Revisiting Rosenzweig-MacArthur: Towards a general approach to population dynamics incorporating individual behavior

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1 Introduction

Game theory is a natural tool to model the behavior of animals, who must respond to the behavior of other animals as well as complex and rapidly shifting environments. A classical application of game-theory is patch-choice models, where the ideal free distribution emerges to explain spatial distributions (**??**). A game theoretical approach has been fruitful in studying habitat choice in simple ecosystems under the assumption of static populations or simplifying the habitat to a few discrete patches. Real-life habitat choice consists of animals choosing where to forage in a continuous landscape, with varying intra-specific competition and outside risk. Models that can handle such systems allow for better models of habitat distribution, and represent a significant step forward in understanding natural systems (**?**).

A common simplification when including behavior in population models is to assume that at least one payoff is linear in the choice of strategy, (**?**). Linear models are sufficient to explain simple predator-prey dynamics with optimal behavior, (**?**), but non-linear effects in natural systems are substantial (**?**). A model for population games is set out in (**?**). Optimal behavior is introduced by every population maximizing the pr. capita growth at every instant. This implicitly assumes monomorphic populations, where all individuals intrinsically act as one (**??**). We propose a modification of the approach from (**?**) in the vein of (**?**), based on individual optimization. Instead of assuming a population where all individuals act in lockstep, we assume that each animal acts independently, but that its risk-reward calculus is affected by the population mean behavior. This marks a return to the ideas of playing the field, (**??**). If we assume large populations and that the animals of each type are indistinguishable, the game can be modeled as a static mean field game with multiple types.

The evolution of mean-field games has followed two parallel tracks, one in mathematical biology through the ideal free distribution (**??????**), and the other in mathematical optimization based directly on anonymous actors (**???**).

The main focus in ecology has been studying specific families of games in depth **?**, while the focus in mathematical optimization has been in establishing uniqueness and existence of Nash equilibria through the toolbox of variational inequalities (**???**). We demonstrate that in certain cases, a mean-field game can be rephrased equivalently as a normal-form game. This allows us to bring the entire toolbox of variational inequalities to bear on population games.

Using the theory of variational inequalities, we show that population games based on individual optimization have a unique equilibrium under very general assumptions. Our approach allows us to handle both continuous and discrete strategy spaces, but more technical assumptions are required for existence in the continuous setting. The classical ideal free distribution emerges as a special case of our approach, providing a compelling argument for the mean-field approach. We demonstrate the fundamental difference between working with direct pr. capita optimization and using the mean field approach, explicitly quantifiying the difference in expected payoff for the case of the ideal free distribution. Behavior based on individual optimization appears more cautios than predicted when optimizing pr. capita consumption, which we demonstrate with an example and conjecture as a general property. We demonstrate our approach by applying it to a behaviorally modified Rosenzweig-MacArthur system in continuous space. We show that the system satisfies the criteria for existence and uniqueness as a population game.

In addition to our theoretical advances, we implement a simple and efficient numerical method of finding Nash equilibria and equilbria of population games. The approach is applied to our case of the behaviorally modified Rosenzweig-MacArthur system. We examine the population dynamics through a phase portrait, where they appear to be asymptotically stable. We study the population levels and spatial distribution at equilibrium as a function of the carrying capacity, intraspecific predator competition. The rest of the paper is organized as follows: We start with the general setting. After building the general setting, we introduce the machinery of variational inequalities in the context of game theory. Here we show the general uniqueness and existence results. We proceed to study the concrete Rosenzweig-MacArthur model, showing existence and uniqueness of the Nash equilibrium and population equilibrium. We analyze the results, and discuss the implications of both the results and our theoretical results.

2 General setting

We build the general setting piece-by-piece, from the environment to the foraging strategies. First we define the environment, then we introduce the mean-field setting, as it is necessary to handle the strategy of an entire population. Once we have laid the building blocks for our setting, we prove a proposition. This proposition demonstrates that our setting generalizes the ideal free distribution and is preferential to assuming monomorphic populations from the outset. The generalization allows for a birds-eye view of population games.

We envision a setting with M different types of animals co-existing in an environment. More rigorously, we assume that the environment is a measure space (X, μ). Modeling the environment as a measure space allows us to model environments which are continuous, discrete and mixtures thereof in the same context. As an example, bats forage over a continuous area while the caves where they rest are discrete and disconnected (**?**). We model that the populations N_i, $i \in \{1, \ldots, M\}$ are large compared to a single individual. This allows us to consider the population as continuous, consisting of infinitely many individuals.

We suppose that the migration dynamics happen on a faster time-scale than the population dynamics, as is seen in e.g. marine ecosystems (**?**). This slow-fast dynamic allows us to model the migrations as instantaneous, with each individual picking the optimal foraging ground at every instant (**??**).

We assume that every animal has an area where it forages at every instant. For an animal of type i this is described by a probability distribution σ_i over the environment X. We require that the distribution σ_i is absolutely continuous with respect to the measure μ. In an abuse of notation, we will denote this density by σ. We denote the space of probability densities with respect to μ space by $P_\mu(X)$. By requiring absolute continuity we remove degenerate Nash equilibria e.g. Dirac-type distributions in a continuous setting, avoiding for example all gazelles stacked exactly at a single point in space. By working in this generality, we generalize both the continuous and continuous approach to habitat selection (**???**).

2.1 Foraging strategies and mean-field

An animal actively chooses where it forages, and we model that an animal is always foraging. Hence the density σ_i describing where it forages is a strategic choice for an animal. In order to inform this choice, we need to establish the playing field. An animal of type i faces the environmental state and the foraging choices of all other inhabitants. Modeling the influence of the foraging choices necessitates the introduction of the mean-field-strategy, $\bar{\sigma}_j$ for type j. The mean-field strategy $\bar{\sigma}_j$ is the average strategy of all individuals of type j. As a consequence, we can describe the foraging presence from type j at a point $x \in X$ by $N_j \bar{\sigma}_j(x)$.

The choice of optimal foraging strategy σ_i^* for an animal of type i is a trade-off based on the presence of competitors, predators and prey. The mean density of competitors, predators and prey at a point x is described by $N_j \bar{\sigma}_j(x)$. We capture this trade-off in a payoff function $U_i(\sigma_i, (N_j \bar{\sigma}_j)_{j=1}^M)$. The goal of a single animal of type j is then to find the optimal strategy σ_j^* such that

$$\sigma_j^* = \operatorname{argmax}_{\sigma_j \in P_\mu(X)} U_i(\sigma_j, (N_j, \bar{\sigma}_j)_{j=1}^M) \tag{1}$$

The fundamental assumption in a mean-field is that the populations are assumed to consist of infinitely many individuals so the choice of a single individual does not change the mean-field strategy (**?**). At the Nash equilibrium of a mean-field game every individual of type i follows the same strategy σ_i^*, (**?**). Heuristically,