JOURNAL OF THE ROYAL SOCIETY Interface

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J. R. Soc. Interface 2013 **10**, 20130544, published 21 August 2013

JOURNAL OF THE ROYAL SOCIETY Interface

rsif.royalsocietypublishing.org

Perspective

Cite this article: McNamara JM. 2013 Towards a richer evolutionary game theory. J R Soc Interface 10: 20130544.
http://dx.doi.org/10.1098/rsif.2013.0544

Received: 19 June 2013
Accepted: 29 July 2013

Subject Areas:
biomathematics

Keywords:
strategy, variation, decision process, mechanism, flexibility

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Towards a richer evolutionary game theory

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Most examples of the application of evolutionary game theory to problems in biology involve highly simplified models. I contend that it is time to move on and include much more richness in models. In particular, more thought needs to be given to the importance of (i) between-individual variation; (ii) the interaction between individuals, and hence the process by which decisions are reached; (iii) the ecological and life-history context of the situation; (iv) the traits that are under selection, and (v) the underlying psychological mechanisms that lead to behaviour. I give examples where including variation between individuals fundamentally changes predicted outcomes of a game. Variation also selects for real-time responses, again resulting in changed outcomes. Variation can select for other traits, such as choosiness and social sensitivity. More generally, many problems involve coevolution of more than one trait. I identify situations where a reductionist approach, in which a game is isolated from is ecological setting, can be misleading. I also highlight the need to consider flexibility of behaviour, mental states and other issues concerned with the evolution of mechanism.

1. Introduction

All models are wrong, but some are useful [1].

In natural populations, the fitness of an organism often depends both on its own strategy and on the strategies of other population members. For example, if an animal contests over a resource with a conspecific, then the benefits of being aggressive depend on whether the opponent is liable to be aggressive. Evolutionary game theory is a standard tool that is used to predict evolutionary outcomes when there is such frequency dependence. Most game-theoretic models used by behavioural ecologists and other evolutionary biologists are simple schematic models that are manifestly unrealistic in that they vastly simplify the world. They usually have some uses, but I contend that they are often too simple, and that adding richness to the models can radically alter predictions; so that the simple models often mislead. In this paper, I outline some of my concerns about the way much of game theory is applied in behavioural biology and suggest some future directions for the field.

For definiteness, I focus on two-player games between members of the same species, although many remarks apply to multi-player games and those between members of different species. My focus is also on the stable endpoints of the evolutionary process, rather than the evolutionary dynamics that led to an endpoint (for an account of dynamics, see [2]). At an endpoint, the strategy adopted by population members is evolutionarily stable; i.e. no mutant adopting a different strategy can invade the population under the action of natural selection. In game-theoretical terms such a strategy is necessarily a Nash equilibrium strategy; i.e. the strategy maximizes the pay-off given other population members also adopt this strategy. As the Nash equilibrium condition does not exclude the possibility that rare mutants may have an equal pay-off to resident population members, and these mutants may be able to invade as they become more common, it must be strengthened to ensure evolutionary stability against all mutants. Maynard Smith's concept of an evolutionarily stable strategy (ESS) is one suitable strengthening of the Nash condition [3].

Two classic examples of two-player games are the hawk–dove game of aggression [3] and the Houston–Davies parental effort game [4]. In the standard

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hawk–dove game, individuals are identical and there are no role differences, and each contestant must choose whether to play hawk or dove. In the Houston–Davies game, one contestant is male and the other is female and each must choose its level of effort invested in care. In both games, the pay-off (fitness increment) to an individual depends on the action of the individual and its opponent.

These games share some common features:

— *Variation*. All individuals in a role have the same attributes (e.g. ability) although they may differ in what action they choose. Thus, in the Houston–Davies game all males are assumed to have the same ability to care, and all females are assumed to have the same ability to care.

— *Process*. Individuals choose their action without knowing the action of the opponent, and cannot later change their mind once their opponents' action becomes known. Games with this property are sometimes referred to as simultaneous-choice games. They are also known as 'sealed bid' games.

— *Ecological context*. The games are considered in isolation rather than being embedded in a wider model that specifies the ecological and life-history context. In particular, the pay-offs are specified in advance rather than arising in a consistent manner from these outside considerations.

— *Traits*. The trait that is subject to evolution is either the probability of choosing between two actions (e.g. hawk or dove), or if the trait is fundamentally continuous rather than a probability, is one dimensional (e.g. parental effort).

— *Mechanism*. The games concentrate on optimal behaviour, assuming this is achievable, and ignore the underlying psychological mechanisms that lead to behaviour.

These features are shared by a host of game-theoretical models such as vigilance games [5], predator inspection [6] and which parent deserts (Model 2 of [7]). One theme of this paper that I will elaborate on is that these features are often related. For example, if there are no individual differences this may mean that at evolutionary stability all individuals are doing the same thing and there is nothing to learn about the partner, whereas differences select for strategies that gain information about the partner. As an illustration of why games cannot be considered in isolation, consider the pay-off from breaking contact with the current partner and seeking a new partner. This pay-off depends on the availability of more suitable partners and their behaviour, and hence on the range of individual differences in the population and what occurs outside the narrow confines of the game under consideration. For example, in games of divorce, the quality of potential new partners in the pool of single individuals depends on the divorce strategies of all population members [8].

So how restrictive or misleading are these five assumptions? How do predictions of these simple models change when richness is added? For example, how are predicted levels of aggression between rivals or cooperation between parents changed when an interaction is put into an ecological setting, and when individuals differ and can gain information about each other?

2. Variation and its consequences

Between- and within-individual differences in behaviour are widely documented and sources of variation (such as genetic mutation) have been extensively discussed [9]. Here, I am mainly concerned with the consequences of variation rather than its source, although, as I will describe, adding richness to models allows more degrees of freedom and this can lead to the maintenance of variation through frequency-dependent selection. I focus on three classes of consequences; when small amounts of variation stabilize a game, when the direction of evolution depends on the amount of variation in a trait, and when the selection pressure on one trait depends on the amount of variation in another trait.

To conceptualize the types of variation that occur, we can think of the state of an organism as a vector specifying quantities, such as energy reserves, size and other physiological variables; abilities such as foraging or fighting and external information such as the reputation of an opponent or the number of offspring under care. A strategy is a rule for choosing actions as a function of state that is determined by genetics and by development. The actual behaviour of the organism in a particular situation is determined by the organism's strategy and its current state. Within-individual variation in behaviour occurs because, although an individual is always using the same strategy, its state varies over time or there is inherent randomness in its choice of actions. Between-individual variation in behaviour can occur because different individuals have different strategies or because they are in different states.

2.1. Errors stabilize games

Small random deviations from optimal behaviour provide a source of variation. Within game-theoretical models, these deviations are often referred to as errors. It is well known that occasional errors/small differences in behaviour are important in stabilizing games [10]. In particular, it has been argued that because errors do occur, evolutionary outcomes are predicted to be subgame-perfect Nash equilibria [11]. Loosely speaking, a Nash equilibrium strategy is subgame perfect if individuals playing the strategy take the best action (apart from rare errors) in whatever circumstance they find themselves in while playing the game.

For example, consider a game between two parents that are caring for their common young. Each parent can either care for the young or desert. Suppose that if the female cares the male does best if he deserts, while if she deserts he does best if he cares. Similarly, the female does best to desert if the male cares and care if he deserts. Suppose that the male chooses first, then the female chooses on the basis of the male's decision. One Nash equilibrium for this game is for the female to desert regardless of the male's decision and for the male to care. At this Nash, the male is forced to care because of the female's threat to desert regardless of his action. Note that this equilibrium is not subgame perfect, because the female would desert even if the male deserted, which would not be the best decision in the circumstances. However, she never faces this circumstance because he always cares. Now suppose the male makes the occasional error and deserts—or equivalently does not care because he has been killed by a predator. Then a female that carried out her threat to desert would be worse off than a mutant female that deserted if the male cared but cared if he deserted. As this mutant female would do equally well as a resident when the male cared and do better when he deserted, the mutant could invade. In other words, the Nash equilibrium would not be evolutionarily stable

[12,13]. This illustrates a general point — occasional errors or small differences mean that the whole game tree is explored. It is for this reason that we expect that what evolves should be a subgame-perfect Nash equilibrium [11].

Errors are important in affecting the stability of many games [14]. For applications of these ideas to the repeated prisoner's dilemma game, see Leimar [15].

2.2. Variation may change the fitness landscape

The above is concerned with rare errors. However, if errors or other sources in variation in the behaviour of an opponent are sufficiently commonplace, then this may change the fitness landscape by so much that the evolutionary equilibrium shifts dramatically. McNamara *et al*. [16] considers a repeated prisoner's dilemma game played between two contestants in which there is between-individual variation maintained by mutation. In this game, there is a fixed maximum number of rounds, N, and this maximum is known to both individuals. The game ends either immediately after the defection of at least one of the contestants or after N rounds if both players always cooperate. For this game, it is always best to defect on round N if this round is reached. For the pay-offs considered, the usual backward induction argument means that the only Nash equilibrium strategy is to defect always on the first round (at which time the game ends). McNamara *et al*. [16] consider a population in which the number of rounds to cooperate before defecting is genetically determined. In an evolutionary simulation, the evolved value of this trait depends on the mutation rate. When this rate is low, selection acts to reduce cooperation and at evolutionary stability the modal trait value is zero; i.e. the most common strategy is to defect on the first round, as predicted by backward induction. By contrast, when the probability of mutation exceeds a critical level, the direction of evolution switches and high levels of cooperativeness evolve. This occurs because, when there is sufficient variation in the population (maintained by mutation), it is worth an individual taking a risk that its partner is cooperative. In this model, it is phenotypic variation that selects for individuals to 'take a chance' with their partner, but the phenotype needs to be correlated with the underlying genetics if high levels of cooperation are to evolve.

For an example where noise in the centipede game leads to cycling in replicator dynamics rather than convergence to the subgame-perfect Nash equilibrium, see Ponti [17].

These examples illustrate a general issue that applies to both rare and frequent 'errors'. When a game can be solved analytically, then the result is a Nash equilibrium at which there is no variation. By contrast, evolutionary simulations automatically maintain variation through mutation and crossover. Variation is inherent in all biological systems, so when the two do not agree I suggest that it is the analytical solution that gives an unrealistic prediction.

2.3. The selection pressure on one trait depends on the amount of variation in another trait

The above example shows that the degree of cooperativeness that evolves can depend on the amount of variation in this trait. Here, I consider how the amount of variation in the trait also affects the selection pressure on the degree of choosiness for partners and the need to be socially aware.

2.3.1. Variation leads to choosiness

In many situations, it may be advantageous to break off interacting with an uncooperative or poor-quality partner and seek a better partner. However, searching for a new partner is liable to be costly, so that it will only be worth searching if there is a good possibility that the new partner is significantly better than the current partner. Here, the variation in the desired partner trait in the population is crucial; if all population members are equally uncooperative, then there is no point in changing partner. Only if there is sufficient variation will a change of partner be common.

McNamara *et al*. [18] illustrate the above point for a pairwise game in which individuals contribute to a common good but at a cost to themselves. Thus, there is a conflict of interest in that each benefits from a high contribution by their partner but would do best if at the same time their own contribution were low. The Nash equilibrium level of cooperation involves a low contribution to the common good, whereas both individuals would do better if they both contributed substantial amounts. McNamara *et al*. [18] consider a large population with an annual breeding season. Each year, before the breeding season, every population member plays a round of the game against another population member. The pay-off to an individual from the game is a resource that enhances its reproductive output that year. After two individuals play the game against one another in a year, they both decide whether they wish to keep the same partner to play next year's game; the pairing is maintained if and only if both players wish it and both survive until next year. If an individual is unpaired at the beginning of a year, it pairs with another randomly chosen unpaired individual. Offspring produced in a year are mature by the next year and are initially unpaired.

In the study of McNamara *et al*. [18], it is assumed that each individual is characterized by two genetically determined traits; the individual's contribution to the common good in the game and its choosiness about partner. For this game, the only Nash equilibrium solution is for individuals to give a low contribution to the common good and to be un-choosy about their partner. However, levels of cooperation that evolve in the population depend crucially on the amount of variation generated by mutation and on the lifespan of individuals (a parameter of the model). It is only worth being choosy and changing partner if there are liable to be other population members that are more cooperative and there is sufficient time to find a better partner and reap the benefits of this relationship. When variation is low, it is not worth being choosy and Nash levels of cooperation evolve. By contrast, when the mutation rate is high enough to maintain significant variation in the degree of cooperativeness, and individuals live a long time, it is worth being choosy. Consequently, choosiness increases in the population and this penalizes uncooperative individuals because these individuals are 'divorced' by their partners. The level of cooperation and the degree of choosiness thus coevolve to high levels.

2.3.2. Variation selects for social sensitivity

When individuals in a population interact with different opponents in a series of games, it is crucial whether these interactions can be observed by others. If observation is possible, then the action of an individual in a game has two distinct consequences; it affects the current pay-off and affects the reputation of the individual. Reputation then affects whether others later choose to interact with the individual or the action of others in future games against the individual. The existence of reputation can be crucial in determining whether cooperative behaviour evolves, as in models of indirect reciprocity (e.g. [19]).

When obtaining information about the traits of others (social sensitivity) is costly, it pays to be socially sensitive only if there is something valuable to be learnt. In particular, if all individuals in the population have the same trait value, and this value persists over evolutionary time, individuals will evolve to behave as if they 'know' this trait value and will not pay the cost of social sensitivity. Social sensitivity will only be maintained if there is between-individual variation in the trait. Variation might be maintained by mutation and developmental noise. However, it can also be maintained by a feedback mechanism; variation in social sensitivity can exert a selection pressure on individuals that maintains variation in the trait that is observed, and variation in this trait can, in turn, maintain the variation in social sensitivity. For example, McNamara *et al*. [20] consider a trust game. In this game, at evolutionary equilibrium, there is a stable mixture of socially sensitive individuals and highly trusting individuals that do not pay the cost of obtaining information. This maintains a mixture of trustworthy individuals that impress socially sensitive individuals with their reputation and untrustworthy individuals that rely on exploiting highly trusting partners. The proportion of these two types evolves so that the socially sensitive individuals and the highly trusting individuals do equally well, maintaining their mix. R. A. Johnstone & S. R. X. Dall (2003, unpublished data) consider a game in which population members play a sequence of rounds of the hawk–dove game, where each round is against a new opponent. Individuals have the possibility to eavesdrop; i.e. to have observed the result of their current opponent's last contest with another partner. Eavesdroppers only play hawk against individuals who previously lost their contest. The presence of eavesdroppers selects other population members to be consistent in their behaviour, either always playing hawk or always playing dove, because this reduces the chances of getting into costly fights. In turn, the presence of a mix of individuals consistently playing hawk and consistently playing dove maintains the need to eavesdrop. As a result, evolution leads to a polymorphic population composed of a mix of consistent individuals and eavesdroppers. For a more general analysis of this type of phenomena, see Wolf *et al*. [21].

3. Process, differences and their relationship

For all the two-player games mentioned above, the pay-off to an individual depends on its own action and that of its opponent. To predict evolutionary outcomes, it is not, however, sufficient to specify the pay-off structure; the process by which actions are chosen is also crucial. To illustrate this, consider two parents caring for their common young. Suppose that the possible actions of each are care or desert, and that pay-offs are specified in terms of the combination of actions chosen. McNamara & Houston [13] consider pay-offs for this game such that the best action of the male for given fixed action of the female is to care regardless of whether the female's action is to care or to desert, and the best action of the female is to care if the male deserts and desert if the male cares. McNamara & Houston [13] contrast two versions of the game; a simultaneous-choice version in which both individuals make their decision without knowing the action of the other, and a sequential-choice version in which the male chooses first and the female then bases her own decision on that of the male. In the simultaneous version of this game, at the unique Nash equilibrium, the male cares and the female deserts. In the sequential version of the game, at the subgame-perfect Nash equilibrium, the male deserts and the female cares; the male deserts to prevent the female from deserting. Thus, predicted evolutionary outcomes are reversed by changing the process by which actions are chosen.

In many real interactions between organisms, actions are not chosen simultaneously, i.e. without knowledge of the action of the opponent. For example, when penduline tits breed, there is either uniparental care by the male or uniparental care by the female or biparental desertion [22]. This pattern cannot be explained as the Nash equilibrium in a simultaneous game between the parents as there would then also be biparental care in some cases [23]. The process by which the combination of actions is reached by the birds is not clear, but it seems to involve information gathering; for example, the female attempts to hide the fact she has already laid eggs from the male [24]. To predict the pattern of care in evolutionary terms, it is necessary to first understand this process. This is an area where theory can only proceed with the necessary observations.

In economics, the field of extensive form games is concerned with decision processes, and there is an extensive literature (e.g. [25]). There have previously been some consideration of process in evolutionary game theory (e.g. [26,27]), but much more needs to be done.

Differences drive the process by which two individuals interact with each other. If the state, ability or motivation of a partner is not completely known, this selects for strategies to find out about the partner. We might then expect the process by which actions are chosen to involve interaction between the partners rather than being a sealed bid. To illustrate this with the parental effort game, suppose that each parent must choose the level of effort it expends in care of the young. In the version of the game studied in Houston & Davies [4], efforts are chosen as a sealed bid; the effort of each sex is genetically determined and it is predicted that they should coevolve to a Nash equilibrium at which each is the best effort given that of the other parent. In this game, parents do not adjust their efforts to the effort of their partner in real time. This has a perverse logic; at evolutionary stability, all males are assumed to be the same and all females are the same, thus there is nothing to be learnt about a partner that is not already coded for genetically. However, this seems unrealistic. Individual differences do exist, and when they are present, it is worth an individual taking note of the effort of the partner and possibly adjusting its own effort as a consequence. As the partner will also do the same, we may expect a period of adjustment (or continual adjustment during care). The situation is then completely different to that considered by Houston & Davies [4]. Now it is the rules for responding to a partner and choosing efforts that are genetically determined, rather than the efforts themselves. At evolutionary stability, the response rule of males (which specifies how to react to both a partner and internal private state variables) is expected to be the best given the response rule of females, and vice versa.

As McNamara *et al*. [28] show, the resulting negotiated efforts need not be best responses to each other; so that efforts are not as predicted by the model of Houston & Davies [4].

In the parental effort context, it has been suggested, or implicitly assumed, that an evolutionarily stable response rule is for each parent to continually adjust its effort to be the best effort given the current effort of their partner (e.g. [29]). This is wrong. In a population that behaved in this way, mutant individuals that put in low effort would do better than residents by exploiting their partner's willingness to compensate [28]. McNamara *et al.* [28] consider a model of negotiation between parents in which individuals differ in quality, with low-quality individuals paying a greater cost for a given level of parental effort. It appears difficult to find Nash equilibrium response rules in general, but McNamara *et al.* [28] do so in the special case in which the costs and benefits are quadratic functions of effort and the pay-offs to the parents are a function of the final negotiated efforts. This latter assumption might be reasonable when efforts settle down to their limiting values in a time which is short compared with the length of the period of care, so that efforts are close to their final values for most of this period. McNamara *et al.* [28] show that a Nash equilibrium response rule is for each parent to adjust to the effort of the partner using a specific function that is linear in the current effort of the partner and their own quality. At this Nash equilibrium, negotiated efforts are less than predicted by the simultaneous-choice game of Houston & Davies [4]. This occurs because both parents attempt to exploit their partner's willingness to partly compensate for their low effort.

The above reasoning applies to many standard games in behavioural ecology, such as those that model vigilance and predator inspection. For example, a predator inspection game might be concerned with the distances that each of two fish approach a suspicious object. Assuming these distances are chosen as a sealed bid and are not adjusted to the behaviour of partner is totally unrealistic. Instead of evolving the distances, any reasonable model would have to consider the evolution of rules that specify how to adjust distance as a function of the behaviour of the partner. Note that if fish were to adjust their distance to be the best given the distance chosen by partner (as assumed by [6]), then the population would not be evolutionarily stable for the same reason real-time best responses are not stable in the parental effort game. In a population that was evolutionarily stable, we might expect individuals to be less responsive to the partner than this (by analogy with the parental effort game). In such a population, the distance that a fish approached the suspicious object would not be the best given the distance chosen by its partner. In all of these games, we need to build future theory taking into account what information is actually used by the organisms to respond in real time.

The specific model of responding in McNamara *et al.* [28] has shortcomings. One is that at the Nash equilibrium a given change in a parent's effort provokes a change in their partner's effort that is the same for all partners. Individuals in the population are adapted to this level of responsiveness and hence 'know' the responsiveness of their partner in advance. However, if mutation maintained a distribution of responsiveness in the population, there would be selection to estimate the responsiveness of partners in real time. Individuals would then be expected to adjust their effort, not just to the current effort of the partner, but taking into account how much the previous efforts of the partner had changed in response to changes in their own effort—a much more complex rule.

A second limitation of the model of McNamara *et al.* [28] is the assumption that pay-offs are just functions of final negotiated efforts. Thus, the model is essentially an average reward model with no real final time. To remedy this shortcoming, Lessells & McNamara [30] model a finite series of interactions between parents with a final time that is known to both parents. One of their main conclusions is that efforts are predicted to increase over the period of care. This model is, however, limited in that there are no quality differences. New models which include both quality differences and time structure are needed. Such models may have to incorporate sources of noise in order to maintain selection on the need to continually monitor and respond to the partner.

McNamara *et al.* [28] are concerned with repeated interactions between a pair of individuals who initially have no information about one another. When individuals have a sequence of partners, their reputation in previous interactions may also be important.

4. Ecological context

Many games in behavioural ecology are considered in isolation, with costs and benefits specified in advance. However, costs and benefits often cannot be specified in advance but emerge from placing a game within an ecological or life-history context. In particular, outside options to the game are often important [10,31], but the value of the options may only emerge as a solution of the game.

For example, in the standard hawk–dove game, the contested resource has value V and the cost of losing a fight is C. At the unique Nash equilibrium, the probability a randomly selected population member plays hawk is p^*, where $p^* = V/C$ when $V < C$ and $p^* = 1$ when $V \geq C$. V and C are usually specified in advance, but is this reasonable? In the case where the resource is a territory, it is certainly not, because the strategy of an individual determines the probability of being in the role of owner, and the value of a territory depends on how easy it is to get an alternative, which depends on the strategy of conspecifics. (cf. [32,33]).

Houston & McNamara [34] consider a version of the hawk–dove game in which each male in a population encounters a series of females during his life. If a given female he encounters is uncontested by another male, he mates with her. If, on the other hand, a rival male contests the female, the two competitors play a hawk–dove game over access to her; if they both play dove, each gets to mate with her with probability 0.5 at no cost; if one male plays hawk and the other dove, the hawk mates with her; if they both play hawk, the winner of the fight mates with her and the loser dies with probability z. Between encounters with successive females, a male dies of other causes with some fixed probability. The pay-off to a male is his lifetime number of matings (which I denote by W).

For this game, it is reasonable to take the value of mating with a female to be $V = 1$; however, C cannot be set to some arbitrary value. This is because the cost of dying is the resultant loss in future reproductive success. Thus, $C = zW$. But the value of W for a male depends on his future behaviour and the behaviour of other population members. Thus W, and hence C, emerge from solving the game and cannot be specified in advance. Houston & McNamara [34] show that there is a range of parameter space in which there are two Nash equilibrium values of the probability of playing hawk, p_1^* and p_2^*, that satisfy $0 < p_1^* < p_2^* = 1$. When the resident strategy is to play hawk with probability p_1^*, it can be shown that $W = 1/zp_1^*$. Thus, $C = 1/p_1^*$, and hence $p_1^* = V/C$. When the resident strategy is to play hawk with probability $p_2^* = 1$, we have $W \leq 1/z$, so that $V \geq C$. Thus, at each Nash equilibrium, V and the cost C that emerges after solving the game are consistent with a single round of the hawk–dove game. However, this cost cannot be specified in advance.

This example shows the need to place games into an ecological setting in which consequences rather than pay-offs are specified in advance, and then treat the game as a life-history problem in which fitness is maximized. Having solved this holistic problem, costs and benefits for individual actions can be derived, if desired [35].

An early model of desertion illustrates how not adopting a holistic perspective leads to lack of consistency. In model 2 of Maynard Smith [7], a male and female each decide whether to care for their common young or to desert. It is envisaged that males get a benefit from desertion because they can then re-mate. This benefit is specified in advance. At one of the Nash equilibrium solutions given in Maynard Smith [7], females care and males desert. This is despite the fact that because all females are caring, there are none for males to re-mate with. This inconsistency was identified and the model was modified to remove the inconsistency by Webb *et al*. [36] (see also [37]).

In desertion games and games that analyse coy female behaviour [38], predictions on whether polymorphic behaviour within a sex evolves depend crucially on the assumptions about re-mating probabilities. If these probabilities are fixed, then a general result ([39], see also [40]) implies that any mixed strategy Nash equilibrium cannot be an ESS. By contrast, when re-mating probabilities are determined by population behaviour mixed strategy ESSs are possible [36,41–43]. The resultant variability that is generated in the coyness game of McNamara *et al*. [43] is essential to the maintenance of female choosiness (coy behaviour) in this game.

It is particularly important not to treat games that involve parental care and sexual selection in isolation. This is because the solution of one simple game is often related to the solution of another game. For example, if females are choosing males partly because of the care these males will give to young, preferred males will have more mating opportunities and hence be selected to care less. Thus, the value of mating with a particular type of male depends on the solution of the game, and the solution depends on the value [44]. For other examples of interrelations between components in this general area, see, for example, [35,45–47]. Ultimately, parental care and sexual selection models need to consider an ecological and life-history context in which quantities such the operational sex ratio, paternity allocation by females, mating preferences, mate choice behaviour and care behaviour emerge from the analysis, rather than being assumed at the beginning. As Houston *et al*. [48] emphasize, a reductionist approach is too limited in this area.

5. Traits

5.1. Discrete versus continuous traits

In the standard hawk–dove game, hawk and dove are the two possible actions and a strategy specifies the probability of playing hawk rather than dove. In reality, whether an animal is aggressive is liable to be contingent on circumstance; for example, it might be aggressive over a contested item of food only if it is sufficiently hungry, and a strategy specifies the critical level of hunger [49] above which to be aggressive, so that strategies fall on a continuum. In addition, there may be a continuum of levels of aggression.

Like the hawk–dove game, many situations are modelled as a simple game with a strategy taken to be a probabilistic rule for choosing between two actions, whereas there is a continuum of strategies in the real-world situation which the model is meant to represent. When cooperativeness and choosiness coevolve in the model of McNamara *et al*. [18], these two traits each lie on a continuum, and this is essential to their coevolution, as a small increase in one leads to a small increase in the other. In what other models would predictions be qualitatively altered if a more realistic set of strategies were considered?

In investigating the degree of cooperation that is predicted in a population, most focus has been on direct and indirect reciprocity in the prisoner's dilemma game (e.g. [50]). In this game, not only are there only two actions, but also the best response to any action of an opponent is always to be as uncooperative as possible. As many games in nature are unlikely to have this extreme form, we need to analyse more general games, allowing for continuous action spaces and individual differences. For what game structure does allowing interaction and negotiation lead to direct reciprocity-like behaviour and high levels of cooperation? For what game structures does allowing individuals to establish reputations result in a population that is more cooperative than that at the sealed-bid Nash equilibrium? McNamara, Doodson & Wolf (2012, unpublished data) establish a partial answer to this latter question for a special class of pay-off functions. In their game, individuals choose the level of their own resources to invest in a common good. Each individual meets a sequence of opponents chosen at random from a population, playing one round of a game against each. McNamara, Doodson & Wolf show that when the best response to an opponent on a single round is to decrease investment as the opponent increases investment, allowing reputation reduces mean population cooperativeness. This occurs because it pays to have a reputation of not being very cooperative because opponents will tend to compensate for this by investing more in the common good. By contrast, cooperativeness is enhanced by allowing reputations when the best response to an increase in investment by the partner is to also increase investment. Much more needs to be done in this area.

5.2. Multiple traits

Instead of considering the evolution of a single trait, we often should be considering the coevolution of two (or more) traits, because this can lead to different predictions. For example, in the parental effort game of Houston & Davies [4] and most games based on it, effort is taken to be a single non-negative number. Suppose that the benefit to young is a decelerating function of the total effort of the parents, and the cost to each parent is an accelerating function of its effort. Then, if both parents have the same cost function, it is predicted that both will expend the same effort on care. By contrast, suppose a parent's physiology influences its ability to care, with parents that are good at care paying a cost to maintain the relevant physiology. Then allowing physiology and parental effort to coevolve can lead to disruptive selection, resulting in one sex developing the ability to care and having high parental effort while the other sex evolves to be poor at care and put in low effort (McNamara & Wolf 2013, unpublished data). If instead of allowing physiology to change, effort is taken to be a vector specifying effort at providing food, effort at defending against predators, etc., then again there can be selection for role specialization, e.g. with one parent providing food and the other defending the young (Z. Barta, T. Szekely, A. Liker & F. Harrison 2013, unpublished data).

In the above example, going from the evolution of a single trait to the coevolution of two traits leads to sex role specialization. If there are no roles, increasing the dimension of the problem often leads to the evolution of polymorphism in traits. For example, Wolf & McNamara [51] consider a version of the hawk–dove game in which behaviour in a contest and physiology coevolve. At the resultant Nash equilibrium, some members of the population play hawk and have high fighting ability, others play dove and have poorer fighting ability. We have also seen that in the trust game [20] and the eavesdropping game of Johnstone & Dall, allowing social sensitivity to coevolve with the focal behavioural trait can lead to the evolution of polymorphism.

6. Mechanism

6.1. Mechanism

Most game-theoretical models ignore the psychological mechanism by which actions are chosen. Psychological mechanisms are typically general purpose and have evolved to deal with many situations in a complex world [52–55]. It follows that in any particular game, it is likely that a general mechanism is used rather than one specific to this game. Indeed, behaviour in games may just be determined by the usual learning rules of psychology that are not even specific to the fact the situation is a game [56]. If psychological mechanisms have evolved to cope with many situations, in order to predict behaviour in a game we cannot just model this game. Instead, we need to build models that identify the generic problem (e.g. pairwise competition over a resource) that includes this game as a specific instance, find what behavioural rule evolves assuming the rule does well (on average or is robust, as appropriate) over a range of situations that are instances of the generic situation, and then analyse the behaviour that the rule produces in the focal game (cf. [52]).

6.2. Flexibility

As organisms use rules based on mechanisms, these rules have limited complexity. Although there is much work on bounded rationality, especially in economic game theory (e.g. [57]), one aspect of limited complexity that needs further analysis concerns the lack of flexibility that results. If a population of organisms use rules of limited complexity in a complex world, then individuals will take the same (or similar) decisions across similar circumstances (every situation is unique). If there is also between-individual variation in the rules used, there will be population-level correlations in the behaviour across different situations. Thus, we can expect personality variation. Within such a population, past behaviour is then predictive of future behaviour. A consequence is that reputation is important when interacting with others. It may then be crucial whether reputation is a perfect predictor of future behaviour or only gives partial information. For example, consider the evolution of trustworthiness. Suppose that individuals are sometimes observed in their actions, so affecting their reputation, and sometimes unobserved. If individuals have some flexibility but this is limited, then they may have to establish an especially high reputation for trustworthiness when observed in order to convince potential partners of their trustworthiness when not observed.

The above discussion takes the degree of flexibility as a constraint. Instead, it might be reasonable to assume that flexibility can evolve, but that the greater the flexibility of the psychological machinery the greater the cost to maintain it. In some cases, even if flexibility is possible at low cost it might not evolve because there may be social pressures to be consistent. For example, it may pay for population members to observe the consistency of others and prefer to interact with those that are consistent. This latter topic has been little explored but deserves more attention.

6.3. Mental representations

How should the evolution of mechanism be modelled? One approach is to take a known psychological mechanism within some well-defined class and to analyse which specific mechanism within the class evolves (cf. [52,53,56,58]). Another more difficult approach is to try to evolve the class of mechanism without assuming its general form [53]. Whichever approach is adopted, it may be important to consider mental representations such as the degree of trust, love or anger felt for others. Although humans (and possibly other animals) may remember how trustworthy another individual was in all past interactions, they still summarize this information in feelings such as trust. This feeling is then important in influencing decisions about whether to trust the individual in a current interaction. Emotions such as trust may be assumed in models, or may emerge. As an example of the latter, state-space models allow the probabilities of transition between states to be under selection. At evolutionary stability, the rule that has evolved can then often be interpreted in terms of mental states [15].

Future work in this area needs to consider both the evolution of mental states and the consequences of this evolution for evolutionary game theory. For example, what are the consequences of channelling all previous information into a few summary variables which then determine current behaviour? Does this lead to more trust or cooperative behaviour in a population or less?

7. Final remarks

This perspective is not intended as a criticism of game theory as a whole, just the way it is applied in behavioural biology. Many of the tools to make richer models already exist, particularly in economic game theory, and biologist might profitably learn from that literature. However, even in economics the value of a model depends on its assumptions (cf. [59]) and may be very limited; so methods and models should not be uncritically imported from that field.

Models vastly simplify the world, but that is not a criticism of modelling. Good models give insights. However, it is always important to understand what a particular model can tell us, and what its limitations are. To gain insights, it is usually best to start with simple models and to understand what they can reveal and their limitations, and only then move on to models of greater realism and complexity. Applications of evolutionary game theory started with very simple models. Many of these models had their uses, but many are extremely limited, and their limitations have not always been appreciated. In particular, it has not always been appreciated that adding a little richness to many models completely changes their predictions. It is time to move on to less limited models.

Acknowledgements. I thank Zoltan Barta, Sasha Dall, Tim Fawcett, Alasdair Houston, Alex Kacelnik, Olof Leimar, Pete Trimmer and Max Wolf for comments on previous versions of this paper.

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