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The conservation game

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ABSTRACT

Conservation problems typically involve groups with competing objectives and strategies. Taking effective conservation action requires identifying dependencies between competing strategies and determining which action optimally achieves the appropriate conservation goals given those dependencies. We show how several real-world conservation problems can be modeled game-theoretically. Three types of problems drive our analysis: multi-national conservation cooperation, management of common-pool resources, and games against nature. By revealing the underlying structure of these and other problems, game-theoretic models suggest potential solutions that are often invisible to the usual management protocol: decision followed by monitoring, feedback and revised decisions. The kind of adaptive management provided by the game-theoretic approach therefore complements existing adaptive management methodologies.

1. Introduction

Many decisions in conservation biology and natural resource management occur in contexts of conflicting interests. Formal tools and behavioral methods adopted to assist conservation decision-making typically manage this conflict with an idealization. Decisions involving groups with competing interests—community delegates, conservation agencies, governments, industries, etc.—are modeled as decisions of a single agent attempting to maximize satisfaction of different objectives representing those interests: preserving indigenous land-use, protecting biodiversity, ensuring recreational access to natural areas, minimizing economic cost, etc. Such formal models presuppose intra- and inter-group consensus exists about relevant probabilities and utilities, which would ensure the optimal single-agent decision accurately reflects the best group outcome.

The focus on consensus is often reasonable. It facilitates using well-studied multi-criteria decision analysis methods to evaluate conservation problems. These tools include the analytic hierarchy process (Saaty, 2005), multi-attribute utility theory (Dyer, 2005), and other formal methods for gaining consensus recently applied to conservation decisions (Regan et al., 2006; Steele et al., 2007). Some natural resource management problems even mandate consensus decisions (Shields, 1998), although only consensus about the final outcome, not about every aspect of the decision, is typically required. Even so, the wisdom of always or usually seeking consensus is debatable (Brower et al., 2001; Peterson et al., 2005). Emphasizing consensus too often obscures, rather than illuminates, the structure of decisions about conservation. Often the conflicts of interests involved are irresolvable and thus seeking consensus is inappropriate. Guidance about such situations is nonetheless necessary for successful conservation action.

The literature on these issues has primarily emphasized explicitly acknowledging the conflict and negotiating (Peterson et al., 2005), and even appealing to higher authorities to force resolution. The first strategy is effective only if something resembling consensus can be cultivated, and the second is problematic if the "higher authority" is (or perceived to be) a stakeholder or non-impartial arbitrator (Helvey, 2004). In general, attempting to build consensus is futile if conflict is irreconcilable or cooperation is stubbornly partial. Moreover, powerful authorities benevolent to conservation are unfortunately rare. How to manage conflict without relying on authority or consensus is therefore crucial to effective conservation decision-making. In particular, non-cooperative strategies different

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stakeholders might possess, possible interactions between them, and how conservation decisions are structured bear significantly on what conservation goals are achievable.

Game theory is the appropriate framework for approaching these issues. Several types of conservation and natural resource management decisions correspond to different game-theoretic scenarios. Some scenarios have non-cooperative optimal solutions, others require cooperation to achieve optimal outcomes. If cooperation is infeasible, game theory still helps determine what decision strategies optimize conservation outcomes. For example, a game-theoretic perspective provides insights about: the strategies different stakeholders will likely adopt given their objectives when consensus, compromise, or cooperation are feasible; what types of cooperation best reflect stakeholder interests and achieve their objectives; which stakeholders are likely to form coalitions; the range of possible outcomes under non-cooperative and cooperative decision-making dynamics; and, whether an optimal or satisfactory solution for all stakeholders can be reached simultaneously.

Game-theoretic decision-making about conservation is a form of adaptive management where conservation advocates adapt their strategy based on expected responses from business interests, community delegates, governments, and other stakeholders. Section 2 introduces the basic concepts of game theory and some commonly-encountered games, and considers how multinational cooperative conservation efforts can be analyzed in a game-theoretic framework. Section 3 shows how common-pool resource management is modeled game-theoretically, and reviews applications of game theory to conservation problems.

Game theory's scope is not restricted to strategic interactions between conscious, deliberative players such as humans. Nature itself can be represented as a player in a conservation game, dynamically responding to attempts to conserve it in sometimes surprising and challenging ways. Game theory helps anticipate such responses to management actions and identify the best adaptive counter-strategies. Section 4 describes these conservation games against nature and shows how game theory provides guidance about their resolution. Section 5 discusses the issue of uncertainty about determining which game is being played. Combining standard decision theory with game theory makes this potentially debilitating problem tractable.

Applications of game theory to conservation problems are not new (see Walters, 1994; Milner-Gulland and Mace, 1998, and Sections 3 and 4 below), but have been of limited scope. Most have analysed a single game-theoretic structure, have been employed post-hoc to describe decision-making retrospectively, and/or have focused on hypothetical, idealized problems. Besides reviewing previous game-theoretic treatments of multi-stakeholder conservation decisions, we survey different types of games, discuss their possible outcomes, and show how they provide prescriptive guidance, as well as descriptive information, about a range of conservation problems. That stakeholder interests often conflict is highlighted throughout this discussion. Conflict and disagreement are the status quo, not the exception. Representing such decisions as games where stakeholders employ competing strategies is a first step in understanding, representing, and addressing the complexity of decision-making in conservation and natural resource management.

2. Game theory, multinational decisions and adaptive management

In many situations more than one party is both involved in a conservation decision and its implementation. Consider an animal species with a declining population, whose range spans two countries. Such real-life examples abound in the literature on transboundary conservation (e.g. Roca et al., 1996; Goodale et al., 2003; Wolmer, 2003; Zbicz, 2003; Hanley and Folmer, 1999). Conservation efforts in such cases will be most effective if both countries cooperate to protect the species. This requires general agreement that the conservation efforts are warranted and worthwhile, but the two countries may be motivated differently about the details of the conservation plan in ways that produce game-theoretic, rather than decision-theoretic, dynamics. These dynamics can take several forms, which we describe below.

First consider the case where conservation efforts would fail unless both countries commit to a particular conservation strategy that comes at no cost to either party. Assume also that unilateral commitment by one country would yield partial success in curbing species decline but that this is unacceptable to either party. This can be represented in the standard game-theory matrix (see Table 1). Each country (or player in the game) either cooperates or defects, and the four possible outcomes are assigned ordered-pairs of preference rankings. The first number is the ranking for player 1 "row" and the second for player 2 "column"; higher numbers represent outcomes more preferable to that player than lower number outcomes (in this paper we focus primarily on games with direct outcomes or payoffs to players, but see Ule et al., 2009 for the ramifications for cooperation of indirect rewards or punishment).

In this game, the solution is straightforward: both parties should cooperate and commit to the recommended conservation strategy since it is in both their interests. It is worth spelling out the game-theoretic reasoning that supports this intuitive conclusion. Here, cooperation has two very desirable properties. First, it is optimal in the sense that no player can do better without the other player being worse off. Solutions with this property are called Pareto optimal. Second, no player would unilaterally change his or her action from this solution. Solutions with this property are called *Nash equilibria*. The coincidence of these desirable properties makes cooperation such a compelling and robust solution (see Binmore, 2007; Luce and Raiffa, 1957, and Osborne, 2003 for more on game theory). In other cases, things are not so straightforward.

Alter the example so that defection from the agreed conservation strategy is a realistic option. Suppose that unilateral support of the conservation strategy would yield a cost to the country supporting the strategy but benefits would accrue to both countries. If both countries consider the conservation benefits and economic costs of different strategies, a game of "chicken" can emerge. Similar game-theoretic dynamics occurred in the cold war arms race (Table 2). There are two (uncoordinated) Nash equilibria but no Pareto optimal solutions.

Now change the example again so that each country can unilaterally achieve results with less cost, but where the result of the cooperative conservation effort would be preferable. For example, each country could defect from a bilateral conservation program by implementing a unilateral, less expensive but less effective, program. This yields the "stag hunt game" (Skyrms, 2004), where

Table 1
Simple cooperative game.

		Player 2 "column"	
		Cooperate	Defect
Player 1 "row"	Cooperate	2, 2	1, 1
	Defect	1, 1	0, 0

Table 2
The game of chicken.

		Player 2 "column"	
		Cooperate	Defect
Player 1 "row"	Cooperate	1, 1	1, 2
	Defect	2, 1	0, 0

Table 3
The stag hunt game.

		Player 2 "column"	
		Cooperate	Defect
Player 1 "row"	Cooperate	2, 2	0, 1
	Defect	1, 0	1, 1

Table 4
Prisoners' dilemma/free-rider problem/tragedy of the commons.

		Player 2 "column"	
		Cooperate	Defect
Player 1 "row"	Cooperate	3, 3	0, 5
	Defect	5, 0	1, 1

there is a Pareto optimal Nash equilibrium (both parties cooperate), but also a risk-averse, sub-optimal Nash equilibrium (parties do not cooperate) (Table 3). Non-cooperation is risk averse because if one party defects the other is better off defecting as well, so the safest strategy is defection.

A final variation produces a model of multi-national cooperation. Assume several countries cooperate and agree to share the costs of a conservation plan. Suppose also that defection by one country would benefit that country by reducing cost without noticeable detrimental effects to the overall conservation goal. Defection therefore seems rational. But if every country defects, there is a significant cost—failure of the conservation effort. This is the well-known free-rider problem, or prisoners' dilemma (Table 4). If, however, conservation success requires all nations to cooperate completely, the game is an *n*-player stag hunt. Uncertainty about the structure of conservation decisions can therefore yield uncertainty about which game is being played, and games can be changed by subtle empirical matters (e.g. how many countries must cooperate to achieve conservation goals).

There are several advantages to viewing such conservation scenarios as games. First, game theory can help discover solutions to these decision problems. Even when a definitive solution cannot be found, game-theoretic analyses often clarify the structure of conservation problems and provide insights about how they are best managed. For example, in a game of chicken, signaling credible commitment to the defection strategy is rational. This signal is expected, and unless the commitment really is credible (and ideally irreversible) the signal should not be taken seriously. Although this is well known within the game theory literature, it may not be apparent in conservation contexts until a game-theoretic analysis reveals a game of chicken is being played (Osborne, 2003).

Game theory may also indicate what the likely outcomes of a conservation scenario will be in advance. In some cases, the best advice is to avoid setting things up as initially planned. For example, (discussed at length in the next section) the best way of dealing with the tragedy of the commons is, in effect, to change the game by penalising non-cooperation until it is no longer rational. Table 5 summarizes the range of games described here, their characteristics, optimal strategies and appropriate applications.

These potential benefits of the game-theoretic perspective show how game theory is a kind of adaptive management. The key to adaptive management is that the outcomes of management strategies are monitored and then assessed against clearly-specified goals. Management strategies are then revised accordingly, often mid-stream (Walters, 1986). Usually, implementation of the initial strategy, monitoring, assessment, and strategy revision occur sequentially, but it need not. Game theory supplies adaptive information about the probable efficacy of strategies before the actual outcomes of implementation. Strategies can then be adapted prior to being adopted because the likely outcomes are sometimes clear beforehand. Moreover, game theory requires agents be explicit about goals, strategise about the best ways to achieve those goals, monitor strategy success, and modify strategies given the impact of other agents on those goals. These are all key elements of successful adaptive management. Game theory mandates attention to these elements of environmental decision making, and by doing so enhances and affirms the role of adaptive management methods in conservation planning.

One idealization employed in game theory should be highlighted. Game theory assumes each agent is self-interested and that their interests are reflected in a preference ordering (see Dodds, 2008 for a full discussion of this issue). Each agent tries to obtain the best outcome for themselves. Game theory does not prohibit an agent from considering the interests of others. For example, an agent may prefer an outcome that less (directly) benefits them because it benefits someone else they care about (e.g. see Ule et al., 2009). But this apparent altruism must produce some (perhaps indirect) benefit to the agent, according to game theory. (Perhaps they "feel good" about helping others.) Being "self-interested" in game theory only requires that all such considerations are fully reflected in the agent's preference ordering.

3. Management of common-pool resources: game-theoretic examples

In conservation contexts, a common-pool resource is a natural resource available for consumption, from which it is difficult to exclude or limit users (Ostrom, 1999). Users can be individuals,

Table 5
Game-theoretic scenarios often found in conservation and environmental decision making.

Game (structure)	Characteristics	Optimal strategy	Conservation application examples
Simple cooperative game (Table 1)	Cooperation has no cost, but non-cooperation does; acceptable conservation outcomes require both parties cooperate	Cooperate (Pareto optimal, Nash equilibrium)	Reducing harvest yields beyond some minimum threshold (e.g. fisheries management), trans-boundary species conservation requiring multi-national cooperation (e.g. poaching abatement), forging binding climate change agreements
Chicken (Table 2)	Unreciprocated cooperative action is costly to the acting party but benefits non-acting parties; mutual defection is the worst outcome	Defect if the other party will cooperate; otherwise cooperate	Managing common-pool resources, trans-boundary species conservation (where only some parties must act to achieve a satisfactory conservation outcome)
Stag hunt (Table 3)	Defection is beneficial, but is not as much as mutual cooperation	Cooperate (Pareto optimal, Nash equilibrium); risk averse defection (Nash equilibrium)	Land-use management, managing common-pool resources (e.g. fish stocks)
Prisoners' dilemma/free-rider problem/tragedy of the commons (Table 4)	Unreciprocated cooperative action is costly to the acting party but benefits non-acting parties	Defect (Nash equilibrium) unless mutual cooperation can be guaranteed	Land-use management, utilization of common-pool resources (e.g. management of fish stocks)

communities, institutions, states, or nations. Examples of natural common-pool resources are fishing grounds, forests, populations of animal and plant species, wetlands and grazing lands. For common-pool resources, one user's consumption decreases other users' potential consumption. If left unchecked, this can lead to conflict, over-use and depletion as users strive to appropriate more and more of the resource. Unconstrained use of common-pool resources is a major conservation concern and continues to be a major cause of decline in biodiversity. This section reviews some of the game-theoretic approaches to understanding and managing the consumption of common-pool resources. Although the review is not exhaustive, it highlights a range of game-theoretic conservation problems and describes the insights they give into the social dimension of decision making.

3.1. Tragedy of the commons

Tragedy of the commons is the most widely understood outcome of unconstrained consumption of common-pool resources (Dodds, 2005). Hardin (1968) coined the term to refer to situations where each individual in a commons independently attempts to maximize his/her gain of the common-pool resource. In acquiring resources, an individual exclusively appropriates each additional unit of positive utility but the negative utility associated with removing the resource from the common pool is shared across all individuals. The positive utility of resource appropriation to an individual therefore almost always outweighs the negative utility of reducing the resource. Hence, when individuals operate independently, acquiring more and more of the resource maximizes each individual's utility, and "therein lies the tragedy" (Hardin, 1968).

The solution has traditionally been to impose top-down regulation of all users' resource appropriation through sanctions, reprisals, individual limits, and incentives. This has been the case with the International Whaling Commission (IWC), the Convention on International Trade in Endangered Species (CITES) and the Convention on Biological Diversity (CBD) (for a review see DeSombre, 2007). These institutions often oversee a game of chicken where some players agree to cooperate while others refuse, and where the nature of the game evolves through time and across spatial scales due to changes in the status of the resource, the consequences of prior decisions and actions, and changes in player composition. When effective enforcement is infeasible, users "who would willingly reduce their own appropriation if others did are unwillingly to make a sacrifice for the benefit of a large number of free riders" (Ostrom, 1999). The free-rider problem lies at the heart of the tragedy of the commons and thus cooperation, at least in part, is crucial to successful regulation of common-pool resources. This example also shows that some conservation problems involve embedded games: games nested as sub-modules in other, broader games, where the structure of one may determine the outcome of the other, and vice versa.

Empirical studies show that in many conservation contexts cooperation is more likely to emerge from bottom-up community-based programs than top-down enforced regulation. In bottom-up programs, users are usually local residents that have traditionally relied upon the common-pool resource for subsistence and self regulate consumption by imposing their own enforcement of restrictions, or partnering with local authorities to do so (Gibson and Marks, 1995; Ostrom, 1999; Goodale et al., 2003; Sirén, 2006). The formal game-theoretic approaches that have been used to date to address the potential for tragedies of the commons include both top-down and bottom-up approaches. We survey examples of game-theoretic applications to conservation management in the next section. The aim is to show how game theory can characterise the conflicts involved, and assist in improving conservation management and decreasing the over-use of common-pool resources.

3.2. Poaching and enforcement

Most game-theoretic analyses of conservation issues have focused on poaching or overharvest of common-pool resources in both terrestrial and marine environments. The games considered run the gamut from non, to partially, to fully cooperative, and most have been modeled as the stag hunt, chicken, or prisoners' dilemma (or free rider).

Gibson and Marks (1995) use non-cooperative game theory to analyse the failure of community-based wildlife management programs to abate poaching in Africa. The illegal hunting of wildlife in Zambia is their case study. They describe the choices confronting wildlife scouts and rural residents and examine a range of incentives and motives to show that the assumptions underpinning many wildlife management programs do not represent the incentives and motives of rural hunters and scouts. As a result, local hunters continue to kill game at unsustainable rates. Increased enforcement has, however, shifted their tactics and prey selection. Gibson and Marks (1995) conclude that wildlife management schemes have failed because they poorly represent the motives of rural residents and do not sufficiently incentivise against hunting. The extant incentive structure only targets individual hunters through punishment rather than benefits, while non-hunters reap tangible rewards from a successful wildlife management program—the consequence is that hunters reject the management regime. The game-theoretic analysis suggests a bottom-up approach where rural residents are invested with greater authority over wild animals would be most effective.

Mesterton-Gibbons and Milner-Gulland (1998) extend this example to focus on Zimbabwe's Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) project. This project is intended to provide incentives for local residents to refrain from poaching rhinos. Local residents must decide on whether to poach and whether to enforce the law in what is essentially a stag hunt game. Each individual can cheat in two ways: by poaching (in the role of resident) and by electing not to enforce the law (in the role of potential scout). They use cooperative game theory to determine the conditions under which community self-monitoring would ensure conservation occurs and conclude that "no self-monitoring agreement can be sustainable without a payment to each individual that exceeds the opportunity cost of monitoring—even if no one is poaching" (Mesterton-Gibbons and Milner-Gulland, 1998).

Keane et al. (2008) review game-theoretic models of enforcement and compliance to study rule-breaking behavior in conservation, using African elephants as a case study. They review individual-, group- and institution-level models and identify a few important game-theoretic results about elephant conservation: (i) fines proportional to the number of trophies in a poacher's possession are more effective than fixed fines, (ii) increasing the effort devoted to detecting and prosecuting poachers is more effective than increasing the severity of punishment to poachers (Milner-Gulland and Leader-Williams, 1992; Leader-Williams and Milner-Gulland, 1993), and (iii) the success of bans on international ivory trade is ambiguous, depending on the assumptions in the model. The fact that banning ivory could increase elephant poaching is particularly interesting. It could be caused, at least in part, by an expected rise in ivory prices that would enhance incentives to poach elephants (Kremer and Morcom, 2000). Bulte et al. (2003) also claim that trade bans can accelerate species toward extinction if speculators bet on future price increases by stockpiling, with the intention of cashing in on their stock once the species becomes extinct.

The most extensive application of game theory in wildlife management has been to fisheries (see Sumaila, 1999 for a review). Few applications of game-theoretic models to fisheries have targeted *conservation* management, but the current state of fisheries makes these applications relevant to conservation. We review two game-theoretic fisheries applications that emphasize conservation.

Burton (2003) uses a game-theoretic model based on the stag hunt to investigate community-based sanctions to maintain quota and entry limit restrictions in a fishery. The model shows that sanctions remove the incentive for small coalitions to defect; larger groups usually do not defect because the effects on fish stocks would reduce the rewards of doing so. The type of restriction and whether the fisher's operation is low or high cost determines whether there is an incentive to defect. Burton demonstrates that the heterogeneity of fishers and how they interact in the absence of external regulation drives the game-theoretic dynamics.

Byers and Noonburg (2007) investigate the impacts of poaching on marine reserve effectiveness with a game-theoretic model. In their model, individual fishers "maximize profit from a fixed amount of fishing effort but compete with one another in the harvest." The goal is to assess what level of enforcement and penalisation for poaching is necessary to achieve a desired level of compliance. Their game-theoretic analysis of poaching questions the reliability of previous models, which assume that setting aside reserves is equivalent to implementing catch quotas (with complete compliance).

3.3. Land-use change and trans-boundary management

Although most game-theoretic treatments in conservation management have focused on poaching and enforcement, game theory is also being used to assess other social choice issues in land-use change and trans-boundary management. Rodrigues et al. (2009) study a two-person game where each landowner manages a single land parcel that can change states through time to forested, agricultural or abandoned. One landowner's choice to deforest his/her land affects the utility of the adjacent landowner's parcel. Landowners decide to conserve or deforest based on their opponent's choice and future state changes in the parcels. Interestingly, Rodrigues et al. (2009) show that two types of social dilemma arise in this game based on how quickly the forest regenerates. When the forest regenerates very slowly but agricultural abandonment occurs rapidly, the stag hunt dilemma is most likely. When the forest regenerates quickly and agricultural abandonment occurs slowly, a prisoners' dilemma is likely. The likelihood of a social dilemma in this scenario (i.e. stag hunt or prisoners' dilemma) is uninfluenced by socio-economic factors but determined by the environment, in this case forest regeneration and agricultural abandonment rates. Section 5 considers the difficult issue of how to deal with uncertainty about game structure.

4. Games against nature

Competition and cooperation between governments, NGOs, and other groups about conservation issues are obviously game-theoretic. The game-theoretic character of more mundane conservation decisions is much less appreciated. Consider three typical conservation optimization problems: selecting areas to protect species on limited land-acquisition budgets (Joseph et al., 2009), monitoring species to evaluate potential threats with limited time and fixed budgets (Grantham et al., 2009), and managing species recovery plans to maximize persistence probabilities with similar monetary and temporal constraints (Pressey et al., 2007). These problems share a common structure. They require decisions about actions that attempt to maximize some quantity while others—typically resources of some kind—are fixed. Representing these problems decision-theoretically, rather than game-theoretically, involves two oversimplifications. First, resource constraints are often more flexible than fixed (Colyvan et al., 2009; Colyvan and Steele, 2011). Constraints are typically negotiated, and the appropriate framework for such negotiations is game-theoretic, usually as Nash bargaining games (Nash, 1950; Binmore, 1998, Chapter 1). In fact, results of optimization analyses in conservation planning alone can supply compelling reasons to modify proposed constraints, particularly initial budgets (see Justus et al., 2008).

The second oversimplification is assuming that nature's response is straightforward and easily predictable following conservation actions such as monitoring or managing species. Nature often responds dynamically and unexpectedly to such actions. Recent studies suggest, for example, that some marking methods used in conservation monitoring negatively affect marked animals, thereby changing their behavior and distorting the information acquired (see McCarthy and Parris, 2008). In these cases, representing nature as part of the fixed background structure of the conservation problem is inaccurate. Rather, it should be treated as another player in the game.

This may sound counterintuitive, especially given economists' typical assumptions about players—that they are perfectly rational expected utility maximisers for instance. These assumptions effectively require players be expert game theorists: they must know not only what their strategy should be, but also what other players' strategies should be. (Typically, these strategies cannot be determined in isolation and both must be determined simultaneously.) Whether these assumptions are reasonable approximations or unrealistic idealisations of actual human decision-makers is controversial (see Henrich et al., 2005), but their implausibility for nature—which is neither conscious nor rational—is obvious. Rather than attempting to approximate some idealised human decision-maker, in conservation biology the objective of treating nature as a game-theoretic player is to capture the dynamic response of what is being conserved to attempts to conserve it. Conscious agents and their deliberate, considered responses to various strategies are replaced with species and other natural entities responding to conservation strategies. In hydrology, for example, nature can be represented as an agent that prefers liquids to attain their lowest level and it schemes to make this happen. Humans attempting to increase water tables or construct artificial lakes are players with different intentions and they must play against nature.

It is useful to distinguish between nature as a player in a game and nature as a rule maker. There will be structural features of the game—such as, which moves are available to a player—that are immutable and non-negotiable. Laws of physics and laws of nature more generally are inviolable, at least in the context of the games being considered (Colyvan and Ginzburg, 2003). Such external constraints on games can be understood as being dictated by "nature as a rule maker". "Nature as a player in the game" can make moves left open by the structural features of the game. Note that background constraints and possible moves in a game will often vary across contexts. For example, when governments unalterably fix conservation budgets, this constitutes a constraint in the game and governments are acting as rule makers. But sometimes budgets are negotiable and then governments are acting as players. So too with nature. It both sets constraints and makes moves. Determining which role it plays in any given context is difficult but part of the art of good modeling. Nested games are particularly challenging. At one level nature may act as a player. The outcome of that game may then serve as a constraint in game at another level. At this level, nature is acting as a rule maker.

Considerable work on these so-called "games against nature" has been done outside conservation contexts (e.g. Luce and Raiffa, 1957, Chapter 13), but applications to conservation biology are rare (e.g. Palmini, 1999). Similar to the conservation-focused competition and cooperation between groups discussed above, a game-theoretic perspective also offers important insights about conservation games against nature. Consider a core conservation concern: ensuring species (and environmental resources more generally) never reach irreversible thresholds below which population decline and ultimate extinction are inevitable. This was the motivation behind the original "safe minimum standard," "minimum viable population," and related concepts (Ciriacy-Wantrup and Phillips, 1970; Frankel and Soulé, 1981). Besides controversies about the uncertainty, predictive accuracy, and empirical validation of methods used to assess these concepts (see Morris and Doak, 2002, Chapter 12; Brook et al., 2002), such analyses were also criticized for generally failing to consider how the value of species to humans—economic value in particular—may impact viability (Bulte et al., 2003). Modeling attempts to maximize species viability as types of games against nature provides a more comprehensive account of what adequate conservation requires.

How the game is represented significantly affects what conservation actions are defensible and/or whether a compelling rationale for conservation exists. For example, decisions about irreversible destruction of natural resources, such as species extinction, can be formulated as two kinds of games against nature: insurance and lottery games (Ready and Bishop, 1991). Both games involve two potential actions: development that precipitates species extinction (with certainty), or preservation that guarantees species persistence. Both games also involve two kinds of uncertainty about nature: that the species threatened with extinction *could* contain the cure for a future *possible* disease epidemic. The insurance game assumes at least one threatened species contains a cure that would be completely effective against an epidemic. The game structure is depicted in Table 6, where $D > 0$ is the net development benefit, $-L$ is the uncured outbreak's net negative value, $L > D$, and no information about the probability of outbreak is available. In this game, preservation is insurance against the threat of outbreak. A minimax decision criterion, for example, recommends one consider the greatest possible losses and then choose the action that minimises those. It favors preservation because development risks the maximum possible loss, $D - L$. This is one form of a precautionary principle.

Even this simple game can be reformulated differently on reasonable grounds. Rather than assume a certain cure and an uncertain outbreak, the lottery game assumes, perhaps more realistically, a certain outbreak and an uncertain cure (Table 7). In this game, preservation constitutes a lottery, not insurance, about whether protected species contain a cure to the upcoming disease outbreak. Development is now favored on the minimax criterion because $-L$ is the worst possible outcome. Differences in the kind of uncertainty between the insurance and lottery games therefore yield different conclusions about the legitimacy of conservation actions.

These examples highlight the salience of a game-theoretic perspective on conservation decision-making, even in the absence of human players with strategic intentions and deliberations. As models of real-world conservation decisions, these games are more illustrative than representative. Ready and Bishop (1991) stress that uncertainty realistically exists both about the probability of outbreak and that preserved species would contain a cure, and that several other assumptions are similarly simplistic. Applying other decision criteria—maximization of expected utility, minimax with regret, maximax, and many others—can yield different guidance about conservation in games against nature as well. Of course, many, perhaps most, conservation problems involve not only nature as an opponent, or groups with competing interests (see Sections 2 and 3), but both simultaneously (see Bulte et al., 2003). This formidable complexity partially explains why so many conservation problems remain unresolved.

Table 6
State of nature 1.

		Player "column"	
		Outbreak	No outbreak
Player "row"	Outbreak	$D - L$	D
	No outbreak	0	0

Table 7
State of nature 2.

		Player "column"	
		Cure	No cure
Player "row"	Cure	$D - L$	$D - L$
	No cure	0	$-L$

5. Uncertainty about the game

The above examples show that quite different games arise out of very similar circumstances. Although game theory offers advice about optimal strategy when the details of games are fixed, it offers little unequivocal advice when there is uncertainty about what the game is. Consider multi-national cooperation on conservation efforts. As Section 2 noted, whether the game is chicken or a stag hunt depends on how many countries must cooperate to achieve the conservation goal. But suppose this information is unavailable or only probabilistic information exists about the relevant number of countries. The game being played would be unknown. This variety of model uncertainty—not knowing which theoretical model (stag hunt or chicken) appropriately represents the situation—is difficult to quantify and potentially debilitating (Regan et al., 2002).

Section 3 showed that the best way to achieve cooperation in such games is to introduce penalties and rewards that effectively change the game to one of simple cooperation, where cooperation is a Pareto optimal Nash equilibrium. What rewards and penalties are required depend on the game details, but uncertainty about which game is being played yields uncertainty about which reward and penalty regime to introduce. The apparent limits of game theory techniques therefore threaten an impasse.

Game theory alone cannot solve this problem, but it is a classic problem of decision making under uncertainty. The various games we are uncertain about can be represented as states of the world in a decision problem. Our possible actions include penalty and reward regimes and each outcome's payoff is the value of each game for each player under the reward regime employed. Probabilities should be assessed for each game (i.e. the probability that a particular game is being played) and expected utilities of actions are calculated by weighing outcome utilities with their respective probabilities. The devil, however, is in the details. Successful implementation will depend on much about the specific case, which will often be very complicated. The general idea is quite straightforward and an example will help illustrate.

Suppose it is known that a multi-national conservation game is either chicken or stag hunt but it is unknown which. Although it is an empirical matter which game is being played, available data may not easily resolve the issue. Modeling can help. The probability that all countries must cooperate, versus the probability that only some countries must cooperate is needed. Suppose our models deliver (with the available data) probability p for all countries having to cooperate (i.e. the probability a stag hunt is being played) and $1 - p$ for the probability only some countries must cooperate (i.e. the probability chicken is being played). If there is no chance the conservation goal can be achieved without cooperation, three policy regime options are available: transform chicken to a simple cooperative game, transform stag hunt to a simple cooperative game, or do nothing. Value of information analyses can be performed to determine whether (and what) further information may be required (see Gould, 1974; Raiffa, 1968; Peck and Teisberg, 1993; Runge, 2011). The payoffs for each regime are the summed payoffs of the relevant games less the costs associated with the regime transformations. Whichever penalty regime maximizes expected utility would then be the regime implemented.

Such hybrid decision analyses make use of both game theory and decision theory and are the best way of dealing with model uncertainty. In such cases, neither game theory nor decision theory alone provides guidance. But together they are capable of dealing with many difficult decisions encountered in conservation management.

6. The potential of game theory

Many useful applications of game theory to conservation await successful implementation. But game theory is not a panacea for all difficult decision problems in conservation and resource management. As with other formal decision tools—decision theory, operations research, consensus methods, and others—appropriate implementation by skilled decision makers is crucial. Game theory should prominently feature among the suite of decision tools at the disposal of conservation and natural resource managers.

Even if using formal methods does not prove to be practical in a given situation, thinking about decisions from a game-theoretic perspective can often clarify and improve informal decision making (see Lindenmayer et al., in preparation for an example of informal game-theoretic reasoning in identifying potential problems for carbon sequestration schemes). For example, noticing that a decision will evoke a response from the natural world, seeing the situation as a game against nature helps decision makers anticipate how things will pan out. This improves on the static picture presented by decision theory. Thinking game-theoretically requires possible responses to decisions be considered and, if necessary, anticipatory revisions to those decisions. This engenders a more dynamic, adaptive view of the environment and our place in it. As a form of adaptive management, game theory also prompts attention to appropriate time scales and whether the games will be repeated. These issues, in turn, often favor a more long-term perspective on environmental decisions and their possible long-term consequences. Herein lies the real value of game theory: it provides a general and powerful framework for analysing environmental decisions, one that adopts a dynamical approach to decisions and naturally lends itself to an appreciation of the ongoing and far-reaching consequences of major environmental decisions.

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