

Phenotype adjustment promotes adaptive evolution in a game without conflict



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HIGHLIGHTS

- We study the evolutionary outcomes of adaptive phenotypic plasticity in a game.
- We consider the sex allocation of a lifelong pair with no conflicts of interest.
- Dynamics with phenotype adjustment always evolve states of maximum fitness.
- No-adjustment dynamics sometimes fail to evolve states of maximum fitness.

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ABSTRACT

Organisms may adjust their phenotypes in response to social and physical environments. Such phenotypic plasticity is known to help or retard adaptive evolution. Here, we study the evolutionary outcomes of adaptive phenotypic plasticity in an evolutionary game involving two players who have no conflicts of interest. A possible example is the growth and sex allocation of a lifelong pair of shrimps entrapped in the body of a sponge. We consider random pair formation, the limitation of total resources for growth, and the needs of male investment to fertilize eggs laid by the partner. We compare the following three different evolutionary dynamics: (1) No adjustment: each individual develops a phenotype specified by its own genotype; (2) One-player adjustment: the phenotype of the first player is specified by its own genotype, and the second player chooses the phenotype that maximizes its own fitness; (3) Two-player adjustment: the first player exhibits an initial phenotype specified by its own genotype, the second player chooses a phenotype given that of the first player, and finally, the first player readjusts its phenotype given that of the second player. We demonstrate that both one-player and two-player adjustments evolve to achieve maximum fitness. In contrast, the dynamics without adjustment fails in some cases to evolve outcomes with the highest fitness. For an intermediate range of male cost, the evolution of no adjustment realizes two hermaphrodites with equal size, whereas the one-player and two-player adjustments realize a small male and a large female.

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1. Introduction

Evolutionary adaptation is realized through natural selection, where the genotype with the highest fitness increases its fraction and eventually occupies the entire population. This adaptation process may be hindered if a conflict exists among individuals or among different genes in the same individual (Arnqvist and Nilsson, 2000; Chapman et al., 2003; Cosmides and Tooby, 1981).

Organisms with the same genotype may have different phenotypes in a manner adapted to the environment. This phenotypic plasticity may be useful in achieving a higher fitness when the local environment and social status of each individual are heterogeneous. Whether this phenotypic plasticity enhances evolutionary adaptation in genetic dynamics has been a theme of evolutionary biology. For example, the Baldwin effect is caused by the phenotypic plasticity that allows an organism to cope with a new environment that is otherwise very harmful to the species, and subsequent genetic evolution gives rise to a new genotype that produces a phenotype adapted to the new environment (Baldwin, 1896; Ancel, 2000; Pigliucci and Murren, 2003; Yeh and Price, 2004; Crispo, 2007; Lande, 2009; Scheiner and Holt, 2012). Thus,

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a combination of phenotypic plasticity and genetic evolution can realize adaptation that achieves a higher fitness or at a faster rate than purely genetic evolution (Ancel, 2000; Lande, 2009).

In behavioral ecology, adaptive phenotypic adjustment has been discussed in the evolution of parental care in birds (Houston and Daview, 1985; McNamara et al., 1999; Houston et al., 2005). They have introduced an infinite number of alternating steps of phenotype adjustment, where each player shifts to take the step that maximizes its own fitness given the partner's phenotype (best response dynamics). The endpoint of best response dynamics is assumed to represent the behavior observed in the field. They observed some differences between the case in which players adjust their parental care to each other's investment and the case in which players perform parental care as determined by their genotype. The main target of these analyses is the conflict of interest between mother and father in parental care because each parent has the potential to reduce its own investment to the current brood so that it may gain more offspring in future broods or acquire new mates. Thus, perfect cooperation is difficult to evolve due to the conflict of interest between players.

In this paper, we study the role of phenotypic plasticity in promoting adaptive evolution. We focus on a game situation in which no conflict of interest exists among players. As an illustrating biological example, we consider the sex allocation and the growth propensity of a pair of reproducing individuals forced to engage in lifetime monogamy, such as two shrimps confined within a sponge (Saito et al., 2001; Saito, 2002). The shrimps enter the sponge when they are both small in size and grow within it to reach a body size such that leaving is impossible. Their fitnesses are equal, because the reproductive success of each shrimp is the sum of the number of eggs laid by one and sired by the other, and each offspring has one father and one mother who have exactly the same genetic contribution. In this way, we can perfectly remove the effect of conflict of interest between players. Thus we conjecture that efficient evolutionary dynamics might achieve the highest fitness at the evolutionary endpoint.

We compare the evolutionary dynamics of three situations, differing in the participation of phenotypic adjustment of players. In the first situation, genetic evolution is represented by replicator dynamics in which the phenotype of each player is determined by its own genotype (no adjustment). In the second situation, the phenotype of one player is specified by its own genotype, but the other player chooses the phenotype that attains its own optimum given the phenotype of the first player (one-player adjustment). In the third situation, the first player takes an initial phenotype given by its own genotype, which is followed by the choice of the second player who takes the optimal phenotype given that of the first player, and finally, the first player readjusts its phenotype to a value according to the phenotype of the second player (two-player adjustment).

In general, shrimps have diverse sexual systems, ranging from simultaneous hermaphrodites (e.g., genus *Lysmata*: Bauer, 2006) to sex changers (e.g., genus *Pandalus*: Charnov, 1979 and Koeller et al., 2000) and to separate sexes (e.g., genus *Spongicola*: Saito and Koya, 2001; Saito et al., 2001 and Saito, 2002), with the last group encompassing the largest number of species. Because physiological changes such as growth and sex allocation take much longer than behavioral changes (e.g., parental care), we consider the adjustment occurring in one or two steps rather than an infinite number of steps.

We show that both one-player and two-player adjustments evolve to the same state that attains maximum fitness. In contrast, the dynamics without adjustment sometimes fail to evolve outcomes with the highest fitness. Both no-adjustment dynamics and one-player adjustment dynamics converge to evolve separate sexes with a large female and a small male when the minimum cost

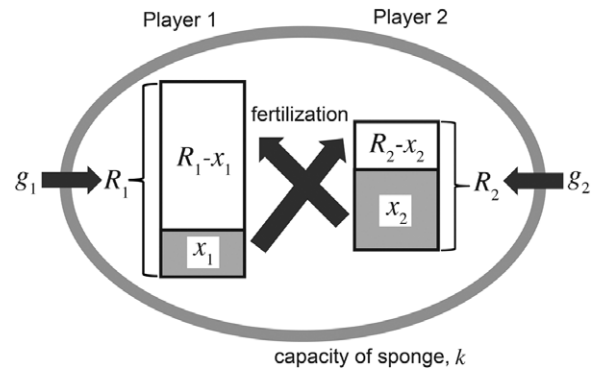


Fig. 1. Scheme of the model. A pair of shrimps is confined within the body of a sponge. The shrimps can choose growth propensity (g_1, g_2) and allocation to male function (x_1, x_2). Parameters are the capacity of the sponge, k ; the minimum cost of male function, c ; and the efficiency of male function, a . The reproductive investment (R_1, R_2) is determined by the growth propensities and the capacity of the sponge. The fitness of the two individuals is exactly the same because it is the sum of eggs laid by them and fertilized by the partner, and no conflicts of interest exist. We consider three different processes for the evolution.

of male function is large. In contrast, both dynamics converge to evolve hermaphrodites of equal size when the minimum male cost is small. For an intermediate range of male cost, no adjustment evolution realizes two hermaphrodites with equal size, whereas the one-player adjustment realizes a large female and a small male.

2. Model

Fig. 1 illustrates the scheme of the model. Let R_1 and R_2 be the total amount of reproductive resources of the first and second individuals, respectively. Let x_1 and x_2 be the amounts of investment to male reproductive function, and let $R_1 - x_1$ and $R_2 - x_2$ be the amounts of investment to female function by the first and second individuals, respectively. Both individuals obtain the same fitness, which is equal to:

$$\phi = (R_1 - x_1) \bullet s(x_2; a, c) + (R_2 - x_2) \bullet s(x_1; a, c). \quad (1)$$

The first term on the right-hand side is the number of eggs produced by the first individual that are fertilized by the sperm of the second individual, and the second term is the number of eggs produced by the second individual that are fertilized by the first individual. Here we assume that self-fertilization does not occur in the modeled animal, which is an acceptable assumption because self-fertilization is less common in animals than in plants (Jarne and Charlesworth, 1993; Jarne and Auld, 2006). An individual who performs male function must develop male sexual organs that require investment c . $s(x; a, c)$ is the fertilization success of a male who invests to reproduction x defined as follows:

$$s(x; a, c) = 1 - \exp(-a[x - c]_+), \quad (2)$$

where $[m]_+ = \max\{m, 0\}$. a is the fertilization efficiency and c is the minimum cost of male function. Because the fitness effect as a sperm donor (or father) and egg producer (or mother) is exactly the same, the fitness of the two individuals is the same.

We distinguish the two individuals as Players 1 and 2. Player 1 is the individual who arrived to the mating site first, and Player 2 is the one who arrived later. We consider two quantities, g_1 and g_2 , that represent the growth propensities of Player 1 and Player 2, respectively. We assume that these quantities are constrained within the intervals $0 \leq g_1 \leq 1$ and $0 \leq g_2 \leq 1$. Therefore, the total amount of reproductive resources available to Player 1 and Player 2, denoted by R_1 and R_2 , respectively, are written as follows:

$$R_1 = r_0 \frac{g_1}{1 + (g_1 + g_2)/k} \quad \text{and} \quad R_2 = r_0 \frac{g_2}{1 + (g_1 + g_2)/k}. \quad (3)$$

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