Asymmetric Games in Monomorphic and Polymorphic Populations

Mark Broom · Jan Rychtář

Abstract Evolutionary game theory is an increasingly important way to model the evolution of biological populations. Many early models were in the form of matrix games, or bi-matrix games in asymmetric situations when individuals occupy distinct roles within the contest, where rewards are accrued through independent contests against random members of the population. More recent models have not had the simple linear properties of matrix games, and more general analysis has been required. In this paper we carry out a general analysis of asymmetric games, comparing monomorphic and polymorphic populations. We are particularly interested in situations where the strategies that individuals play influence which role that they occupy, for example in a more realistic variant of the classical Owner-Intruder game. We both prove general results and consider specific examples to illustrate the difficulties of these more complex games.

Keywords Bi-matrix games · ESS · Population games · Uncorrelated asymmetry · Role

1 Introduction

Evolutionary game theory has its origins in important work carried out in the 1960s and early 1970s, see [21] and [8]. Using ideas from classical game theory, the central feature is that of the population and the frequencies of strategies (or traits) within it. The most important contribution is perhaps the work of Maynard Smith and co-workers, in particular [14] and [12] which set out the underlying theory essentially in the way that we understand it today. The

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central concept of the theory is the Evolutionarily Stable Strategy (ESS), a strategy which, if all individuals play it, resists invasion by alternatives and thus persists through time. It is thus essentially a static concept, and much of the early theory did not concern itself with how populations reached the ESS. The concept of evolutionary dynamics, which addressed this question, was introduced in [20], see also [6] and [10].

1.1 Matrix Games

Perhaps the simplest type of evolutionary game is the matrix game. Here individuals play games against opponents randomly selected from the population. An individual playing S_i facing one playing S_j receives reward a_{ij}, so one playing mixed strategy $\mathbf{p}$ against an opponent playing $\mathbf{q}$ receives reward $\mathbf{p}A\mathbf{q}^{\mathrm{T}}$, where A is the $n \times n$ matrix (a_{ij}). An important feature of matrix games is that the expected payoff to an individual does not depend upon the composition of the population, except through its mean (thus matrix games always have the *polymorphic–monomorphic equivalence* property, see Sect. 2). Thus for a population with mean strategy $\mathbf{q}$, and denoting $\mathcal{E}\left[\mathbf{p}; \mathbf{q}\right]$ as the expected payoff to a player playing strategy $\mathbf{p}$ in a population playing $\mathbf{q}$, we have

$$\mathcal{E}\left[\mathbf{p}; \mathbf{q}\right] = \mathbf{p}A\mathbf{q}^{\mathrm{T}}. \tag{1}$$

This payoff is linear in both the vector $\mathbf{p}$ (linear on the left, or linear in the focal player strategy) and the vector $\mathbf{q}$ (linear on the right, or linear in the population strategy). This leads to much simplification, and the ESS conditions reduce to a form that is easier to work with. In particular, classical games like the Hawk-Dove game and the Prisoner's Dilemma are examples of matrix games. For example in the Hawk-Dove game, individuals compete for a resource of value V with two available strategies, Hawk and Dove. Hawks always beat Doves, contests between players with the same strategy are won with probability 0.5, with the loser of a Hawk-Hawk contest incurring an additional cost C. Thus, indicating Hawk as strategy 1 and Dove as strategy 2, we have payoffs $a_{11} = (V - C)/2$, $a_{12} = V$, $a_{21} = 0$, and $a_{22} = V/2$. For more on matrix games see [12], [2], and [3].

1.2 Nonlinear Games

Not all games have the nice properties described above. One of the earliest examples of an evolutionary game, the sex ratio game (see [9]), considers a focal female producing a proportion p of male offspring in a population with equivalent proportion q. The payoff to the focal female is

$$\mathcal{E}\left[p; q\right] = \frac{p}{q} + \frac{1-p}{1-q}, \tag{2}$$

which is linear in p (focal strategy), but not in q (population mean). The game here cannot be thought of in terms of individual contests, but it is a game against the population as a whole. This is called a playing the field game, or a population game [3, 15, 16]. We note that such games also satisfy polymorphic–monomorphic equivalence (see Sect. 2). For examples of games that do not satisfy polymorphic–monomorphic equivalence, see [3, Chap. 7] and [19].

In general the payoff to an individual is a function of its strategy and the composition of the population. We write the payoff to an individual playing $\mathbf{p}$ within a population Π as $\mathcal{E}\left[\mathbf{p}; \Pi\right]$. A monomorphic population all playing $\mathbf{q}$ is indicated by $\Pi = \delta_{\mathbf{q}}$, whereas if the population is polymorphic with the proportion playing $\mathbf{q_i}$ being α_i, we write $\Pi = \sum_i \alpha_i \delta_{\mathbf{q_i}}$.

1.3 Games with Distinct Roles

In the above we have considered populations with indistinguishable individuals. What if individuals can be distinguished? Maynard Smith and Parker [13] identified two main types of difference between individuals: correlated asymmetries, where there is some real difference between them, and uncorrelated asymmetries where individuals are effectively identical, but can be distinguished by the role they occupy, for example territory owner or intruder.

We will mainly consider uncorrelated asymmetries. The classical Owner-Intruder game involves a territory owner meeting an intruder. Each individual chooses Hawk or Dove, and the usual contest as described above occurs. Here an individual can be an owner or an intruder in different contests (it is assumed to occupy each role with probability 0.5), and can choose its strategy conditional on which role it occupies. This yields results of different character to the original game, where mixed strategies now do not occur. In fact for this class of game it was shown in [18] that mixed strategies are impossible, Selten's classic Theorem (see Sect. 3, and also 3, p.142).

The owner intruder game is an example of a bi-matrix game: a two role game where payoffs are determined by a set of independent contests between a focal individual using strategy $(\mathbf{p}_1, \mathbf{p}_2)$ (i.e. a strategy $\mathbf{p}_1$ as an owner and $\mathbf{p}_2$ as an intruder) and a randomly selected opponent using a strategy $(\mathbf{q}_1, \mathbf{q}_2)$. The payoff to the focal individual is given by

$$\mathcal{E}\left[(\mathbf{p}_1, \mathbf{p}_2); (\mathbf{q}_1, \mathbf{q}_2)\right] = \frac{1}{2}\mathcal{E}_1\left[\mathbf{p}_1; \mathbf{q}_2\right] + \frac{1}{2}\mathcal{E}_2\left[\mathbf{p}_2; \mathbf{q}_1\right], \tag{3}$$

where

$$\mathcal{E}_1\left[\mathbf{p}_1; \mathbf{q}_2\right] = \mathbf{p}_1 A \mathbf{q}_2^{\mathrm{T}}, \tag{4}$$
$$\mathcal{E}_2\left[\mathbf{p}_2; \mathbf{q}_1\right] = \mathbf{p}_2 B \mathbf{q}_1^{\mathrm{T}}. \tag{5}$$

The evolution of such populations can be analysed using replicator dynamics [17], [10], (but see [1]). Here, rather than each individual being able to switch roles, we must consider individuals which are permanently in one (given) role, and the composition of the population of each role through time is dynamically changing. We might think of the roles being male and female, for example.

Although, for the sake of simplicity, our formulations suggest our focus on static games, the content can be readily adapted to dynamic games such as parental care games [11], in which individuals pass between different states according to their sex and the strategy they use, or food-stealing games, e.g. [5], where individuals can be a food handler or challenger, and the probability of occupying each role depends upon their strategy within contests.

2 Definitions

We consider a population where individuals can occupy more than one role, in this case two. We assume that every game involves precisely one individual in each role (for example, an owner and an intruder). We note that it would be possible to consider a wider class of games which are not based upon pairwise interactions as a full generalisation of playing the field games. However, the problem as considered is still complex, possesses some useful structural features, and is the natural extension from classical asymmetric games. A population is represented by a measure on the strategy space. We can view a given population Π as a pair (Π_1, Π_2), where Π_r represents the population structure (i.e. the distribution of strategies) of individuals in role r.

2.1 Strategies and Payoffs

We shall denote $\mathcal{E}_1[\mathbf{p}_1; \Pi_2]$ as the payoff to the focal individual in role 1 when using strategy $\mathbf{p}_1$ when it is effectively playing in a population of "role 2 players" described by Π_2, which happens with probability $\rho_1((\mathbf{p}_1, \mathbf{p}_2), \Pi)$. Similarly we shall use $\mathcal{E}_2[\mathbf{p}_2; \Pi_1]$ as the corresponding payoff in role 2. Our player must be in one of the two roles, and so $\rho_2((\mathbf{p}_1, \mathbf{p}_2), \Pi) = 1 - \rho_1((\mathbf{p}_1, \mathbf{p}_2), \Pi)$.

Definition 1 We define $\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi]$, the *payoff* to a strategy $(\mathbf{p}_1, \mathbf{p}_2)$ in a population $\Pi = (\Pi_1, \Pi_2)$, by

$$\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi] = \rho_1((\mathbf{p}_1, \mathbf{p}_2), \Pi)\mathcal{E}_1[\mathbf{p}_1; \Pi_2] + \rho_2((\mathbf{p}_1, \mathbf{p}_2), \Pi)\mathcal{E}_2[\mathbf{p}_2; \Pi_1]. \tag{6}$$

Later we shall consider populations that consist of two distinct classes of individuals, where the interaction of strategies and roles may be different for each class. For example, at its simplest, females and males, where females are always in role 1 and males are always in role 2. In such a case we define the probability of a class k individual being in role 1 when faced by an individual of class l in role 2 by $\rho_{1kl}((\mathbf{p}_1, \mathbf{p}_2), \Pi)$.

Definition 2 A strategy $(\mathbf{p}_1, \mathbf{p}_2)$ is an *Evolutionarily Stable Strategy (ESS)* of the game if for every other strategy $(\mathbf{q}_1, \mathbf{q}_2)$ there exists $\varepsilon_0 > 0$ such that for all $\varepsilon \in (0, \varepsilon_0)$

$$\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi] > \mathcal{E}[(\mathbf{q}_1, \mathbf{q}_2); \Pi], \tag{7}$$

where $\Pi = (1 - \varepsilon)\delta_{(\mathbf{p}_1, \mathbf{p}_2)} + \varepsilon\delta_{(\mathbf{q}_1, \mathbf{q}_2)}$.

2.2 Strategies and Roles

Definition 3 We will say that a game is *strategy-role independent* if the probability of an individual occupying a particular role does not depend upon their chosen strategy, i.e. if the function $\rho_1((\mathbf{p}_1, \mathbf{p}_2), \Pi)$, and so $\rho_2((\mathbf{p}_1, \mathbf{p}_2), \Pi)$, does not depend on an individual's strategy $(\mathbf{p}_1, \mathbf{p}_2)$.

Definition 4 We can say that a game is *population-role independent* if $\rho_1((\mathbf{p}_1, \mathbf{p}_2), \Pi)$ does not depend on Π.

Lemma 1 *When there is only one class of individual, the concepts of strategy-role independence and population-role independence are equivalent.*

Proof Assume that ρ does not depend on the population. Because every game involves precisely one individual in each role, half of the population is in role 1 and the other half in role 2. Thus $\rho_1(\mathbf{p}, \delta_{\mathbf{p}}) = 1/2$ for every $\mathbf{p}$, and for any population Π and any pair of strategies $\mathbf{p}$ and $\mathbf{q}$,

$$\rho_1(\mathbf{p}, \Pi) = \rho_1(\mathbf{p}, \delta_{\mathbf{p}}) = \frac{1}{2} = \rho_1(\mathbf{q}, \delta_{\mathbf{q}}) = \rho_1(\mathbf{q}, \Pi). \tag{8}$$

Conversely, when the game is strategy-role independent and there is just one class of individual, then (in any population) any individual must have a probability of exactly 1/2 to be in role 1. Consequently, ρ does not depend on the population. □

Strategy-role independence means that the payoff in Equation (6) to a strategy $(\mathbf{p}_1, \mathbf{p}_2)$-player in a population $\Pi = (\Pi_1, \Pi_2)$, becomes

$$\mathcal{E}[(\mathbf{p}_1, \mathbf{p}_2); \Pi] = \frac{1}{2}\mathcal{E}_1[\mathbf{p}_1; \Pi_2] + \frac{1}{2}\mathcal{E}_2[\mathbf{p}_2; \Pi_1]. \tag{9}$$

Lemma 1 should be contrasted with games when individuals can be different as we see in Sect. 5, Example 5.

Note, that in a population $\Pi = \sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}$, the population of individuals in role 2 can in general be described by

$$\Pi_2 = \sum_i \beta_{i2}\delta_{q_{i2}}, \tag{10}$$

where

$$\beta_{i2} = \frac{\alpha_i \rho_2\big((\mathbf{q}_{i1}, \mathbf{q}_{i2}), \Pi\big)}{\sum_j \alpha_j \rho_2\big((\mathbf{q}_{j1}, \mathbf{q}_{j2}), \Pi\big)}. \tag{11}$$

Similarly, we have

$$\Pi_1 = \sum_i \beta_{i1}\delta_{q_{i1}}, \tag{12}$$

where

$$\beta_{i1} = \frac{\alpha_i \rho_1\big((\mathbf{q}_{i1}, \mathbf{q}_{i2}), \Pi\big)}{\sum_j \alpha_j \rho_1\big((\mathbf{q}_{j1}, \mathbf{q}_{j2}), \Pi\big)}. \tag{13}$$

Note that in the case with identical individuals and strategy-role independence, $\rho \equiv 1/2$ and thus $\beta_i = \alpha_i$ for all i.

2.3 Monomorphic and Polymorphic Populations

Definition 5 In a population without roles, we say that a game has *polymorphic–monomorphic equivalence* if for every strategy $\mathbf{p}$, for any finite collection of strategies $\{\mathbf{q}_i\}_{i=1}^m$ and for any corresponding collection of m constants $\alpha_i \geq 0$ such that $\sum_i^m \alpha_i = 1$ we have

$$\mathcal{E}\left[\mathbf{p}; \sum_i \alpha_i \delta_{\mathbf{q}_i}\right] = \mathcal{E}\left[\mathbf{p}; \delta_{\sum_i \alpha_i \mathbf{q}_i}\right]. \tag{14}$$

We note that polymorphic–monomorphic equivalence holds only in respect of the static notion of ESSs, and there is no such equivalence in terms of dynamics, since any dynamics depends directly on the specific combination of strategies within the population.

Definition 6 We say that an asymmetric game has *polymorphic–monomorphic equivalence* if individuals cannot distinguish between a polymorphic mixture $\sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}$ and a monomorphic population $\delta_{(\sum_i \alpha_i \mathbf{q}_{i1}, \sum_i \alpha_i \mathbf{q}_{i2})}$, so that the total payoff, as well as the probability of being in role 1, are the same in both populations, for all individuals.

Specifically, a game has polymorphic–monomorphic equivalence if for every $(\mathbf{p}_1, \mathbf{p}_2)$, any finite collection of strategies $\{\mathbf{q}_{i1}, \mathbf{q}_{i2}\}_{i=1}^m$ and any corresponding collection of m constants $\alpha_i \geq 0$ such that $\sigma_{i=1}^m \alpha_i = 1$, we have

$$\mathcal{E}\left[(\mathbf{p}_1, \mathbf{p}_2); \sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}\right] = \mathcal{E}\left[(\mathbf{p}_1, \mathbf{p}_2); \delta_{(\sum_i \alpha_i \mathbf{q}_{i1}, \sum_i \alpha_i \mathbf{q}_{i2})}\right] \tag{15}$$

and

$$\rho_1\big((\mathbf{p}_1, \mathbf{p}_2), \sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}\big) = \rho_1\big((\mathbf{p}_1, \mathbf{p}_2), \delta_{(\sum_i \alpha_i \mathbf{q}_{i1}, \sum_i \alpha_i \mathbf{q}_{i2})}\big). \tag{16}$$

For example, if the game has polymorphic–monomorphic equivalence and the population is given by $\Pi = (1-\varepsilon)\delta_{(\mathbf{p}_1,\mathbf{p}_2)} + \varepsilon\delta_{(\mathbf{q}_1,\mathbf{q}_2)}$, then an individual in role 1 will effectively play against a population described by $\Pi_2 = (1-\varepsilon)\delta_{\mathbf{p}_2} + \varepsilon\delta_{\mathbf{q}_2}$. Note that this concept first appeared in [3, p.143], but that there only the condition (15) was stipulated (and for the cases considered the condition (16) was satisfied). However, if (16) does not hold, the probability of an individual being in role 1 would depend on whether the individual is in a polymorphic or in a monomorphic population and hence the two populations would not be truly equivalent.

Definition 7 A game has *polymorphic–monomorphic equivalence within roles* if individuals already in role 1 (or 2) cannot distinguish between polymorphic and monomorphic populations. Thus whenever $\Pi = \sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}$ and $\Pi' = \delta_{\sum_i \alpha_i (\mathbf{q}_{i1},\mathbf{q}_{i2})}$, then

$$\mathcal{E}_1\left[\mathbf{p}_1; \Pi_2\right] = \mathcal{E}_1\left[\mathbf{p}_1; \Pi_2'\right], \tag{17}$$

$$\mathcal{E}_2\left[\mathbf{p}_2; \Pi_1\right] = \mathcal{E}_2\left[\mathbf{p}_2; \Pi_1'\right]. \tag{18}$$

Explicitly, a game has polymorphic–monomorphic equivalence within roles if for every strategy $(\mathbf{p}_1, \mathbf{p}_2)$, every m-tuple of strategies $(\mathbf{q}_{i1}, \mathbf{q}_{i2})_{i=1}^m$ and scalars $(\alpha_i)_{i=1}^m$ such that $\alpha_i \geq 0$ and $\sum_i \alpha_i = 1$ we have

$$\mathcal{E}_1\left[\mathbf{p}_1; \sum_i \beta_{i2}\delta_{\mathbf{q}_{i2}}\right] = \mathcal{E}_1\left[\mathbf{p}_1; \delta_{\sum_i \beta_{i2}\mathbf{q}_{i2}}\right] \tag{19}$$

whenever $\rho_1\left((\mathbf{p}_1, \mathbf{p}_2), \sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}\right) \neq 0$ or $\rho_1\left((\mathbf{p}_1, \mathbf{p}_2), \delta_{\sum_i \alpha_i (\mathbf{q}_{i1},\mathbf{q}_{i2})}\right) \neq 0$, and

$$\mathcal{E}_2\left[\mathbf{p}_2; \sum_i \beta_{i1}\delta_{\mathbf{q}_{i1}}\right] = \mathcal{E}_2\left[\mathbf{p}_2; \delta_{\sum_i \beta_{i1}\mathbf{q}_{i1}}\right] \tag{20}$$

whenever $\rho_2\left((\mathbf{p}_1, \mathbf{p}_2), \sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}\right) \neq 0$ or $\rho_2\left((\mathbf{p}_1, \mathbf{p}_2), \delta_{\sum_i \alpha_i (\mathbf{q}_{i1},\mathbf{q}_{i2})}\right) \neq 0$, where the β_{ij} are defined as in (11) and (13).

3 General Results

The following classical theorem was introduced and proved in [18]. It was reformulated to be consistent with the more general (in some ways, but not others) terminology of this paper in [3]. The proof given below comes from [3, p.143], and we show it here for completeness.

Theorem 1 *Assume that the population satisfies strategy-role independence, and that the payoff functions $\mathcal{E}_1\left[\mathbf{p}_1; \Pi_2\right]$ and $\mathcal{E}_2\left[\mathbf{p}_2; \Pi_1\right]$ are linear on the left, i.e. that there are functions $(f_{1i})_{i=1}^{n_1}$, $(f_{2i})_{i=1}^{n_2}$ such that*

$$\mathcal{E}_1\left[\mathbf{p}_1; \Pi_2\right] = \sum_{i=1}^{n_1} p_{1i} f_{1i}(\Pi_2), \tag{21}$$

$$\mathcal{E}_2\left[\mathbf{p}_2; \Pi_1\right] = \sum_{i=1}^{n_2} p_{2i} f_{2i}(\Pi_1). \tag{22}$$

Then $(\mathbf{p}_1, \mathbf{p}_2)$ can be an ESS only if $\mathbf{p}_1$ and $\mathbf{p}_2$ are pure strategies.

Proof Let $(\mathbf{p}_1, \mathbf{p}_2)$ be given and let i_0 be such that

$$f_{1i_0}(\delta_{\mathbf{p}_2}) = \max_i\{f_{1i}(\delta_{\mathbf{p}_2})\}. \tag{23}$$

Now, assume that $\mathbf{p}_1$ is not a pure strategy, in particular it is not the pure strategy S_{i_0}. Since $(\mathbf{p}_1, \mathbf{p}_2)$ is an ESS, it has to resist invasion by $(S_{i_0}, \mathbf{p}_2)$ which by (7) means that

$$\mathcal{E}\left[(\mathbf{p}_1, \mathbf{p}_2); \Pi\right] > \mathcal{E}\left[(S_{i_0}, \mathbf{p}_2); \Pi\right] \tag{24}$$

where $\Pi = (1-\varepsilon)\delta_{(\mathbf{p}_1,\mathbf{p}_2)} + \varepsilon\delta_{(S_{i_0},\mathbf{p}_2)}$. Inequality (24) is, by (9), equivalent to

$$\mathcal{E}_1\left[\mathbf{p}_1; \delta_{\mathbf{p}_2}\right] > \mathcal{E}_1\left[S_{i_0}; \delta_{\mathbf{p}_2}\right]. \tag{25}$$

However, the last inequality is not possible since otherwise we would have the following

$$\mathcal{E}_1\left[S_{i_0}; \delta_{\mathbf{p}_2}\right] = f_{1i_0}(\delta_{\mathbf{p}_2}) = \sum_i p_{1i} f_{1i_0}(\delta_{\mathbf{p}_2}) \tag{26}$$

$$\geq \sum_i p_{1i} f_{1i}(\delta_{\mathbf{p}_2}) = \mathcal{E}_1\left[\mathbf{p}_1; \delta_{\mathbf{p}_2}\right] \tag{27}$$

$$> \mathcal{E}_1\left[S_{i_0}; \delta_{\mathbf{p}_2}\right]. \tag{28}$$

Thus $\mathbf{p}_1$ must be pure for $(\mathbf{p}_1, \mathbf{p}_2)$ to be an ESS. A similar argument holds for $\mathbf{p}_2$. Thus the only possible ESSs are pure. □

This is an important result, since it suggests that the mixed strategies commonplace in evolutionary games such as the Hawk-Dove game are in fact not possible whenever animals can distinguish themselves in some way. No two animals are identical, so it suggests that mixtures are rare and pure solutions (or no ESSs at all) are commonplace. However, strategy-role independence is needed for the proof to work. What if this condition is not satisfied? We shall explore this question later, see Sect. 4, Example 2.

Theorem 2 *If the game has polymorphic–monomorphic equivalence, then it has polymorphic–monomorphic equivalence within roles.*

Proof Let us fix a strategy $(\mathbf{p}_1, \mathbf{p}_2)$, an m-tuple of strategies $(\mathbf{q}_{i1}, \mathbf{q}_{i2})_{i=1}^m$ and scalars $(\alpha_i)_{i=1}^m$ such that $\alpha_i \geq 0$ and $\sum_i \alpha_i = 1$. Let $\Pi = \sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}$ and let $\Pi' = \delta_{(\sum_i \alpha_i \mathbf{q}_{i1}, \sum_i \alpha_i \mathbf{q}_{i2})}$. We have to prove that

$$\mathcal{E}_1\left[\mathbf{p}_1; \sum_i \beta_{i2}\delta_{\mathbf{q}_{i2}}\right] = \mathcal{E}_1\left[\mathbf{p}_1; \delta_{\sum_i \beta_{i2}\mathbf{q}_{i2}}\right] \tag{29}$$

whenever $\rho_1\big((\mathbf{p}_1, \mathbf{p}_2), \Pi\big) \neq 0$ or $\rho_1\big((\mathbf{p}_1, \mathbf{p}_2), \Pi'\big) \neq 0$, and the analogous equality for $\mathcal{E}_2$, where β_{i1} and β_{i2} are given by (13) and (11). The game has polymorphic–monomorphic equivalence and thus, by (16), the coefficients β_{ij} do not depend on whether they are calculated in population Π or Π'. Also, let us denote

$$\rho_1 = \rho_1\big((\mathbf{p}_1, \mathbf{p}_2), \Pi\big) = \rho_1\big((\mathbf{p}_1, \mathbf{p}_2), \Pi'\big). \tag{30}$$

Firstly suppose that we fix $\mathbf{q}_{i1} = \mathbf{q}_1$ for all i. We then have

$$\rho_1\mathcal{E}_1\left[\mathbf{p}_1; \sum_i \beta_{i2}\delta_{\mathbf{q}_{i2}}\right] = \mathcal{E}\left[(\mathbf{p}_1, \mathbf{p}_2); \Pi\right] - (1-\rho_1)\mathcal{E}_2\left[\mathbf{p}_2; \sum_i \beta_{i1}\delta_{\mathbf{q}_1}\right] \tag{31}$$

$$= \mathcal{E}\left[(\mathbf{p}_1, \mathbf{p}_2); \Pi'\right] - (1-\rho_1)\mathcal{E}_2\left[\mathbf{p}_2; \delta_{\mathbf{q}_1}\right] \tag{32}$$

$$= \mathcal{E}\left[(\mathbf{p}_1, \mathbf{p}_2); \Pi'\right] - (1-\rho_1)\mathcal{E}_2\left[\mathbf{p}_2; \delta_{\sum_i \beta_{i1}\mathbf{q}_1}\right] \tag{33}$$

$$= \rho_1\mathcal{E}_1\left[\mathbf{p}_1; \delta_{\sum_i \beta_{i2}\mathbf{q}_{i2}}\right]. \tag{34}$$

Similarly, fixing a strategy $\mathbf{q}_2$ and proceeding as above would give an equivalent equation for role 2 payoffs, and together these give polymorphic–monomorphic equivalence within roles. □

Theorem 3 *If a game is strategy-role independent, then the game has polymorphic–monomorphic equivalence if and only if it has polymorphic–monomorphic equivalence within roles.*

Proof If the game has polymorphic–monomorphic equivalence, it has polymorphic–monomorphic equivalence within roles by Theorem 2. Now, assume that the game has polymorphic–monomorphic equivalence within roles and is strategy-role independent. Then

$$\mathcal{E}\left[\mathbf{p}; \sum_i \alpha_i \delta_{(\mathbf{q}_{i1},\mathbf{q}_{i2})}\right] = \frac{1}{2}\mathcal{E}_1\left[\mathbf{p}_1; \sum_i \alpha_i \delta_{\mathbf{q}_{i2}}\right] + \frac{1}{2}\mathcal{E}_2\left[\mathbf{p}_2; \sum_i \alpha_i \delta_{\mathbf{q}_{i1}}\right] \quad (35)$$

$$= \frac{1}{2}\mathcal{E}_1\left[\mathbf{p}_1; \delta_{\sum_i \alpha_i \mathbf{q}_{i2}}\right] + \frac{1}{2}\mathcal{E}_2\left[\mathbf{p}_2; \delta_{\sum_i \alpha_i \mathbf{q}_{i1}}\right] \quad (36)$$

$$= \mathcal{E}\left[\mathbf{p}; \delta_{\sum_i \alpha_i (\mathbf{q}_{i1},\mathbf{q}_{i2})}\right]. \quad (37)$$

Thus we have polymorphic–monomorphic equivalence. □

Thus when we have strategy-role independence, whether monomorphic and polymorphic populations are equivalent reduces to considering this comparison separately within roles. This equivalence is very useful for analysis, and only having to consider our focal individual in the separate roles independently simplifies significantly the task of ascertaining if the polymorphic–monomorphic equivalence condition holds.

4 Population Properties and Examples

Consider a population of identical individuals playing a game with two roles as previously described. A population may or may not satisfy the properties of strategy-role independence, polymorphic–monomorphic equivalence and polymorphic–monomorphic equivalence within roles. There are eight potential combinations of such properties, but which combinations can occur, and which cannot? We explore this in the current section. Our results are summarised in Table 1. In what follows, we will use a shorthand notation; for example "the game is **SR N, PM N, PMR Y**" which will mean that the game does not satisfy the properties of strategy-role independence (SR), and polymorphic–monomorphic equivalence (PM), but satisfies the property of polymorphic–monomorphic equivalence within roles (PMR).

Example 1 (*Owner-Intruder game with strategy-role independence*) Consider a contest over a territory between an owner and an intruder, based upon the Hawk-Dove game. In each role an individual can play either Hawk or Dove, leading to the following pure strategies [12].

Hawk – play Hawk when both owner and intruder,
Dove – play Dove when both owner and intruder,
Bourgeois – play Hawk when owner and Dove when intruder,
Marauder – play Dove when owner and Hawk when intruder.

The term "Marauder" was used for this type of behaviour in [4] and [3]. Maynard Smith [12] simply called it "Strategy X".

In the original game with pairs of individuals meeting at random with each occupying the owner role with probability 1/2 (i.e. with strategy-role independence) if $V \geq C$ then Hawk is the unique ESS, and if $V < C$ then there are two pure ESSs, Bourgeois and Marauder, see for example [3, Sect. 8.3]. Thus we can see that Theorem 1 is satisfied for this game.

It is clear that the original game satisfies all three properties, which we denote by **SR Y, PM Y, PMR Y**.

From Theorem 2 we know that polymorphic–monomorphic equivalence implies polymorphic–monomorphic equivalence within roles, so that neither **SR Y, PM Y, PMR N** nor **SR N, PM Y, PMR N** can hold.

From Theorem 3 we know that the conditions for polymorphic–monomorphic equivalence and polymorphic–monomorphic equivalence within roles are identical under strategy-role independence, and so we cannot have **SR Y, PM N, PMR Y**.

Example 2 (*Owner-Intruder game without strategy-role independence*) Now consider a population consisting only of Hawks (play Hawk with probability 1 in either role, which we denote by $(1, 1)$) and Bourgeois (play Hawk with probability 1 if owner and with probability 0 if intruder, denoted by (1,0)) individuals, which has contested some territories for some time, with repeated fights (see [3], p.150). After a contest, the winner of a Hawk-Dove contest will be an owner, and the loser will be an intruder. If the proportion of Hawks is q, then if $q > 0.5$ then all Bourgeois will be intruders, and similarly if $q < 0.5$ all Hawks will be owners. The role probabilities are thus

$$\rho\big((1,1),q\big) = \begin{cases} 1, & q < 0.5; \\ \frac{0.5}{q}, & q > 0.5 \end{cases} \tag{38}$$

$$\rho\big((1,0),q\big) = \begin{cases} \frac{0.5-q}{1-q} & q < 0.5; \\ 0, & q > 0.5 \end{cases} \tag{39}$$

When $q > 0.5$ the conditional probability of facing a Hawk when in role 1 is $(q - 0.5)/0.5$ (and we can similarly find other conditional probabilities) and so we have the following payoffs, see [3, p.150],

$$\mathcal{E}\big[(1,1);\Pi\big] = \frac{0.5}{q}\left(\frac{V-C}{2}\frac{q-0.5}{0.5} + V\frac{1-q}{0.5}\right) + \left(1 - \frac{0.5}{q}\right)\frac{V-C}{2} \tag{40}$$

$$= \frac{V-C}{2} + \frac{1-q}{q}\frac{V+C}{2}, \tag{41}$$

$$\mathcal{E}\big[(1,0);\Pi\big] = 0. \tag{42}$$

It is shown in [3, Sect. 8.3] that there is a unique ESS for $V < C$ at $q = (V + C)/(2C)$. Note that this mixed ESS can occur because the assumptions of Selten's Theorem 1 are violated, because we do not have strategy-role independence. Clearly we do have polymorphic–monomorphic equivalence within roles, but we do not have polymorphic–monomorphic equivalence since the role probabilities of playing against a population comprising of half Hawks and half Bourgeois are clearly different from playing against a population of the monomorphic equivalent strategy $(1, 0.5)$. This game is thus of type **SR N, PM N, PMR Y**.

Example 3 Now consider a game with two pure strategies available in each role, where the payoffs are governed by the variance of the population strategy within each role. Specifically,

Table 1 The abbreviations SR, PM and PMR refer to the properties of strategy-role independence, polymorphic–monomorphic equivalence and polymorphic–monomorphic equivalence within roles, respectively

SR	PM	PMR	Possible combination
Y	Y	Y	Yes (Example 1)
Y	Y	N	No (Theorem 2)
Y	N	Y	No (Theorem 3)
Y	N	N	Yes (Example 3a)
N	Y	Y	Yes (Example 4)
N	Y	N	No (Theorem 2)
N	N	Y	Yes (Example 2)
N	N	N	Yes (Example 3b)

Games may or may not have any of these three properties, giving eight potential combinations. The table shows whether or not each of these combinations is actually possible or not, and indicates the result which demonstrates this in each case

we assume that:

$$\mathcal{E}_1\left[\mathbf{p}_1; \sum_i \beta_{i2}\delta_{q_{i2}}\right] = \sum_i \beta_{i2}(q_{i2} - \bar{q_2})^2, \tag{43}$$

$$\mathcal{E}_1\left[\mathbf{p}_2; \sum_i \beta_{i1}\delta_{q_{i1}}\right] = \sum_i \beta_{i1}(q_{i1} - \bar{q_1})^2, \tag{44}$$

where q_{ij} is the probability of the ith type playing pure strategy 1 in role j, and $\bar{q_j} = \sum \beta_{ij} q_{ij}$. A potential scenario is if strategies represent genes with each role corresponding to a different locus, so that one set of genes contributes to fitness on some occasions, and the other contributing on the other occasions. Fisher's Fundamental Theorem of Natural Selection [7] states that the increase in fitness of an organism is proportional to its genetic variance, and in our population fitness can similarly depend upon the variance of the terms in each role.

Clearly all monomorphic populations yield a payoff of zero, and all polymorphic ones yield positive payoffs. Thus there is neither polymorphic–monomorphic equivalence nor polymorphic–monomorphic equivalence within roles. We can select the role probabilities as we like; in particular choosing them either to be always 1/2, or to be (suitable) functions of the strategies $\mathbf{p}_1$ and $\mathbf{p}_2$. Thus from this example we can have either **SR Y, PM N, PMR N** (role probability always equal to 1/2, Example 3a) or **SR N, PM N, PMR N** (role probabilities vary, Example 3b).

For a population to satisfy polymorphic–monomorphic equivalence but not strategy-role independence we require that the probability of playing in role 1 depends on the population strategy only through the mean values $\mathbf{q}_1 = \sum_i \alpha_i \mathbf{q}_{i1}$ and $\mathbf{q}_2 = \sum_i \alpha_i \mathbf{q}_{i2}$. Thus the role probabilities in any polymorphic population are the same as the equivalent monomorphic one, so they only depend upon the population through the mean, and can be written in the form $\rho_1\big((\mathbf{p}_1, \mathbf{p}_2), (\mathbf{q}_1, \mathbf{q}_2)\big)$. Note that the means here written as $\mathbf{q}_j$ are different in form to the earlier ones in Example 3. They are unconditional mean strategies, as opposed to those above in Example 3 which are conditional on individuals being in a particular role.

Example 4 Consider a population where there are only two pure strategies within each role, and p_1 and p_2 are the probabilities of choosing strategy 1 in role 1 and role 2, respectively. Assume that the role probabilities depend only upon the mean strategies as above, and are given by

$$\rho_1\big((\mathbf{p}_1, \mathbf{p}_2), (\mathbf{q}_1, \mathbf{q}_2)\big) = \frac{2 + (p_1 - q_1) - (p_2 - q_2)}{4}. \tag{45}$$

It should be noted that the expected value of ρ_1 over any population is 1/2, which is necessary for the function defined in (45) to be allowable (i.e. that it is possible to construct a game with these role probabilities). Further note that, by (13),

$$\begin{aligned}\beta_{i1} &= \frac{\alpha_i\big(2 + (q_{i1} - q_1) - (q_{i2} - q_2)\big)/4}{\sum_j \alpha_j\big(2 + (q_{j1} - q_1) - (q_{j2} - q_2)\big)/4} \\ &= \alpha_i \frac{2 + (q_{i1} - q_1) - (q_{i2} - q_2)}{2}.\end{aligned} \tag{46}$$

Similarly we obtain

$$\beta_{i2} = \alpha_i \frac{2 + (q_{i2} - q_2) - (q_{i1} - q_1)}{2}. \tag{47}$$

We shall define the payoffs to a p_i-player in role i to simply be $p_i q_{3-i}$, which gives

$$\begin{aligned}&\mathcal{E}\left[(\mathbf{p}_1, \mathbf{p}_2); \sum_i \alpha_i \delta_{(\mathbf{q}_{i1}, \mathbf{q}_{i2})}\right] \\ &= p_1 q_2 \frac{2 + (p_1 - q_1) - (p_2 - q_2)}{4} + p_2 q_1 \frac{2 - (p_1 - q_1) + (p_2 - q_2)}{4}.\end{aligned} \tag{48}$$

The population satisfies polymorphic–monomorphic equivalence (and thus polymorphic–monomorphic equivalence within roles) but not strategy-role independence. Thus we have **SR N, PM Y, PMR Y**.

5 Distinct Classes of Individuals

There are many ways that individuals can be different, such as size, age, sex and so on. This might affect either the payoff that an individual receives within a particular role, its probability of occupying that role or both. Thus, assuming that there are m classes of individuals, in Equation (6) the payoff to an individual of class k in role 1 or 2 can be denoted by $\mathcal{E}_{1k}\left[\mathbf{p}_1; \Pi_2\right]$ and $\mathcal{E}_{2k}\left[\mathbf{p}_2; \Pi_1\right]$, respectively, and the probability of that individual occupying role i in contests against an individual of class l can be denoted by $\rho_{ikl}\big((\mathbf{p}_1, \mathbf{p}_2), \Pi\big)$. Naturally, $\rho_{2kl}\big((\mathbf{p}_1, \mathbf{p}_2), \Pi\big) = 1 - \rho_{1kl}\big((\mathbf{p}_1, \mathbf{p}_2), \Pi\big)$ for all k, l.

In this section we consider only differences in the role probability, assuming that

$$\mathcal{E}_{1kl}[\mathbf{p}_1; \Pi_2] = \mathcal{E}_{1k'l'}[\mathbf{p}_1; \Pi_2], \tag{49}$$

for all k, l and k', l' and all $\mathbf{p}_1$ and Π_2 (and similarly for role 2), and look at a small number of ways in which this difference in role probability can affect our results.

Considering polymorphic–monomorphic equivalences of different types (and there may be extra different possibilities now we have more than one class, for instance depending upon whether different classes among the opposing population are considered distinct or not) is a more complex problem which we shall not discuss here. We define the payoff to an individual in class k by

$$\mathcal{E}_{(k)}\left[(\mathbf{p}_1,\mathbf{p}_2);\Pi\right]=\sum_l \rho_{1kl}\big((\mathbf{p}_1,\mathbf{p}_2),\Pi\big)\mathcal{E}_{1kl}[\mathbf{p}_1;\Pi_2]+\rho_{2kl}\big((\mathbf{p}_1,\mathbf{p}_2),\Pi\big)\mathcal{E}_{2kl}[\mathbf{p}_2;\Pi_1]. \quad (50)$$

There are cases where individual classes and roles are equivalent, so that for instance all games involve one male and one female, and there is a male role and a female role in such a game. Recall from Sect. 1 that the dynamic version of bi-matrix games is such a case. Denoting females as class 1 and males as class 2, then role probabilities are independent of strategy and population. We can thus write $\rho_{ikl}\big((\mathbf{p}_1,\mathbf{p}_2),\Pi\big)$ simply as ρ_{ikl} and we have $\rho_{112}=1$ and $\rho_{121}=0$. Technically we do not need to define ρ_{111} and ρ_{122} here, as individuals never face another of the same type (although the only logical choice in such a case for the probabilities would be 1/2).

We can now extend the independence concepts introduced in Sect. 2.2 to the case where there is more than one class of individuals.

Definition 8 We say that a game is *strategy-role independent* if the function $\rho_{1kl}\big((\mathbf{p}_1,\mathbf{p}_2),\Pi\big)$, and so $\rho_{2kl}\big((\mathbf{p}_1,\mathbf{p}_2),\Pi\big)$, does not depend on an individual's strategy $(\mathbf{p}_1,\mathbf{p}_2)$, for all classes k,l.

Definition 9 We say that a game is *population-role independent* if $\rho_{1kl}\big((\mathbf{p}_1,\mathbf{p}_2),\Pi\big)=\rho_{1kl}\big((\mathbf{p}_1,\mathbf{p}_2),\Pi'\big)$ for all classes k,l and all populations Π and Π' that have the same distribution of individuals over the classes.

Example 5 Consider an Owner-Intruder game with two classes of individuals, old and young. After each contest, the old individuals do not move so widely about the habitat as the young ones, and in any contest between an old and a young individual, there is a probability $\rho>0.5$ that the old individual takes the role of the owner. This yields the probabilities $\rho_{111}=\rho_{122}=1/2$, $\rho_{112}=\rho$, $\rho_{121}=1-\rho$ where ρ_{ikl} stands for a probability of a class k individual in role $i\in\{1,2\}$ in a contest against a class l individual in role $3-i$ ($k,l=1$ for an old individual, $k,l=2$ for a young individual). Thus, we have a game that is strategy-role and population-role independent (but with ρ not equal to 0, 1/2 or 1).

Recall that for one class of individual, the two concepts of strategy-role independence and population-role independence are identical. For two or more roles this is not true, as we see from the following example.

Example 6 Consider a population consisting of large individuals (class 1) and small individuals (class 2). Each picks a foraging time fraction, which we shall denote by L and S, respectively. We shall consider a focal large individual with strategy denoted by l in a population playing L, similarly a focal small individual with strategy s in a population playing S. When not foraging, for the remainder of the time they rest. Large individuals find objects at rate $f_L(d)$, small ones $f_S(d)$, where $d(L,S)$ is the food density, which decreases with the population choices L and S. It may, for example, be that $f_S(d)>f_L(d)$ but $f_S(d)/f_L(d)$ decreases with d. For simplicity we shall assume that switching between periods of search and rest are sufficiently fast that we can effectively consider search as following a Markov process with rate given by the product of their search rate and search probability. When an object is found, a random searching individual (i.e. one not resting) contests the resource with probability p, taking the role of Challenger versus an Owner.

Assume that there are N_L large individuals, and N_S small ones. We track one large focal individual using strategy l and would like to see how often it interacts with a small individual (and in which role). First, we determine what kind of Owner-Intruder contest the next one will be. There are SN_S searching small individuals, each using strategy S, $L(N_L - 1)$ searching large individuals each using strategy L and one focal large individual using strategy l. The rate at which these types discover food are $SN_S f_S(d)$, $L(N_L - 1) f_L(d)$ and $l f_L(d)$. Thus, the focal individual will be the next to discover the object (and become an owner) with probability

$$\frac{l f_L(d)}{SN_S f_S(d) + L(N_L - 1) f_L(d) + l f_L(d)}.$$

The probability that the randomly drawn opponent (from the ones that are searching) it will face is a small individual is

$$\frac{SN_S}{SN_S + L(N_L - 1)}.$$

Thus, the probability that the next contest will be l as an owner versus S as an intruder is

$$p_{lS} = \frac{l f_L(d)}{SN_S f_S(d) + L(N_L - 1) f_L(d) + l f_L(d)} \cdot \frac{SN_S}{SN_S + L(N_L - 1)}. \tag{51}$$

Similarly, a small individual will be the next to discover the object and become an owner with probability

$$\frac{SN_S f_S(d)}{SN_S f_S(d) + L(N_L - 1) f_L(d) + l f_L(d)}.$$

The probability that the randomly drawn opponent (from the ones that are searching) it will face is a focal large individual is

$$\frac{l}{S(N_S - 1) + L(N_L - 1) + l}.$$

Thus, the probability that the next contest will be S as an owner versus l as an intruder is

$$p_{Sl} = \frac{SN_S f_S(d)}{SN_S f_S(d) + L(N_L - 1) f_L(d) + l f_L(d)} \cdot \frac{l}{S(N_S - 1) + L(N_L - 1) + l}. \tag{52}$$

Since our process is Markov, we clearly have

$$\rho_{112}(l) = \frac{p_{lS}}{p_{lS} + p_{Sl}}. \tag{53}$$

Thus, when we fix the ratio N_L/N_S and send both N_L and N_S to ∞, we get

$$\rho_{112}(l) = \frac{1}{1 + \frac{f_S(d)}{f_L(d)}}. \tag{54}$$

Similarly we get $\rho_{121}(s) = 1/\left(1 + f_L(d)/f_S(d)\right)$ and $\rho_{111}(l) = 1/2$, $\rho_{122}(s) = 1/2$. Thus, the role probability does not depend on l or s but does depend on the population (through $d = d(L, S)$).

However we do have the following result, which implies that population-role independence is a stronger concept than strategy-role independence.

Theorem 4 *If a game in a population with more than one class is population-role independent, then it is also strategy-role independent.*

Proof We shall focus on the interaction between an individual in class k and one in class l. Let $\mathbf{p}(k)$ and $\mathbf{p}'(k)$ be two alternative strategies of a focal player in class k. Consider a population Π and let M_{kl} denote a population which has the same distribution of individuals over the classes as Π, and such that individuals in classes k and l are monomorphic $\delta_{\mathbf{p}(k)}$ and $\delta_{\mathbf{p}(l)}$. Let $M_{k'l}$ denote a population where individuals in class k are monomorphic $\delta_{\mathbf{p}'(k)}$ and in class l they are monomorphic $\delta_{\mathbf{p}(l)}$.

Note that

$$\rho_{1kl}\big(\mathbf{p}(k), M_{kl}\big) + \rho_{1lk}\big(\mathbf{p}(l), M_{kl}\big) = 1, \tag{55}$$

$$\rho_{1kl}\big(\mathbf{p}'(k), M_{k'l}\big) + \rho_{1lk}\big(\mathbf{p}(l), M_{k'l}\big) = 1, \tag{56}$$

because the populations are monomorphic in classes k and l, and for contests between class k and class l individuals precisely one of the individuals has to be in role 1.

Assume that the game is population-role independent. Thus,

$$\rho_{1kl}\big(\mathbf{p}(k), \Pi\big) = \rho_{1kl}\big(\mathbf{p}(k), M_{kl}\big) = 1 - \rho_{1lk}\big(\mathbf{p}(l), M_{kl}\big) \tag{57}$$

$$= 1 - \rho_{1lk}\big(\mathbf{p}(l), M_{k'l}\big) = \rho_{1kl}\big(\mathbf{p}'(k), M_{k'l}\big) \tag{58}$$

$$= \rho_{1kl}\big(\mathbf{p}'(k), \Pi\big), \tag{59}$$

and hence the game is strategy-role independent. □

In this section we have thus seen just a few ways in which populations with different classes of individuals can make analysis more complex, and where the kind of simplifications we are used to use do not always hold. This is, of course, only the briefest of explorations of this area.

6 Discussion

In this paper we have investigated asymmetric games, and the consequences of departures from the classical bi-matrix game format. We are particularly interested in the effects of there being a correlation between an individual occupying a particular role, and the strategies that they play when in that role. This seems likely to happen in many real scenarios, such as the Owner-Intruder example (Example 2) that we discuss. We have seen that, naturally, this significantly complicates analysis.

Using three concepts, strategy-role independence, polymorphic–monomorphic equivalence and polymorphic–monomorphic equivalence within roles, we have investigated general populations of individuals which are identical (except possibly in their strategies). Classical games generally satisfy all three properties, and we have considered all eight combinations of the presence or absence of the property in a population. We have shown that polymorphic–monomorphic equivalence is stronger than polymorphic–monomorphic equivalence within roles. It is not stronger than strategy-role independence, as we see in Example 4. We have shown that in general populations can satisfy only five of the eight possible combinations, giving examples of each type.

We note that the payoff functions of our examples (in particular that from Example 4) are in some cases very different from the kind that we have so far seen in mainstream evolutionary games, and so perhaps although we have shown that these are theoretically possible, the relationship with real populations is still open. The concepts that we discuss here will be relevant to investigate real populations, and developing more realistic models. For instance, Kokko and Johnston [11] discuss the concept of the operational sex ratio (the ratio of the number of males searching for mates to the number of females searching for mates), which is effectively the sex ratio when mating occurs, as opposed to the adult sex ratio in the population (the ratio of the number of adult males to the number of adult females). This concept is of relevance precisely when the usual assumptions of independent contests proportional to population frequency break down, and is closely linked to that of polymorphic–monomorphic equivalence.

Finally, populations are not composed of identical individuals, and this will have consequences for analysis. Potentially all individuals could be different, but the simplest case is clearly two different classes of individuals, and we have briefly looked into this in Sect. 5. Examples are large and small individuals, or males and females. In fact, the classical replicator dynamics considers two distinct classes, which each correspond to a role (so in our terminology would have ρ values of 1 and 0, respectively). We have seen that a fourth concept of population role independence (which we show is weaker than strategy-role independence) is useful, and using examples we see some new phenomena which cannot occur for the single class population.

Finally, the investigation of the concepts that we have introduced in this paper, in particular in the case of multiple types, has only just started. It would be of particular interest to see how often real populations fail the standard assumptions of evolutionary game theory, and how they can be related to the concepts that we discuss here.

Acknowledgments The research was supported by Simons Foundation grant 245400. We would also like to thank the reviewers whose comments helped to improve the clarity of the manuscript. This paper was handled by the Editor-in-Chief.

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