Asymmetric Population Games and the Legacy of Maynard Smith: From Evolution to Game Theory and Back?

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1. Introduction

Among the numerous contributions of Maynard Smith to the theory of evolution, maybe the most widely recognized one concerns a not less important contribution to a different field of research, namely that of *Game Theory*.

In 1973, attempting to characterize candidates for stable resolutions of a conflict within animal populations, Maynard Smith and Price have first introduced the concept of an *Evolutionarily Stable Strategy, ESS*. In order to define it, they have assumed that individuals in the population encounter each other at random (this assumption was later relaxed, e.g. Bomze 1986, Vickers and Cannings 1987, Lessard 1990 and references there), that, once encountered, each individual (player) has the same set of strategies (rules of behavior, later to be replaced, more generally, by phenotypes), and that the expected payoff (survival probability, fitness, or inclusive fitness), gained by an individual at the end of the encounter, is determined by both its own strategy and that of its opponent. Assuming such a structure, Maynard Smith and Price have opened a new field of research, namely that of *Population Game Theory*, now a solid branch of game theory (e.g. see Hammerstain and Selten 1993, Weibull 1995, Hofbauer and Sigmund 1998). Concentrating on symmetric population games, and following Hamilton's concept of *Unbeatable Strategy* (Hamilton 1967), they have defined an ESS as a strategy that strictly outcompetes (yields higher expected payoff than) any single alternative (mutant) strategy that occurs in low enough, but positive, frequency in the population (For equivalent definitions and further developments of the concept see Maynard Smith 1974, Bishop and Cannings 1976, Eshel and Motro 1981, Bomze 1986, 1990, Bomze and Potscher 1989, Bomze and Burger 1995, Vickers and Cannings 1987, Taylor 1989, and a most extensive survey by Lessard 1990).

Indeed, the situation in which each individual in a population has to best adjust its or his or her behavior to that of an anonymous random opponent from the same population, is by no means restricted to the biological context of natural selection. Such a situation may be, all the same, typical to a population of rational individuals, seeking each to maximize his or her own payoff. Population game theory as a useful model for the investigation of conflicts within a population of rational players has thus become widely employed in micro-economy and other social sciences.

Rather controversial remained just the original attempt of Maynard Smith and Price (as well as that of Williams, Hamilton, Wilson and other) to explain phenomena of animal behavior on a pure phenotypic basis, ignoring inevitable restrictions, imposed by the genetic structures (e.g. Feldman and Cavalli Sforza, 1981). This controversy has been relaxed with later studies, in which plausible (though not universal) conditions have been established for long-term convergence to an ESS, if exists.

Having expressed my view on the subject elsewhere, it is not my intention to return here to this controversy. Instead, I wish to concentrate on another, rather overlooked, difficulty in applying models of population game theory to natural populations, regardless of whether they consist of rational human players, or of biological organisms under natural selection. Part of this difficulty follows from the simple fact that individuals in natural populations are quite often different from one another in *some* conspicuous parameter. A qualitatively more serious difficulty stems, as we shall see, from the fact that such individuals are usually different from one another in *many* parameters, even if differences are small.

2. Asymmetric Population Games And Evolutionary Paths.

A first crucial step toward the understanding of some difficulties, concerning evolutionarily stable resolutions of asymmetric conflicts, was made in a later seminal work of Maynard Smith, this time with Parker (1976). In that work, concentrating on the simplest situation of an asymmetric conflict, where encounters are limited to individuals of two different roles (e.g. male or female, owner or intruder), Maynard Smith and Parker have demonstrated *Asymmetric Population Games* as a qualitatively new subject of research. In order to generalize the concept of ESS to such a situation, they have defined a pure strategy of an individual, *regardless of its role*, as a behavioral rule that determines its behavior under each of the roles it may assume. This way, any asymmetric population game is formally transformed into a symmetric one (though with a richer space of strategies). An *Asymmetric ESS* of the original (asymmetric) population game, was naturally defined in the traditional way, as an ESS of the symmetrized, richer space form of the population game, namely as a strategy that strictly out-competes any alternative strategy that occurs in low enough, but positive, frequency in the population.

One revolutionary result of the work of Maynard Smith and Parker was the finding that even the most minor asymmetry between players may drastically change the set of ESS's corresponding to a conflict. Following that work, it was shown, more generally, by Selten (1980) that an ESS of an asymmetric population game can only be obtained in pure strategies. For the bulk of well studied (symmetric) population games that allow only for mixed ESS's, this finding indeed implies that even the slightest asymmetry,

when introduced into a population game, may drastically change its outcome. For a parallel, dynamic version of Selten's theorem see Eshel and Akin (1983). For a further study of asymmetric ESS, see Taylor (1979), Hammerstain (1981), Samuelson and Zhang (1992).

A first, somehow disturbing, problem for the mainstream (symmetric) theory of population games has, thus, followed from the fact that most, if not practically all, natural conflicts involve at least some sort of asymmetry between the participants, e.g. in age, in height or, say, in color. Selten's theorem implies that in any such a case, previous analysis, ignoring the effect of such minor asymmetries, should be revised, with possibly radical changes in the predicted outcome of the conflict.

But then, an essentially more serious problem stems from the fact that most (if not practically all) natural conflicts involve *many sorts of asymmetries*. While this may not create an apparent difficulty in the construction of a theoretical model, as long as one arbitrarily concentrates on one single parameter of asymmetry (e.g. Ownership, as the only source of asymmetry in the work of Maynard Smith and Parker), the situation is different when multiple asymmetry is involved (Eshel and Sansone 2002). The problem is even more serious when concerning predictions about the outcome of a conflict within a *natural* population. In such a case, it is not necessarily clear which, out of the innumerable parameters of asymmetry that express themselves in the population, are actually observed by the participants as relevant to the conflict. Yet, concentrating on different sets of asymmetries, a population game analysis of the conflict may lead to radically different predictions.

Unfortunately, there is no hope to build, notwithstanding to analyze, a population game model that would take into consideration all possible asymmetries among individuals in a natural population. Moreover, such an endeavor, even if successful, would not be realistic because it is quite unlikely that the participants themselves are actually able to take into consideration all conceivable asymmetries between them. As a simple example, it is easy to see that in any Hawk-Dove conflict within a human society, a behavioral rule of giving priority to the contender with, say, longest thumb can well replace Ownership-Priority, demonstrated by Maynard Smith and Parker as a strict, asymmetric ESS. Moreover, Thumb-Priority would be as efficient as Ownership-Priority in preventing aggressive confrontations within the population. Yet as far as we know, this sort of asymmetry, like many others, is a most unlikely factor to be observed in real conflicts within human populations.

Concerning conflicts within natural populations, a preliminary question to be asked is, therefore: *What is the set of relevant asymmetries, expected to be observed by individuals in a given population?*

To a certain level, the answer to this question is almost obvious, though maybe not quite satisfactory: Given an evolutionarily stable situation, any individual in the relevant population is better off observing exactly those parameters of asymmetry that are traditionally observed by the other. Indeed, migrant from a population with the behavioral rule of Thumb-Priority, would suffer twice when facing a population in which the behavioral rule is that of Ownership-Priority: As a potential intruder, he would suffer the danger of aggressive encounters with shorter-thumb owners, and as an owner, he would loose by unnecessarily renouncing his rights of ownership to potential intruders with

longer thumbs. Yet, the same is true for a migrant from an Ownership-Priority population, to a Thumb-Priority one.

On a somehow higher level, a more meaningful question would, therefore, be: *Why is it, that a certain asymmetry, or set of asymmetries (and, consequently, a certain ESS), out of innumerable possible combinations, has been established as relevant in a certain population.*

I indeed do not claim that the establishment of Ownership Priority rather than Thumb Priority populations as a common evolutionarily stable rule in human and in other is a surprising phenomenon. No doubt, there are simple explanations why the first is more likely to establish itself in real populations than the latter. Other evolutionarily stable rules, based on specific asymmetries rather than on other, may or may not be that simple to explain. My main claim is that, given the high dimensionality of asymmetry in natural populations, *none of the behavioral rules, observed in such populations, can be explained on the pure basis of population game theory,* without resorting to further information about historical facts and evolutionary paths. This is so because virtually almost any set of asymmetries, once established as relevant in large enough majority of the population, can lead to an evolutionarily stable situation (for a different view, based on arguments of group selection, see Binmore 2004).

From this point of view, it seems that a circle was closed. While the pioneering work of Maynard Smith and Price has first provided a, still most useful, tool for examining candidates for evolutionary stable resolutions of a conflict within a population, it was the, as well pioneering, work of Maynard Smith and Parker to suggest a first step toward further understanding of the limitation of this important tool, when not backed by further knowledge of evolutionary paths.

3. The Example of the Hawk-Dove Game: One Payoff Matrix, Many Interpretations.

Following Maynard Smith and Parker, we now concentrate on the simple payoff matrix of the Hawk-Dove game, as shown in figure I.

Figure I: The hawk-Dove Payoff Matrix

	Dove	Hawk
Dove	$v/2$ $v/2$	0 v
Hawk	0 v	$pv - q\theta$ $qv - p\theta$

where $v < \theta$ and $p = 1 - q$. We see that this same payoff matrix, when corresponding to different sorts of a conflict, may lead to different sets of "rational" outcomes.

3.1 Interpretation I: A two-player symmetric game.

Story: Two persons are holding a 100$ bill they have found on the street, when a policeman arrives. Each of the two can play either a Dove, telling the truth, or a Hawk, claiming ownership of the bill. If both tell the truth, the sum of 100$ would be equally split between them. If only one claims ownership, he would get it all. If both claims ownership, a decision would have to be made in court, the winner would then get the amount of 100$, and the other would have to pay expanses of $\theta > 100\$$.

This situation is characterized by a simple Hawk-Dove game, in which $p = q = 1/2$, and $v = 100\$ < \theta$. As it is well known, the equilibria of this game are:

i)   (0,1) - First player claims ownership. The other yields.

ii)   (1,0) - Second player claims ownership. First player yields.

iii) (x,x) - Each of the two plays Dove in positive probability $x = 1 - v/\theta < 1$.

The first two are pure, strict, and efficient equilibria (i.e. they are maximizing the total payoff). The third one is neither strict, nor efficient, allowing a positive probability of a costly conflict.

3.2 Interpretation II: A symmetric population game (Maynard Smith and Price 1972).

Story: The same as before, except for the fact that each of the two contenders is interrogated separately, and that they have no previous information about one another, except for the fact that they both belong to the same population. Consequently, their decisions should be made, independently of one another, on the mere basis of some behavioral rule, prevailing in this population.

Suppose a behavioral rule that determines a probability $0 \leq y \leq 1$ for playing Dove. By straightforward calculations one can verify that if $y > x = 1 - v/\theta$, then it is advantageous to decrease one's probability of playing Dove, and vice versa if $y < x = 1 - v/\theta$. It follows that if players only want to increase their personal payoffs (or, maybe, if they are so selected to), a probability $x = 1 - v/\theta$ of Dove-playing is the only one that can remain at equilibrium in the population. Moreover, this equilibrium is now *Evolutionarily Stable*, in the sense that any deviation from it, renders it advantageous for any individual in the population to change his behavior in a direction opposite to the original deviation.

3.3-a Interpretation III-a: A population game with asymmetry in respect to ownership (Maynard Smith and Parker 1976).

Story: The same as the previous case, except for the fact that one of the two contenders is actually the owner of the bill, and both (but not the police) know it.

A behavioral rule, in this case, may naturally be different for owner and for non-owner. Consequently, even in the case $p = 1/2$ (e.g. Grafen 1987), the ESS (x, x) of the symmetric Hawk-Dove conflict is no more stable: Since encounters only occur between owners and intruders, any deviation of the owners from (x, x) would render only it advantageous for non-owners to deviate in the opposite direction, and vice versa. Once deviating from (x, x), the population is, therefore, bound to end up either in (0,1) or in (1,0).

On the other hand, once the population strategy (0,1) of *Ownership Priority* (coined the *Bourgeois Principle* by Maynard Smith and Parker) is established as a behavioral rule in the population, an owner can only gain by claiming his rights, knowing that his opponent would then always yield, and an intruder can only loose by doing so, knowing that his opponent would never yield. Ownership Priority is, therefore, a strict equilibrium, hence an ESS. By the same argument, however, so is also the "Paradoxical" rule (1,0) of "Owner always gives up".

Assuming, more generally, that the owner has a better chance $p \geq 1/2$ to win in a discord conflict, Ownership Priority (0,1) always remains an ESS, while the Paradoxical rule (1,0) remains so if and only if $p < \theta / (\theta + v)$.

3.3-b Interpretation III-b: A population game with asymmetry in respect to body-size (still a version of Maynard Smith and Parker 1976).

Story: The same as in 3.2, except for the fact that this time, no policeman is seen around. If both claim ownership, they just have to fight, with damage θ to the loser. One of the two is larger, and thus is expected to have a higher chance $p > 1/2$ to win.

The analysis and results of this case are exactly as in the previous one, 3.3-a, with Body Size Priority replacing Ownership Priority with $p > 1/2$.

3.4 Interpretation IV: A population game with asymmetry in respect to both ownership and body-size.

As before, two persons are holding a 100$ bill. There is no policeman at the vicinity. One of the two is larger than the other, but the other is now the owner of the bill.

Following Maynard Smith and Parker, a pure strategy is defined, in this case, as a behavioral rule that determines one's action, given his status as owner or intruder, his own body size, and that of his opponent. It is easy to see that *Body Size Priority* is always an ESS, in this case. The question is: What other ESS's can be maintained in the population, especially – Can *Ownership Priority* still be then an ESS?

For any $k \geq 1/2$, let Γk be the strategy: "*Obey Owner Priority if and only if the intruder's probability of winning a fight is smaller than k, otherwise obey Body Size Priority*". One can readily recognize $\Gamma_{1/2}$ as the pure *Body Size Priority*, while for k larger than the maximal probability of one member of the population to defeat another, Γk is the *Ownership Priority*. For any value of k in between, Γk is the strategy of giving priority to the owner, if difference in body size is not too large.

It is easy to verify that Γk is an ESS if and only if $k < \theta/(\theta+v)$. As a special case we see that *Total Ownership Priority* can still remain evolutionarily stable in face of differences in body size, provided no individual in the population can entertain a probability larger than $\theta/(\theta+v)$ to win a discord conflict with another. This is possible if fighting is hazardous, and if the value v of the good under contention is small relative to the damage θ, inflicted on the loser. As the value v in stake increases relative to θ, the maximal value of k, for which Γk is still an ESS, decreases, hence the range of *Body Size Priority* increases on the expense of *Ownership Priority*. Any respect to ownership disappears as v reaches the value θ and above. For $v = \theta$, *Body Size Priority* is the only ESS. When v grows larger than θ, even *Body Size Priority* is no more anywhere-respected. Smaller contenders are then expected to challenge slightly bigger ones.

For a (non linear) biologically oriented variation of this model, where competition is about breeding territories, see Eshel and Sansone (2002). The paper assumes that the loser, if survives, still has a positive probability to get hold of another territory in the future, depending, in turn, on the population strategy, but also on its body size. Differently from the more simplistic model described above, the value v of a territory appears to be different for different players, depending on one's perspective of getting hold of territory in the future. Instead, it is shown that the set of ESS's depends then on a single parameter α, which is determined, in turn, by the availability of new habitats, by the population density, by the expected longevity of owners and of intruders, and by the damage θ, inflicted on the loser. It is shown that for high values of α (corresponding, among other, on high availability of new habitats), *Ownership Priority* is evolutionarily stable. As α decreases, the range of *Body Size Priority* increases on the expense of *Ownership Priority*. *Ownership Priority* remains the only ESS when α reaches some critical value α_0. Below this level, even *Body Size Priority* is no more totally respected. In this case, differently from the case of the linear model, only individuals of a relatively low rank (small body size) challenge slightly larger ones. As long as α does not drop further down, larger individuals still respect Body Size Priority, waiting their turn when confronted with even slightly larger opponents.

3.5 Interpretation VI: A population game with multiple asymmetries - The importance of historical events and evolutionary dynamics.

Assume the same payoff matrix as before, with $p = 1/2$, and assume now a large number, say N, of *inessential* asymmetries (i.e. such that do not affect the payoff matrix). Any encounter is characterized, in this case, by a vector of N pairs of values, measuring the asymmetry parameters of ego and opponent respectively. Let Ω be the set of all such

vectors. A pure strategy Γ of is, then, a mapping of Ω into the set $\{D, H\}$, where $\Gamma(v)$ is the realization (i.e. a choice between D and H) of the strategy Γ at the encounter $v \in \Omega$. For any encounter $v \in \Omega$, denote by $\tilde{v} \in \Omega$ the adjacent encounter, in which the roles of participants have been exchanged.

Proposition: *The ESS's of the Multiple Asymmetry Population Game are exactly the pure strategies Γ, for which $\Gamma(\tilde{v}) \neq \Gamma(v)$ for essentially all $v \in \Omega$.*

Proof: *From Selten's theorem it follows that the only possible ESS's of this population-game, are pure. Let, thus, Γ be any pure strategy. For any encounter $v \in \Omega$, it follows from the Hawk-Dove payoff matrix that the best response to $\Gamma(\tilde{v})$ is playing D if $\Gamma(\tilde{v}) = H$, and playing H if $\Gamma(\tilde{v}) = D$. Moreover, this best response is also strict. On one hand, this means that any pure strategy Γ, such that $\Gamma(\tilde{v}) \neq \Gamma(v)$ for essentially all $v \in \Omega$, is a strict best response to itself, hence a strict equilibrium, hence an ESS. On the other hand, any pure strategy Γ, such that $\Gamma(\tilde{v}) = \Gamma(v)$ for a positive-measure set of encounters $v \in \Omega$, cannot be a best response to itself, hence it cannot be an equilibrium, notwithstanding an ESS.*

It follows that there is a one to one correspondence between the ESS's Γ of the population game, and those mappings of Ω into $\{D, H\}$, for which $\Gamma(\tilde{v}) \neq \Gamma(v)$. It further follows that even if all asymmetries were based on a dichotomy (as is the case for Owner versus Intruder, but not for differences in Body-Size), the number of possible ESS's were 2^N. Concerning natural populations, in which the number N of potential parameters of asymmetry is likely to be of the order of hundreds, the number 2^N of possible ESS's must be of the order of billions of billions. Indeed, with this number of potential attractors, any mechanism of natural selection in asymmetric population games (e.g. Gaunersdorfer et al 1991, Hofbauer and Sigmund 1998), becomes useless as a means to predict which ESS is to be established in a population, *without resorting to a further knowledge of social structure or historical events*. Moreover, it is hard to imagine any evolutionary mechanism that would allow a population to converge, within a reasonable evolutionary time, to any specific ESS, as this means coming to agreement about a common behavioral rule, concerning any of the, at least 2^N, possible sorts of an encounter.

One possible mechanism for this, as it appears to be the case in real situations of either human or animal conflict, is to concentrate on a small number of asymmetries, ignoring all other ones as irrelevant. This may leave us with a relatively not too big number of possible ESS's (just two for a one dimensional dichotomy, as is the case in the Owner-Intruder Conflict). It still leaves us with the question of how could a choice of specific small number of parameters out of many have evolved in a population.

The situation is different when, in addition to numerous *inessential* asymmetries, there exist few *essential* ones. From arguments, similar to the ones given in the previous section, it appears that in such a case, scarcity of the good under contention may eliminate any behavioural rule, which is not an essential, *Strength-Oriented* ESS. For this, a relatively short period of scarcity may be sufficient, as the newly established

behavioural rule would then remain evolutionarily stable also in normal situations. This, however, still leaves us with a question about the ubiquity of *Ownership Priority*.

4. Evolutionary Stability and Evolution – Back to Ownership Priority, a Brief Discussion.

When Maynard Smith and Parker (1976) introduced the *Owner-Intruder Conflict* as first example of an asymmetric population game, they have kept in mind a bulk of field observations, apparently indicating an *essentially asymmetric* situation, in which the owner has, by and large, a better chance than his opponent to win an aggressive confrontation, once the situation escalates to. Thus, their main claim was that even the most minor deviation from the symmetric case of the Hawk-Dove conflict is sufficient for a drastic change in the evolutionarily stable outcome of the conflict. As a rather mathematical curiosity, they have demonstrated it to be true also for the limit case of an *inessential* asymmetry.

In a later paper, Grafen (1987) has harshly criticized both the theoretical and empirical arguments, traditionally given for owner advantage in aggressive confrontations. Consequently, his claim was that the null hypothesis of an *inessential* owner-intruder asymmetry was never rejected. Without expressing an opinion about the actual debate, I find it productive, at this stage, to put forward the theoretical question of how crucial for the evolution of *Ownership Priority* is the alternative hypothesis of an *essential* (and, in fact, significant) owner-intruder asymmetry. I maintain that *the answer to this question depends on the (maybe different) roles one attributes to Population Game Theory and to Population Game Dynamics, within the process of Evolution, either genetic or cultural*.

Indeed, if ownership is an inessential factor in the conflict, *Owner-Priority*, as we have seen, must be just one out of a huge number of possible evolutionarily stable resolutions of the conflict, all of which being equally efficient in preventing aggressive confrontations. In such a case, it might be difficult to explain, on the mere basis of Population Game Dynamics, the *establishment* of one specific inessential ESS, out of the innumerable, inessential alternatives, and it is even more so with the most likely presence of some essential alternative (as, e.g. Body Size Priority); This, to be distinguished from the long-term *stability* of such a behavioral rule, once it has been already established in the population, for one reason or another.

A speculative explanation for the emergence of Ownership Priority, on the basis of a complex Population Game Dynamics, may be possible in some special cases. Concerning territorial contests, for example, one can think of a temporal period of scarcity which, if harsh enough, may be sufficient, as we have seen, to render inevitable the combination of *Strength Priority* and *aggressive confrontations*. During such a period, ownership may emerge as the most trustful marker of strength. We have further seen that with the relaxation of scarcity, aggressive confrontations are likely to be continuously replaced by efficient, concord strategies of *Strength Priority*. But in this case, differently from the situation described in 3.4 (and much in agreement with the original model, suggested by Maynard Smith and Parker, 1976) *Strength Priority* is best represented by *Ownership Priority*. Indeed, once the latter is established as a non aggressive behavioral rule in the population, *Ownership* alone is sooner or later bound to lose its value as a marker of

Strength. Thus, now in agreement with the observations of Grafen (1981), this might well be the commonplace in normal, stationary situations. Yet we know that in such situations, either full or partial *Ownership Priority*, once established in a population, remains Evolutionarily Stable, even if one out of innumerable alternative (all the same inessential) ESS's.

I do not know whether such a speculative explanation can be actually served as a valid one for the emergence of Ownership Priority in some real situations, and I cannot think of any way to check it. It sure cannot be valid for other observed situations of Ownership Priority, in which ownership can never be a marker of strength. In addition to obvious phenomena of Ownership Priority, observed in virtually all human societies, this is the case, for example, when concerning meat (but not other sorts of food) in baboon troops. First priority is then reserved to the provider of the meat, even if low in rank and power. But Ownership Priority, in this case, as well as in most, if not all, other natural examples, cannot be separated from a more complex social structure, nor its path of evolution can be understood on the mere basis of Population Game Dynamics.

I believe that this is true for most, if not all Evolutionarily Stable Strategies, apparently observed in natural situations, either in human or in animal societies. Yet, in the perspective of more than thirty years, it appears that the very introduction of population game theory, even if often insufficient for the prediction of real evolutionary paths, especially in natural situations of multiple asymmetries, still provides us with an indispensable tool to understand which sort of animal (and maybe human) behavior can be long maintained in a population. This was the original objective of Maynard Smith and Price. I believe that even now, after thirty years of extensive development, this is what population game theory is mainly about.

References

Binmore, K.: *Game Theory and the Social Contract,* parts 1&2.

Bishop, D.T. and Cannings, C.: Models of animal conflicts. Adv. Appl. Prob. **8**, 616–691 (1976).

Bomze, I.M.: Non-cooperative two-person games in biology: A classification. International Journal of Game Theory. **15**, 31-57 (1986).

Bomze, I.M.: Dynamical aspects of evolutionary stability. Monatshefte fur Math. **110**, 189–206 (1990).

Bomze, I.M. and B¨urger, R.: Stability by mutations in evolutionary games. Games and Econ. Behav. **11**, 146–172. (1995).

Bomze, I.M., P¨otscher, B.M.: *Game Theoretical Foundations of Evolutionary Stability.* Springer. Berlin-Heidelberg-N.Y. (1989).

Eshel, I. and E. Akin: Coevolutionary instability of mixed Nash solutions. Jour. Math. Biol. **18**, 123-33 (1983).

Eshel, I. and U. Motro. Kin selection and strong evolutionary stability of mutual help. Theor. Pop. Biol. **19**, 420-33 (1981).

Eshel, I. and Sansone, E.: Multiple asymmetry and concord resolution of a conflict. Jour. Theor. Biol. 213/2. 209-222 (2002).

Feldman, M. W. and Cavalli Sforza, L.L.: Further remarks on Darwinian selection and "altruism". Pop. Biol. **19**, 251-260 (1981).

Gaunersdorf, A., J. Hofbauer, and K. Sigmund. On the dynamic of asymmetric games. Theor. Pop. Biol. **39** (3), 345-357 (1991).

Grafen, A. The logic of divisively asymmetric contests: respect for ownership and the desperado effect. Animal Behavior, **35**. 462-467 (1987).

Hamilton,W. D.: Extraordinary sex ratio. Science **156**: 282-290 (1967).

Hammerstein, P.: The role of asymmetries in animal conflicts. Anim. Behav., 29.193-205 (1981).

Hammerstein, P. and Selten, R.: Evolution Game Theory. In: *Handbook of Game Theory with Economic Applications*, Vol 2, R.J. Auman, S. Hart (eds), North Holland: Elsevier Science Publications, (1993).

Hofbauer, J.P. and Sigmund, K.: *Evolutionary Games and Population Dynamics*. Cambridge: Cambridge University Press, (1998).

Lessard, S.: Evolutionary stability – One concept, many meanings. Theor. Pop. Biol. **37**, 159-170 (1990).

Maynard Smith, J.: The theory of games, and the evolution of animal conflict. Jour. Thero. Biol. **47**, 209-221 (1974).

Maynard Smith, J.: *Evolution and the Theory of Games*. Cambridge, UK. Cambridge Univ. Press (1982).

Maynard Smith, J., and Price, G.: The logic of animal conflict. Nature (London) **246**, 15–18, (1973)

Maynard Smith, J. and Parker, J.: The logic of asymmetric contests. Anim. Behav. 25. 1-9. Jour. Theor. Boil **25**, 93-101 (1976.).

Samuelson, L. and J. Zhang. Evolutionary stability in asymmetric games. Journal of Economic Theory 57, 363-391. (1992).

Selten, R.: A Note on Evolutionary Stable Strategies in Asymmetric Animal Conflicts, J. Theor. Biol. **84**, 93-101 (1980).

Taylor, P.D.: Evolutionary stable strategies with two types of player. Jour. App. Prob. 16, 76-83 (1979).

Taylor, P.D.: Evolutionary stability in one-parameter models with weak selection. Theor. Pop. Biol. **34**, 654–674 (1989)

Vickers, G.T., and Cannings, C.: On the definition of an evolutionarily stable strategy. Jour. Theor. Biol. **129**, 349–353 (1987).

Weibull, J.W.: *Evolutionary Game Theory*. Cambridge: MIT Press (1995).