

PROBLEMS WITH CLASSICAL MODELS OF SEX-RATIO EVOLUTION

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Abstract. The classical theory of the sex-ratio evolution, known as the sex-ratio game, is based on the maximization of the number of grandchildren, treated as a fitness measure of a female producing offspring of the sex ratio that is coded in her genes. The theory predicts that it is more profitable to produce offspring with less numerous sex. We can find in the literature mutually exclusive conclusions based on this prediction: some textbooks say that populations with the equal number of sons and daughters are evolutionarily stable, others identify this ratio as a stable state of a population with different individual strategies being allowed. It is also not clear whether a primary or secondary sex ratio is a target of evolution. Moreover, the classical theory ignores the role of males, who host non-expressed sex-ratio genes. Our new approach, based on multipopulation dynamic evolutionary games, shows that in populations of players with individual strategies, the secondary sex ratio is attracted by the current value of the primary sex ratio, which slowly converges to the unique stable value of 0.5. Male hosts of the sex-ratio gene are important because perturbations of a stable state of males subpopulation can destabilize the whole system.

1. Introduction. In nature, the observed ratio of males to females is in most cases 0.5. However, a single male individual can fertilize many females. In many species, dominant males can monopolize all females in the population, thus making reproduction of other males impossible. Nevertheless, also in this case the 0.5 sex ratio can be observed. The question is: what mechanism is responsible for what seems to be a suboptimal sex ratio? When males, unlike females, do not produce offspring, half of individuals are excluded from reproduction. Such a population has a lower mean fitness than a population in which majority of individuals reproduce. The question arises: what is the origin of the

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0.5 sex ratio? This problem was considered by Darwin. Unfortunately, he has not solved it. First attempts to explain this phenomenon were made in the end of the 19-th century. They were also the first applications of mathematical methods in evolutionary biology. Their author was a German biologist, Carl Dusing. Using the mathematical reasoning, he argued that the natural selection could lead to the stabilization of the sex ratio on the level of 0.5. His results are founded on one basic assumption - the number of grandchildren is assumed as a fitness measure of a female who produces offspring of a sex ratio that is coded in her genes. It is known that the sex of an offspring is an effect of both a mother and a father. But a female can express her individual strategy by spontaneous abortions of foetuses with a wrong sex. This assumption has become the cornerstone of sex-ratio models. Ronald A. Fisher used a similar argument in his book and the concept is often attributed to him (see Fisher [4], Queller [9]). The Dusing-Fisher approach produces the following predictions. In the case of a shift of the population sex ratio to males, a female who produces proportionally more female offspring than other females will have a higher number of grandchildren. Similarly, when the population sex ratio is shifted to females, the production of a higher proportion of males will ensure a higher number of grandchildren. Formalization of this reasoning can be obtained by the construction of a fitness function whose arguments are: an individual strategy (that is the sex ratio in a female brood) and the population sex ratio. It can be done in the following way.

Let us take a game-theoretic perspective. Players are females, and the proportion of males in the brood of a single female, described by P_{ind} is her individual strategy. Let P denote the population sex ratio (interpreted as the proportion of males), N the number of all individuals in the population, and x the number of children of a single female. Now we can derive a payoff function which describes the number of grandchildren of a female with a strategy P_{ind} . A female with the strategy P_{ind} will have $P_{ind}x$ sons, and these sons will produce $P_{ind}x^2 \frac{(1-P)N}{PN}$ grandchildren. This female will also have $(1 - P_{ind})x$ daughters, who will produce $x^2(1 - P_{ind})$ grandchildren. Hence the total number of grandchildren is given by the following expression:

$$\begin{aligned} P_{ind}x^2((1 - P)N/PN) + x^2(1 - P_{ind}) &= x^2 \left[\frac{P_{ind}(1 - P)}{P} + (1 - P_{ind}) \right] \\ &= x^2(1 - P) \left[\frac{P_{ind}}{P} + \frac{1 - P_{ind}}{1 - P} \right]. \end{aligned} \quad (1)$$

Let us assume for simplicity that $x = 1$, then the right-hand side of (1) can be written as $(1 - P)F(P_{ind}, P)$, where $F(P_{ind}, P) = \frac{P_{ind}}{P} + \frac{1 - P_{ind}}{1 - P}$.

As we can see, $F(P_{ind}, P)$ can be used to compare numbers of grandchildren of females with different individual strategies. This function is a payoff function of an evolutionary game, which in the literature is called the SEX-RATIO GAME (see [2], [3], [7], [8], [9], [11]). In a situation when $P = 0.5$, all strategies will obtain equal payoffs, hence this is an equilibrium. When this equilibrium is disturbed to the advantage of one of the sexes, it is more profitable to produce more individuals of the less numerous sex. In the biological literature we can find different conclusions based on this mathematical reasoning, sometimes mutually exclusive. Generally, in textbooks there exist two main variants:

- Natural selection promotes females with an individual strategy $P_{ind} = 0.5$ (see [5]).
- Natural selection leads to the 0.5 population sex ratio without favoring any individual strategy. Population is non-homogenous, there are different individual strategies (see [10]).

In biology, there is a very important distinction between the sex ratio among zygotes (called the primary sex ratio) and the sex ratio among adult individuals (called the secondary sex ratio). In textbooks, two types of relations between the primary and secondary sex ratio can be found:

- Primary sex ratios converge to 0.5 and there are no compensations of the secondary sex ratio perturbations (see [10]).
- The primary sex ratio can be biased away from 0.5, but the secondary sex ratio converges to 0.5 (see [6]).

An advantage of the Dusing-Fisher approach is its simplicity. As we have seen above, the derivation of this model takes only a few lines of text. Still, there are some questions. Does an arbitrary assumption that the number of grandchildren is a measure of fitness allows to extrapolate a reproductive success to future generations? If a female \hat{P}_{ind} has more grandchildren than a female P_{ind} , then in the following generations, will \hat{P}_{ind} also have more descendants than P_{ind} ? Let us recall that the classical model depends on two variables: the individual strategy P_{ind} and the population sex ratio P . It is obvious that the value of P is determined by a combined influence of all individual strategies in the population. However, this effect is not present in the classical approach. If an individual strategy \hat{P}_{ind} will spread in the population, then we can expect convergence of P to the value of \hat{P}_{ind} . The Dusing-Fisher model analyzes only the effect of the population sex ratio P on the fitness of individual strategies; the effect of individual strategies on P is not considered. The second problem with the classical model is that it takes into account only female reproductive success. An individual strategy is interpreted as a decision process performed by a female. But since a fitness measure is assumed to be the total number of grandchildren, the gene transfer takes place through sons as well. This is an inconsistency because the fitness function is constructed for females only. It is possible that a male carrier of genes for a strategy P_{ind} will have a greater reproductive success than a female having this strategy. The question is: what influence the unconsidered effects described above will have on the predictions of the Dusing-Fisher model?

2. Multipopulation model. In order to address the above problems we need to construct an alternative model which would involve both males and females effects on the gene proliferation. The new model is very complicated from the mathematical point of view and therefore in this paper we limit ourselves to an overview of the new approach. It is based on a multi-population evolutionary game with a replicator dynamics (Argasiński [1]). We assume here that there are 3 different individual strategies in the population, for example $P_1 = 0.5$, $P_2 = 0.2$, and $P_3 = 0.8$. As in the classical approach, the individual strategy is the sex ratio (proportion of males) in a female brood. Now we construct a two-population model. The first subpopulation consists of males and the second of fe-

males. Individuals are distinguished by their sex and the strategy coded in their genes. A strategy is expressed only in females; male individuals are only its carriers. Current population state is described by

- $F = [f_1, f_2, f_3]$ – a vector of proportions of individual strategies in the female subpopulation,
- $M = [m_1, m_2, m_3]$ – a vector of proportions of individual strategies in the male subpopulation,
- P – a proportion of males in the population (or the population sex ratio).

The space of states of the population can be described as the product of two three-dimensional simplexes and a unit interval (one-dimensional simplex). Our model focuses on the dynamics of changes of the population state described by the replicator dynamics. Therefore, the fitness function does not describe the number of grandchildren but the number of direct descendants. The derivation of the fitness function is based on the computation of the probability of the number of descendants of an individual of a given sex and strategy. We assume that the production of a single descendant is a single Bernoulli trial, where the success means the transfer of the strategy gene to the new individual. For a male with the strategy P_i , the probability of such transfer to a male descendant is equal to $\theta_m^m(P_i) = 0.5(0.5f_1 + 0.2f_2 + 0.8f_3)$, an analogous value for a female descendant is $\theta_m^f(P_i) = 0.5(1 - (0.5f_1 + 0.2f_2 + 0.8f_3))$ (a haploid probability of a gene transfer multiplied by a probability of a proper sex choice according to the mean strategy of a potential mothers population). Analogously for a female we have $\theta_f^f(P_i) = 0.5(1 - P_i)$ and $\theta_f^m(P_i) = 0.5(P_i)$. A female makes x trials (a number of her kids) and a male individual makes $a_f x$ trials (a number of his kids), where a_f is the number of females per one male (analogously a_m is the number of males per one female, later on an additional upper index P_i will mean that we take into account only hosts of this strategy). Then we can calculate mean values of numbers of male and female descendants produced by a single male or a female parent with the strategy P_i denoted by $\mu_x^y(P_i)$, where the lower index describes the sex of a parent and the upper index describes the sex of an offspring. Hence for the strategy P_i we have $\mu_f^f(P_i) + a_m^{P_i} \mu_m^f(P_i)$ new female individuals per a single female parent, and an analogous value for males equals to $\mu_m^m(P_i) + a_f^{P_i} \mu_f^m(P_i)$. The mortality of parents may be treated as a negligible background fitness, so these values can be interpreted as per capita growth rates. According to Argasiński [1], these functions can be described in variables F, M and P . Therefore, depending on the sex of an individual, we obtain two kinds of the fitness (payoff) functions,

$$\begin{aligned} F_f(P_i, F, M, P) &= \frac{x}{2} \left((1 - P_i) + \frac{m_i}{f_i} (1 - (0.5f_1 + 0.2f_2 + 0.8f_3)) \right) \text{ for females,} \\ F_m(P_i, F, M, P) &= x \frac{1 - P}{2P} \left(0.5f_1 + 0.2f_2 + 0.8f_3 + \frac{f_i}{m_i} P_i \right) \text{ for males.} \end{aligned} \quad (2)$$

These functions describe per capita growth rates of an individual characterized by the sex and an inherited strategy. Arguments of these functions are: the strategy P_i inherited by the individual and the population state described by vectors F, M and the value of P . Payoffs are interpreted as the per capita growth rate of an individual described by the

sex and its strategy at the moment when the population is in the state F, M, P . We can now derive the mean fitness function for the female subpopulation

$$\bar{F}_f(F, M, P) = f_1 F_f(P_1, F, M, P) + f_2 F_f(P_2, F, M, P) + f_3 F_f(P_3, F, M, P),$$

and the mean fitness function for the male subpopulation

$$\bar{F}_m(F, M, P) = m_1 F_m(P_1, F, M, P) + m_2 F_m(P_2, F, M, P) + m_3 F_m(P_3, F, M, P).$$

Subsequently, we can derive the mean fitness function for the whole population

$$\bar{F}(F, M, P) = P \bar{F}_m(F, M, P) + (1 - P) \bar{F}_f(F, M, P).$$

We may now form the multi-population replicator equations (see [1]) which describe changes in proportions of strategies among females:

$$\dot{f}_i = f_i(F_f(P_i, F, M, P) - \bar{F}_f(F, M, P)); \quad i = 1, 2,$$

changes in proportions of strategies among males:

$$\dot{m}_i = m_i(F_m(P_i, F, M, P) - \bar{F}_m(F, M, P)); \quad i = 1, 2,$$

and the evolution of sex ratio:

$$\dot{P} = P(\bar{F}_m(F, M, P) - \bar{F}(F, M, P))$$

Then we obtain the following system of equations:

$$\begin{aligned} \dot{f}_i &= x \left(\frac{f_i}{2} (1 - P_i) + \left(\frac{m_i}{2} - f_i \right) (1 - (0.5f_1 + 0.2f_2 + 0.8f_3)) \right) \quad \text{for } i = 1, 2, \\ \dot{m}_i &= x \frac{1}{2} \left(\frac{1}{P} - 1 \right) (f_i P_i - m_i (0.5f_1 + 0.2f_2 + 0.8f_3)) \quad \text{for } i = 1, 2, \\ \dot{P} &= x(1 - P)(0.5f_1 + 0.2f_2 + 0.8f_3 - P). \end{aligned} \tag{3}$$

Solutions of the above equations show that:

- Natural selection does not favor the individual strategy 0.5 (or any other strategy). Trajectories of the system converge to restpoints. For every rest point, the mean strategy of the female subpopulation (that is the primary sex ratio) is equal 0.5 and the proportion of carriers of a strategy P_i must satisfy the following condition: $f_i P_i = m_i (0.5f_1 + 0.2f_2 + 0.8f_3)$.

- A trajectory of the population sex ratio (the secondary sex ratio) P can pass the value 0.5, which is stable from the point of view of the classical theory. P is attracted by the current value of the primary sex ratio and follows it until the whole system reaches a stable state. This happens when the primary sex ratio (and in effect the secondary sex ratio) is equal to 0.5.

- Changes of initial conditions of the male subpopulation may affect the behavior of the whole system.

3. Conclusions. Our model shows that superiority based on the number of grandchildren of a female cannot be extrapolated to future generations. Trajectories of the evolution of the male subpopulation may strongly affect the behavior of the whole system. Our major conclusion is that the role of male hosts of sex-ratio genes has been completely disregarded in the classical theory. Numerical solutions of replicator equations show that

dynamics of this system is very complex. Continuation of this work may provide new interesting results.

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