., 2003. Crossover from scale-free to spatial networks. *EPL (Europhysics Letters)* 63, 915.
- 330 Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences* 100, 9383–9387.
- Bell, J., Galzin, R., 1984. Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series* 15, 265–274.
- 335 Bellisario, B., Cerfolli, F., Nascetti, G., 2010. Spatial network structure and robustness of detritus-based communities in a patchy environment. *Ecological research* 25, 813–821.

- Bono, J.M., 2007. Patterns of kleptoparasitism and inquilinism in social and non-social duna thrips on Australian acacia. *Ecological Entomology* 32, 411–418.
- Brooks, C.P., Antonovics, J., Keitt, T.H., 2008. Spatial and temporal heterogeneity explain disease dynamics in a spatially explicit network model. *The American Naturalist* 172, 149–159.
- Broom, M., Cannings, C., 2013. A dynamic network population model with strategic link formation governed by individual preferences. *Journal of Theoretical Biology* 335, 160–168.
- Broom, M., Lafaye, C., Pattni, K., Rychtář, J., 2015. A study of the dynamics of multi-player games on small networks using territorial interactions. *Journal of Mathematical Biology* , 1–24.
- Broom, M., Rychtář, J., 2012. A general framework for analysing multiplayer games in networks using territorial interactions as a case study. *Journal of Theoretical Biology* 302, 70–80.
- Broom, M., Rychtář, J., 2013. *Game-theoretical models in biology*. CRC Press.
- Bruni, M., Broom, M., Rychtář, J., 2013. Analysing territorial models on graphs. *Involve, a Journal of Mathematics* 7, 129–149.
- Carlo, T.A., Yang, S., 2011. Network models of frugivory and seed dispersal: challenges and opportunities. *Acta Oecologica* 37, 619–624.
- Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D’Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., et al., 1996. The report of the ecological society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6, 665–691.
- Cosner, C., 2005. A dynamic model for the ideal-free distribution as a partial differential equation. *Theoretical Population Biology* 67, 101–108.

- Crooks, K.R., Sanjayan, M., 2006. Connectivity conservation: maintaining
 365 connections for nature. Conservation Biology Series-Cambridge 14, 1.
- Dale, M., Fortin, M., 2010. From graphs to spatial graphs. Annual Review of
 Ecology, Evolution, and Systematics 41.
- Diamond, J., 1975. Assembly of species communities. in ecology and evolution
 of communities.(eds ml cody and jm diamond.) pp. 342–444.
- 370 Economo, E.P., Keitt, T.H., 2008. Species diversity in neutral metacommunities:
 a network approach. Ecology letters 11, 52–62.
- Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N.P.,
 Dalsgaard, B., Sassi, C., Galetti, M., Guimarães, P.R., et al., 2013. The
 dimensionality of ecological networks. Ecology letters 16, 577–583.
- 375 Farine, D.R., 2014. Measuring phenotypic assortment in animal social networks:
 weighted associations are more robust than binary edges. Animal Behaviour
 89, 141–153.
- Farine, D.R., Firth, J.A., Aplin, L.M., Crates, R.A., Culina, A., Garroway, C.J.,
 Hinde, C.A., Kidd, L.R., Milligan, N.D., Psorakis, I., et al., 2015. The role
 380 of social and ecological processes in structuring animal populations: a case
 study from automated tracking of wild birds. Royal Society open science 2,
 150057.
- Ferrari, J.R., Lookingbill, T.R., Neel, M.C., 2007. Two measures of landscape-
 graph connectivity: assessment across gradients in area and configuration.
 385 Landscape ecology 22, 1315–1323.
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat frag-
 mentation: a synthesis. Global Ecology and Biogeography 16, 265–280.
- Fortuna, M.A., Albaladejo, R.G., Fernández, L., Aparicio, A., Bascompte, J.,
 2009. Networks of spatial genetic variation across species. Proceedings of the
 390 National Academy of Sciences 106, 19044–19049.

- Fortuna, M.A., Bascompte, J., 2006. Habitat loss and the structure of plant–animal mutualistic networks. *Ecology Letters* 9, 281–286.
- Franks, N.R., Partridge, L.W., 1994. Lanchester’s theory of combat, self-organization, and the evolution of army ants and cellular societies. *Behavioral Mechanisms in Evolutionary Ecology* , 390–408.
- Galanter, N., Silva Jr., D., Rowell, J., Rychtář, J., 2015. The territorial raider game and graph derangements [arXiv:1507.06286](#).
- Ginsberg, J.R., Macdonald, D.W., 1990. Foxes, wolves, jackals, and dogs: an action plan for the conservation of canids. volume 5. IUCN.
- Hadjichrysanthou, C., Broom, M., Kiss, I.Z., 2012. Approximating evolutionary dynamics on networks using a neighbourhood configuration model. *Journal of Theoretical Biology* 312, 13–21.
- Heinsohn, R., Packer, C., 1995. Complex cooperative strategies in group-territorial african lions. *Science* 269, 1260–1262.
- Higashi, M., Yamamura, N., Abe, T., Burns, T.P., 1991. Why don’t all termite species have a sterile worker caste? *Proceedings of the Royal Society of London B: Biological Sciences* 246, 25–29.
- Hölldobler, B., 1981. Foraging and spatiotemporal territories in the honey ant *myrmecocystus mimicus wheeler* (hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 9, 301–314.
- Hölldobler, B., Wilson, E.O., 1990. The ants. Harvard University Press.
- Jacoby, D.M., Brooks, E.J., Croft, D.P., Sims, D.W., 2012. Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods in Ecology and Evolution* 3, 574–583.
- Jacoby, D.M., Freeman, R., 2016. Emerging network-based tools in movement ecology. *Trends in ecology & evolution* 31, 301–314.

- Jeong, H.C., Oh, S.Y., Allen, B., Nowak, M.A., 2014. Optional games on cycles and complete graphs. *Journal of Theoretical Biology* 356, 98–112.
- Jetz, W., Carbone, C., Fulford, J., Brown, J.H., 2004. The scaling of animal
420 space use. *Science* 306, 266–268.
- Johnson, D.D., MacKay, N.J., 2015. Fight the power: Lanchester’s laws of combat in human evolution. *Evolution and Human Behavior* 36, 152–163.
- Jordano, P., Bascompte, J., Olesen, J.M., 2003. Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology letters* 6, 69–81.
- 425 Keeling, M.J., Danon, L., Vernon, M.C., House, T.A., 2010. Individual identity and movement networks for disease metapopulations. *Proceedings of the National Academy of Sciences* 107, 8866–8870.
- Kelley, S.W., Ransom Jr, D., Butcher, J.A., Schulz, G.G., Surber, B.W., Pinchak, W.E., Santamaria, C.A., Hurtado, L.A., 2011. Home range dynamics,
430 habitat selection, and survival of greater roadrunners. *Journal of Field Ornithology* 82, 165–174.
- Kurokawa, S., Ihara, Y., 2013. Evolution of social behavior in finite populations: A payoff transformation in general n -player games and its implications. *Theoretical Population Biology* 84, 1 – 8.
- 435 Lanchester, F.W., 1916. *Aircraft in warfare: The dawn of the fourth arm.* Constable Limited.
- Lázaro, A., Mark, S., Olesen, J.M., 2005. Bird-made fruit orchards in northern europe: nestedness and network properties. *Oikos* 110, 321–329.
- Lewinsohn, T.M., Inácio Prado, P., Jordano, P., Bascompte, J., M Olesen, J.,
440 2006. Structure in plant–animal interaction assemblages. *Oikos* 113, 174–184.
- Lieberman, E., Hauert, C., Nowak, M.A., 2005. Evolutionary dynamics on graphs. *Nature* 433, 312–316.

- Luckhurst, B., Luckhurst, K., 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* 49, 317–323.
- 445 Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London B: Biological Sciences* 271, 2605–2611.
- Meyers, L., 2007. Contact network epidemiology: Bond percolation applied to infectious disease prediction and control. *Bulletin of the American Mathematical Society* 44, 63–86.
- 450 Montoya, J.M., Pimm, S.L., Solé, R.V., 2006. Ecological networks and their fragility. *Nature* 442, 259–264.
- Mosser, A., Packer, C., 2009. Group territoriality and the benefits of sociality in the african lion, *panthera leo*. *Animal Behaviour* 78, 359–370.
- 455 Noss, R.F., 1991. Landscape connectivity: different functions at different scales. *Landscape linkages and biodiversity*. Island Press, Washington, DC, USA , 27–39.
- Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. *Nature* 359, 826–829.
- 460 Packer, C., Scheel, D., Pusey, A.E., 1990. Why lions form groups: food is not enough. *American Naturalist* , 1–19.
- Pielou, E., 1972. Niche width and niche overlap: a method for measuring them. *Ecology* 53, 687–692.
- Radford, A.N., du Plessis, M.A., 2004. Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. *Animal Behaviour*
- 465 68, 803–810.
- Rand, D.G., Armao IV, J.J., Nakamaru, M., Ohtsuki, H., 2010. Anti-social punishment can prevent the co-evolution of punishment and cooperation. *Journal of Theoretical Biology* 265, 624–632.

- 470 Rayfield, B., Fortin, M.J., Fall, A., 2011. Connectivity for conservation: a framework to classify network measures. *Ecology* 92, 847–858.
- Rowell, J.T., 2009. The limitation of species range: a consequence of searching along resource gradients. *Theoretical Population Biology* 75, 216–227.
- Rowell, J.T., 2010. Tactical population movements and distributions for ideally
475 motivated competitors. *The American Naturalist* 176, 638–650.
- Sah, P., Singh, L.O., Clauset, A., Bansal, S., 2014. Exploring community structure in biological networks with random graphs. *BMC bioinformatics* 15, 220.
- Schmidt, K., Jedrzejewski, W., Okarma, H., 1997. Spatial organization and
480 social relations in the eurasian lynx population in białowieża primeval forest, poland. *Acta Theriologica* 42, 289–312.
- Shakarian, P., Roos, P., Johnson, A., 2012. A review of evolutionary graph theory with applications to game theory. *Biosystems* 107, 66–80.
- Shirley, M.D., Rushton, S.P., 2005. The impacts of network topology on disease
485 spread. *Ecological Complexity* 2, 287–299.
- Sorato, E., Gullett, P.R., Creasey, M.J., Griffith, S.C., Russell, A.F., 2015. Plastic territoriality in group-living chestnut-crowned babbler: roles of resource value, holding potential and predation risk. *Animal Behaviour* 101, 155–168.
- Strandburg-Peshkin, A., Farine, D.R., Couzin, I.D., Crofoot, M.C., 2015.
490 Shared decision-making drives collective movement in wild baboons. *Science* 348, 1358–1361.
- Szolnoki, A., Perc, M., 2012. Conditional strategies and the evolution of cooperation in spatial public goods games. *Physical Review E* 85, 026104.
- Taylor, C., Fudenberg, D., Sasaki, A., Nowak, M.A., 2004. Evolutionary game
495 dynamics in finite populations. *Bulletin of Mathematical Biology* 66, 1621–1644.

- Taylor, P., 2013. Inclusive and personal fitness in synergistic evolutionary games on graphs. *Journal of Theoretical Biology* 325, 76–82.
- Urban, D., Keitt, T., 2001. Landscape connectivity: a graph-theoretic perspective. *Ecology* 82, 1205–1218.
- Watts, D.P., Mitani, J.C., 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* 138, 299–327.
- Williams, J.M., Oehlert, G.W., Carlis, J.V., Pusey, A.E., 2004. Why do male chimpanzees defend a group range? *Animal Behaviour* 68, 523–532.
- Wilson, M.L., Britton, N.F., Franks, N.R., 2002. Chimpanzees and the mathematics of battle. *Proceedings of the Royal Society of London B: Biological Sciences* 269, 1107–1112.

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.

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.

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.

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.

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 .

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.