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A genetic approach to the rock-paper-scissors game

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ABSTRACT

Polymorphisms are usually associated with defenses and mating strategies, affecting the individual's fitness. Coexistence of different morphs is, therefore, not expected, since the fittest morph should outcompete the others. Nevertheless, coexistence is observed in many natural systems. For instance, males of the side-blotched lizards (*Uta stansburiana*) present three morphs with throat colors orange, yellow and blue, which are associated with mating strategies and territorial behavior. The three male morphs compete for females in a system that is well described by the rock-paper-scissors dynamics of game theory. Previous studies have modeled the lizards as hermaphroditic populations whose individual's behavior were determined only by their phenotypes. Here we consider an extension of this dynamical system where diploidy and sexual reproduction are explicitly taken into account. Similarly to the lizards we represent the genetic system by a single locus with three alleles, *o*, *y*, and *b* in a diploid chromosome with dominance of *o* over *y* and of *y* over *b*. We show that this genotypic description of the dynamics results in the same equilibrium phenotype frequencies as the phenotypic models, but affects the stability of the system, changing the parameter region where coexistence of the three morphs is possible in a rock-paper-scissors game.

1. Introduction

In ecology, polymorphism is the presence of two or more distinct morphs determined genetically and in stable frequencies that are too high to be considered a consequence of recurrent mutations (Gray and McKinnon, 2007; Huxley, 1955). Even very simple organisms such as bacteria may present more than one morph in some communities. Individuals of *Escherichia coli*, for instance, can produce, be resistant, or be sensitive to colicin (Kerr et al., 2002). Colicin production is determined by a gene present in the plasmid *col*, while the bacterial resistance against the toxicity of colicin is frequently a mutation that prevents colicin binding on the outer membrane (Jeanteur et al., 1994).

Polymorphism can also be related to strategies used by individuals to escape from their predators (Brodie III, 1992; Carlson and Holsinger, 2010). For instance, the damselfish (*Acanthochromis polyacanthus*) may exhibit different colors in the Great Barrier Reef (Planes and Doherty, 1997). In the southern half of the Great Barrier Reef, the damselfish present an uniform black color morph. On north reefs, the damselfish are bicolored. In the central region, they present an intermediate character. In some areas, at least two morphs coexist. The damselfish colors resemble the colors of other fish present in these areas. The rarest color in a given area is exposed to a higher chance to be found by predators. The differences in body color are determined by the combination of three alleles (Planes and Doherty, 1997).

In some cases, polymorphism is associated with different behaviors among males with different mating strategies (Brockmann, 2001; Jukema and Piersma, 2006; Sinervo and Lively, 1996; Tuttle, 2003; Zhang et al., 2013), affecting directly the individual's fitness. In these cases, monomorphism of the fittest morph is expected, making the evolution of different morphs and their coexistence a challenge. The common side-blotched lizard (*Uta stansburiana*) is one of the these challenging cases and one of the most known examples of coexistence of different morphs (Sinervo and Lively, 1996). Males of *U. stansburiana* present up to three morphs in natural populations. The morphs have different colors on their throat, which is an indicator trait of the different male strategies in territory defense and aggressiveness (Ferguson, 1966). The territories attract females for reproduction. Once in a territory, the female becomes exclusive to its male owner. The greater the number of females attracted by a male, the greater is the fitness of this male (Sinervo and Lively, 1996). The orange-throated males are the most aggressive and have large territories, attracting many females. The blue-throated males defend smaller territories, with fewer females that are assiduously guarded by them. The yellow-throated males

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do not own territories but resemble the female in throat color and behavior, easing their entrance into other males territories to sneak females (Sinervo and Lively, 1996; Sinervo et al., 2000).

Sinervo and collaborators have studied this system in great detail and developed models to understand how the different morphs (linked to alternative male reproductive strategies) coexist in *U. stansburiana* lizards across different areas (Corl et al., 2012; Sinervo et al., 2001; Sinervo and Clobert, 2003; Sinervo and Lively, 1996; Sinervo and Svensson, 2002). Most of these works used game theory in the context of the rock-paper-scissors (RPS) to characterize males fitness, oscillation frequencies, and the equilibria found in natural populations (Smith, 1982). The RPS game qualitatively elucidates the coexistence of the three morphs through the payoffs (number of females) each morph earns defending (or not defending) the territories and monopolizing (or not monopolizing) the females (Sinervo and Lively, 1996). Because each morph can out-compete only one of the other two, the coexistence is maintained by negative frequency-dependent selection, where each male morph has an advantage when it is rare (Bleay et al., 2007). The *Uta* lizards are one of the most studied examples of RPS-game in nature but coexistence of three morphs with similar hierarchical strategies also occur in other organisms, such as bacteria, ruffs and other lizards (Jukema and Piersma, 2006; Kerr et al., 2002; San-Jose et al., 2014).

Models based only on the morphs and the associated behaviors qualitatively describe the dynamics observed in natural populations (Sinervo and Lively, 1996). Lizards, however, are diploid individuals with a well known genetic system associated with the morphs (Sinervo et al., 2001; Sinervo and Clobert, 2003; Sinervo and Svensson, 2002). The genetic system of throat colors and male behavior are described by a single locus called OBY (Sinervo, 2001). This locus has three alleles, *o, b*, and *y*, resulting in six possible genotypes that give rise to the three male strategies. The letter of the allele refers to throat color and they follow a sequence of dominance decreasing from orange to yellow, and blue (Sinervo, 2001; Sinervo et al., 2001). Therefore, lizards with an allele *o* have orange throat color whereas individuals with the *y* allele have yellow throats if homozygous or heterozygous with the allele *b*. Finally blue-throat individuals are always homozygotes at the locus *OBY* (Sinervo, 2001; Sinervo et al., 2001).

In the lizards and damselfish examples, the sexual reproduction between individuals with the same phenotype can, therefore, generate offspring of other types, affecting the frequency of the morphs. Phenotype frequencies depend not only on the fitness (as the number of mates) acquired, but also on the allele frequencies in the population and on the dominance of the alleles in diploid individuals (Sinervo, 2001; Sinervo et al., 2001; Sinervo and Clobert, 2003; Sinervo and Svensson, 2002). Our goal here is to investigate the dynamics of populations with three morphs, considering the genetics of the different morphs, as opposed to considering only the phenotypes. Here, we used the *Uta* lizards as inspiration to develop our theoretical model. However, the model we propose can be adapted to many other systems with three morphs or strategies defined genetically (Jukema and Piersma, 2006; Planes and Doherty, 1997; San-Jose et al., 2014)

In order to compare our results with previous works we also use the same game theoretic approach proposed by Sinervo, but we define the morphs by their genotypes and we show how the allele frequencies of this system affect the coexistence of the morphs in the populations. We show that the equilibrium populations in the genetic model coincides with those in the purely phenotypic model. However, the parametric region of payoffs where coexistence of the three morphs is stable increases considerably. We also calculate the period of oscillations around the equilibrium and find that it is even larger than that obtained in the phenotypic model (Sinervo and Lively, 1996). This suggests that a simple RPS model may not be able to explain the duration of the cycles in the system and that other factors, such as density dependent female selection (Sinervo, 2001) and spatial distribution might be crucial ingredients.

(a) Player 2

$$\text{Player 1}\quad \begin{array}{c|ccc|} & R & P & S \\ \hline R & a_1 & b_1 & c_1 \\ P & c_2 & a_2 & b_2 \\ S & b_3 & c_3 & a_3 \\ \hline \end{array}$$

(b) Individual J

$$\text{Individual } I\quad \begin{array}{c|ccc|} & O & B & Y \\ \hline O & M_{OO} & M_{OB} & M_{OY} \\ B & M_{BO} & M_{BB} & M_{BY} \\ Y & M_{YO} & M_{YB} & M_{YY} \\ \hline \end{array}$$

Fig. 1. Payoff matrix of the rock-paper-scissor (RPS) game. (a) General matrix, where the matrix elements (payoffs) satisfy the inequalities $b_i < a_i < c_i$. (b) Notation used for the *Uta* lizards where M_{IJ} is the payoff an individual of the color I gets when interacting with an individual of the color J. The coefficients M_{IJ} satisfy the same inequalities as in the payoff matrix represented in (a).

2. Dynamics in the phenotypic rock-paper-scissors game

The **R**ock-**P**aper-**S**cissors game is defined by the strategies R, P, S, in which S wins against P, P wins against R, and R wins against S. The game is defined by a payoff matrix where the elements represent the payoff the strategy indicated in the row earns when playing against the strategy indicated in the column. The payoff matrix of an RPS game is illustrated in Fig. 1(a) where coefficients satisfy the inequalities $b_i < a_i < c_i$ (Nowak, 2006).

One of the most remarkable models of population dynamics for three morphs was proposed for the *Uta* lizards case, using the RPS game introduced by Sinervo and Lively (1996). For the sake of simplicity we will use the same nomenclature of the lizards to analyze how sexual reproduction in diploid populations changes the dynamics of a RPS game. Notwithstanding morphs and alleles names are the same used by Sinervo and collaborators, any sexual populations with three morphs or strategies defined genetically may use the same approach we use here.

The original work by Sinervo and Lively considers a hermaphroditic population reproducing clonally. The three morphs are represented by orange (O), blue (B), and yellow (Y) strategies in the game theoretic sense. Since the model is based solely on the lizard's phenotypes, we shall call it the *Phenotypic-RPS* model here, to distinguish it from the genotypic model we will introduce. For the specific case of the *Uta* lizards we use the more explicit notation for the payoff matrix elements, defining M_{IJ} as the payoff that a lizard of color I gets when interacting with a lizard of color J (see Fig. 1(b)), where $I, J = \{O, B, Y\}$. In the *Phenotypic-RPS* model the dynamics of the three phenotypes/strategies are described by discrete time equations:

$$p_{I,n+1} = p_{I,n}\frac{W_{I,n}}{W_n} \tag{1}$$

where $p_{I,\,n}$ is the frequency of males with strategy I at generation n,

$$W_{I,n} = \sum_J M_{IJ}\, p_{J,n} \tag{2}$$

is the average fitness of the strategy I and

$$W_n = \sum_I W_{I,n}\, p_{I,n} \tag{3}$$

is the total average fitness of the population at generation n.

The equilibrium frequencies where the three morphs coexist, $\overline{p}_I$, are obtained by solving $p_{I,n+1} = p_{I,n} \equiv \overline{p}_I$ together with the conditions

$$W_{O,n} = W_{Y,n} = W_{B,n}$$