Analysing territorial models on graphs

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Evolutionary graph theory combines evolutionary games with population structure, induced by the graph. The games used are limited to pairwise games occurring on the edges of the graph. Multiplayer games can be important in biological modelling, however, and so recently a new framework for modelling games in structured populations allowing games with arbitrary numbers of players was introduced. In this paper we develop the model to investigate the effect of population structure on the level of aggression, as opposed to a well-mixed population for two specific types of graph, using a multiplayer hawk-dove game. We find that the graph structure can have a significant effect on the level of aggression, and that a key factor is the variability of the group sizes formed to play the games; the more variable the group size, the lower the level of aggression, in general.

1. Introduction

Evolutionary graph theory has been developed to more realistically model evolution in populations [Lieberman et al. 2005; Antal and Scheuring 2006; Nowak 2006; Broom and Rychtář 2008]. These models use standard games like the Prisoner's Dilemma and the hawk-dove game, and embed them within a graph structure [Ohtsuki et al. 2006; Santos and Pacheo 2006; Hadjichrysanthou et al. 2011] representing a finite inhomogeneous population, as opposed to traditional evolutionary game theory models which generally consider infinite well-mixed populations. Earlier work also considered similar models which depart from the infinite well-mixed case, in particular [Schaffer 1988] considered a hawk-dove game in a finite population, and [Killingback and Doebeli 1996] considered a hawk-dove game on a lattice. A limitation of the evolutionary graph theory approach is that games can only involve two players, which interact through the graph edges. However, many real animal interactions can involve many players, e.g., in African wild dogs [Ginsberg and Macdonald 1990] or roadrunners [Kelley et al. 2011]. In addition useful theoretical

models which we might want to utilise also describe such multiplayer interactions. In some cases many groups can interact at significant food sources, and often food loss to neighbours can be considerable [Jetz et al. 2004].

In [Broom and Rychtář 2012] we developed a new framework of territorial behaviour modelling how a structured population involved the interaction of different sized groups of individuals at different times. As well as developing the general framework, they also introduced some specific models of interaction. One such was the territorial raider model, where individuals each owned a territory and could either stay in their own territory or move to a neighbouring territory at each time point. Whenever a group of individuals met on a territory, they interacted by means of playing a (potentially) multiplayer game. In the same paper we considered an example of a multiplayer hawk-dove game on a star. One important conclusion was that the level of aggressiveness was less on the star graph than on the equivalent well-mixed graph, i.e., an unstructured population. Thus it is possible that the population structure can have a significant effect on how the population behaves, and it may be that in real structured populations aggression is lower than that predicted by models which do not take the structure into account.

In this paper we follow [Broom and Rychtář 2012] and model the same interaction using different example graphs, again comparing these structured populations with their equivalent well-mixed population model. We show that in different circumstances the level of aggression can be noticeably higher or lower than would be expected in the equivalent well-mixed population, and that even graphs with superficially similar structures can lead to either a significant increase or decrease in the level of aggression. Indeed a particular graph structure can lead to either more or less aggression than the well-mixed population, depending upon other parameter values. Thus to model group interactions properly, it may be important to develop a strong understanding of the nature of interactions and the population structure.

We consider N individuals $I_1, \ldots, I_N$ living in their own respective territories $P_1, \ldots, P_N$. The individuals can also move to one of the territories neighbouring theirs. This situation is modelled by a graph (V, E) where the vertices represent the individuals and the territories that they occupy, and an edge between two vertices means that they are neighbours, and so one individual can raid the territory of the other.

2. A territorial raider model on the circle

A circle is a connected graph with every vertex having degree 2. In this model, each individual can go from its territory to one next to its own with a probability λ and stays on its territory with a probability $1 - 2\lambda$. The circle model is shown in Figure 1.
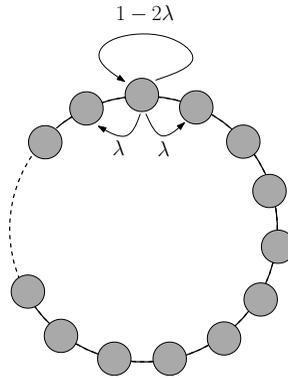
Figure 1. The circle representation. In this model, each individual starts on one of the vertices which represent their territories. From this vertex they can either "stay at home" with a probability $1 - 2\lambda$ or explore a neighbouring territory connected to it through an edge with a probability λ to go to each neighbour (every individual has two neighbours in this model).

2.1. *Group sizes.* For any population of size $N \geq 3$ in the circle model, we have the following probabilities that a given individual is in a group of size i, denoted by $P(|G| = i)$:

$$P(|G| = 1) = (1 - 2\lambda)(1 - \lambda)^2 + 2\lambda(2\lambda)(1 - \lambda)$$
$$= 1 - 4\lambda + 9\lambda^2 - 6\lambda^3,$$
$$P(|G| = 2) = 2(1 - 2\lambda)(1 - \lambda)\lambda + 2\lambda((1 - 2\lambda)(1 - \lambda) + 2\lambda^2)$$
$$= 4\lambda(1 - 3\lambda + 3\lambda^2),$$
$$P(|G| = 3) = 3\lambda^2(1 - 2\lambda),$$
$$P(|G| = k) = 0, \quad k > 3.$$

Note that these probabilities do not depend on N. From here, we find that the mean group size is

$$E[|G|] = 1 + 4\lambda - 6\lambda^2. \tag{1}$$

2.2. *A multiplayer hawk-dove game.* We suppose that the individuals on the circle structure play a multiplayer hawk-dove game as in [Broom and Rychtář 2012]; i.e., if several individuals are on the same territory then they compete for a reward of value V. If all individuals are doves, they split the reward equitably and if there are hawks all the doves give up and get nothing, while the hawks fight for the reward so that one hawk receives the reward V and all the other hawks get a cost C (see [Broom and Rychtář 2012] for more details on the calculations). If all individuals

play hawk with a probability α, except our focal individual, we find that the average payoff for a dove player will be

$$E_d(\alpha) = V\left\{1 - 2\lambda + 4\lambda^2 - 2\lambda^3 + \alpha(4\lambda^2 - 2\lambda - 2\lambda^3) + \alpha^2(\lambda^2 - 2\lambda^3)\right\}$$

and the average payoff for a hawk player will be

$$E_h(\alpha) = V\left\{1 + \alpha(3\lambda^2 - 2\lambda) + \alpha^2(\lambda^2 - 2\lambda^3)\right\} + C\left\{-2\alpha\lambda + 3\alpha\lambda^2 + \alpha^2\lambda^2 - 2\alpha^2\lambda^3\right\}.$$

Then the difference of payoff between a hawk player and a dove player, will be given by the incentive function

$$\begin{aligned} h_C(\alpha) &= E_h(\alpha) - E_d(\alpha) \\ &= V\{2\lambda - 4\lambda^2 - \alpha\lambda^2 + 2\lambda^3 + 2\alpha\lambda^3\} - C\{2\alpha\lambda + 3\alpha\lambda^2 + \alpha^2\lambda^2 - 2\alpha^2\lambda^3\}. \quad (2)\end{aligned}$$

In [Broom and Rychtář 2012] we considered examples involving $V = 1$ and $C = 2$, and here we shall also use these values. In this case

$$h_C(\alpha) = 2\lambda - 4\lambda^2 + 2\lambda^3 + \alpha(-4\lambda + 5\lambda^2 + 2\lambda^3) + \alpha^2(2\lambda^2 - 4\lambda^3).$$

To find mixed evolutionarily stable strategies, i.e., with $0 < \alpha < 1$, we need to set $h_C(\alpha) = 0$. We then have the discriminant for α given by

$$\Delta = 36\lambda^6 - 60\lambda^5 + 73\lambda^4 - 56\lambda^3 + 16\lambda^2$$

and obtain the roots

$$\alpha_1 = \frac{-5\lambda^2 + 4\lambda - 2\lambda^3 + \sqrt{\Delta}}{2(2\lambda^2 - 4\lambda^3)} \quad \text{and} \quad \alpha_2 = \frac{-5\lambda^2 + 4\lambda - 2\lambda^3 - \sqrt{\Delta}}{2(2\lambda^2 - 4\lambda^3)}.$$

We now have to see if those values are in $(0, 1)$ or not to find possible ESSs.

Example 1. For any population size N, if we take $\lambda = \frac{1}{3}$, we find that the roots of $h_C(\alpha) = 0$ are $\alpha_1 = 9.0584$ and $\alpha_2 = 0.4416$. The first root is outside of $[0, 1]$ and it is easy to show that the other is stable, whilst the two pure strategies 0 and 1 are unstable, so that 0.4416 is the unique ESS of this case.

More generally the value of α_2 is shown for the full range of values of λ in Figure 2. α_2 is low for intermediate values of λ when the variability of group size is the largest, and high for the extreme values when group size variability is lower.

2.3. *The equivalent well-mixed population model.* As described in [Broom and Rychtář 2012], to find an equivalent well-mixed population, we want to identify a p so that we have a Binomial$(N - 1, p)$ distribution with equal mean group size to that of the circle. Here we have the equation $E[|G|] = 1 + (N - 1)p$, which is to say,

$$p = \frac{\lambda(4 - 6\lambda)}{N - 1}. \quad (3)$$
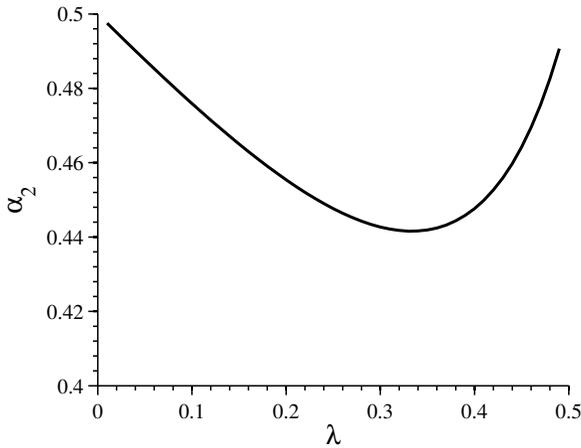
Figure 2. The values of the biological meaningful root α_2 for the multiplayer hawk-dove game with $V = 1$ and $C = 2$ on the circle, representing the probability of playing hawk in the mixed ESS. The values of α_2 for all allowable λ are shown.

Following [Broom and Rychtář 2012], the same hawk-dove game as played above leads to

$$E_h(\alpha) = V \frac{1 - (1 - p\alpha)^N}{Np\alpha} + C\left(-1 + \frac{1 - (1 - p\alpha)^N}{Np\alpha}\right)$$

and

$$E_d(\alpha) = V\left(\frac{(1 - p\alpha)^N - (1 - p)^N}{Np(1 - \alpha)}\right);$$

i.e., the incentive function is

$$h_W(\alpha)$$
$$= V \frac{1 - (1 - p\alpha)^N}{Np\alpha} + C\left(-1 + \frac{1 - (1 - p\alpha)^N}{Np\alpha}\right) - V\left(\frac{(1 - p\alpha)^N - (1 - p)^N}{Np(1 - \alpha)}\right),$$

or again

$$h_W(\alpha) = \frac{1}{Np\alpha(1 - \alpha)}\left\{(1 - \alpha)(V + C) - (V + C)(1 - p\alpha)^N\right.$$
$$\left. + C\alpha(1 - p\alpha)^N - CNp\alpha(1 - \alpha) + \alpha V(1 - p)^N\right\}. \quad (4)$$

In [Broom and Rychtář 2012] it was stated that there is at most one root of (4) in the interval [0, 1]. A proof of this statement is given in Appendix A, where it is shown that there is a root between 0 and 1 for $p \neq 0$ and $C > 0$ if and only if

$$\frac{V}{C} < \frac{Np + (1 - p)^N - 1}{1 - (1 - p)^N - Np(1 - p)^{N-1}}. \quad (5)$$

Example 2. We again take $\lambda = \frac{1}{3}$, and find the ESS value α_N for the well-mixed population of size N, for various N.

a) We consider $N = 3$, corresponding to the smallest possible circle. We find the same result as in the circle case: $\alpha_{\text{circle}} = \alpha_3 = 0.4416$. This is as we would expect as for $N = 3$ the circle and the well-mixed population are identical for $\lambda = \frac{1}{3}$.

b) For $N = 5$, we find $\alpha_5 = 0.4208 < \alpha_{\text{circle}}$.

c) For $N = 50$ we find $\alpha_{50} = 0.4046 < \alpha_5 < \alpha_{\text{circle}}$.

Thus for the well-mixed population the ESS hawk probability declines with the population size. In particular, except for $N = 3$, the ESS hawk proportion is higher for the circle than for the well-mixed population. This is in contrast to the star form from [Broom and Rychtář 2012]. These results are consistent because in the circle case, the hawk cannot be in a territory with more than two other hawks whereas the equivalent well-mixed population allows bigger groups which disfavour hawk players. The star in turn allowed such bigger groups to form with greater probability.

3. A territorial raider model on a complete bipartite graph

A bipartite graph is a graph whose vertices can be divided into two disjoint sets U and V, with n and m elements respectively, such that every edge connects a vertex in U to one in V. A complete bipartite graph is a special kind of bipartite graph where every vertex of the first set is connected to every vertex of the second set. We shall assume that each individual in U has a probability λ of going to each territory in V and a probability $1 - m\lambda$ of staying in its own territory, and similarly each individual in V has probability μ of going to each territory in U and a probability $1 - n\mu$ of staying in its own territory. The general bipartite model is illustrated in Figure 3.

We shall again find the distribution of group sizes, and compare these to the equivalent well-mixed population.

3.1. *Group size.* Without loss of generality we assume that $m \leq n$. For an individual in a territory on the right side (in the smaller side, with m individuals), we find:

For any $1 \leq k \leq \min(n+1, m+1) = m+1$:

$$P(|G| = k) =$$
$$\binom{n}{k-1}(1 - n\mu)\lambda^{k-1}(1 - \lambda)^{n-k+1} + n\mu(1 - m\lambda)\binom{m-1}{k-2}\mu^{k-2}(1 - \mu)^{m-k+1}$$
$$+ nm\lambda\mu\binom{m-1}{k-1}\mu^{k-1}(1 - \mu)^{m-k}.$$
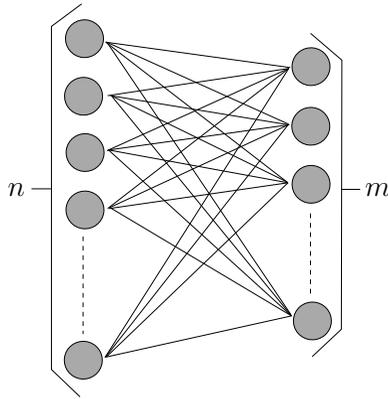
Figure 3. The *n-m* complete bipartite graph representation. The vertices represent territories. The edges represent the possible moves from one territory to another. Here we assume that each individual on the left has a probability λ to go to each of the right territories and a probability $1 - m\lambda$ to stay in its own territory, and similarly each individual on the right has a probability μ to go to each territory on the left and a probability $1 - n\mu$ to stay in its own territory.

For any $m + 2 \leq k \leq \max(n + 1, m + 1) = n + 1$ we have

$$P(|G| = k) = \binom{n}{k-1}(1 - n\mu)\lambda^{k-1}(1 - \lambda)^{n-k+1}.$$

Similarly for an individual in a territory on the left, we find:

For any $1 \leq k \leq m + 1$:

$$P(|G| = k) =$$

$$\binom{m}{k-1}(1 - m\lambda)\mu^{k-1}(1 - \mu)^{m-k+1}$$

$$+ m\lambda(1 - n\mu)\binom{n-1}{k-2}\lambda^{k-2}(1 - \lambda)^{n-k+1} + nm\lambda\mu\binom{n-1}{k-1}\lambda^{k-1}(1 - \lambda)^{n-k}.$$

For any $m + 2 \leq k \leq n + 1$, we find:

$$P(|G| = k) =$$

$$m\lambda(1 - n\mu)\binom{n-1}{k-2}\lambda^{k-2}(1 - \lambda)^{n-k+1} + nm\lambda\mu\binom{n-1}{k-1}\lambda^{k-1}(1 - \lambda)^{n-k}.$$

Finally we find the average probability for an individual on this structure:

For any $1 \leq k \leq m + 1$:

$$P(|G| = k) = \frac{n}{n+m}\binom{m}{k-1}(1 - m\lambda)\mu^{k-1}(1 - \mu)^{m-k+1}$$

$$+ \frac{n}{n+m}\binom{n-1}{k-2}m\lambda(1 - n\mu)\lambda^{k-2}(1 - \lambda)^{n-k+1}$$

$$+ \frac{n}{n+m}\binom{n-1}{k-1}nm\lambda\mu\lambda^{k-1}(1 - \lambda)^{n-k}$$

$$+ \frac{m}{n+m}\binom{n}{k-1}(1 - n\mu)\lambda^{k-1}(1 - \lambda)^{n-k+1}$$

$$+ \frac{m}{n+m}n\mu(1 - m\lambda)\binom{m-1}{k-2}\mu^{k-2}(1 - \mu)^{m-k+1}$$

$$+ \frac{m}{n+m}nm\lambda\mu\binom{m-1}{k-1}\mu^{k-1}(1 - \mu)^{m-k}.$$

For any $m + 2 \leq k \leq n + 1$:

$$P(|G| = k) =$$

$$\frac{n}{n+m}\left(m\lambda(1 - n\mu)\binom{n-1}{k-2}\lambda^{k-2}(1 - \lambda)^{n-k+1} + nm\lambda\mu\binom{n-1}{k-1}\lambda^{k-1}(1 - \lambda)^{n-k}\right)$$

$$+ \frac{m}{n+m}\left((1 - n\mu)\binom{n}{k-1}\lambda^{k-1}(1 - \lambda)^{n-k+1}\right).$$

Now we can use these results (see [Appendix B](#)) to show that the mean group size is given by

$$\mathbf{E}(|G|) =$$

$$1 + \frac{2nm\mu - 2nm^2\lambda\mu + 2nm\lambda - 2n^2m\lambda\mu + n^2m\lambda^2 - nm\lambda^2 + n\mu^2m^2 - nm\mu^2}{n+m}. \quad (6)$$

3.2. The equivalent well-mixed population. In the equivalent well-mixed population with $N = n + m$ individuals, with the number of individuals in the same patch as a focal individual following a Binomial$(N - 1, p)$ distribution, we want the same mean group size as before. For a well-mixed population equivalent to the *n-m* structure, we will have

$$1 + p(n + m - 1) = E(|G|).$$

This leads directly from the previous calculation to

$$p = \frac{2nm\mu - 2nm^2\lambda\mu + 2nm\lambda - 2n^2m\lambda\mu + n^2m\lambda^2 - nm\lambda^2 + n\mu^2m^2 - nm\mu^2}{(n+m)(n+m-1)}.$$

$$(7)$$

Example 3. If we take $n = m$ and $\lambda = \mu = 1/(n+1)$, clearly the probability distribution of the group size of an individual from the left is identical to that of an individual from the right. For any $1 \leq k \leq n+1$,

$$
\begin{aligned}
P(|G| = k) &= \binom{n}{k-1}\left(1 - \frac{n}{n+1}\right)\left(\frac{1}{n+1}\right)^{k-1}\left(1 - \frac{1}{n+1}\right)^{n-k+1} \\
&\quad + \frac{n}{(n+1)^2}\binom{n-1}{k-2}\left(\frac{1}{n+1}\right)^{k-2}\left(1 - \frac{1}{n+1}\right)^{n-k+1} \\
&\quad + \frac{n^2}{(n+1)^2}\binom{n-1}{k-1}\left(\frac{1}{n+1}\right)^{k-1}\left(1 - \frac{1}{n+1}\right)^{n-k} \\
&= \frac{n^{n-k+1}}{(n+1)^{n+1}}\left(\frac{n!}{(k-1)!\,(n-k+1)!} + \frac{n!}{(k-2)!\,(n-k+1)!} + \frac{n!}{(k-1)!\,(n-k)!}\right) \\
&= \left(\frac{1}{n+1}\right)^{k-1}\left(1 - \frac{1}{n+1}\right)^{n-(k-1)}\binom{n}{k-1}.
\end{aligned}
$$

Thus this bipartite graph with equally sized parts has a binomially distributed group size, and this is equivalent to a well-mixed population with $n+1$ individuals and mean group size $(2n+1)/(n+1)$. For large n this is approximately a Poisson distribution which is also a good approximation for the well-mixed population with $2n$ individuals and mean group size $(2n+1)/(n+1)$. Thus for large n this graph is approximately the same as its equivalent well-mixed population.

3.3. *A complete bipartite graph with $n = 3$ and $m = 2$.* We now consider a complete bipartite graph with $n = 3$ and $m = 2$. There is a representation of this model in Figure 4.

The group size probabilities are as follows. For an individual on the right,

$$
\begin{aligned}
P(|G| = 1) &= (1 - 3\mu)(1 - \lambda)^3 + 3\mu(2\lambda)(1 - \mu), \\
P(|G| = 2) &= 3(1 - 3\mu)\lambda(1 - \lambda)^2 + 3\mu(1 - 2\lambda)(1 - \mu) + 3\mu^2(2\lambda), \\
P(|G| = 3) &= 3(1 - 3\mu)\lambda^2(1 - \lambda) + 3\mu^2(1 - 2\lambda), \\
P(|G| = 4) &= (1 - 3\mu)\lambda^3,
\end{aligned}
$$

and for an individual on the left,

$$
\begin{aligned}
P(|G| = 1) &= (1 - 2\lambda)(1 - \mu)^2 + 2\lambda(3\mu)(1 - \lambda)^2, \\
P(|G| = 2) &= 2(1 - 2\lambda)\mu(1 - \mu) + 2\lambda((1 - 3\mu)(1 - \lambda)^2 + 6\lambda\mu(1 - \lambda)), \\
P(|G| = 3) &= (1 - 2\lambda)\mu^2 + 2\lambda(2(1 - 3\mu)\lambda(1 - \lambda) + 3\lambda^2\mu), \\
P(|G| = 4) &= 2(1 - 3\mu)\lambda^3.
\end{aligned}
$$

Thus we find the mean group size as
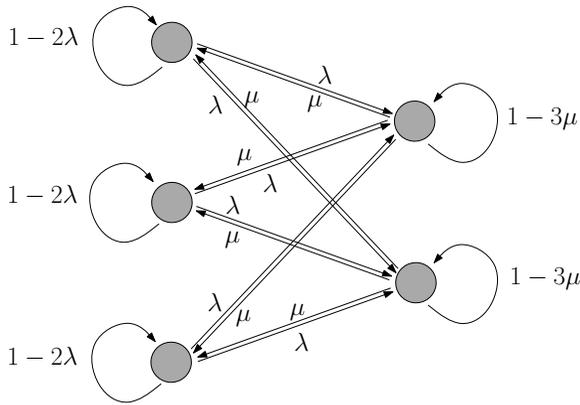
Figure 4. The complete bipartite graph with $n = 3$ and $m = 2$ representation. The vertices represent territories and the edges represent the possible moves from one territory to another. Here λ is the probability for an individual on the left to move to each of its neighbours on the right; it stays in its own territory with probability $1 - 2\lambda$. μ is the equivalent probability for an individual on the right.

$$E[|G|] = 1 + \tfrac{12}{5}\lambda + \tfrac{12}{5}\mu - 12\mu\lambda + \tfrac{6}{5}\mu^2 + \tfrac{12}{5}\lambda^2. \tag{8}$$

As for the circle we consider the multiplayer hawk-dove game. We find then for a hawk-dove game, with probability α of playing hawk, the following payoffs: For a hawk player the payoff is

$$
\begin{aligned}
E_h(\alpha) = C\big\{&(-\tfrac{6}{5}\mu - \tfrac{3}{5}\mu^2 + 6\mu\lambda - \tfrac{6}{5}\lambda - \tfrac{6}{5}\lambda^2) \\
&+ \alpha^2(\tfrac{3}{5}\mu^2 - \tfrac{6}{5}\mu^2\lambda - \tfrac{18}{5}\mu\lambda^2 + \tfrac{6}{5}\lambda^2 + \tfrac{2}{5}\lambda^3) + \alpha^3(-\tfrac{2}{5}\lambda^3 + \tfrac{6}{5}\mu\lambda^3)\big\} \\
+ V\big\{&1 + \alpha(-\tfrac{6}{5}\mu - \tfrac{3}{5}\mu^2 - \tfrac{6}{5}\lambda + 6\lambda\mu - \tfrac{6}{5}\lambda^2) \\
&+ \alpha^2(\tfrac{3}{5}\mu^2 - \tfrac{6}{5}\mu^2\lambda + \tfrac{6}{5}\lambda^2 - \tfrac{18}{5}\mu\lambda^2 + \tfrac{2}{5}\lambda^3) + \alpha^3(-\tfrac{2}{5}\lambda^3 + \tfrac{6}{5}\mu\lambda^3)\big\}.
\end{aligned}
$$

For a dove player the payoff is

$$
\begin{aligned}
E_d(\alpha) = V\big\{&1 - \tfrac{6}{5}\mu - \tfrac{6}{5}\lambda + 6\lambda\mu - \tfrac{6}{5}\mu^2\lambda - \tfrac{18}{5}\mu\lambda^2 + \tfrac{6}{5}\mu\lambda^3 \\
&+ \alpha(-\tfrac{6}{5}\mu - \tfrac{6}{5}\lambda + 6\lambda\mu - \tfrac{6}{5}\mu^2\lambda - \tfrac{18}{5}\mu\lambda^2 + \tfrac{6}{5}\mu\lambda^3) \\
&+ \alpha^2(\tfrac{3}{5}\mu^2 - \tfrac{6}{5}\mu^2\lambda + \tfrac{6}{5}\lambda^2 - \tfrac{18}{5}\mu\lambda^2 + \tfrac{6}{5}\mu\lambda^3) + \alpha^3(-\tfrac{2}{5}\lambda^3 + \tfrac{6}{5}\mu\lambda^3)\big\}.
\end{aligned}
$$

Example 4. We consider the case when $C = 2$, $V = 1$, $\mu = 0.2$ and $\lambda = \tfrac{1}{3}$. Here there is an ESS on the graph with hawk probability $\alpha = 0.4086$.
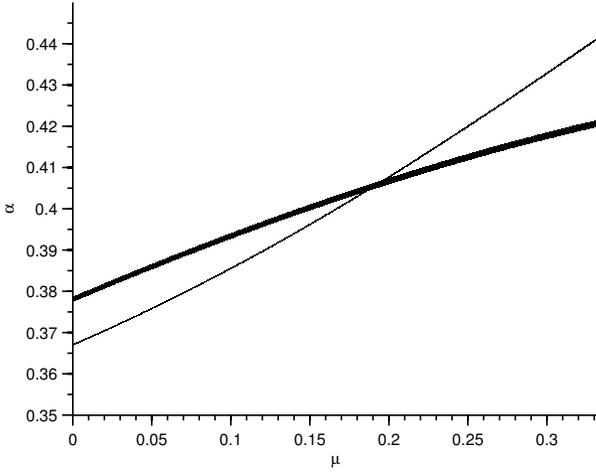
Figure 5. The evolutionarily stable proportion of hawks on a complete bipartite graph with $n = 3$ and $m = 2$ (thin line) and a well-mixed population (thick line), where $\lambda = \frac{1}{3}$ and μ varies from 0 to $\frac{1}{3}$.

For the well-mixed population we obtain

$$p = \tfrac{3}{5}\lambda + \tfrac{3}{5}\mu - \tfrac{15}{5}\mu\lambda + \tfrac{3}{10}\mu^2 + \tfrac{3}{5}\lambda^2 = \tfrac{79}{375}.$$

We find for $\mu = 0.2$, that in the well-mixed population there is an ESS with hawk probability $\alpha = 0.4066 < 0.4077$. Thus it appears that the hawk probability is somewhat bigger in this 3-2 model than the corresponding well-mixed population.

However, if we vary the parameter μ as in Figure 5, we see that for small μ the level of aggression is higher in the well-mixed population, and for large μ it is bigger on the graph.

3.4. *A complete bipartite graph with n = 5 and m = 2*. Let us now study another concrete example of this *n-m* bipartite graph model. Taking $n = 5$ and $m = 2$, we find that the corresponding probabilities are as follows, where we denote $P(|G| = k)$ by P_k:

$$P_1 = \tfrac{1}{7}\big(7 - 20\mu + 5\mu^2 - 20\lambda + 20\lambda^2 - 20\lambda^3 + 10\lambda^4 - 2\lambda^5 + 140\lambda\mu$$
$$- 30\mu^2\lambda - 300\mu\lambda^2 + 400\mu\lambda^3 - 250\mu\lambda^4 + 60\mu\lambda^5\big),$$

$$P_2 = \tfrac{1}{7}\big(20\mu - 20\mu^2 - 140\mu\lambda + 20\lambda - 80\lambda^2 + 120\lambda^3 - 80\lambda^4 + 20\lambda^5$$
$$+ 60\mu^2\lambda + 600\mu\lambda^2 - 1200\mu\lambda^3 + 1000\mu\lambda^4 - 300\mu\lambda^5\big),$$

$$P_3 = \tfrac{1}{7}\big(15\mu^2 + 60\lambda^2 - 180\lambda^3 + 180\lambda^4 - 60\lambda^5 - 30\mu^2\lambda - 300\mu\lambda^2$$
$$+ 1200\mu\lambda^3 - 1500\mu\lambda^4 + 600\mu\lambda^5\big),$$

$$P_4 = \tfrac{1}{7}\big(80\lambda^3 - 160\lambda^4 + 80\lambda^5 - 400\mu\lambda^3 + 1000\mu\lambda^4 - 600\mu\lambda^5\big),$$
$$P_5 = \tfrac{1}{7}\big(50\lambda^4 - 50\lambda^5 - 250\mu\lambda^4 + 300\mu\lambda^5\big),$$
$$P_6 = \tfrac{1}{7}\big(12\lambda^5 - 60\mu\lambda^5\big).$$

We can calculate the payoff for a dove player as

$$
\begin{aligned}
E_d(\alpha) = {} & P_1 + \frac{P_2}{2} + \frac{P_3}{3} + \frac{P_4}{4} + \frac{P_5}{5} + \frac{P_6}{6} - \alpha\Big(\frac{P_2}{2} + 2\frac{P_3}{3} + 3\frac{P_4}{4} + 4\frac{P_5}{5} + \frac{P_6}{6}\Big) \\
& + \alpha^2\Big(\frac{P_3}{3} + 3\frac{P_4}{4} + 6\frac{P_5}{5} + 10\frac{P_6}{6}\Big) - \alpha^3\Big(\frac{P_4}{4} + 4\frac{P_5}{5} + 10\frac{P_6}{6}\Big) \\
& + \alpha^4\Big(\frac{P_5}{5} + 5\frac{P_6}{6}\Big) - \frac{P_6}{6}\alpha^5.
\end{aligned}
$$

The payoff for a hawk player is similarly

$$
\begin{aligned}
E_h(\alpha) = {} & V - \alpha(V + C)\Big(\frac{P_2}{2} + P_3 + \frac{3P_4}{2} + 2P_5 + \frac{5P_6}{2}\Big) \\
& + \alpha^2(V + C)\Big(\frac{P_3}{3} + P_4 + 2P_5 + \frac{10P_6}{3}\Big) - \alpha^3(V + C)\Big(\frac{P_4}{4} + P_5 + \frac{5P_6}{2}\Big) \\
& + \alpha^4(V + C)\Big(\frac{P_5}{5} + P_6\Big) + \alpha^5\Big(\frac{41V P_6}{6} - \frac{C P_6}{6}\Big).
\end{aligned}
$$

Example 5. For $\lambda = \tfrac{1}{3}$ and $\mu = \tfrac{1}{6}$ we obtain

$$P_1 = \tfrac{289}{756}, \ P_2 = \tfrac{590}{1701}, \ P_3 = \tfrac{1255}{6804}, \ P_4 = \tfrac{40}{567}, \ P_5 = \tfrac{25}{1701} \ \text{and} \ P_6 = \tfrac{2}{1701}.$$

Using the payoffs $V = 1$ and $C = 2$ we find that the ESS occurs when $\alpha = 0.3603$.

For the equivalent well-mixed population, we find that for the same values of λ and μ as above, we have

$$E[|G|] = P_1 + 2P_2 + 3P_3 + 4P_4 + 5P_5 + 6P_6 = 1.9921.$$

So according to [Broom and Rychtář 2012] we have $1 + 6p = 1.9921$, or

$$p = 0.1653.$$

We then find $\alpha = 0.3785$ as the unique ESS in this equivalent well-mixed population. We notice that $\alpha_{5\text{-}2} = 0.3603 < 0.3785 = \alpha_7$. Thus in this case hawks prefer the equivalent well-mixed population to the corresponding 5-2 model.

However, again, if we vary the parameter μ as we did in Figure 5, we see that for small μ the level of aggression is much higher in the well-mixed population, and for large μ this advantage is reduced (see Figure 6). There is nevertheless a higher level of aggression for the well-mixed population in all cases. As we see in Figure 7, this is not the case for the alternative value of $\lambda = \tfrac{1}{4}$.

Thus different bipartite graphs can inhibit or encourage aggression, in comparison to the baseline well-mixed populations. In the multiplayer hawk-dove game,
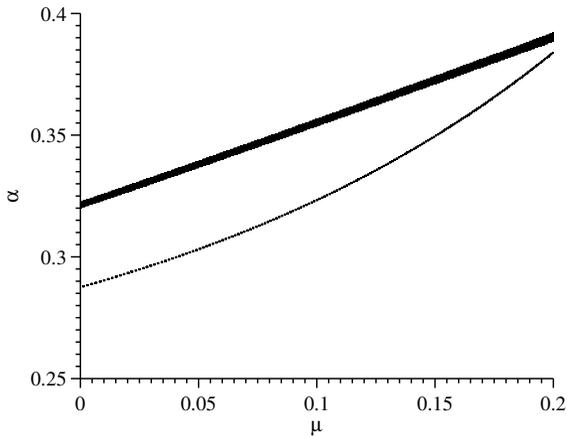
Figure 6. The evolutionarily stable proportion of hawks on a complete bipartite graph with $n = 5$ and $m = 2$ (thin line) and a well-mixed population (thick line), where $\lambda = \frac{1}{3}$ and μ varies from 0 to 0.2.
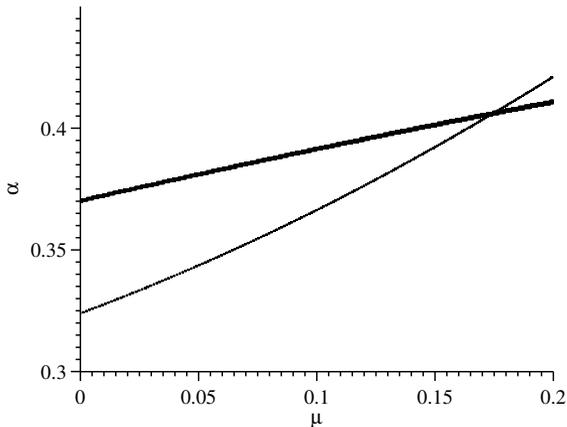
Figure 7. The evolutionarily stable proportion of hawks on a complete bipartite graph with $n = 5$ and $m = 2$ (thin line) and a well-mixed population (thick line), where $\lambda = \frac{1}{4}$ and μ varies from 0 to 0.2.

hawks do particularly badly in large groups. Thus when there is a significant risk of a large group forming, selection will favour lower aggression. This is the case in more asymmetric bipartite graphs like the 5-2 model when the parameter λ is large (and the star which is an $(N-1)$-1 bipartite graph), where vertices on the smaller side can play host to such large groups.

4. Discussion

Evolutionary graph theory has made a valuable contribution to the understanding of evolution in structured populations [Lieberman et al. 2005; Nowak 2006; Broom and Rychtář 2008]. However it has certain limitations; in particular the interactions between individuals, usually modelled by evolutionary games, are limited to pairwise ones. Hence a new framework was introduced in [Broom and Rychtář 2012] for modelling structured populations which allows interactions between an arbitrarily large number of individuals. The main purpose of the paper was to introduce the framework, and a secondary purpose was to give examples of different models of interaction, one of which was the territorial raider model. However, no single model was considered in any great detail. In this paper we applied results from [Broom and Rychtář 2012] to several different examples of graphs for the territorial raider model and compared the multiplayer hawk-dove game played on these graphs to equivalent well-mixed populations.

We studied two main graphs: the circle and the n-m complete bipartite graph. The observation of the different cases leads to interesting results. First we notice that for the same mean group size, hawks favour the model in which it is less likely to meet many other individuals, i.e., be a member of a large group; comparing different populations with identical means, it seems that small variance is preferred by hawks. In the circle case, since the maximal number of individuals in one territory is three no matter the number of individual considered, and since the equivalent well-mixed population will allow N individuals in one territory, hawks prefer the circle model for any N larger than three. In the n-m bipartite model the results observed are different. For the 3-2 bipartite graph hawks prefer the 3-2 graph to the equivalent well-mixed population except for small values of μ but for the 5-2 graph, hawks generally prefer the equvalent well-mixed population. In [Broom and Rychtář 2012] we considered the star, the n-1 bipartite graph, and in particular the 4-1 model, where hawks also prefer the equivalent well-mixed population. Here for large numbers of individuals, hawks favour the well-mixed population. From these observations, we understand that the structure of a model has a major influence on the strategy of the individuals.

One of the key components of our population model is the evolutionary game used. We considered a multiplayer hawk-dove game, but there are a number of alternatives that could have been applied. Multiplayer matrix games [Broom et al. 1997] provide a more general class of games, and it is possible to have games which involve coalitionary behaviour, so that perhaps forming large groups can be beneficial, in contrast to the hawk-dove game example. The results will be game-specific, in general. For instance we demonstrated the fact that there is at most one mixed ESS in the well-mixed population model, however for arbitrary multiplayer games there can be many ESSs.

Potential future work will thus include investigating different example games and structures as mentioned above. An important future direction of this research is the incorporation of evolutionary dynamics in the new structure, as at present the theory has concentrated on the development of the framework and key static properties. The type of dynamics used in evolutionary graph theory, such as the invasion process where a random individual gives birth with probability proportional to its fitness and then replaces one of its neighbours at random, will be applicable to our system with suitable redefinition of the term neighbour to more properly interpret the interactions between individuals, though there may be other potential dynamics as well. The combination of dynamics, game and structure will provide a flexible framework for analysing population interactions.

Appendix A: A proof that Equation (4) has at most one root, and conditions for such a root to occur

Set $v = V/C$. Then

$$h_W(\alpha) = \frac{C}{Np\alpha(1-\alpha)} \big((1-\alpha)(v+1) - (v+1)(1-p\alpha)^N$$
$$+ \alpha(1-p\alpha)^N - Np\alpha(1-\alpha) + \alpha v(1-p)^N \big).$$

Denoting $1-\alpha$ by β, we then have

$$h_W(\alpha) =$$
$$\frac{C}{Np\alpha(1-\alpha)} \big(\beta(v+1) - (v+\beta)(1-p+p\beta)^N - Np\beta(1-\beta) + (1-\beta)v(1-p)^N \big).$$

We now define

$$f(\beta) = \beta(v+1) - (v+\beta)(1-p+p\beta)^N - Np\beta(1-\beta) + (1-\beta)v(1-p)^N.$$

This function is differentiable as many times as we want and its third derivative is

$$f'''(\beta) =$$
$$-3p^2 N(N-1)(1-p+p\beta)^{N-2} - (v+\beta)N(N-1)(N-2)p^3(1-p+p\beta)^{N-3}.$$

It is clear that $f'''(\beta) < 0$. Moreover, we have $f(0) = -v(1-p)^N + v(1-p)^N = 0$, and $f(1) = (v+1) - (v+1) = 0$.

Thus f' is concave, increasing and then decreasing, and therefore f' can't have more than two roots. From there we can say that f has at most three roots. Since we know that $f(0) = f(1) = 0$, there is at most one other root in $\mathbb{R}$ so at most one root in $(0, 1)$.

Since we have

$$\frac{C}{Np\beta(1-\beta)} > 0 \quad \text{for all } \beta \in (0, 1),$$

(i.e., there is no root in $(0, 1)$), we can say that $f(\beta)$ has at most one root in this interval. From here, we can also conclude that $h_W(\alpha)$ has at most one root in this interval. That concludes the proof.

We now investigate what are the conditions on V and C to give a root in $(0, 1)$. First, let us calculate $h_W(\alpha)$ when $\alpha = 0$ and $\alpha = 1$. We have, for $p \neq 0$

$$h_W(0) = V\left(1 - \frac{1}{Np} + \frac{(1-p)^N}{Np}\right) > 0$$

and

$$h_W(1) = (V + C)\frac{1 - (1-p)^N}{Np} - C - V(1-p)^{N-1}.$$

So h_W is positive if $p \neq 0$ when $\alpha = 0$ and h_W has at most one root in $(0, 1)$. Thus we can say that either h_W is nonnegative for any α if $h_W(1) \geq 0$ or there is one α in $(0, 1)$ such as $h_W(\alpha) = 0$ (and then we have $h_W(1) \leq 0$).

Let us now study the sign of $h_W(1)$ for $p \neq 0$. We have

$$(V + C)\frac{1 - (1-p)^N}{Np} - C - V(1-p)^{N-1} \geq 0$$

$$\Longleftrightarrow \left(1 - (1-p)^N - Np(1-p)^{N-1}\right)V \geq \left(Np + (1-p)^N - 1\right)C$$

$$\Longleftrightarrow \frac{V}{C} \geq \frac{Np + (1-p)^N - 1}{1 - (1-p)^N - Np(1-p)^{N-1}}.$$

So there is a root between 0 and 1 for $p \neq 0$ and $C > 0$ if and only if

$$\frac{V}{C} < \frac{Np + (1-p)^N - 1}{1 - (1-p)^N - Np(1-p)^{N-1}}. \tag{9}$$

Appendix B: Mean group size for the complete bipartite graph

The mean group size can be expressed as the sum

$$\mathbf{E}(|G|) = \sum_{k=1}^{n+1} P(|G| = k)k.$$

This is divided into nine distinct terms from the calculations from Section 3.1, six for group sizes less than or equal to $m + 1$ and three for larger groups. These nine terms are simplified below, and the final expression for the mean group size from Equation (6) is found by summing them.

$$\sum_{k=1}^{m+1} \frac{nk}{n+m}\binom{m}{k-1}(1 - m\lambda)\mu^{k-1}(1-\mu)^{m-k+1}$$

$$= \sum_{k=0}^{m} \frac{n(k+1)}{n+m} \binom{m}{k}(1-m\lambda)\mu^k(1-\mu)^{m-k}$$

$$= \frac{n(1-m\lambda)}{n+m}\left(1+\sum_{k=0}^{m} k\binom{m}{k}\mu^k(1-\mu)^{m-k}\right)$$

$$= \frac{n(1-m\lambda)}{n+m}\left(1+\sum_{k=1}^{m} \frac{m!}{(k-1)!\,(m-k)!}\mu^k(1-\mu)^{m-k}\right)$$

$$= \frac{n(1-m\lambda)}{n+m}\left(1+m\mu\sum_{k=0}^{m-1} \frac{(m-1)!}{(k)!\,(m-1-k)!}\mu^k(1-\mu)^{m-k-1}\right)$$

$$= \frac{n(1-m\lambda)}{n+m} + \frac{nm\mu(1-m\lambda)}{n+m}.$$

$$\sum_{k=1}^{m+1} \frac{nk}{n+m}\binom{n-1}{k-2}m\lambda(1-n\mu)\lambda^{k-2}(1-\lambda)^{n-k+1}$$

$$+ \sum_{k=m+2}^{n+1} \frac{nmk}{n+m}(1-n\mu)\binom{n-1}{k-2}\lambda^{k-1}(1-\lambda)^{n-k+1}$$

$$= \sum_{k=0}^{m} \frac{n(k+1)}{n+m}\binom{n-1}{k-1}m\lambda(1-n\mu)\lambda^{k-1}(1-\lambda)^{n-k}$$

$$+ \sum_{k=m+1}^{n} \frac{nm(k+1)}{n+m}(1-n\mu)\binom{n-1}{k-1}\lambda^k(1-\lambda)^{n-k}$$

$$= \frac{nm\lambda(1-n\mu)}{n+m} \sum_{k=0}^{n} \binom{n-1}{k-1}(1+k)\lambda^{k-1}(1-\lambda)^{n-k}$$

$$= \frac{nm\lambda(1-n\mu)}{n+m} \sum_{k=1}^{n} \binom{n-1}{k-1}(1+k)\lambda^{k-1}(1-\lambda)^{n-k}$$

$$= \frac{nm\lambda(1-n\mu)}{n+m} \sum_{k=0}^{n-1} \binom{n-1}{k}(2+k)\lambda^k(1-\lambda)^{n-k-1}$$

$$= 2\frac{nm\lambda(1-n\mu)}{n+m} + \frac{nm\lambda(1-n\mu)}{n+m} \sum_{k=0}^{n-1} \binom{n-1}{k}k\lambda^k(1-\lambda)^{n-k-1}$$

$$= 2\frac{nm\lambda(1-n\mu)}{n+m} + \frac{nm\lambda(1-n\mu)}{n+m} \sum_{k=1}^{n-1} \frac{(n-1)!}{(k-1)!\,(n-k-1)!}\lambda^k(1-\lambda)^{n-k-1}$$

$$= 2\frac{nm\lambda(1-n\mu)}{n+m} + \frac{nm\lambda^2(n-1)(1-n\mu)}{n+m} \sum_{k=0}^{n-2} \binom{n-2}{k}\lambda^k(1-\lambda)^{n-k-2}$$

$$= 2\frac{nm\lambda(1-n\mu)}{n+m} + \frac{nm\lambda^2(n-1)(1-n\mu)}{n+m}.$$

$$\sum_{k=1}^{m+1} \frac{nk}{n+m}\binom{n-1}{k-1}nm\mu\lambda^k(1-\lambda)^{n-k} + \sum_{k=m+2}^{n+1} \frac{nmk\lambda\mu}{n+m}\binom{n-1}{k-1}n\lambda^{k-1}(1-\lambda)^{n-k}$$

$$= \sum_{k=0}^{m} \frac{n(k+1)}{n+m}\binom{n-1}{k}nm\mu\lambda^{k+1}(1-\lambda)^{n-k-1}$$

$$\quad + \sum_{k=m+1}^{n} \frac{nm(k+1)\lambda\mu}{n+m}\binom{n-1}{k}n\lambda^k(1-\lambda)^{n-k-1}$$

$$= \sum_{k=0}^{n} \frac{n(k+1)}{n+m}\binom{n-1}{k}nm\mu\lambda^{k+1}(1-\lambda)^{n-k-1}$$

$$= \frac{n^2m\lambda\mu}{n+m} \sum_{k=0}^{n}(k+1)\binom{n-1}{k}\lambda^k(1-\lambda)^{n-k-1}$$

$$= \frac{n^2m\lambda\mu}{n+m} \sum_{k=0}^{n-1}(k+1)\binom{n-1}{k}\lambda^k(1-\lambda)^{n-k-1}$$

$$= \frac{n^2m\lambda\mu}{n+m}\left(1 + \sum_{k=1}^{n-1}k\binom{n-1}{k}\lambda^k(1-\lambda)^{n-k-1}\right)$$

$$= \frac{n^2m\lambda\mu}{n+m}\left(1 + \sum_{k=0}^{n-2}\frac{(n-1)!}{(k)!\,(n-2-k)}\lambda^{k+1}(1-\lambda)^{n-k-2}\right)$$

$$= \frac{n^2m\lambda\mu}{n+m}\left(1 + (n-1)\lambda\sum_{k=0}^{n-2}\binom{n-2}{k}\lambda^k(1-\lambda)^{n-k-2}\right)$$

$$= \frac{n^2m\lambda\mu}{n+m} + \frac{n^2m(n-1)\lambda^2\mu}{n+m}.$$

$$\sum_{k=1}^{m+1} \frac{mk}{n+m}\binom{n}{k-1}(1-n\mu)\lambda^{k-1}(1-\lambda)^{n-k+1}$$

$$\quad + \sum_{k=m+2}^{n+1} \frac{mk}{n+m}(1-n\mu)\binom{n}{k-1}\lambda^{k-1}(1-\lambda)^{n-k+1}$$

$$= \sum_{k=0}^{m} \frac{m(k+1)}{n+m}\binom{n}{k}(1-n\mu)\lambda^k(1-\lambda)^{n-k}$$

$$+ \sum_{k=m+1}^{n} \frac{m(k+1)}{n+m}(1-n\mu)\binom{n}{k}\lambda^k(1-\lambda)^{n-k}$$

$$= \frac{m(1-n\mu)}{n+m} \sum_{k=0}^{n}(k+1)\binom{n}{k}\lambda^k(1-\lambda)^{n-k}$$

$$= \frac{m(1-n\mu)}{n+m}\left(1+\sum_{k=1}^{n}k\binom{n}{k}\lambda^k(1-\lambda)^{n-k}\right)$$

$$= \frac{m(1-n\mu)}{n+m} + \frac{m(1-n\mu)}{n+m}n\lambda\sum_{k=0}^{n-1}\frac{(n-1)!}{k!\,(n-k-1)!}\lambda^k(1-\lambda)^{n-k-1}$$

$$= \frac{m(1-n\mu)}{n+m} + \frac{nm\lambda(1-n\mu)}{n+m}.$$

$$\sum_{k=1}^{m+1}\frac{nmk\mu}{n+m}(1-m\lambda)\binom{m-1}{k-2}\mu^{k-2}(1-\mu)^{m-k+1}$$

$$= \sum_{k=0}^{m}\frac{nm(k+1)\mu}{n+m}(1-m\lambda)\binom{m-1}{k-1}\mu^{k-1}(1-\mu)^{m-k}$$

$$= \frac{nm(1-m\lambda)\mu}{n+m}\sum_{k=1}^{m}(k+1)\binom{m-1}{k-1}\mu^{k-1}(1-\mu)^{m-k}$$

$$= \frac{nm(1-m\lambda)\mu}{n+m}$$

$$\cdot\left(\sum_{k=0}^{m-1}\binom{m-1}{k}\mu^k(1-\mu)^{m-1-k}+\binom{m-1}{k}(k+1)\mu^k(1-\mu)^{m-1-k}\right)$$

$$= \frac{2nm(1-m\lambda)\mu}{n+m}$$

$$+ \frac{nm(m-1)(1-m\lambda)\mu}{n+m}\sum_{k=1}^{m-1}\frac{(m-2)!}{(k-1)!\,(m-1-k)!}\mu^k(1-\mu)^{m-1-k}$$

$$= \frac{2nm(1-m\lambda)\mu}{n+m}$$

$$+ \frac{nm(m-1)(1-m\lambda)\mu^2}{n+m}\sum_{k=0}^{m-2}\frac{(m-2)!}{(k)!\,(m-2-k)!}\mu^k(1-\mu)^{m-2-k}$$

$$= \frac{2nm(1-m\lambda)\mu}{n+m} + \frac{nm(m-1)(1-m\lambda)\mu^2}{n+m}.$$

$$\sum_{k=1}^{m+1} \frac{nm^2 k \lambda \mu}{n+m} \binom{m-1}{k-1} \mu^{k-1} (1-\mu)^{m-k}$$

$$= \sum_{k=0}^{m} \frac{nm^2(k+1)\lambda\mu}{n+m} \binom{m-1}{k} \mu^k (1-\mu)^{m-1-k}$$

$$= \frac{nm^2\lambda\mu}{n+m} \sum_{k=0}^{m} \binom{m-1}{k} (k+1)\mu^k (1-\mu)^{m-1-k}$$

$$= \frac{nm^2\lambda\mu}{n+m} \left(\sum_{k=0}^{m-} \binom{m-1}{k} \mu^k (1-\mu)^{m-1-k} + \sum_{k=1}^{m-1} \binom{m-1}{k} k \mu^k (1-\mu)^{m-1-k} \right)$$

$$= \frac{nm^2\lambda\mu}{n+m} \left(1 + \mu(m-1) \sum_{k=0}^{m-2} \frac{(m-2)!}{k!\,(m-2-k)!} \mu^k (1-\mu)^{m-2-k}\right)$$

$$= \frac{nm^2\lambda\mu}{n+m} + \frac{nm^2(m-1)\mu^2\lambda}{n+m}.$$

So we have

$$\mathbf{E}(|G|)$$

$$= \frac{n(1-m\lambda)}{n+m} + \frac{nm\mu(1-m\lambda)}{n+m} + 2\frac{nm\lambda(1-n\mu)}{n+m} + \frac{nm\lambda^2(n-1)(1-n\mu)}{n+m}$$

$$\quad + \frac{n^2m\lambda\mu}{n+m} + \frac{n^2m(n-1)\lambda^2\mu}{n+m} + \frac{m(1-n\mu)}{n+m} + \frac{nm\lambda(1-n\mu)}{n+m}$$

$$\quad + \frac{2nm(1-m\lambda)\mu}{n+m} + \frac{nm(m-1)(1-m\lambda)\mu^2}{n+m} + \frac{nm^2\lambda\mu}{n+m} + \frac{nm^2(m-1)\mu^2\lambda}{n+m}$$

$$= 1 + \frac{2nm\mu - 2nm^2\lambda\mu + 2nm\lambda - 2n^2m\lambda\mu + n^2m\lambda^2 - nm\lambda^2 + n\mu^2m^2 - nm\mu^2}{n+m}.$$

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