



# A general structured model of a hermaphrodite population

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## ABSTRACT

Both empirical and theoretical studies, have dealt with the question how to best optimize reproductive fitness for hermaphrodites, using models such as game theory or complicated energetic costs and benefits of mating displays. However, hermaphrodites exhibit a broad spectrum of sexual behaviors like simultaneous, sequential or lifetime gonochorist that cannot be explained using a unique formalism.

A possible explanation of this diversity relies on the way these species maximize their fitness: Does the individual hermaphrodite split its time between strategies maximizing its instantaneous reproductive fitness or its evolutionary fitness?

Here, we compare these two points of view and extend a game theoretical formalism to a sex allocation model that underlies all sexual behaviors as a result of a dynamic game whose payoff depends on the costs and benefits of sexual reproduction. Using this formalism, we prove that a simultaneous hermaphrodites strategy is stable even for high values of sex changing costs. Moreover, we prove that the stability of a sequential hermaphrodite is linked to the average energy allocated to the pure female strategy.

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## 1. Introduction

Evolutionary theory teaches us that the two components of evolutionary fitness are survival and reproduction. In asexually reproducing species, adaptations that increase reproductive fitness are relatively easy to analyze (Jaekle, 1994). In sexual reproducers, evolution has yielded magnificent diversity of adaptations intended to increase reproductive fitness (Stearns, 1992; Tuomi et al., 1983); however, quantifying their impact on the success of a species as a whole is certainly more challenging (Frankham et al., 2014).

Many studies, both empirical and theoretical, have dealt with the question of how to best optimize reproductive fitness as a sexual reproducer, and with such simple yet ubiquitous subjects as the game theory of sex ratios (Hamilton, 1967) and with such complicated yet specific topics as energetic costs and benefits of mating displays (Szamado, 2015). Among sexual reproducers, the most complicated analyses of fitness are required for hermaphrodites: those who can perform either sexual function (*i.e.* male or female) (Ghiselin, 1969; Jarne and Charlesworth, 1993; Munday et al., 2006a; 2006b; Warner et al., 1975). Even among hermaphrodites,

there is diversity in the expression of reproductive role: protandry (where males change to females Wang et al., 1990), protogyny (where females change to males Schlessman and Barrie, 2003), simultaneous hermaphroditism (where individuals of the species can play both roles at the same time, sometimes with the ability to self-fertilize Jarne and Charlesworth, 1993), and repeated sequential hermaphroditism (where individuals can switch between sexes multiple times throughout their lifespan Munday et al., 2006a; Munday et al., 2006b).

For these species, a fundamental and fascinating question then arises: is a hermaphrodite simply splitting its time between maximizing its reproductive fitness as a female and maximizing its reproductive fitness as a male, or is fitness as a hermaphrodite optimized by an entirely different, longer-term strategy?

If we explore the first topic, the idea that hermaphrodites are spending some time optimizing each sexual function could be explained as a clever mechanism by which to increase their total reproductive fitness. By performing both functions (*i.e.* female and male roles), they may be able to increase their total number of opportunities to reproduce (*cf.* Kokko and Jennions, 2008). They may also be hedging the bet of differential success in mate selection: those with characteristics that may not make them the most successful sexual competitors for mates as males might have precisely the perfect set of characteristics with which to attract high-quality mates as females, or vice-versa. Similarly, a single individ-

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ual may have attributes that make its eggs and sperm themselves differentially able to yield viable offspring. Particularly if these relative successes are dependent on external and fluctuating conditions (either demographic or externally environmental), then the ability to perform both functions may drastically increase evolutionary fitness. These arguments, however, by themselves, may be insufficient. In addition to the potential benefits, individuals must bear the physiological costs of producing both types of gametes (in some cases constantly, and in other cases, undergoing metamorphosis/metamorphoses). These costs may themselves curtail the number or quality of the gametes produced in either or both functions and/or may negatively affect survival (e.g. by increasing energetic requirements). To be of evolutionary benefit, the increased reproductive fitness must outweigh the incurred costs.

Furthermore, this idea of increasing fitness by following an intermediate (i.e. split) strategy may run philosophically contrary to the concept of evolutionary competition. Theory suggests that in an environment with limited resources (in this case, opportunities for mating and/or successful gamete development into the next generation), any relative advantage over others should be selectively favored. In this context, this notion implies that individuals who split their effort between both sexual functions must still be able to compete successfully within each sex against individuals who focus all their energy on that one function. These are the same mathematical foundations that examine the emergence of anisogamy from isogamy (cf. Bulmer and Parker, 2002). This line of reasoning suggests either that there is little to be gained from increased effort within either sexual function or that much is to be gained by adding the capacity to play both roles.

This logic leads us to the second topic, where something fundamentally different is happening in hermaphroditic species. Rather than switching between optimizing two independent strategies, they may be following a truly mixed strategy, optimizing their lifetime reproduction complete in the knowledge that this approach will include both functions. To test whether this might be the case, we focus on hermaphrodites with the most freedom and/or opportunity to diverge from single-sexual-function optimization: hermaphrodites. In this case, sex is a flexible affair and we are dealing with a sexual function instead of a state. Simultaneous and sequential hermaphrodites exhibit both similarities and differences in the way in which they respond to sexual conflict. As examples of similarities, Okumura (2001) confirms that sex reversal goes in both directions in *Epinephelus akaarai* (a sequential hermaphrodite species). He showed the presence of both male and female gonadal tissues for this fish. Simultaneous hermaphrodites also show a preference in sex allocation response as *Lythrypnus dalli* individuals behave as male or female only and maintain only one active gonadal tissue Mary (1997).

In previous studies (Kebir et al., 2010; Miled et al., 2010), we proved that deterministic-density-dependent models lead to a chaotic dynamic for a simultaneous hermaphrodite and that individual-based models tend to stabilize the population for a sequential hermaphrodite. Therefore, here, using game theory, we investigate the origin of stability of different kinds of hermaphroditism in general, such as sequential and simultaneous hermaphrodites. In our previous study (Kebir et al., 2015), we constructed and analyzed a general dynamical game model structured by size and sex that we refer to as the *instantaneous* game (IG) model. The main objective is to study how and when sexual strategies (i.e. a sequential hermaphrodite or simultaneous hermaphrodite) are stable when sex is viewed as a flexible function.

A behavior decision depends on direct cues in the environment (i.e. decisions based on local information) or instead depends on long-term fitness, even if each independent decision does not maximize fitness within the immediate environmental context (i.e.

choices made to maximize long-term payoffs, focusing on global system outcomes). To this end, we contrast the analysis of the already-presented IG model (Kebir et al., 2015) with the formulation of a new model called the residual game (RG) model. Our goal is to determine how these types of fitness shape the evolutionary stability of hermaphroditic species.

The article is organized as follows: Section 2 describes the IG model and introduces the payoff matrix of the RG model. Mathematical analysis of the local asymptotic stability of several types of sexual strategies is discussed in Section 3. We then examine, by numerical analysis: the conditions for which different kinds of hermaphrodites should exist. The conclusion is reported in Section 4, where we discuss these results and offer a few concluding thoughts. Finally, the Appendix concludes this study with proofs of two theorems that summarize our main results of the model analysis: conditions when the entirely male population or the entirely female population states are unstable and circumstances where sequential-hermaphrodite strategies are locally asymptotically stable for the game.

## 2. Model description

Gender conflict (also called the hermaphrodite dilemma by Leonard, 1990) is defined as the tendency for a pair of prospective (sequential and simultaneous) hermaphrodite couplers to elect the less expensive sexual function (Dwitt, 1996; Wethington and Dillon, 1996). Besides, at the individual level, gender conflict can be viewed as a game where sexual behaviors are the strategies, and payoffs depend on “fitness” (Alonzo and Warner, 2000; Leonard, 1990; Mary, 1997; Parker et al., 2013). “Fitness” can be understood either as long-term fitness—i.e. a long-term average per capita growth rate of any given clone—or as the instantaneous per capita growth rate at any given moment (e.g. next mating). We use the qualifications “mean fitness” and “instantaneous fitness” to denote the two concepts, respectively (Ripa and Dieckmann, 2013). On the basis of these concepts, we present a new model called the residual game (RG) model, where payoffs are based on an evaluation of mean fitness: precisely the potential reproductive value,  $RV$  (Keyfitz and Caswell, 2005). We assess the potential reproductive value through “instantaneous fitness”—that takes into account sexual competition cost and/or sex change cost—defined in ref. (Kebir et al., 2015) via the *instantaneous* game (IG) model.

### 2.1. Game strategies

We consider a stable size-structured population of individuals able to change sex at each mating. This population is subdivided into four kinds of sexual strategies corresponding to four categories of players (Kebir et al., 2015): Strategy 1, the cooperative female, denoted by  $FM$  (i.e. a female that changed to a male, knowing that “male” is the present status); strategy 2, a pure or uncooperative female, denoted by  $F$  (i.e. a female that stayed female, knowing that “female” is the present status); strategy 3, the cooperative male, denoted by  $MF$  (i.e. a male that changed to a female, knowing that “female” is the present status); and strategy 4, the pure or uncooperative male, denoted by  $M$  (i.e. a male that stayed male, knowing that “male” is the present status).

Because sex allocation energy depends on individual size, we suppose that the population is structured by size over a finite set,  $S = \{s_0, \dots, s_{max}\}$ , (with  $s_0$  and  $s_{max}$  respectively the initial and maximum magnitude of fertility). During the mating period, when the game is played, we assume that the total number of individuals for each size  $s$  is constant, while the proportion of individuals adopting each strategy changes. Let  $X(s, t) = (x_1(s, t), x_2(s, t), x_3(s, t), x_4(s, t))^T$  be the vector of frequencies of players for each strategy for a population of size  $s$  at time point

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