Journal of Theoretical Biology 341 (2014) 102–110

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Cooperation promotes the evolution of separate sexes from hermaphrodites with unitary growth

Ying Xu, Jiang-Nan Yang*

School of Life Sciences, Nanjing University, Jiangsu 210093, China

HIGHLIGHTS

- Investments that increase less than linearly with offspring number promote dioecy.
- Modular growth linearizes investments in most plants and promotes hermaphroditism.
- Males and females cooperate with each other and promote sexual differentiation.
- Mutant phenotypes at low frequency can come into cooperation despite genetic drift.

ARTICLE INFO

Article history:
Received 19 March 2013
Received in revised form
25 September 2013
Accepted 26 September 2013
Available online 12 October 2013

Keywords:
Sex allocation
Sex ratio
Genetic drift
Coevolution
Fixed costs

ABSTRACT

Most animals have specialized into separate sexes but most plants remain hermaphroditic. The underlining cause for this is still unclear. Here we address this question by evolutionary stable strategy analysis and exact calculation of frequency-dependent selection and genetic drift in geographically structured populations. Reproductive investments of hermaphrodites are divided into male and female functions, and each sex requires linear investments that increase linearly with successful gamete number and reusable investments (RIs) that increase less than linearly. Individuals specializing into one sex require RIs of only this sex and thus can produce more gametes. However, these gametes suffer strong kin competition as they are of the same sex and gamete number of the other sex decreases. The success of individuals specializing into one sex requires individuals specializing into the other sex to cooperate with them, providing them with more opposite-sex gametes and relaxing them of the same-sex competition. The evolution of this cooperation does not require two rare mutations to happen simultaneously at the same place, because single-sex mutants can sparsely spread in a hermaphroditic population with RIs despite genetic drift and wait for mutants of the other sex to arise. RI resembles fixed cost in previous theories. However, previous theories considered all costs except for costs for gametes as fixed costs and this does not capture an important plant–animal difference; modular growth of sexual organs in most plants and some animals promotes reproductive investments to increase linearly with offspring number, so their investments in sexual organs are linear investments rather than fixed costs. This study shows the evolution of separate sexes from hermaphrodites as an example of the evolution of cooperation and mutualism as in harmony games, and highlights modular growth as an important factor that prevents most plants and some animals from evolving into separate sexes.

1. Introduction

Separate sexes of different mating types, which were presumably to avoid inbreeding and gain offspring diversity (Whitfield, 2004), appeared in the early evolution of sex in haplont species (such as protozoa and most fungi). The gamete size differentiation (known as the evolution of anisogamy, see models of Parker (1982) and Yang (2010)) of the two mating types of some multicellular haplont species, such as many bryophyta, may have given rise to the first form of separate males and females. These haplont males and females mitotically produce sperm and eggs that fuse to form diploid zygotes. Then the zygotes or their mitotic derivatives (sporophytes) regenerate the haploid males and females through meiosis. So, the diploid zygotes may be viewed as the earliest hermaphrodites that gave rise to both sperm and eggs (through male and female offspring), though the males and females (gametophytes) still lived independently. Then, the diploid phase was prolonged relative to the haploid phase in the life cycles of some clades of organisms and became the dominant phase in all animals and most vascular plants (Mable and Otto, 1998), with haploid gametophytes usually only “parasitizing” the diploid (Campbell et al., 2003). As a result, the “early hermaphrodites” (diploid sporophytes) became evident as what people usually mean by saying hermaphrodites.

---

* Corresponding author. Tel.: +86 13612940315.
E-mail address: yangjiangnan@qq.com (J.-N. Yang).

0022-5193/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jtbi.2013.09.033

However, as evolution continued, the hermaphrodites of many animals, such as ancestors of vertebrates and arthropods, gave up one sex and differentiated into separate sexes of male and female again (but with diploid bodies and meiosis), though most plants still remain hermaphroditic. Many theories have been proposed to explain hermaphroditism and separate sexes. However, an important question still remains unclear: what is the fundamental difference between plants and animals that causes their very different tendency to evolve into separate sexes or to remain hermaphrodites? There are many case-by-case analyses, but we do need a simpler, general and long-term stable explanation.

For example, although avoiding inbreeding (or selfing) depression is still viewed as an important reason for the evolution of separate sexes by many researchers (Charlesworth and Charlesworth, 1978), its generality is a problem (Iyer and Roughgarden, 2008), as most hermaphrodites can avoid inbreeding or selfing (De Nettancourt, 2001; Goodwillie et al., 2005; Jarne and Auld, 2006), especially for most animals that have freer control of their gametes. Besides, separate sexes are more costly than many other mechanisms of avoiding selfing, so avoiding selfing should not be a stable and general explanation for separate sexes.

The theory of sex allocation (Campbell, 2000; Charnov, 1982; Charnov et al., 1976) can partly explain hermaphroditism. Hermaphrodites will use the limited resources more efficiently if the marginal increase of fitness of a sex is diminished when the cost of the sex increases further. In the theory of sex allocation, many factors, such as sibling competition caused by lack of locomotion, for plants are listed to show why male or female investments have diminishing marginal returns. However, this theory explains more about plants and more about the costs of differentiation, but says little about the benefits of differentiation, especially for animals. The theory relies on the shape of the fitness function to explain hermaphroditism, which is important and fundamental to our following model, but does not clearly imply the mechanisms for the shape of the fitness function. Exploring these mechanisms will be important for better understanding the exact biological reasons for the evolution of hermaphroditism and separate sexes.

What is more, hermaphrodites can avoid the failure to find mates, which may help hermaphrodites succeed in natural selection (Campbell, 2000; Darwin, 1859), especially for plants that cannot move by themselves. However, many species, including many hermaphrodites, can also reproduce asexually (de Meeus et al., 2007), which is more efficient than selfing as there are no costs for meiosis or inbreeding depression. So, ensuring reproduction should not be a general explanation for hermaphroditism either.

As differentiation means that individuals have to depend more on each other, cooperation is probably closely associated if two differentiated individuals can be functionally considered together as a "cooperation whole" (or a couple of a male and a female here) (Yang, 2010), which is a dynamic structure, formed when a male and a female meet and reproduce, and generates benefit for both the male and the female. What is the problem cooperation solves here? Some biologists (Bawa, 1980; Charnov, 1979; Heath, 1977; Lloyd, 1982) argued that hermaphrodites suffer an energetic cost because they maintain two reproductive systems. However, all hermaphrodites maintain two reproductive systems; why are plants different from animals? So, these biologists are close to the right answer, but more efforts are still needed to better understand how separate sexes evolved. In our opinion, it is sexually different reusable investments (SDRIs, mathematically defined in Section 2) rather than two reproductive systems that promote the evolution of separate sexes. SDRIs are defined as investments that are specifically required for one sex and can be re-used when additional gametes/offspring can be produced, i.e., SDRIs increase less than linearly (i.e., with negative second derivative) with total offspring number (the actual payoff). SDRIs are similar to "fixed costs" used by some other theorists (Charnov, 1979; Heath, 1977). However, an investment does not need to be "fixed" to promote sexual differentiation, as increasing less than linearly with offspring number will be sufficient.

Multicellular organisms have two basic types of growth, modular and unitary (Halle, 1986; Ryland and Warner, 1986). Most plants and some sessile animals show modular growth, with some basic units replicate again and again at multiple places and remain totipotent (i.e., new organs/body segments, especially sexual organs, can be generated if more resource is available), while the body plans of most animals are genetically pre-determined (unitary growth) (Walbot, 1985). Most plants do not have obvious SDRIs, because their modular growth makes investments in sexual organs increase linearly with total offspring number and thus cannot be viewed as SDRIs or fixed costs. We think this is possibly the main reason why most plants remain hermaphroditic.

SDRIs can cause the evolution of cooperation of individuals to differentiate into males and females to produce more offspring as a whole (by using the saved reusable investments from the unused sex). Then, males and females can promote the success of each other by providing each other with more opposite gametes and relieving each other of the local competition pressure (Charnov, 1982; Charnov et al., 1976; Eppley and Jesson, 2008; Ghiselin, 1969) from the same sex. We consider this mutual relationship as cooperation between males and females as in harmony games (Helbing and Johansson, 2010), which does not have large cost for cooperation as in Prisoner's dilemma (Nowak, 2006) and does not have cheaters, as hermaphrodites do not gain from males and females. We define cooperation simply as a relationship with all sides working together and benefiting each other, and this cooperative interdependence fits in the context of increasingly high levels of organization (Okasha, 2006; Yang, 2013) and mutual evolution (Holland and DeAngelis, 2010; Holland et al., 2002).

We will first build a model that tries to unify previous theories as well as incorporating SDRIs and cooperation. Then we will apply the model to more general conditions and show the evolutionary dynamics in a stochastic model of selection and genetic drift in ring-shaped structured populations by exact calculation. Finally, we will further discuss why plants and animals are fundamentally different in the evolution of separate sexes. We do not attempt to cover all previous theories here. Rather, we seek for the most simple and general patterns that are important in the differences of plants and animals.

2. Basic assumptions of the model

Assume that $N-1$ individuals of a hermaphroditic population can directly compete with a focal individual, especially a mutant. These N individuals are defined as the competition region of the focal individual. When N increases, an individual directly competes with more individuals, so kin competition is diluted. N describes the density and mobility (dispersal) of individuals in a population. The idea of regional competition in a structured population has been used a lot in the study of the evolution of cooperation, often to introduce kin selection (Fisher, 1930; Mitteldorf and Wilson, 2000; Raimondi and Martin, 1991; Yang, 2013). Here we use it to measure the degree of self-competition (local frequency-dependent selection) and the freedom degree of competition among different individuals, the same with the model of Yang (2010). Furthermore, we assume that sperm and egg dispersal completely overlap with survival competition in region to avoid the unnecessary complexity of sexual differences. For example, dispersal of only females can lead to local mate competition of males and a biased sex ratio