

Evolution of Frequency-Dependent Sexual Selection Using Agent-Based Model

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Abstract

Nonindependent mate choice occurs when a female is influenced in her choices of mate by the social environment. Frequency-dependent selection (FDS) is a typical example of a nonindependent mate choice and comes in two forms: positive or negative. In the positive form, any rare variant is at a disadvantage, whereas rare variants are favored in the negative form. Both forms of FDS have been confirmed in many species, and several mathematical and theoretical biology studies have reported the advantages of each. However, few studies have focused on the evolution of the two forms of FDS together. In this work, we simulated FDS using an agent-based model consisting of imported mating strategy as gene and female preference influenced by the social environment as meme. Experimental results revealed a relation between the operational sex ratio of males and the FDS strategy of females. A similar tendency was observed among real animals.

Introduction

Most models of sexual selection assume that females exhibit a genetically based preference for males with specific traits (Kirkpatrick and Ryan, 1991). However, female mate choice is a complex process involving not only genetic but also non-genetic factors (Westneat et al., 2000). There is increasing evidence that social factors have an important influence on mate-choice decisions (Witte and Noltemeier, 2002). Numerous studies have reported that social environment may influence mate preferences.

Individuals usually mate with opposite-sex others based on their own assessment of the suitability prospective mate, but this assessment can also be modulated by observing the decisions of others, so-called nonindependent mate choice (Vakirtzis and Roberts, 2010). One example of nonindependent mate choice is frequency-dependent selection (FDS). Positive FDS is a form of selection in which genotypes are favored when they are common and negative FDS is a form of selection in which genotypes are favored when they are uncommon (Hughes et al., 2013). Many experimental studies have confirmed positive FDS and negative FDS in nature separately (Singh and Sisodia, 2000; Vakirtzis, 2011).

There are also many studies on FDS using agent-based models in the fields of artificial life. Kawata et al. have examined the possibility of speciation without viability selection by positive FDS (Kawata and Yoshimura, 2000), and Kokko et al. have investigated how negative FDS evolved (Kokko et al., 2007). Some studies have demonstrated the advantages of mate-choice copying (Sirota, 2001; Dubois, 2007). However, these studies are tightly focused and there is no research on both positive and negative FDS for mate choice, together.

Guppies are known to copy the mate choice of other females (Dugatkin, 1992), and has been said that such mate-choice copying produces positive FDS (Kirkpatrick and Dugatkin, 1994). However, there have been cases in which guppies have exhibited negative FDS behavior (Hughes et al., 2013). This indicates that different forms of FDS occur in the same species. We expect that the FDS strategy is dictated by the individuality of the agents. Servedio and Kirkpatrick have shown that the mate-choice copying is hereditary (Servedio and Kirkpatrick, 1996), and Dubois defined the copier female and non-copier female to choose a mate by nature (Dubois, 2007). In this work, we propose an agent-based model for both positive and negative FDS to study how to evolve.

Until now, we have expressed inborn bodily characteristics as genes and acquired preferences as memes. In the previous work, we configured an evolutionary model of artificial life (agents) that combine genes and memes and observed their influence on changes in preferences concerning mate selection (Tokuhara et al., 2005; Mutoh et al., 2010). In this paper, we propose a model that adds genes expressing the mating strategy of the female in order to determine how social factors influence female mate choice. By doing so, we can computationally observe mate selection behavior by agents and discuss the evolution of mating strategy on the basis of agent responses to the environment as generations proceed. Finally, we compare our proposed model with 32 kinds of real animals.

Agent Model

We have previously described an enhanced Lerena model (Lerena, 2000) in the form of an agent-based model consisting of both hereditary traits (genes) and acquired traits (memes) (Tokuhara et al., 2005; Mutoh et al., 2010). The concept of memes was proposed by R. Dawkins (Dawkins, 1989), who defined a meme as both a base factor and a unit of cultural information. Our agent model was able to represent constant (i.e., hereditary) and variable (i.e., acquired) information as genes and memes, respectively. However, previous models had no individual difference to change their memes. In this paper, we describe a new model that reflects the concept of FDS and how to change memes is decided by their genes.

Agents

An agent a_i consists of sex sex_i , age age_i , dyad genes $gene_i$, and meme $meme_i$, as

$$a_i(sex_i, age_i, gene_i, meme_i). \quad (1)$$

Genes are hereditary. The first one is for inborn gene traits and the second for newly added ones related to mating strategy. Memes relate to preferences for gene traits.

$$gene_i = (g_i^{trait}, g_i^{strategy}), \quad (2)$$

$$meme_i = meme_i^{pref}, \quad (3)$$

where g_i^{trait} is a gene trait of an agent a_i , $g_i^{strategy}$ is a mating-strategy gene of an agent a_i , and $meme_i^{pref}$ is the preference of the g^{trait} in mate choice. The expression of the mating-strategy gene and meme preference is limited to females ($sex_i = \text{female}$) and the expression of the gene trait is limited to males ($sex_i = \text{male}$). For the sake of simplicity, we set the trait of each male to be fixed throughout his life; that is, males do not have a meme trait.

Mating-strategy genes

We think that common males likely to be popular males. This is because it is easy for popular males to leave offspring. We assume that whether a female prefers popular or unpopular males is decided by her hereditary gene; that is, her mating-strategy gene.

We assume a gene $g^{strategy}$ encoded by bit-strings that determine the mating-strategy of females but is not expressed in males. The length of strings is one bit (0 or 1). When the $g^{strategy}$ of a female agent is one, her mating-strategy is positive FDS, which means she prefer males with popular traits. Conversely, when the $g^{strategy}$ of a female agent is zero, her mating-strategy is negative FDS, which means she prefers males with unpopular traits. We describe later how to discriminate between popular and unpopular traits.

As mentioned above, we represent individuals having traits and mating-strategies as genes and preferences as memes.

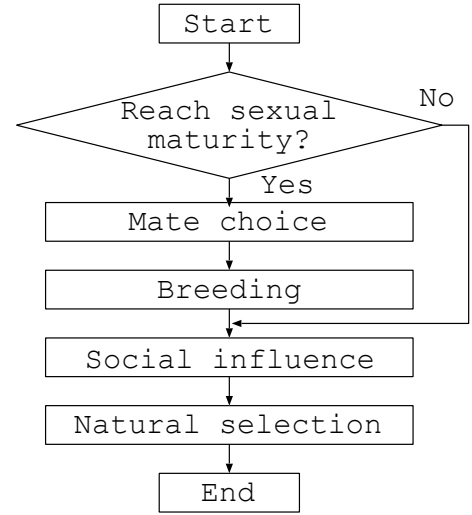


Figure 1: A flow of agent actions during each step.

Action

A single run for each step is mostly a repetition of the following three procedures:

1. Mate choice
2. Breeding
3. Social influence

A flow of agent actions is shown in Figure 1. First, each female reaching sexual maturity selects a male mate on the basis of her preference. Males and females whose mates are determined by mate choice then breed. After breeding, the mate preference of each female is influenced by social environment. This means that the meme preference of each female is rewritten. Finally, agents reaching life end are removed from the population and a certain number of agents are randomly picked to form the next step, which mirrors the process of natural selection. For simplicity, the energy consumed by each action and the fitness used in selection process are not considered. Next, we explain each action in detail.

Mate choice A female a_i selects the best-matched male a_j as a mate from L sampled males. The sampled population consists of randomly selected L males. The female evaluates a male by calculating the hamming distance between her own preference and the traits displayed by the male. The evaluation value $P_{i,j}$ for mate choice is determined using agent a_i 's meme preference $meme_i^{pref}$ and agent a_j 's gene trait G_j^t as

$$P_{i,j} = H(meme_i^{pref}, G_j^t), \quad (4)$$

where $H(A, B)$ is the hamming distance between A and B . Agent a_i prefers a_j to a_k when $P_{i,j} < P_{i,k}$. Among L

males, a female a_i chooses a single mate a_j , where $P_{i,j}$ is smallest. Male choice tactics is based on a method (Kawata and Yoshimura, 2000) that is a reasonable assumption for real animals (Gibson and Langen, 1996; Widemo and Sæther, 1999). After choosing a mate, a female a_i is added to the *potential_mate_j* list for selected male a_j . A male decides on N females randomly in the *potential_mate_j* list after all females have selected a single mate.

A male can breed with N females per step. When the sex ratio between males and females is equal, we can explain N as the operational sex ratio (OSR) (i.e., the ratio between sexually active males and females in a population) of males. From now, we call N the OSR of the males.

Breeding Suppose that female a_i selects male a_j each other. A new agent a_l is produced as the child of a_i and a_j . This new agent a_l has the following composition.

$$a_l(\text{sex}_l, 0, (g_l^{\text{trait}}, g_l^{\text{strategy}}, \text{meme}_{DV}^{\text{pref}}), \quad (5)$$

where sex_l is either male or female with an even probability; age_l is zero; genes $(g_l^{\text{trait}}, g_l^{\text{strategy}})$ are determined by genetic operations of Equation (6)(7).

$$g_l^{\text{trait}} = \text{mutb}(\text{crb}(g_i^{\text{trait}}, g_j^{\text{trait}})), \quad (6)$$

$$g_l^{\text{strategy}} = \text{mutb}(\text{crb}(g_i^{\text{strategy}}, g_j^{\text{strategy}})), \quad (7)$$

where $\text{mutb}(A)$ is a mutate-function that reverses each bit of A with probability γ ; $\text{crb}(A, B)$ is a cross-function that returns either A and B with an even probability. Meme is not inherited from parents. Thus, its default is $\text{meme}_{DV}^{\text{pref}}$.

A female a_i is limited to only one round of breeding for each step. On the other hand, a male a_j is limited to N round of breeding with females in his *potential_mate_j* list for each step.

Social influence Next, the preference of a female a_i is influenced by the social environment. This means that a female a_i prefers the trait g_k^{trait} of a male a_k who is the most popular or unpopular as indicated by mate choice from other females. That is, a female a_i imitates the gene trait g_k^{trait} with her meme preference $\text{meme}_i^{\text{pref}}$. Females judge whether a male is popular or unpopular by the number of females in his *potential_mate_j* list. The mating-strategy gene g_i^{strategy} is encoded by a bit-string with a length of one bit. Specifically, when the mating-strategy gene g_i^{strategy} of a female a_i is zero, her imitation target is the male agent whose *potential_mate* list has the least number of females in L males selected randomly from a population. Conversely, when the mating-strategy gene g_i^{strategy} is one, her imitation target is the male agent whose *potential_mate* list has the most number of females in L sampled males.

Here, a female a_i can change her $\text{meme}_i^{\text{pref}}$ by reversing multiple bits in her bit string data to come close to the gene trait g_k^{trait} of target male a_k . The number of reversing bits is randomly spread over half the total number of all bits.

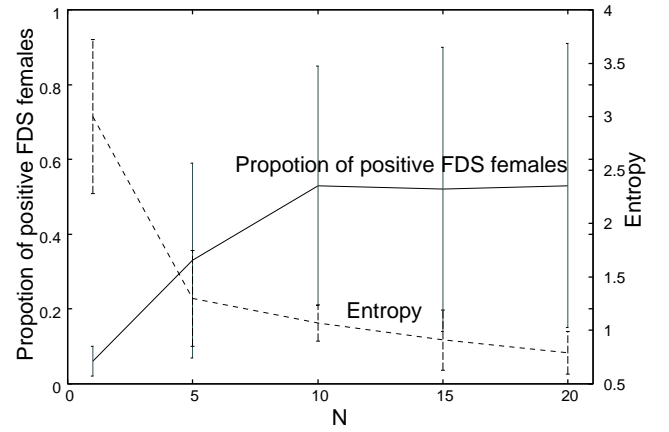


Figure 2: The average proportion of positive FDS females and the entropy of male traits after 3,000 steps at each OSR of males (N) for 40 trials.

Experiments

Next, we describe our experiments with the proposed model, where many male and female agents exist and are evolvable.

Experimental settings

All females can breed after $2[\text{step}]$, and select a mate described above. All parents produce two offspring for each breed. All agents are dead after $20[\text{step}]$ (life time). An initial population of 1,000 agents, consisting of 500 females and 500 males, is evolved from an initial state where: (1) gene g^{trait} and meme $\text{meme}^{\text{pref}}$ are encoded by bit-strings; the length of these strings is 10 bits each; (2) the initial values of genes g^{trait} and g^{strategy} , and meme $\text{meme}^{\text{pref}}$ are given randomly to all agents. In each step, 1,000 agents are randomly picked to form the next step. The parameterization used in these sets of simulation runs is (1) mutation rate $\gamma = 0.01$; (2) simulation steps = 3,000; (3) the number of sampled males $L = 40$.

In the experiments, we focus on the transition of mating-strategy genes and the gene diversity of male traits. An alternative approach to summarizing and forecasting gene diversity can be based Shannon's entropy (Shannon, 2001). Gene diversity E is calculated as

$$E = - \sum_{i=1}^S p_i \log_2 p_i, \quad (8)$$

where p_i is the occurrence probability of i th agents that have the same gene trait in a population and S is the number of gene traits patterns.

Results

We changed the OSR of males, N , in the range of $1 \leq N \leq 20$ and studied the evolution of the mating-strategy gene. Figure 2 shows the average proportion of female agents

whose mating-strategy is positive FDS and the average entropy of male traits at each N . Results showed that as N becomes larger, the proportion of positive FDS females becomes higher and comes nearer to 0.5. The entropy of male traits becomes lower as N becomes larger.

Discussion

As mentioned above, a female is added to the *potential_mate* list of a male selected as a mate. A male can breed with N females in his *potential_mate* list per step. When the number of females in his list exceeds N , some of the females cannot breed. The mating-strategy genes of females failing to breed then decrease at the next generation. The point here is that the mating-strategy of a female preferring a male whose *potential_mate* list exceeds a breeding capacity (N) is disadvantageous in terms of survival.

The proportion of positive FDS females in Figure 2 becomes higher as N becomes larger. We assume this is because, as N becomes larger, 1) it is harder for the number of females in a male's *potential_mate* list to become more than N , 2) females leave offspring more easily despite of preferring popular males, and 3) it is easy to increase the mating-strategy genes of preferring popular males; that is, the proportion of positive FDS females becomes higher. Conversely, as N becomes smaller, 1) it is easier for the number of females in male's *potential_mate* list to become more than N , 2) females preferring popular males have a harder time leaving offspring, and 3) it is easy to decrease the mating-strategy genes of preferring popular males; that is, the proportion of positive FDS females becomes lower.

Also, as shown in Figure 2, the proportion of positive FDS females comes nearer to 0.5 as N becomes larger. This is because the mating success of females approaches 100% regardless of female mating-strategy as N becomes larger. This means that the incidence of positive or negative FDS is irrelevant.

Effect of number of males sampled for female choice

Next, we changed the number of males sampled for female choice, L , in the range of $5 \leq L \leq 60$, and studied the resulting evolution of the mating-strategy gene. The OSR of males (N) is fixed to one. Figure 3 shows the average proportion of female agents whose mating strategy is positive FDS and the average entropy of male traits after 3,000 steps at each L sampled males for 40 trials.

Experimental results showed that as the size of the males sampled (L) became larger, the proportion of positive FDS females became lower and the entropy of male traits became higher. This is because it was easy for the sampled males to overlap as the sample size becomes larger. Duplicate sampling caused concentration of popularity. Then, as mentioned above, it was easy for the number of females in

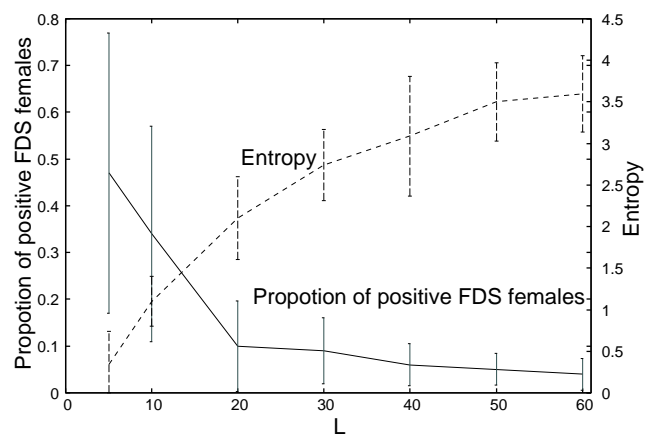


Figure 3: The average proportion of positive FDS females and the entropy of male traits after 3,000 steps at each L sampled males for 40 trials.

a male's *potential_mate* list to exceed his capacity and the proportion of positive FDS females became smaller.

Inversely, as the size of sampled males became smaller, the proportion of positive FDS females became higher, approaching 0.5. This means that the incidence of positive or negative FDS is irrelevant, since as the size of sampled males becomes smaller, there seems to be no effect of the FDS. FDS only exhibits an effect for animals with a large enough number of sampled males.

Comparison with real animals

In this section, we compare the experimental results with real animals. According to Singh et al. (Singh and Sisoia, 2000), negative FDS has been observed in 14 kinds of animals (parasitic wasp, flour beetle, etc.) while the mate-choice copying has been observed in 25 kinds of animals (sailfin molly, Japanese medaka, etc.) (Vakirtzis, 2011). Here, we treat mate-choice copying as positive FDS, since mate-choice copying has been shown to produce positive FDS (Kirkpatrick and Dugatkin, 1994).

The operational sex ratio (OSR) is an important environmental factor that influences mating behaviors (Clutton-Brock and Parker, 1992). We consider the OSR of each mating system. The OSR in monogamous species is approximately equal (Zug et al., 2001). The OSR in polyandrous species is typically strongly female biased (Schamel et al., 2004) while that in polygynous species is male biased (Jorgensen and Fath, 2008). The OSR in promiscuous species is not clear, but it might be male biased since males might have relatively higher potential reproductive rate than females. Then, we can explain the OSR of males as *Polyandrous* < *Monogamous* < *Polygamous*, *Promiscuous*.

Figure 4 shows the number of species having been confirmed to practice FDS at each mating system. White and black boxes indicate the distribution of 11 species exhibiting

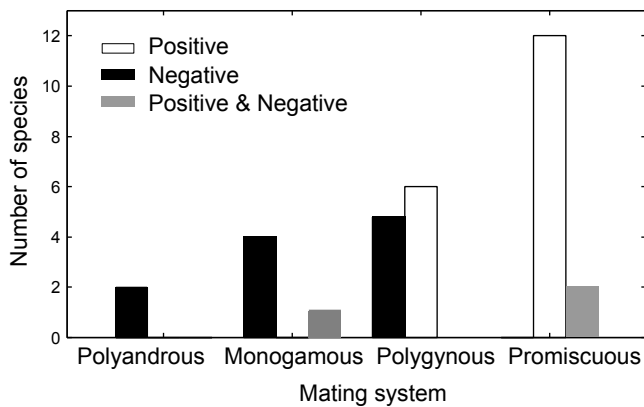


Figure 4: Number of species having been confirmed to practice FDS at each mating system. White boxes indicate positive FDS. Black boxes indicate negative FDS. Gray boxes indicate 3 species exhibiting both positive and negative FDS.

only positive FDS and 18 species¹ exhibiting only negative FDS, respectively. Gray boxes indicate the distribution of 3 species (guppy, drosophila, and humans) exhibiting both positive and negative FDS. In this figure, we can confirm that positive FDS occurs only in species whose OSR of males is large whereas negative FDS occurs in species whose OSR of males is small. This result partially matches our experimental results in Figure 2.

Several experiments (Doucet et al., 2004; Slagsvold and Viljugrein, 1999) and studies (Vakirtzis and Roberts, 2009, 2010; Dubois, 2007) have argued that mate-choice copying is highly unlikely to evolve in monogamous species due to the increasing costs of female competition. The OSR of males belonging to monogamous species is less than that of polygamous males. Our experimental results showing that as the OSR becomes smaller, the positive FDS females becomes lower, confirm these hypotheses.

On the other hand, the number of sampled males (L) of real animals is not clear. We still need to clarify whether the experimental results agree with the behavior of real animals.

Conclusion

We proposed a new model for mate choice involving genes and memes that introduces mating-strategy genes. The mating-strategy gene means that females prefer whether popular or unpopular males. We expressed female agents that have the mating-strategy gene and the meme preference influenced from other mate choice. The results of experiments using our proposed model demonstrated that as the operational sex ratio (OSR) of males becomes larger, the number of positive FDS females increases. A similar tendency was observed among real animals. We also discov-

¹This is with the exception of four species; two species whose mating system is uncertain, one species with reversed sex roles, and one genotypic species.

ered that as the size of males sampled for female choice became larger, the number of positive FDS females decreased. However, we have not matched the results of this experiment against real-world animals. We need to examine the number of sampled males of actual animals and compare it with our experimental results.

We would like to point out here that despite strong evidence for the negative FDS, the evolutionary processes that account for its prevalence are not known (Hughes et al., 2013). From the results of experiments using our proposed model, we can build two hypotheses for this question. One, the OSR is not strongly male biased. Two, the sampled male size is too big.

However, mate choice in the real world is not as simple as in our model. There are a variety of factors involved in propagation, such as cost, fitness and asymmetry in the roles between males and females. We need to consider the existence of male meme traits such as decoration and mimesis. In our future work, we will improve the model based on the findings of this paper so that it better conforms to the real world.

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