Applications of Game Theory

Game theory is applicable to almost all aspects of strategic human interaction. Simply, game theory can accurately model interaction between human agents in diverse settings. However, the purpose of this essay is to consider the veracity of game theoretical models in an ecological context, specifically the Prisoner's Dilemma ("P.D.") model; this will concern strategic preferences (e.g. combative and non-egoistical) of non-human populations. With brief analysis of ecological models, this essay will conclude that the theory is consistently applicable to ecological decision arenas.

Ecological models involve multi-individual interactions; these interactions have consequences for the organisms involved, hence there are implicit costs. Finite resources exist in these models which are "up-for-grabs" by competing organisms who must expend energy. Clearly, any outcome will involve some balance of benefits (resources) and costs (energy) for participants. This balance is considered a net-loss payoff and the methods of competition considered strategic preferences—known ecologically as phenotypes (Cowden, 2012). Described in these broad terms, the parallels between the ecological model and conventional economic theory are self-evident. Despite this, what is not immediately clear is whether these phenotypes actually reflect strategic preference or just stochastic behaviour. Analysing interaction in context will elucidate the fact that behaviour is often equivalent to strategy—wherein natural selection is the engine of strategy, not intelligence (Glimcher, et al., 2009).

Competition is abundant in non-human populations; it is not difficult to imagine groups of individuals ***X*** and ***Y*** in a non-human population fiercely vying for resources. The individualistic motivation behind this competition is in line with evolution by natural selection: individuals compete for resources to further their genealogy. Although the resources being sought after are the same, the behaviour of individuals will not necessarily be homogenous; for example, some individuals may have a propensity to be aggressive in interactions whilst some are yielding. This creates an interesting dynamic in the population whereby one group will not dominate entirely. Instead the population will reach an equilibrium (Frank & Cartwright, 2013). The P.D. model emulates equilibrium in competitive populations extremely well. As such, biologists have found the model useful in modelling several antagonistic populations—not just Hawks and Doves.

Given a population of types ***X*** and ***Y***, competing for resource C_i (i.e. calories in) and expending energy C_o (i.e. calories out), a P.D. payoff matrix for interaction between two individuals would be:

		Individual$_1$	
		***X* (Aggressive)**	***Y* (Yield)**
Individual$_2$	***X* (Aggressive)**	$\frac{1}{2}(C_i - C_o)$ $\frac{1}{2}(C_i - C_o)$	0 C_i
	***Y* (Yield)**	C_i 0	$\frac{1}{2}C_i$ $\frac{1}{2}C_i$

Table 1: Payoff Matrix for Antagonistic Competition

Providing$(C_i - C_o) > 0$ the dominant strategy for both individuals will be ***X***. Therefore, *Nash equilibrium* occurs when both individuals pursue strategy ***X*** despite a *Pareto efficient* outcome of ***Y-Y***. Seemingly, the aggressive trait will displace the tendency to yield in the population. Despite this, in nature, there are very few—if any—populations which are entirely dominated by aggressive behaviour. The P.D. model accounts for this fact:

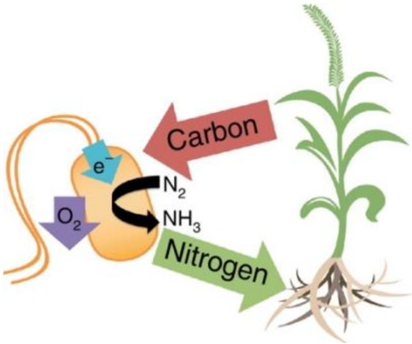
$$\frac{1}{2}C_i > \frac{1}{2}(C_i - C_o)$$

This inequality highlights the fact that when both individuals yield, each receives more total calories than they otherwise would. In a population dominated by strategy ***X,*** there is incentive for some individuals to follow strategy ***Y***; this fact will cause a population dominated by aggression to breakdown. The result is that populations are mixed, just as is observed in natural ecosystems.

Mixed populations are a strong indication of the fact that phenotypes are equivalent to strategy: the propensity of an individual to be aggressive or yielding in this model will determine their share of resources, so individuals must choose strategy appropriately. In time, the success of a particular strategy will determine average payoffs and, thereby, relative population shares (Frank & Cartwright, 2013). Intuitively, this is in line with Darwinian competition: individuals who access more of the available resources on average will take up a growing share of the population over time. Natural selection has provided individuals with strategic preferences which maximise their chances of survival (Cowden, 2012). The P.D. model appears to be a practical synthesis of competition in ecological settings.

Despite this, the model makes assumptions which oversimplify interactions. For example, the expectation that individuals behave consistently in competition for resources is unrealistic—doves may fight, hawks may concede. Furthermore, the model will breakdown if the condition: $(C_i - C_o) > 0$ does not hold. That said, **C_i** may not be the only payoff individuals receive; arguably, there are implicit payoffs from winning competitions (e.g. signalling dominance to potential mates/rivals) which would suggest that the P.D. model explains competition over even trivial calorie-sources. However, it would be difficult to quantify these benefits to incorporate them into the model.

Inasmuch as the P.D. model accounts for competitive interactions, the iterated version of the model appears to account for non-egoistical interactions. At first, it's difficult to reconcile coalition behaviour with Darwinian individualism: why would competitive individuals operate in mutual interest? If it were the case that individuals only interacted once, cooperation would not persist under the P.D. model. However, in many ecosystems, individuals interact frequently. Given a population with high frequency of interactions, P.D. is iterated—over evolutionary timescales (i.e. generations)—and payoffs converge on the *Pareto efficient* outcome. Individuals adopt strategy based on simple reciprocity and cooperative feedback loops develop, similar to *tit-for-tat* strategies in Axelrod games, whereby fidelity is rewarded; for example, symbiosis between legume and the nitrogen-fixing bacteria in their roots (see Figure 1)[1]. Repetition of this process develops the altruism witnessed in many ecosystems: individuals will do what is best for the population to promote their own long-term survival (e.g. warning calls).



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[1] Symbiotic relationship between legume and nitrogen-fixing bacteria (Geddes , et al., 2015)

Some question the validity of using the iterated P.D. as a model for altruism. Noe et al (1991) present three limitations of using the model to explain altruistic non-human behaviour:

1. Communication is critical in collaboration, the P.D. model prohibits explicit communication.
2. Resources may be indivisible, the P.D. model assumes that resources may be allocated according to strategy;
3. Individuals may cooperate with a third-party, the P.D. model strictly involves two players.

These limitations highlight what seem to be important issues with using the iterated P.D. model to explain ecological coalition behaviour. I would contest that some of these limitations may be explained away by the workings of the model.

Regarding issue one, communication is implicit in the behaviour of participants: action expresses priorities. Therefore, strategies are effectively signalling—communicating—to the other player and explicit communication is ancillary to this (Bshary & Grutter, 2005).

Issue two may be solved by assuming that, within a *tit-for-tat* context, an individual will sacrifice an indivisible morsel in one iteration expecting the action to be subsequently reciprocated. Although this strategy would be open to exploitation, in small populations individuals would likely show greater fidelity due to a high probability of repeated interactions and potential punishments (Chen & Jacobs, 2005). Alternatively, indivisible morsels may be allotted to relatively important individuals in a population to improve the overall survival rate of the population—this is just conjecture.

Issue three may be disputed if we consider that over evolutionary timescales phenotypes, if not the individuals who possess them, will interact repeatedly. Populations are finite so all iterations of strategy are bound to occur even if individuals entirely defer from interactions occasionally.

Based on the analysis I would conclude that the iterated P.D. sufficiently explains non-egoistic behaviour in non-human populations. Noe et al (1991) reach a similar conclusion, labelling the model as a 'practical paradigm'.

Thus far this essay has focussed on applying the P.D. model to simplified, symmetric interactions. A natural question to ask is whether the model can be applied to complex interactions; in which, payoffs may vary in size and individuals are not homogenous.

The assumption that individuals are identical is clearly inappropriate for analysing any population. Therefore, it is important that the model can accommodate differences in players. This is in fact the case: strategies are flexible to the constraints on the individual (e.g. smaller individuals have a propensity to avoid conflict with larger individuals). The model also accommodates the strategies of individuals facing similar constraints [e.g. ritualised combat among closely matched male fiddler crabs (Cowden, 2012)].

Payoffs will not always be symmetric, especially in combative interactions; for example, payoffs will vary significantly between the occupier and intruder of a given territory: the occupier stands to lose more than the intruder and will often act more aggressively because of this—also predicted by the P.D. model.

Evidently the P.D. model is extremely flexible. Not only does the model explain combative and non-egoistical interactions but it is also able to incorporate salient asymmetries (Hammerstein, 1979). Whilst there are some important limitations of the model to consider, these may be explained away by considering the model in a dynamic ecological context.

Ultimately, the model ably predicts a stable population equilibrium that results from specific strategies employed by non-human individuals as part of an evolutionary process, whilst still accounting for even more nuanced behaviours. Based on the evidence presented, it seems reasonable to conclude that phenotypes may be considered non-stochastic strategies and, as such, the game theoretical P.D. model is an applicable framework for analysing ecological decision environments.

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