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ESS versus Nash: solving evolutionary games

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ABSTRACT

Question: Can a Nash solution concept be used for the analysis of evolutionary games? What are the advantages of ESS solutions over Nash solutions in evolutionary games?

Mathematical methods: ESS and Nash equilibrium solution concepts and Darwinian dynamics for evolutionary games.

Conclusions: An ESS contains the properties of Nash but not the other way around. The properties of evolutionary games make them fit poorly with the classical notion of a Nash solution. These properties include six key differences between the ESS and Nash concepts: (1) in the evolutionary game, players inherit rather than choose their strategies; (2) the focus of evolutionary games is on the strategies and not on the actual players who come and go via births and deaths; (3) the payoffs in the evolutionary game represent fitness, creating a dynamical link between payoffs and changes in the frequency of strategies; (4) in state-dependent games, players in a classical game may possess forethought and anticipate the consequences of their actions, whereas in the evolutionary game organisms do not; (5) unlike classical games, the actual number of players in the game can expand and contract via changes in population sizes; and (6) evolutionary games have a particular kind of symmetry where collections of individuals may have different strategies, yet their strategies all arise from the same set of evolutionarily feasible strategies (pure or mixed) and each experiences the same fitness consequence of possessing a particular strategy. For these reasons, we argue that the use of Nash as a solution concept in evolutionary games will be misleading, and that the ESS deserves primacy over Nash as the solution concept for evolutionary games.

Keywords: Nash equilibrium, ESS, Darwinian dynamics.

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INTRODUCTION

The Nash solution of classical games has the property of being a ‘no-regret’ strategy. If all players are using their Nash solution, then no player can benefit by unilaterally changing its strategy. The evolutionarily stable strategy (ESS) concept from evolutionary game theory has Nash-like properties. For instance, a population of individuals playing a particular strategy would be invadable (not ESS) if any individual could benefit by unilaterally changing its strategy. In contrast, a Nash solution is not necessarily ESS because an ESS places additional requirements on the game and on the solution. For example, evolutionary games recognize underlying dynamics of strategy frequencies, population sizes, or both, whereas Nash solutions focus on the players rather than their strategies. Evolutionary game theory has evolved dramatically from its roots in 1973 to its present sophistication, which includes adaptive dynamics, evolutionary branching, and strategies that can be continuous, as well as scalar and/or vector-valued. During this theoretical development, the ESS began distinct from Nash, but almost immediately the Nash solution entered as a substitute solution for the ESS in continuous games (Auslander *et al.*, 1978; Mirmirani and Oster, 1978). Today, some authors prefer an ESS solution while others refer to the solutions of evolutionary games as strict Nash (Cressman, 2010; Nowak, 2006, p. 55).

Here, our objective is to evaluate some of this development of terminology and concepts, and suggest a path forward. We detail the properties of evolutionary games that do not make them fit well with the classical notion of a Nash solution. These include six key differences between the ESS and Nash, and their contexts as given in the abstract. There are numerous minor differences that will become apparent, but these six major differences represent the key reasons for our comparison of Nash and ESS (Table 1). We will explain how an ESS, once achieved, contains the properties of Nash, but not the other way around. We hope to show the roles of Nash and ESS in evolutionary game theory, clarify ambiguities that have and can arise, and urge that the ESS should be given primacy over Nash as the solution concept for evolutionary games.

In what follows, we consider both the Nash and ESS solutions for games along the continuum from classical games with no inherent dynamics to evolutionary games with population and strategy dynamics in three ways. First, we begin with a simple two-player

Table 1. The major differences between a Nash equilibrium and an evolutionarily stable strategy, both of which seek to find a ‘no regret strategy’, but the way this is achieved is fundamentally different

Point	Nash equilibrium	Evolutionarily stable strategy
1	Fixed number of players	Number of players changes due to population dynamics
2	Fixed frequency of strategies	Frequency of strategies changes due to population dynamics
3	Players choose strategies rationally, and may switch strategies	Players inherit strategies and may not switch
4	Payoff can be anything of value	Payoff is always fitness
5	Players use forethought for how changing their strategy might change the state variable, and react accordingly	Players have no forethought on state variable change
6	Players are the focus	Heritable strategies are the focus

matrix game, and then move on to the players, strategies, and outcomes of an arbitrary n-player game characterizing the Nash solution for this game. Second, we introduce state variables that can either represent the states of individual players (e.g. hunger, reproductive status) or some state shared by all of the players (e.g. resource availability, population density) (de Roos and Persson, 2013). These states have a dynamic and therefore they change with time, and the state variables influence the payoffs, and even the Nash equilibrium. Finally, we turn this game into an evolutionary game by letting the state variables represent the population sizes or densities of a biological species or of a population of players distinct from other populations of players. With this change, payoffs become fitness defined as the per capita growth rates of the populations. Strategies are inherited from parents within the population, leading to strategy dynamics as well. When considered collectively, each species' payoff function represents 'group fitness' and can be solved for the group optimum. However, in the guise of a fitness-generating function (or 'invasion fitness' function), each individual can be the unit of selection distinct from any population level objective. We will introduce the *G*-function as a formal representation of an evolutionary game (Vincent and Brown, 2005). The *G*-function is the per capita growth rate of individuals possessing a particular strategy in an environment defined by some resident strategies. It permits a seamless consideration of the ecological and evolutionary dynamics of each species or population. The outcome of such a game can have one of several properties, including ESS, convergence stability, and neighbourhood invader strategy (NIS) (Maynard Smith and Price, 1973; Eshel and Motro, 1981; Christiansen, 1991; Apaloo, 1997; Apaloo *et al.*, 2009).

Throughout the following comparisons of the Nash and ESS solutions and concepts, we use example models. These models have been constructed to illustrate the points, and do not necessarily reflect specific scenarios of direct biological relevance. That said, they have been selected to contain the properties of the most common types of evolutionary games (i.e. matrix games and population dynamic games), and therefore the principles and issues demonstrated will apply to all models that share the properties of the models presented herein.

1951 NASH vs. 1973 ESS

In 1951, Nash wrote his seminal paper, giving rise to the solution concept that bears his name. Game theory was advancing beyond the max–min solutions favoured for zero-sum games and was, in fact, moving beyond zero-sum games altogether (Nash, 1951). For two-player, symmetric, zero-sum games, the max–min had both rigorous and intuitive appeal. One player's loss was another player's gain. Placing a floor on one's losses, and by default placing a ceiling on an opponent's takings, resulted in a strategy that gave the highest payoff given the circumstances – that is, where each opponent was trying to do the same to the other. The elegance and logic of a max–min solution begins to break down and does not apply to many n-player games and non-zero-sum games. Nash developed both a formalism and intuition for a 'no regret strategy' as a solution concept for n-player games (Nash, 1951).

The idea is compelling but not immediately obvious. To do its best, a player must select a strategy that maximizes its payoff given the strategies in use by the other $n - 1$ players. At such a strategy, the player can do no better by changing its strategy. The player's payoffs might improve dramatically if it could change the strategies of others, but it does not control these and must be content to manipulate its own strategy within the context of others. Hence we see the player's dilemma as one of evaluating the consequences of unilaterally changing its strategy in response to the strategies of others and the rules of the game. These consequences could involve strategy changes by opponents, or changes in state variables. All players face the same dilemma save for their vantage point of identifying who is self and who are opponents: if I see myself as the focal individual, but another sees me as an opponent, and vice versa. A Nash equilibrium, then, can be thought of as a point in n-dimensional strategy space where each dimension represents the strategy choices of a given individual and where each individual maximizes its payoffs given the strategies of others. No individual can gain from unilaterally changing its strategy, and hence no individual at that point regrets its choice. In a manner similar to the notation in Nash (1951), let $\mathbf{u}^* = (u_1^*, \ldots, u_n^*)$ and $\mathbf{u}^*_{-i} = (u_1^*, \ldots, u_{i-1}^*, u_i, u_{i+1}^*, \ldots, u_n^*)$ is the vector where all players but player i are using their Nash solution. Let H_i be the payoff function to the ith player using u_i, which is drawn from some set of feasible choices denoted by U. The focal strategy $\mathbf{u}^*$ is a Nash solution if and only if for all players $i = 1, \ldots, n$:

$$H_i(\mathbf{u}^*) \geq H_i(\mathbf{u}^*_{-i}) \text{ for all } u_i \tag{1}$$

So at $\mathbf{u}^*$ each player is doing the best it can, given the choices of others.

We can examine a Nash equilibrium for a two-player, two-strategy matrix game. A simple two-player, two-strategy symmetric game given by matrix M might look like:

$$M = \begin{array}{c} \\ \text{A} \\ \text{B} \end{array} \begin{array}{c} \begin{array}{cc} \text{A} & \text{B} \end{array} \\ \begin{bmatrix} 0 & 2 \\ 6 & 1 \end{bmatrix} \end{array} \tag{2}$$

where the rows represent the strategy choice of the focal individual and the columns represent the strategy choice of the opponent. A strategy, u_i, can be defined as the probability of playing one or the other strategy. That is, if a player always plays ‘A’, then $u_i = 1$ is the pure strategy. If a player always plays ‘B’, then $u_i = 0$ is the pure strategy. If a player has a propensity to play A with probability u_i (and B with probability $1 - u_i$), then $0 < u_i < 1$ is the mixed strategy. As a symmetric game, each player has the same choice of strategies and experiences the same payoffs from playing a particular strategy against a particular opponent’s strategy. The only difference between the players is that when player 1 is the focal individual, player 2’s strategy appears on the columns of the matrix, and vice-versa when player 2 is the focal individual. The story can look quite different depending upon whose eyes you are looking through. Let $\mathbf{p}_i$ be the vector $(u_i, 1 - u_i)$, $\mathbf{p}_j$ be the vector $(u_j, 1 - u_j)$, and $i, j = 1, 2$. The payoff function to an individual in matrix notation is as follows:

$$H_i(\mathbf{p}_i) = \mathbf{p}_i M \mathbf{p}_{j \neq i} \tag{3}$$

For such a two-player matrix game, the Nash equilibrium (u_1^*, u_2^*) requires the following:

$$\mathbf{p}_1^* M \mathbf{p}_2^* \geq \mathbf{p}_1 M \mathbf{p}_2^* \text{ and } \mathbf{p}_2^* M \mathbf{p}_1^* \geq \mathbf{p}_2 M \mathbf{p}_1^* \tag{4}$$

The game with the payoff matrix defined in equation (2) has three distinct Nash equilibria (see Appendix A for further details). The first is that player 1 always plays A and player 2 always plays B: $u_1^* = 1$ and $u_2^* = 0$. If player 1 plays A and player 2 plays B, neither can benefit from unilaterally changing their strategy, even though player 1 comes up short relative to player 2. The second equilibrium is the reverse of the first: $u_1^* = 0$ and $u_2^* = 1$. At the third Nash solution, the players might sometimes play A and sometimes play B with frequency $u_1^* = u_2^* = \frac{1}{7}$. The first two solutions are strict Nash equilibria in the pure strategy domain. The third solution, which is a mixed strategy, is not a strict Nash equilibrium. Indeed, no mixed strategy can be a strict Nash equilibrium (Weibull, 1997, p. 15).

Next we ask: how does the solution to this game differ from Nash when applying Maynard Smith and Price's (1973) ESS concept? An ESS is a strategy (or mix of strategies) that cannot be invaded by rare alternative strategies. Note that the emphasis is now on payoffs to strategies rather than payoffs to particular players. This subtle difference will become important in seeing how an ESS may be Nash, but not vice-versa, and in identifying the first feature of evolutionary game theory that does not have any precedent within the Nash solution. Keeping the notation defined above, for a strategy $\mathbf{p}^* = (u^*, 1 - u^*)$ and $\mathbf{p} = (u, 1 - u)$ in a two-player symmetric matrix game to be an ESS:

$$\mathbf{p}^* M \mathbf{p}^* \geq \mathbf{p} M \mathbf{p}^* \qquad (5)$$

and if:

$$\mathbf{p}^* M \mathbf{p}^* = \mathbf{p} M \mathbf{p}^*, \text{ then } \mathbf{p}^* M \mathbf{p} > \mathbf{p} M \mathbf{p} \text{ for all } \mathbf{p} \neq \mathbf{p}^* \qquad (6)$$

It is clear that $\mathbf{p}^*$ is a 'no regret' strategy like the Nash equilibrium strategy, but only in the sense that a rare mutant strategy playing against the ESS will not do better than the ESS playing against itself. Thus, to be ESS, the ESS must be the best response to alternative strategies ($\mathbf{p}$) and also to 'self' strategies ($\mathbf{p}^*$) (Conditions 5 and 6) – a key departure from Nash where one plays against opponents ($\mathbf{p}_j$) but not against oneself ($\mathbf{p}_i$) (Condition 4). This key departure can be seen as the comparison of self strategies ($\mathbf{p}_i^*$) in Nash, versus the comparison of population-wide strategies ($\mathbf{p}^*$) in ESS. This works the other way around as well – that is, if a non-ESS strategy ($\mathbf{p}$) does as well against the ESS ($\mathbf{p}^*$) as the ESS does against itself, then the ESS playing against that non-ESS strategy must do better than that non-ESS playing against itself. This special kind of symmetry ($\mathbf{p}$ is not ascribed to a particular player) that we have alluded to is one key difference between Nash and ESS.

While there are three distinct Nash equilibria in this game, there is only one ESS. Indeed, by the requirements for an ESS, we observe that in this matrix game the strict Nash solutions of $u_1^* = 1$ and $u_2^* = 0$ or $u_1^* = 0$ and $u_2^* = 1$ are not ESS. For instance, at the Nash solution $u_1^* = 1$ and $u_2^* = 0$, player 1 receives a payoff of 2 and player 2 receives 6. While player 1 is doing worse, neither player gains by unilaterally changing their strategy. Player 1's payoff would drop to 1 with a shift in strategy; and player 2's would drop to 0. So, while this is a Nash solution for the two players in this game, it cannot be a solution to the evolutionary game, where the focus is on the payoffs to strategies and not the payoffs to players. With this contest of A played against B, the strategies do not have equal payoffs as required by the ESS. Hence the Nash solution of $u_1^* = u_2^* = u^* = \frac{1}{7}$ is both Nash and ESS. In this case, the ESS places stricter conditions than the Nash solution. This arises because of the requirement that players within a population must play against both individuals using a genetically identical strategy and individuals playing the genetically different alternative strategy, while players in a classical game do not play against self, and must only play against others.

The nature of the evolutionary game relative to classic game theory necessitated the new solution concept of the ESS. In classical game theory, the focus is on the players; they choose their strategies, their payoffs need not be equal at a solution, and payoffs can take many forms in terms of money, fame, utility, etc. In classic game theory, the solution is achieved by assuming that the players act rationally. In that way, the solution is arrived at via teleology – the solution is 'designed' through intent and forethought.

In the evolutionary game, the focus is on the strategies. Players come and go through births and deaths, but strategies are the genes that persist through time (Dawkins, 1976). Individual organisms are the players and they inherit rather than choose their strategies. Payoffs are ultimately in the form of fitness, the per capita growth rate of a population using a particular strategy. This feedback of payoffs to strategies in one 'generation' of the game and the frequency of these strategies in the next generation is what places stricter requirements on the outcome of the evolutionary game. Furthermore, there is a special kind of symmetry to the game by which individuals within a population or species share the same set of evolutionarily feasible strategies and the same fitness consequences of playing any particular strategy. Brown and Vincent (1987) refer to these individuals as 'evolutionarily identical', even if not identical in terms of current extant strategies. Evolutionarily identical individuals of a population or species using the same strategy will have the same expected payoffs, and play against each other as well as individuals within the population playing different strategies. This is a key departure from classical games and, as we showed above, is a key place where the conditions required to solve for ESS become more restrictive than Nash solutions. Finally, the 'design' of the solution is via a teleonomic process – that is, it occurs through trial and error. The utility and function of an adaptation fashioned by means of the ESS does not arise by forethought or intent, but rather by the consequences of a kind of 'creative destruction' where many more individuals are born to a population or species than can possibly survive and reproduce. Heritable variation and the struggle for existence collude to result in natural selection.

In the evolutionary game, strategies with higher fitness will increase in frequency relative to those with lower fitness. For this reason, all of the strategies of the ESS must have the same fitness or payoff. No such requirement is imposed on the Nash equilibrium of classical game theory. The Nash equilibrium was neither formulated for or even anticipated the evolutionary game. We see this as **Reason #1** for seeing the ESS as an appropriate solution concept for evolutionary game theory, and not the Nash equilibrium.

STATE-DEPENDENT NASH EQUILIBRIUM vs. ESS

We have a superficial resemblance between the game played by a fixed number of rational players (generally seen as humans or human institutions) and a game where individuals are part of larger populations of individuals (generally viewed ecologically as populations of individuals of one or more species). Both these classical and evolutionary formulations have the same payoff function, but the contexts of the games are actually quite different. In the classical form, the n players come together, choose their strategies, and receive their payoffs for a given state. The intuition behind the Nash solution is that each player within this context evaluates the consequences of unilaterally changing its strategy. In the evolutionary game context, an individual is part of a larger population and views itself as playing a game against this 'field' (Maynard Smith, 1982, p. 23) even if the actual play involves just n players pulled randomly from this population. The state variable represents a property of the environment that ultimately gets determined by this collective population of individuals, not by any given individual player as in the classical context for the Nash solution.

The intuition behind the ESS is that no rare mutant can invade. Such a rare mutant will not have a substantive effect on the state variable until it increases in frequency within the population. For the classical interpretation of the state-dependent game, it is possible to get the Nash solution to converge on the ESS by assuming the players do not know about the state variable, choose to ignore the externalities of their actions, or there is a sufficient time-lag between action and consequence that the players discount their future. (The social and economic games played by humans that are generating global climate change have all of these properties, making humans behave in a more teleonomic rather than teleologic fashion.) Similarly, for the evolutionary interpretation of this game, it is possible to get convergence of the ESS on the Nash solution by assuming that this is a social game where the animals perhaps intentionally engineer their environment via the state variable. With care and a skilful eye for the nuances between classical and evolutionary games, a modeller may be able to preserve a Nash solution concept for finding the solution to evolutionary games. However, there seems little reason to, given the risk of conflating the two contexts, and the need to stretch the Nash concept beyond its most useful domain.

In the games envisioned by Nash, players come together, choose their strategies, and accept their payoffs. At that point, the game may end and the players go on. In the evolutionary game, payoffs are a hard currency. They influence the survival and reproduction of individuals in the population. Hence they induce changes in population sizes and strategy frequencies within populations. Population size can be defined as the number or density of individuals that use a particular strategy at a given time – an important feature of ecological communities. Individuals come and go via births and deaths, but their strategies either live on or go extinct via inheritance and changes in population size, and new strategies may even take their place via mutation or immigration. Thus, population size becomes an additional state variable that influences payoffs. In this section, we explore state-dependent Nash equilibria where the state may be any type of variable, and in the next section we consider the consequences resulting from a state representing population size.

Imagine n players each with their own payoff function. If each has the same payoff function, then the game is symmetric, otherwise each may have a different set of strategy choices and experience different payoffs even when choosing the same strategy. A player's payoff, H_i, is a function of its own strategy u_i, the strategies of other players ($u_1, \ldots, u_{i-1}, u_{i+1}, \ldots, u_n$), and the state variables, $\mathbf{y} = (y_1, \ldots, y_r)$. Note that here the number of state variables, r, can be greater than or less than the number of players, n. The Nash equilibrium is now a vector of strategies among the players, where each player cannot improve its payoff by unilaterally changing its strategy, given the strategies of others and the current state of the system, $\mathbf{y}$.

Thus far we have not specified how $\mathbf{y}$ occurs. It may be a fixed property of the players' world or a property of the game that is established in advance and remains in effect throughout the duration of the game. Conceivably, the state of the players' environment may change in accord with the players' choice of strategies. If we now include feedbacks where the players' strategies influence the state variables, we may model the dynamics of the state variables as follows:

$$\frac{dy_j}{dt} = F_j(\mathbf{u}, \mathbf{y}) \tag{7}$$

where both the players' strategies and the state variables influence the dynamics of any given state, y_j, $j = 1, \ldots, r$. For our purposes, we assume that the state variables converge on a stable equilibrium, $\mathbf{y}^*$, for any set of strategy values among the players, and this equilibrium may change with the strategies of the players. Hence $\mathbf{y}^*$ is a function of $\mathbf{u}$.

This now places additional restrictions on the Nash equilibrium. For $\mathbf{u}^*$ to be a Nash equilibrium:

$$H_i(\mathbf{u}^*, \mathbf{y}^*) \geq H_i(\mathbf{u}^*_{-i}, \mathbf{y}^*_{-i}), \text{ for each } i = 1, 2, \ldots, n \tag{8}$$

where $\mathbf{y}^*$ refers to the equilibrium state at $\mathbf{u}^*$ and $\mathbf{y}^*_{-i}$ refers to the equilibrium state at $\mathbf{u}^*_{-i}$.

The state-dependent Nash equilibrium introduces two new features. First, the Nash solution will be influenced by the state of the system. Because state influences payoffs, the game itself changes with state. Second, a player should anticipate its effect on the equilibrium state of the system from unilaterally changing its strategy. The state-dependent ESS requires that the population cannot be invaded by a rare alternative strategy. For this reason, the necessary condition for an ESS is as follows:

$$H_i(\mathbf{u}^*, \mathbf{y}^*) \geq H_i(\mathbf{u}^*_{-i}, \mathbf{y}^*), \text{ for each } i = 1, 2, \ldots, n \tag{9}$$

The difference between these two solution concepts may seem subtle but it is important and can be seen in the subscripts of the equilibrium value of state variable. For the Nash solution, the players anticipate the consequences of their strategy for changes in the state variable(s) and has players thinking about how each y^*_j will change with their choice of strategy, u_i. Players incorporate this knowledge into their payoff function H_i and choose strategies accordingly to maximize their payoff against other players' strategies and their and other players' effects on state. For the ESS, an individual is a rare mutant, and its potential for success does not anticipate the consequences for the state variable. The ESS still involves an interaction between u^* and y^* and their influences on each H_i, but the players simply live with rather than control the strategy-dependent changes in each y^*_j. In this sense, the logic behind a Nash equilibrium and an ESS is quite different. The Nash can include, in most cases, the concept of forethought – a Nash equilibrium is teleologic in the sense of 'design with forethought'. On the other hand, natural selection and the basis for the ESS concept is teleonomic and relies on 'design through trial and error'.

The state dependencies discussed above can permit a much broader spectrum of strategies for both classical and evolutionary games beyond awareness of the consequences of one's actions for one's environment. Such strategies may use past and present states, uncertainties in state (regularly or stochastically varying states), or inaccuracies in estimating state to determine the actual action taken by the player or organism. The heritable strategy now includes how information regarding state is processed. Strategies that are derived from information that is acquired and processed by an individual in its lifetime will manifest as phenotypic plasticity and/or real time tracking of environmental circumstances. Just like the 'static' state-dependent Nash and ESS solutions derived above are game theoretic, an information processing strategy may also become part of the solution to a classical or evolutionary game (e.g. Mangel, 1990; Eliassen *et al.*, 2007; Leimar and McNamara, 2015).

State-dependent Nash and ESS: a specific example

To illustrate the role of state dependencies in Nash and ESS solutions, we construct an example game with a continuous strategy. In this example, a player's own strategy influences its payoff according to a quadratic function, while the strategies of others interact in a bi-linear fashion. Such payoff functions may be obtained as an approximation to any continuous games with non-linear and differentiable (at least of order 2) payoff functions. Payoffs increase with the value of the state variable, which serves as the 'constant' of a second-order polynomial. This yields the following payoff functions for this n-player game:

$$H_i(\mathbf{u},y) = a_i u_i - b_i u_i^2 - c u_i \sum_{j=1, j\neq i}^{n} u_j + d_i y \qquad i = 1, \ldots, n \tag{10}$$

This model can be asymmetric or symmetric depending upon whether players share the same parameter values for a_i, b_i, c_i, and d_i. Now, let average payoffs determine changes in the state variable in such a way that increasing a player's strategy increases the growth rate of the state variable:

$$\dot{y} = K - \frac{gy}{\sum_{j=1}^{n} u_j^2} \tag{11}$$

This results in the equilibrium state:

$$y^* = \frac{K \sum_{j=1}^{n} u_j^2}{g} \tag{12}$$

For this game formulation, via the state variable a player provides a public good to the other players by increasing its strategy. The reason is as follows: when a player increases its strategy, there is a resulting increase in the value of the state variable (equation 12) which then results in higher fitness for all (equation 10).

The first-order necessary condition, which is required to hold at $\mathbf{u} = \mathbf{u}^*$ and $y = y^*$, for a Nash equilibrium in this game of n players is as follows:

$$\frac{\partial H_i}{\partial u_i} = a_i - 2b_i u_i - c \sum_{j=1, j\neq i}^{n} u_j + d_i \frac{\partial y}{\partial u_i} = 0 \qquad i = 1, \ldots, n \tag{13}$$

where

$$\frac{\partial y}{\partial u_i} = \frac{2Ku_i}{g} \tag{14}$$

whereas for the evolutionary game, the necessary condition for the ESS is simply thus:

$$\frac{\partial H_i}{\partial u_i} = a_i - 2b_i u_i - c \sum_{j=1, j\neq i}^{n} u_j \qquad i = 1, \ldots, n \tag{15}$$

Since the above game with payoff given in equation (10) is a symmetric game, we can seek a solution where each player uses the same strategy, u^*. We have two equations and two unknowns for evaluating the optimal strategy, u^*, and the equilibrium state, y^*. We can perform this for both the Nash solution and the ESS. The two are not the same, as Nash solutions explicitly involve the state variable, while ESS solutions do not. From Appendix B we have:

$$\text{Nash: } u^* = \frac{a}{2b + c(n-1) - \dfrac{2Kd}{g}} \tag{16}$$

$$\text{ESS: } u^* = \frac{a}{2b + c(n-1)} \tag{17}$$

The Nash solution with forethought on the consequences of unilateral changes, and the ESS with no forethought on the consequences of rare mutations will generally yield different solutions. For both solutions, the optimal strategy, u^*, increases linearly with a. The optimal strategy declines non-linearly with b, and with the number of players, n. In this game, individuals temper their strategy value to mitigate the negative interaction effect between their own strategy and the strategies of others. The difference in the ESS and Nash solutions occurs via the state variable. Note how the ESS (equation 17) is independent of the state variable and the parameters (K and g) that appear in the state equation (11). Not so for the Nash solution where individuals are inclined to increase their strategy with the magnitude of $\frac{Kd}{g}$ (equation 16) as a means of taking advantage of the positive externality – increasing one's own strategy increases the magnitude of the state variable, y^*, which positively influences every player's payoffs. To avoid falling into the realm of negative strategy values for this example game, we assume that $2b + c(n-1) > \frac{2Kd}{g}$; and this can be ensured for any dimension of the game by letting $b > \frac{2Kd}{g}$. For the Nash solution, this prevents a runaway process whereby the individual desires an infinite strategy to induce an infinite state variable that is both private and public good. This consideration does not even surface in the ESS, as individuals are under no selection to 'engineer' the state variable.

State dependencies provide **Reason #2** for using the Nash solution for classical game theory and the ESS solution for evolutionary games. In classical game theory, there is a fixed number of players that can anticipate the consequences for their actions. In the evolutionary game, individuals are part of a population that may engage in games that represent all or just a subset of individuals per play of the game. Because evolution is a teleonomic rather than teleologic process, these individuals do not anticipate the broader consequences of their actions.

WHEN THE STATE VARIABLES ARE POPULATION SIZES

In ecological systems, the population size of a species or group is one of the most important state variables. Much of population ecology deals with models like those first described by Lotka (1925, 1927) and Gause (1931) (see also, for example, Goldberg and Vandermeer, 2013) where population size changes as a function of population size via births and deaths. The context of the Nash equilibrium does not include or anticipate payoffs being influenced by population sizes and changes in population sizes. Rather, payoffs are 'pocketed' by the players, and the number of players remains static. However, an evolutionary game either explicitly or implicitly considers population sizes. Under natural selection, the relevant payoffs are in terms of fitness. Fitness represents the per capita growth rates of individuals possessing a particular strategy. Often games will use surrogates for fitness such as resources harvested, access to mates, and other benefits or costs influencing the survivorship and reproduction of the individuals possessing a particular strategy. Regardless, there is an implicit or explicit connection between the payoffs received during the play of the game and changes in the population sizes and/or frequencies of individuals possessing particular strategies. The evolutionary game therefore has an inner and outer game (Vincent and Brown, 1988). The inner game can be thought of as the actual game (similar to a classical game) where the strategies of the players determine their payoffs. The outer game represents the filter by which payoffs influence population sizes. Strategies with higher payoffs during the inner game increase in frequency in the population as a consequence of the outer game. The Nash solution does not include any such outer game.

Natural selection emerges from (1) heritable variation (individuals possess strategies that are drawn from some set of evolutionarily feasible strategies), (2) struggle for existence (population dynamics can be expressed in terms of per capita growth rates, and while populations can grow exponentially under ideal conditions, at some point there is sufficient crowding such that the population's per capita growth rate declines with population size), and (3) heritable variation influencing the struggle. This last feature of natural selection describes the evolutionary game where the per capita growth rate of an individual is influenced by its own strategy, which we shall call v, the strategies of others in the population or community, $\mathbf{u} = (u_1, \ldots, u_n)$, and the population sizes of each of these strategies, $\mathbf{x} = (x_1, \ldots, x_n)$, where x_i represents the population size of those individuals using strategy u_i. Let $G(v, u, x)$ denote the per capita growth rate for individuals using strategy v in a community determined by strategies u at population sizes x. We call the $G(v, u, x)$ the fitness-generating function (G-function for short). We can use a G-function to incorporate the special kind of symmetry associated with evolutionary games among individuals that possess the same set of evolutionarily feasible strategies and the same fitness consequences of possessing a particular strategy (Vincent and Brown, 2005). The fitness-generating function can describe the 'Darwinian dynamics' that include the ecological dynamics of changes in population sizes and the evolutionary dynamics of changes in strategy values (Vincent and Brown, 2005):

$$\frac{\partial x_i}{\partial t} = x_i G(v, \mathbf{u}, \mathbf{x}) \text{ when } v = u_i \qquad i = 1, \ldots, n \tag{18}$$

and

$$\frac{\partial u_i}{\partial t} = k \frac{\partial G}{\partial v} \text{ when } v = u_i \qquad i = 1, \ldots, n \tag{19}$$

The parameter k simply scales the rate of evolution. Depending upon the explicit circumstances, the scaling term k may be influenced by additive genetic variance, population size and dispersion, mutation rates, and the underlying genetics. The ecological dynamics take on a form easily recognizable to those familiar with models of population ecology. The evolutionary dynamics take on a form easily recognizable to those familiar with quantitative genetics models, Fisher's fundamental theorem of natural selection, and adaptive dynamics.

Based on this description of Darwinian dynamics, we suggest that the evolutionary game must embrace population sizes as a key state variable. When the state variables are population sizes, then the actual number of players in the game can change with time. The game itself is dynamic in the sense that the actual game being played changes with population size. Furthermore, the evolutionary dynamics cause the replacement of less successful strategies by strategy values conferring higher fitness according to the gradient of G with respect to the strategy of an individual, v. A plot of G versus v is also known as the adaptive landscape. Increases in population size will generally depress this landscape. Natural selection favours strategies that move up the slope of this landscape. Hence, at an ecological equilibrium population sizes are such that fitness is zero [either x_i or $G(v, \mathbf{u}, \mathbf{x}) = 0$ when $v = u_i$ and $x_i = x_i^* > 0$). For an evolutionary equilibrium, the fitness gradient must be zero $\left(\frac{\partial G}{\partial v} = 0\right)$ at each $v = u_i^*$. This occurs at minimum, maximum or inflexion points of the adaptive landscape when $v = u_i^*$.

With the immediately preceding section of text, we have made a crucial shift in context. The number of strategies found in the population, n, no longer represents the number of players. The term n describes the number of extant species or sub-populations in the ecological community that have distinct strategies. Hence, there exists some number of players, denoted as x_i, using strategy u_i for $i = 1, \ldots, n$. The sum of all of these population sizes represents the numbers of players in the game. Furthermore, the numbers of players can shrink and grow as the population sizes of the various strategies rise or decline.

For a single strategy, u^*, to be the ESS [and this does not have to be the case; the ESS may contain several co-existing species (Brown and Vincent, 1987; Cohen *et al.*, 2001; Ripa *et al.*, 2009)], the strategy u^* must be a global peak of the adaptive landscape at the equilibrium population size, x^*. At an ESS, the plot of $G(v, \mathbf{u}, \mathbf{x})$ versus v must take on a maximum when $v = u_i^*$ for $i = 1, \ldots, n$, and $\mathbf{x} = \mathbf{x}^*$ [ESS maximum principle (Vincent and Brown, 1988; Vincent and Fisher, 1988)]. At $\mathbf{u}^*$ and $\mathbf{x}^*$:

$$G(v, \mathbf{u}^*, \mathbf{x}^*)\,|_{v = u_i^*} \geq G(v, \mathbf{u}^*, \mathbf{x}^*) \text{ for all } v \neq u_i^* \tag{20}$$

The necessary condition for an ESS (or a coalition of ESSs) is that the ESS or each strategy of the ESS coalition must have maximum fitness given the circumstances. This necessary condition also has the Nash property of making the ESS a no-regret strategy at equilibrium population sizes. However, the complete 'Darwinian dynamics' that encompasses both strategy and population dynamics is entirely within the spirit and intent of the ESS concept, and entirely beyond the domain of the Nash solution. Population dynamics (providing a constantly changing number of players), the ease of separating groups of players into 'species' defined by their strategies (u_i) and their associated population sizes (x_i), and the special form of symmetry that allows a suite of strategies to use the same fitness-generating function, all provide **Reason #3** for reserving the ESS as the solution concept for the evolutionary game (while recognizing its Nash properties); none of these features are necessary for or anticipated by the Nash solution.

EVOLUTIONARY GAMES AND THE PITFALL OF GROUP SELECTION

Additional pitfalls can inadvertently occur when trying to apply classical game theory approaches and concepts to the evolutionary game. We illustrate one of these – namely, the trap of 'group selection' – in the following example.

We imagine n groups of players where each player within a group is using the same strategy, u_i, and where each of these groups has an associated state variable that represents the numbers of individuals or population size of this group. So instead of using y for the state variable, we will use x_i to make clear this state is some density or number of individuals within group i.

Using a slight modification of the prior state-dependent model, we come up with a simple model such that the group' strategy, u_i, influences payoffs according to a quadratic function, and payoffs decline with the sum of population sizes weighted by the strategy of group i:

$$H_i(\mathbf{u}, \mathbf{x}) = -a + bu_i - cu_i^2 - \sum_{j=1}^{n} u_i x_i \qquad i = 1, \ldots, n \tag{21}$$

Since payoffs are now fitness (per capita growth rates of the population possessing the particular strategy) and directly influence the changes in population sizes, we have ecological dynamics given as follows:

$$\dot{x}_i = x_i H_i(\mathbf{u}, \mathbf{x}) \qquad i = 1, \ldots, n \tag{22}$$

Hence equilibrium population sizes require that at $\mathbf{x}^*$,

$$H_i(\mathbf{u}, \mathbf{x}) = 0 \qquad i = 1, \ldots, n \tag{23}$$

One way to interpret the game and to apply the Nash solution is to let each group be its own player in the game. Hence, with $n = 2$ there are two groups, and under this Nash interpretation these two groups represent two players. Because the game is symmetric with each group possessing the same payoff function, someone inappropriately applying Nash to solve this game might seek a Nash solution by assuming all groups use the same strategy and have the same equilibrium population size. For this model, there is a general analytic state-dependent Nash solution for the n-player game with

$$u^* = \frac{[-(1-n)b \pm \sqrt{\{(1-n)b\}^2 + 4ac(-1+2n)}]}{2(-1+2n)c} \tag{24}$$

and

$$x^* = \frac{[nb \mp \sqrt{\{(1-n)b\}^2 + 4ac(-1+2n)}]}{(-1+2n)} \tag{25}$$

For any given number of groups, there are two possible Nash solutions (a positive and negative root) with their associated population sizes. If we consider only the positive root of this solution, we see that as $n \to \infty$, $u^* \to \dfrac{b}{2c}$ and the total population size of $x^* \to \dfrac{b^2 - 4ac}{2b}$.

For sample parameter values of $a = 8$, $b = 20$, $c = 2$, the following table illustrates the results for several different values of n. The common value for u_i^* is listed under u^* and the common value for x_i^* is listed under x^*. The sum of all the x_i^* is also given.

n	u^*	x^*	Σx_i^*
2	3.6943	5.2230	10.4460
3	4.1909	3.2364	9.7093
6	4.6241	1.5036	9.0217
20	4.8928	0.4290	8.5794
50	4.9576	0.1694	8.4710

(26)

As the number of groups (each considered a 'player' in this erroneous way of solving the game) increases, the Nash solution increases and the combined population sizes of all the groups (total population size) declines. By comparing the solution above to the ESS solution obtained from a G-function approach we can clearly illustrate how this Nash solution suffers from the trap of group selection.

We can now use the G-function approach, which avoids the trap of group selection to analyse this game from the 'individual selection' evolutionary game perspective to see how it compares and contrasts with the Nash approach, which must resort to group selection for a solution. Similar to above, the G-function is as follows:

$$G(v, \mathbf{u}, \mathbf{x}) = -a + bv - cv^2 - \sum_{j=1}^{n} u_i x_i \tag{27}$$

Note that $G(u_i, \mathbf{u}, \mathbf{x}) = H_i(\mathbf{u}, \mathbf{x})$, $i = 1, \ldots, n$. The ESS and the corresponding equilibrium population size for this game are given by

$$u^* = \frac{b}{2c} \text{ and } x^* = \frac{b^2 - 4ac}{2b} \tag{28}$$

The ESS solution for the above example is composed of a single strategy ($n = 1$) and its associated equilibrium population size. Darwinian dynamics, which encompass both strategy and population dynamics, drive the strategy value of the population to converge on u^* and the population size to converge on x^*. Both u^* and $x^*$are dependent on each other. Hence, an important distinction between classical games and evolutionary games is how in evolutionary games, the entire population can represent the individual players, yet not be a player itself, allowing the ESS solution to avoid the trap of group selection, while the Nash solution gets caught in the trap. Consequently, the number of players in the evolutionary game and the game itself change with population size.

For the evolutionary game, each individual of the population represents a player. Groups that interact with one another within a larger population do not constitute 'players' in the evolutionary game, even though this can be used as a technique to find Nash equilibria for an evolutionary game where different groups are equated to players. So, why does having one 'group' in the G-function (a population of players all playing one strategy) yield such a different result from setting $n = 1$ and having a single payoff function H_1? When we let groups represent players to find a Nash solution rather than the individuals of a population with size x_i, a kind of group selection occurs where we seek the strategy, u_i, for the group that maximizes H_i. But, in seeking this optimal value for the group's strategy, we are letting all members of the group, x_i, change their strategy collectively rather than unilaterally.

It is known that the solution to an evolutionary game does not necessarily benefit the group, maximize group payoffs, or maximize population size. So, in this example, when we let groups be players and we seek a state-dependent Nash solution where the population sizes are merely viewed as a state variable, when the number of groups is small, the optimal group strategy is small and the total population size is large. As we let the number of groups become larger, each group's population size, x_i, declines. Furthermore, the payoff function for a group, H_i, begins to converge onto that of a rare individual within a G-function. So, only as n goes to infinity does the solution to the state-dependent n-player game of H_i's converge on the ESS for the G-function.

However, the *G*-function seamlessly captures the idea of determining an individual's fitness as a function of its own strategy, *v*, the strategies of others, **u**, and the population sizes of the extant strategies, **x**. In terms of the dimension of the game, both the number of players (sum of the x_i's) and the number of different strategies currently being used, *n*, can change up or down. In contrast, the Nash solution concept is specifically meant for a fixed number of players within a fixed model that determines payoffs to each player as a function of its strategy and the strategies of others, and so it is easy to accidentally fall into the trap of group selection. The ESS solution applies to the evolutionary game where the number of players (population sizes), the number of current strategies, and the game itself may be changing in response to the evolutionary and ecological dynamics. Furthermore, in response to ecological and evolutionary dynamics, the ESS is just one aspect of evolutionary stability that also includes convergence stability and neighbourhood invasion stability (see Gertiz *et al.*, 1998; Apaloo *et al.*, 2009).

Avoiding the trap of group selection is **Reason #4** for using the ESS concept in evolutionary games. Because the focus is on strategies and not players and because evolutionary games have a special symmetry, an ESS approach where the nature of the inner and outer game allows individuals to be 'selected' based on their strategies, rather than a classical game approach where groups of identical players are 'selected' based on their strategies, more elegantly models individual selection and avoids group-selected Nash solutions, which, under particular circumstances (e.g. less than an infinite number of groups) may fail to find the ESS.

DISCUSSION

There are reasons why it may be tempting to think of evolutionary games in terms of a Nash solution, not the least of which is that Nash (Nash, 1951) is an historical antecedent in the 'phylogeny' of game theory, and many of its descendent ideas may be found in the evolutionary games literature of today (e.g. the assumption that players act independently and that each player seeks to minimize their own cost function). Strategies that 'win' evolutionary games (ESS) do have the Nash-like property of being 'no regret' strategies in the sense that at equilibrium, one can do no better by switching strategies (see example on pp. 296–297). However, we argue that it would be a mistake to solve evolutionary games in terms of Nash solutions because evolutionary games have special properties that are absent from classical games, and we have outlined six key ways that Nash differs in aim, context, and substance from an ESS (Table 1). Frameworks specifically designed for solving evolutionary games (e.g. adaptive dynamics and Darwinian dynamics) should be used instead and we have presented four reasons for this.

First, because players inherit rather than choose their strategies, strategies with higher payoffs (fitness) increase in frequency relative to those with lower fitness. The Nash equilibrium was conceived as a solution concept for classical games where each player is allowed to choose its strategy, where each player is rational, and each attempts to maximize its payoff, given the strategies of others. Games of this type can be iterative (e.g. Papavassilopoulos, 1986), and can be adapted to a 'replicator equation' with a dynamic state (e.g. Hofbauer and Sigmund, 2003), but ultimately the classic game is focused on maximizing payoffs to players and the notion that payoff is linked to the frequency of strategies among groups of players is not an embedded part of the classic game. There may be times when a player- rather than strategy-focused game may be appropriate for biological systems (e.g. daily interactions among social organisms, or individual-level plant–plant competition), but evolutionary games are different and this is due to the nature of evolution by natural selection: individuals play the game, but populations evolve. Thus populations, as dynamic state variables, are not only important, but necessary parts of the game, and these can vary with the number of players playing a particular strategy, the number of players in the game, and the frequency of strategies in the game, all of which can influence payoffs. In evolutionary games, payoffs go to strategies – the individuals playing those strategies don't matter – and payoffs are made in terms of fitness, which represents per capita growth rate of a population with a particular strategy.

The second reason not to use Nash for evolutionary games is because evolutionary games have state dependencies and evolutionary dynamics that shape strategy changes exhibit no forethought on state variable change. Because ESS solutions and Nash solutions are 'designed' in different ways, they may not find the same solution to the evolutionary game. In classical games, players can anticipate the effect of their strategy on the state variable and, given this knowledge, players can select a strategy that maximizes their payoff, but for evolutionary games, the ESS is arrived at by trial and error and the state variable is a property of the environment. In this way, Nash solutions can arrive at something 'optimal' but not necessarily evolutionarily stable (e.g. Vincent *et al.*, 2011) or may arrive at a solution that is not ESS (see example on pp. 304–306).

In state-dependent systems, it is possible for Nash solutions to converge on the ESS, but only if the players do not know about the state variable, ignore the externalities of their actions, there is a sufficient time lag between action and consequence, or if players discount their future (all assumptions that could be used, for example, in a model of human actions and climate change); in essence, this is removing the teleology of Nash. There may also be cases where an ESS solution may converge on Nash (for example, when organisms consciously engineer their ecosystems) but for most cases we would argue that even if the ESS solution ends up with Nash-like properties, or the properties of convergent stability, or NIS, this does not necessarily mean that these other solutions are ESS.

The ESS (or the coalition of co-existing strategies of ESS) by definition must take on maxima on the adaptive landscape (Vincent and Brown, 2005). This is the key to finding evolutionarily stable solutions to evolutionary games; other approaches can do no better.

The third and fourth reasons not to use Nash in evolutionary games is that evolutionary games have a special form of symmetry, and because the focus is on strategies and not players. The conditions for evolutionary symmetry are as follows: (1) individuals possessing the same strategy must face the same fitness consequences, and (2) the same set of evolutionarily feasible strategies are available (given the rules of the game) to all individuals playing the game. Because of this symmetry, it is possible to use a *G*-function approach to solving evolutionary games, which allows us to represent the entire population as individual players yet not be a player itself and, therefore, it allows us to 'follow the strategy' through evolutionary time, rather than the player, who only exists for one generation.

The Nash solution concept does not anticipate the outer game this way; Darwinian dynamics does. In contrast, Nash solutions, which are framed in terms of the winning player and not the 'winning' strategy (the one that lasts through evolutionary time), may lead to group selection solutions that are not ESS (see the example on pp. 304–306). Because Darwinian dynamics is inherently an evolutionary game approach, and not a classic approach applied to evolutionary games, it is a much more useful and flexible tool for modelling the evolution of strategies (e.g. phenotypes or behaviours) than the Nash approach. For example, Galapagos finches have different beak 'strategies' (widths) that allow each species to utilize different suites of plant seeds. Because a *G*-function can be used to describe the entire genus of Galapagos finches, Darwinian dynamics can be used to predict co-existence of ESS solutions, or 'species' on particular islands (Vincent and Vincent, 2009).

In addition, this approach is flexible enough that multi-stage *G*-functions (Vincent and Brown, 2005) can be used to model strategies with multiple life stages (like a community of caddisfly species) and even more than one *G*-function may be utilized to define an evolutionary game [(e.g. predators share one *G*-function and prey share another (Brown and Vincent, 1992)]. Pintor *et al.* (2011) suggest that the taxonomic level of Family may provide a good first-cut of who to include within a single *G*-function. The possibilities are as various as the natural systems to be modelled.

This analysis highlights the differences between Nash and ESS, and that it can be used to avoid some of the pitfalls we have described. A careful researcher, with careful attention to the nuances of the game, and evolution by natural selection may well be able to apply Nash to find appropriate solutions to evolutionary games. However, ESS solves this without any potential pitfalls and we suggest it should be adopted as a universal solution concept for the evolutionary game.

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APPENDIX A

In the section entitled '1951 Nash vs. 1973 ESS', we identified the Nash equilibria for the matrix game with the payoff matrix given in equation (2):

$$M = \begin{array}{c c} & \begin{array}{cc} \text{A} & \text{B} \end{array} \\ \begin{array}{c} \text{A} \\ \text{B} \end{array} & \begin{bmatrix} 0 & 2 \\ 6 & 1 \end{bmatrix} \end{array} \tag{29}$$

Here, we show how the Nash solutions given in the text are calculated. To begin we clarify that the payoff matrix in equation (29) is the payoff to player 1 and it implicitly includes the payoff to player 2. More specifically, the payoff to player 2 is given as the transpose of the matrix M, which is given by

$$M^T = \begin{array}{c c} & \begin{array}{cc} \text{A} & \text{B} \end{array} \\ \begin{array}{c} \text{A} \\ \text{B} \end{array} & \begin{bmatrix} 0 & 6 \\ 2 & 1 \end{bmatrix} \end{array} \tag{30}$$

Now suppose player 1 plays strategy A and player 2 plays strategy A as well. Then they each get a payoff of 0. If player 1 changes its strategy to B, but player 2 still plays A, then the payoff to player 1 will increase to 6 and that for player 2 will increase to 2. This suffices to show that each of the players playing strategy A cannot be a Nash solution as players 1 and 2 both do better by this change in strategy. Alternatively, suppose that player 2 changes strategy to B but player 1 still plays A. In this case, player 2 will increase its payoff to 6 and player 1 will get 2.

We consider one more case and it should become clear how the pure strategy Nash solutions are found. For this case, consider the situation where player 1 plays A but player 2 plays B. Here players 1 and 2 get a payoff of 2 and 6 respectively. If player 1 changes its strategy to B, it will receive a (strict) lower payoff of 1 as does player 2. On the other hand, if player 2 changes its strategy to A, then both players 1 and 2 receive a payoff of 0. So player 1 plays A and player 2 plays B is a no-regret strategy (Nash solution) for the game. In fact, this solution is a strict Nash solution since each player has a strictly reduced payoff.

For the mixed strategy Nash solution, we refer the reader to Nowak (2006).

APPENDIX B

In this appendix, we show the details of the calculations for deriving the candidate Nash and ESS solutions given in equation (16) and equation (17) respectively. From the state equation (11) we obtain the equilibrium condition by setting

$$K - \frac{gy}{\sum_{j=1}^{n} u_j^2} = 0 \tag{31}$$

and from the necessary condition in equation (13) we get the Nash necessary condition

$$a_i - 2b_i u_i - c \sum_{j=1, j \neq i}^{n} u_j + d_i \frac{\partial y}{\partial u_i} = 0 \qquad i = 1, \ldots, n \tag{32}$$

Note that these two conditions are required to hold at $\mathbf{u} = \mathbf{u}^*$ and $y = y^*$. Now solving for y from equation (31), we obtain the equilibrium state value

$$y^* = \frac{K\sum_{j=1}^{n} u_j^2}{g} \tag{33}$$

with the corresponding derivative

$$\frac{\partial y}{\partial u_i} = \frac{2Ku_i}{g} \tag{34}$$

Substituting this derivative in equation (32), we get the simpler condition for the Nash solution:

$$a_i - 2b_i u_i - c\sum_{j=1, j\neq i}^{n} u_j + d_i\frac{2Ku_i}{g} = 0 \qquad i = 1, \ldots, n \tag{35}$$

Let $a_i = a$, $b_i = b$ for all i. We seek symmetric solutions, so we set $u_i = u$ for all i. Thus equation (35) becomes

$$a - 2bu - c\sum_{j=1, j\neq i}^{n} u + d\frac{2Ku}{g} = 0 \tag{36}$$

Further simplifications and solving for u^* give the following:

$$a - 2bu - c(n-1)u + d\frac{2Ku}{g} = 0 \tag{37}$$

$$u^* = \frac{a}{2b + c(n-1) - \dfrac{2Kd}{g}} \tag{38}$$

Now we turn our attention to the ESS solution. From equation (15) we get the ESS necessary condition

$$a_i - 2b_i u_i - c\sum_{j=1, j\neq i}^{n} u_j = 0 \qquad i = 1, \ldots, n \tag{39}$$

In the manner similar to the Nash solution derivation above, this equation becomes

$$a - 2bu - c(n-1)u = 0 \qquad i = 1, \ldots, n \tag{40}$$

and solving for u^* we get

$$u^* = \frac{a}{2b + c(n-1)} \tag{41}$$

APPENDIX C

In this appendix, we derive the solutions given in equation (24) and equation (25). For these results, we consider the following general payoff function for a Nash game with n players:

$$H_i(\mathbf{u}, x) = -a + bu_i - cu_i^2 - \sum_{j=1}^{n} u_j x_j$$

with the associated dynamic equation for a non-zero state variable x given by

$$\frac{dx_i}{dt} = x_i H_i(\mathbf{u}, x)$$

For the state and Nash equilibrium, we solve the following equations, evaluated at $\mathbf{u}^*$ and x^* simulatenously:

$$\frac{dx_i}{dt} = 0 \text{ and } \frac{\partial H_i}{\partial u_i} = 0$$

where

$$\frac{\partial H_i}{\partial u_i} = b - 2cu_i - x_i$$

We consider first the case where $n = 1$. Here the equilibrium conditions are:

$$-a + bu_1 - cu_1^2 - u_1 x_1 = 0 \tag{42}$$

$$b - 2cu_1 - x_1 = 0 \tag{43}$$

Solving for x_1 from equation (43) we get $x^* = b - 2cu_1$. Now substitute the value of x_1 into equation (42) and solve for u_1 to get (after some simplification):

$$u_1^* = \sqrt{\frac{a}{c}}$$

Next, we consider the case $n = 2$. In this case, the equilibrium equations are

$$-a + bu_1 - cu_1^2 - (u_1 x_1 + u_2 x_2) = 0 \tag{44}$$

$$-a + bu_2 - cu_2^2 - (u_1 x_1 + u_2 x_2) = 0 \tag{45}$$

$$b - 2cu_1 - x_1 = 0 \tag{46}$$

$$b - 2cu_2 - x_2 = 0 \tag{47}$$

For symmetric solutions with $u_1 = u_2 = u$ and from equations (46) and (47) we get $x^* = b - 2cu$. Substituting the equilibrium x value in any of the equations (44) and (45) and solving for u we get

$$u^* = \frac{b \pm \sqrt{b^2 + 12ac}}{6c}$$

and substituting in the expression for x^* above we get:

$$x^* = \frac{1}{3}\left[2b \mp \sqrt{b^2 + 12ac}\right]$$

In the general case of n players, with $u_1 = u_2 = \ldots u_n = u$, the equilibrium equations are

$$-a + bu - cu^2 - nux = 0 \tag{48}$$

$$b - 2cu - x = 0 \tag{49}$$

Again from equation (49) we have $x^* = b - 2cu$. Substituting in (48) and solving for u we get (after simplifications)

$$u^* = \frac{\left[-(1-n)b \pm \sqrt{\{(1-n)b\}^2 + 4ac(-1+2n)}\right]}{2(-1+2n)c}$$

and

$$x^* = \frac{\left[nb \mp \sqrt{\{(1-n)b\}^2 + 4ac(-1+2n)}\right]}{(-1+2n)}$$