Sex ratio elasticity influences the selection of sex ratio strategy

Yaqiang Wang [1,2] , **Ruiwu Wang** [3] , **Yaotang Li** [1] , **Zhanshan (Sam) Ma** Corresp. [4]

[1] School of Mathematics and Statistics, Yunnan University, Kunming, Yunnan, People’s Republic of China
[2] Institute of Mathematics and Information Science, Baoji University of Arts and Sciences, Baoji, Shanxi, China
[3] Experimental & Theoretical Ecology Lab & State Key Laboratory of Genetic Resources & Evolution, Chinese Academy of Science, Kunming, China
[4] Computational Biology & Medical Ecology Lab & State Key Laboratory of Genetic Resources & Evolution, Chinese Academy of Science, Kunming, China

Corresponding Author: Zhanshan (Sam) Ma
Email address: ma@vandals.uidaho.edu

There are three *sex ratio strategies* (SRS) in nature—male-biased sex ratio, female-biased sex ratio and, equal sex ratio depending on the proportion of male offspring being greater than, less than, or equal to ½. The problem was already noted in Darwin’s (1859) “*Origin of Species,*” and it was R. A. Fisher (1930) who first explained why most species in nature display a sex ratio of ½. Consequent SRS theories such as Hamilton’s (1967) *local mate competition* (LMC) and Clark’s (1978) *local resource competition* (LRC) separately explained the observed deviations from the seemingly universal 1:1 ratio. However, to the best of our knowledge, there is not yet a unified theory that accounts for the mechanisms of the three SRS. Here, we introduce the *price elasticity theory* in economics to define *sex ratio elasticity* (SRE), and present an analytical model that derives three SRSs based on the following assumption: simultaneously existing competitions for both resources and mates influence the level of SRE in both sexes differently. Consequently, it is the difference (between two sexes) in the level of their sex ratio elasticity that leads to three different SRS. Our analytical results demonstrate that the elasticity-based model not only reveals a highly plausible mechanism that explains the evolution of SRS in nature, but also offers a novel framework for unifying two major classical theories (*i.e.,* LMC & LRC) in the field of SRS research.

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2166v1 | CC BY 4.0 Open Access | rec: 27 Jun 2016, publ: 27 Jun 2016

Sex Ratio Elasticity Influences the Selection of Sex Ratio Strategy

Yaqiang Wang[1,3], Ruiwu Wang[2], Yaotang Li*[3] and Zhanshan (Sam) Ma*[4]

[1]Institute of Mathematics and Information Science
Baoji University of Arts and Sciences
Baoji, Shanxi, China

[2]Experimental and Theoretical Ecology Lab &
State Key Laboratory of Genetic Resources and Evolution
Kunming Institute of Zoology
Chinese Academy of Science, China

*[3]School of Mathematics and Statistics,
Yunnan University, Kunming, Yunnan, China
Co-correspondence: liyaotang@ynu.edu.cn

*[4]Computational Biology and Medical Ecology Lab &
State Key Laboratory of Genetic Resources and Evolution
Kunming Institute of Zoology
Chinese Academy of Science, China
Co-correspondence: samma@uidaho.edu

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2166v1 | CC BY 4.0 Open Access | rec: 27 Jun 2016, publ: 27 Jun 2016

Abstract

There are three *sex ratio strategies* (SRS) in nature—male-biased sex ratio, female-biased sex ratio and, equal sex ratio depending on the proportion of male offspring being greater than, less than, or equal to ½. The problem was already noted in Darwin's (1859) "*Origin of Species,*" and it was R. A. Fisher (1930) who first explained why most species in nature display a sex ratio of ½. Consequent SRS theories such as Hamilton's (1967) *local mate competition* (LMC) and Clark's (1978) *local resource competition* (LRC) separately explained the observed deviations from the seemingly universal 1:1 ratio. However, to the best of our knowledge, there is not yet a unified theory that accounts for the mechanisms of the three SRS. Here, we introduce the *price elasticity theory* in economics to define *sex ratio elasticity* (SRE), and present an analytical model that derives three SRSs based on the following assumption: simultaneously existing competitions for both resources and mates influence the level of SRE in both sexes differently. Consequently, it is the difference (between two sexes) in the level of their sex ratio elasticity that leads to three different SRS. Our analytical results demonstrate that the elasticity-based model not only reveals a highly plausible mechanism that explains the evolution of SRS in nature, but also offers a novel framework for unifying two major classical theories (*i.e.,* LMC & LRC) in the field of SRS research.

Keywords: Sex ratio strategy (SRS), Sex ratio elasticity (SRE), Local mate competition (LMC), Local resource competition (LRC), Evolutionary stable strategies (ESS).

Introduction

The *sex ratio* is usually defined as the proportion of males in a population, and it can further be classified as *the primary, secondary*, and *tertiary sex ratio*. We are concerned with the first one, which refers to the ratio of at time of conception (Coney and Mackey, 1998). The *sex ratio strategy* (SRS) is the sex ratio pattern that is exhibited by a species in nature, and its variation can directly affect the structure of population and its mating system (Charnov, 1982; Mabry et al., 2013; West, 2009). In nature, different species choose three different sex ratio strategies: male-biased sex ratio, female-biased sex ratio and, equal sex ratio, depending on sex ratio being greater than, equal, or less than ½, in terms of the proportion of male offspring in the whole population. In spite of the extensive studies in the field since Darwin (1859) and Fisher (1930), the evolution of SRS is still a hotly debated topic in evolutionary biology (*e.g.,* Charnov, 1982; West, 2009).

In 1930, Fisher assumed that males and females are equally costly to produce, equal numbers of both sexes should be produced, leading to the sex ratio of ½ (Fisher, 1930; Charnov 1982; West, 2009). Although it has recently been discovered that this theory was actually first put forward in the 19th century by the German biologist Carl Düsing in his dissertation, who was among the first who resorted to mathematical modeling for solving evolutionary biology problems (Edwards, 2000; West, 2009)， we propose the equal investment theory in this paper as presented by Fisher. An implicit assumption in Fisher's *equal investment theory* is that there are no competitive or cooperative interactions among relatives. Obviously, when populations are structured, competitive interactions between siblings could occur in each patch, such as, mate competition among male offspring, and resource competition among female offspring (Charnov, 1982, Clark 1978, Hamilton 1967, West Stuart 2009).

Mate competition among male offspring in a structured population is termed as local mate competition (LMC), it was first introduced by W. D. Hamilton to explain extraordinary female-biased sex ratios observed in a variety of insects and mites (Hamilton 1967, West Stuart 2009). Hamilton considered the mating system of diploid organisms, and showed that the evolutionary stable strategy (ESS) sex ratio (s*), or what he termed 'unbeatable' sex ratio, can be represented as: $s^* = (n-1)/(2n)$, where n is the number of foundress per patch (Hamilton 1967, West Stuart 2009). In 1979, Hamilton extended his original LMC theory for diploid (Hamilton 1967) to the case of haplo-diploid organism, and noted that inbreeding causes mothers to be relatively more related to their daughters than to their sons, which leads to a slightly more female biased sex ratio being favored. LMC theory predicts female-biased sex ratio is an ESS when mating takes place locally and related male offspring compete for mates. However, W. D. Hamilton (1967, 1979) only explored the effect of competition among male offspring on the SRS, and resource competition among female offspring could also influence the SRS.

In the study of African bush baby (*Galago crassicaudaus*), Clark (1978) found that during breeding season, female's movement is restricted by her 'responsibility' for raising offspring. If male offspring (instead of female offspring) disperse from the natal site while female offspring stay local and compete with each other for resources (such as space, food), then local resource competition (LRC) among females can occur. From the observation, Clark (1978) proposed that female offspring compete for resources (such as space, food), but male offspring leave their birthplace to find new mates. Clark (1978) further postulated with mathematical modeling that female competition for resources can lead to male-biased SRS (Clark 1978, West Stuart 2009).

In summary, existing LMC and LRC models, including their extensions addressed either the effect of competition among male offspring or that among female offspring on the ESS of sex ratio, *respectively*. However, many field observations have discovered that mate competition among male offspring and resource competition (such as nest) among female offspring often occur simultaneously in nature (West Stuart 2009, West Stuart A et al. 2005). Obviously, *mates* can also be considered as a *resource* different from food and shelters.

The simultaneous of these competitions might lead to the difference intensity between male competition and female competition. However, the difference intensity between male competition and female competition could lead to the difference of the sex ratio elasticity of male offspring survival rate and the sex ratio elasticity of female offspring survival rate, which may affect the selection of sex ratio strategy. The concept of elasticity (famous in economics) was first introduced by Wang et al to measure the responsiveness of offspring survival rate to a change in reproductive allocation (Wang et al. 2013). The sex ratio elasticity of male (female) survival rate is a measure used to show the responsiveness of male (female) survival rate to a change in sex ratio. It could be defined as the percentage change in male (female) survival rate divided by the percentage change in sex ratio, and this similar to elasticity concept in economics (Taylor and Weerapana 2011).

Although the existing model do already incorporate the simultaneous mate competition among male offspring and resource competition among female offspring into a single framework (Rodrigues and Gardner 2015), to the best of our knowledge, in the existing literature, how the sex ratio elasticity of male (female) survival rate affects the SRS, which has never been studied before. Therefore, it is still a challenge to incorporate the LMC and LRC into a single framework based on the sex ratio elasticity, and to explore the effect of the sex ratio elasticity of male (female) survival rate on SRS.

In the present study, we construct a new sex ratio model that assumes both the competitions for mates among males and competition for resources among females occur simultaneously in the mating system. Applying MacArthur's product rules (MacArthur 1965). Our analysis reveals that the ESS sex ratio depends on the *sex ratio elasticity* of the male offspring's survival rate (SRE-MSR) and the *sex ratio elasticity* of the female offspring's survival rate (SRE-FSR). Furthermore, we found that both the simultaneous existing competitions could create asymmetricity between males and females in their intensities of competitions. Moreover, the asymmetricity in the intensity can lead to the difference between the *sex ratio elasticity* of the SRE-MSR and SRE-FSR. Then, it is the difference in the sex ratio elasticity that influences the evolution of sex ratio strategy.

The model

Considering a sexual species, which has discrete generations and their offspring remain their natal site. Assuming that male offspring compete for mates and female offspring compete for resources such as nest site and food, there are two competitions occurring simultaneously.

Let m and f be the number of male offspring and the number of female offspring respectively. We further assume that an adult individual can produce N offspring, r is the proportion of male offspring, *i.e.*, the sex ratio, in a clutch, $1-r$ is the proportion of female offspring in the same clutch. S_m is the survival rate of male offspring, and S_f is

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2166v1 | CC BY 4.0 Open Access | rec: 27 Jun 2016, publ: 27 Jun 2016

the survival rate of female offspring.

Based on the above assumptions, the number of male offspring is

$$m = N \cdot r \cdot S_m, \qquad (1)$$

and the number of female offspring is

$$f = N \cdot (1-r) \cdot S_f, \qquad (2)$$

We further assume that the population is effectively infinite, and the brood's sex ratio is determined by the maternal genotype. According to the *de facto* standard treatment in sex-ratio theory, the evolutionary stable strategy (ESS) maximizes the product of $m \times f$, which is known as “MacArthur product rule” in the literature (Charnov Eric L 1982, MacArthur 1965, West Stuart 2009).

From Equations (1) and (2), the product of m and f is given by

$$m \times f = N^2 r(1-r) S_m(r) S_f(r). \qquad (3)$$

Since male offspring compete for mates, the increase of their number should result in the decrease of their survival rate. Similarly, the competition for resources among female offspring should lead to the decrease of their survival rate. In other words, S_m and S_f should be the function of r, *i.e.*, $S_m = S_m(r)$ and $S_f = S_f(r)$, and their derivatives should satisfy the following conditions: $dS_m / dr < 0$ and $dS_f / dr > 0$.

From (3), the product $m \times f$ is a function of the sex ratio r, and it achieves its maximal value with respect to r when $r = r^*$, where r^* is the ESS sex ratio. According to the theory of EES, there are:

$$\left. \frac{d(m \times f)}{dr} \right|_{r=r^*} = 0, \qquad (4)$$

and

$$\left.\frac{d^2(m\times f)}{dr^2}\right|_{r=r^*} \le 0\,. \tag{5}$$

Applying Equation (4) to Equation (3), we obtain the following ESS sex ratio as

$$r^* = \frac{1}{1+\dfrac{1}{1+e_{S_m}+e_{S_f}}}\,, \tag{6}$$

where $e_{S_m} = (dS_m/S_m)/(dr/r)$ is the percentage change in male survival rate divided by the percentage change in sex ratio and $e_{S_f} = (dS_f/S_f)/(dr/r)$ is the percentage change in female survival rate divided by the percentage change in sex ratio. They are similar to the elasticity concepts of economics, corresponding to the well-known *price elasticity of demand* and *price elasticity of supply* (Frank and Bernanke 2007). We therefore define $e_{S_m} = (dS_m/S_m)/(dr/r)$ and $e_{S_f} = (dS_f/S_f)/(dr/r)$ as the *sex ratio elasticity of male survival rate* (SRE-MSR) and the *sex ratio elasticity of female survival rate* (SRE-FSR), respectively.

From male's perspective, the SRE-MSR is a measure of the responsiveness of male survival rate to a change in sex ratio. Similarly, from female's perspective, the SRE-FSR measures the responsiveness of female survival rate to a change in sex ratio.

Obviously, from the definitions of SRE-MSR and SRE-FSR, the value of the SRE-MSR should be negative because male survival rate decreases with the increase of sex ratio, and the value of the SRE-FSR should be positive because female survival rate increases with the increase of sex ratio. The negative or positive sign only represents the direction of variation and the value represents the sensitive degree of survival rate to sex ratio (Taylor and Weerapana, 2011; Wang et al., 2013).

Furthermore, from the definition of sex ratio, the ESS sex ratio must also satisfy $0 < r^* < 1$, (we only consider sexual organisms in this study). From Equation (6) and $0 < r^* < 1$, we have $1 + e_{S_m} + e_{S_f} > 0$; in the following, this constraint is maintained.

Results

From the above model constructions, we conclude the following results:

(i) If $e_{S_m} < -1$, that is, the male survival rate is elastic, then

1) When $0 \le e_{S_f} < 1$ (the female survival rate is inelastic) and $e_{S_f} = 1$ (the female survival rate is unitary elastic), the $1 + e_{S_m} + e_{S_f}$ is less than 0, therefore, these cases is meaningless in our model.

2) When $e_{S_f} > 1$ (the female survival rate also is elastic), *i)* If $\left|e_{S_m}\right| > e_{S_f}$, which means the sensitive degree of the male survival rate to sex ratio is greater than that of female, from Equation (6), we have $r^* < 1/2$ as an ESS sex ratio, i.e., the female-biased sex ratio is an ESS (Figure 1A, blue line); *ii)* If $\left|e_{S_m}\right| = e_{S_f}$, which means the sensitive degree of the male survival rate to sex ratio is equal to that of female, from Equation (6), we have $r^* = 1/2$ as an ESS sex ratio, *i.e.,* the unbiased sex ratio is an ESS (see the red star point of the Figure 1A and 1B); *iii)* If $\left|e_{S_m}\right| < e_{S_f}$, which means the sensitive degree of the male survival rate to sex ratio is less than the female, from Equation (6), we have $r^* > 1/2$ as an ESS sex ratio, *i.e.,* the male-biased sex ratio is an ESS (Figure 1B, green line).

Location for Figure 1

Figure 1. When the male survival rate is elastic, the relationship between the SRE-FSR and the ESS sex ratio

(ii) If $e_{S_m} = -1$, that is, the male survival rate is unitary elastic, then

1) When $0 \le e_{S_f} < 1$ (the female survival rate is inelastic), i.e, $\left|e_{S_m}\right| > e_{S_f}$, which means the sensitive degree of the male survival rate to sex ratio is greater than that of female, from Equation (6), we have $r^* < 1/2$ as an ESS sex ratio, i.e., the female-biased sex ratio is an

ESS (Figure 2A, magenta line);

2) When $e_{S_f}=1$ (the male survival rate is unitary elastic), i.e., $\left|e_{S_m}\right|=e_{S_f}$ which means the sensitive degree of the male survival rate to sex ratio is equal to that of female, from Equation (6), we have $r^*=1/2$ as an ESS sex ratio, *i.e.,* the unbiased sex ratio is an ESS (see the red star point of the Figure 2A and 2B);

3) When $e_{S_f}>1$ (the female survival rate is elastic), i.e., $\left|e_{S_m}\right|<e_{S_f}$, which means the sensitive degree of the male survival rate to sex ratio is less than the female, from Equation (6), we have $r^*>1/2$ as an ESS sex ratio, *i.e.,* the male-biased sex ratio is an ESS (Figure 2, black line).

Location for Figure 2

Figure 2. When the male survival rate is unitary elastic, the relationship between the SRE-FSR and the ESS sex ratio

(iii) If $-1<e_{S_m}\leq 0$, that is, the male survival rate is inelastic, then

1) When $0\leq e_{S_f}<1$ (the female survival rate is inelastic), i) If $\left|e_{S_m}\right|>e_{S_f}$, which means the sensitive degree of the male survival rate to sex ratio is greater than that of female, from Equation (6), we have $r^*<1/2$ as an ESS sex ratio, i.e., the female-biased sex ratio is an ESS (Figure 3A, black line); ii) If $\left|e_{S_m}\right|=e_{S_f}$, which means the sensitive degree of the male survival rate to sex ratio is equal to that of female, from Equation (6), we have $r^*=1/2$ as an ESS sex ratio, *i.e.,* the unbiased sex ratio is an ESS (see the red star point of the Figure 3A and 3B); iii) If $\left|e_{S_m}\right|<e_{S_f}$, which means the sensitive degree of the male survival rate to sex ratio is less than the female, from Equation (6), we have $r^*>1/2$ as an ESS sex ratio, *i.e.,* the male-biased sex ratio is an ESS (Figure 3B, magenta line).

2) When $e_{S_f}=1$ (the male survival rate is unitary elastic) and $e_{S_f}>1$ (the female survival rate is elastic), i.e., $\left|e_{S_m}\right|<e_{S_f}$, which means the sensitive degree of the male

survival rate to sex ratio is less than the female, from Equation (6), we have $r^* > 1/2$ as an ESS sex ratio, *i.e.,* the male-biased sex ratio is an ESS (Figure 3B, magenta line).

Location for Figure 3

Figure 3. When the male survival rate is inelastic, the relationship between the SRE-FSR and the ESS sex ratio

Discussion

To study the evolution of sex ratio, previous models have separately dealt with how the mate competition among male offspring affects the ESS sex ratio and how the resource competition among female offspring affects the ESS sex ratio (Charnov, 1982; Clark, 1978; Fisher, 1930 ; Hamilton, 1967, 1979; West, 2009). Mate competition among male offspring and resource competition among female offspring may occur simultaneous in a same patch, and these competitions could lead to the difference of the SRE-MSR and SRE-FSR (West, 2009; West et al., 2005). However, as to our knowledge, how the SRE-MSR and SRE-FSR affect the ESS sex ratio, which have never been addressed before (West, 2009). The model described in this paper shows that if we assume that mate competition among male offspring and resource competition among female offspring occur simultaneous, the ESS sex ratio depends on the SRE-MSR and SRE-FSR.

Our model firstly shows that if the intensity of the competition among male offspring for mates equals to the intensity of the competition among female offspring for resources, i.e. the sensitive degree of the male survival rate to sex ratio is equal to the female's, the unbiased sex ratio is an ESS. In fact, when the mating is random in a large population and the resource competition among female is random (i.e. there are no competitive interactions between siblings), the intensity of the male competition is equal to the intensity of the female competition, in our model we predict that the ESS sex ratio is ½. This conclusion is similar to Fisher's equal investment theory, i.e., when mating is random, mothers favors equal investment into the two sexes, therefore, the ESS sex ratio is ½ (Fisher, 1930 ; West, 2009).

In addition, our model shows that if the competition among male offspring for mates is more intense than the competition among female offspring for resources, i.e., the sensitive degree of the male survival rate to sex ratio is greater than the female's, the ESS sex ratio is the female-biased. This result is consistent with many empirical studies (West Stuart 2009). For example, for some *Arthropods* (such as, beetles, mites), in this species, a female and her brood occupy a gallery under bark, mating usually occurs before dispersal from the larval host. Therefore, the competition among male offspring for mates is more intense than the competition among female offspring for resources, and strongly female biased sex ratio is observed (Charnov, 1982; Jordal et al., 2002; West, 2009; West et al., 2005). To be noted that when $e_{S_m} = -1/(n+1)$ and $e_{S_f} = 0$, *i.e.*, $\left|e_{S_m}\right| > e_{S_f}$, this result will became to the result of LMC (Hamilton, 1967).

On the contrary, if the competition among male offspring for mates is less intense than the competition among female offspring for resources, we predict that the ESS sex ratio is the male-biased. Moreover, the result of LRC is special case of our results, *i.e.*, if $e_{S_f} = 1/(n-1)$ and $e_{S_m} = 0$ (Charnov, 1982; Clark, 1978; West, 2009). Moreover, this prediction is consistent with some empirical tests (West, 2009). For example, in the African bush baby *Galago Crassicaudaus*, during the breeding season, female's movement are restricted by the burden of raising offspring, consequently, the competition among female offspring for resources is more intense than the competition among male offspring for mates, and so favors a male biased sex ratio reduce the competition among female offspring for resources (Clark, 1978; West, 2009).

Although using a simple sex ratio model and this study achieves several conclusions, there are still some limitations of the model used in this study. The model has disregarded a number of complicating factors, such as density dependence, disperse rate, the spatial structure. To some extent, adding these factors to the model may modify the conclusions reached in this study. We raise these issues to provoke further studies, not to mean that they are of secondary importance to a comprehensive theory of plant reproductive ecology.

Appendix

Elasticity is one of the most basic concepts in economics. Here, let's use the price elasticity of demand to illustrate this concept used in economics (Taylor and Weerapana 2011). Price elasticity of demand is a measure used to show the responsiveness, or elasticity, of the quantity demanded of a good or service to a change in its price. More precisely, it gives the percentage change in quantity demanded in response to a one percent change in price (holding constant all the other determinants of demand, such as income. It can be described as:

$$\text{Price elasticity } (E_P) = \frac{\text{percentage change in quantity demanded}}{\text{percentage change in price}}.$$

Since price and quantity demanded always move in opposite directions, E_P is a negative value. For convenience, however, the absolute value of E_P is used.

If E_P is larger than 1, we say demand is elastic: Consumer response is large relative to the change in price.

If E_P is less than 1, we say demand is inelastic: Consumers are not very responsive to price changes.

If E_P is equal to 1, demand is unitary elastic. In this case, the percentage change in quantity demanded is exactly equal to the percentage change in price.

References

Abe, J., Kamimura, Y., and Shimada, M., 2007. Sex ratio schedules in a dynamic game: the effect of competitive asymmetry by male emergence order. Behavioral Ecology 18, 1106-1115.

Abe, J., Kamimura, Y., Ito, H., Matsuda, H., and Shimada, M., 2003. Local mate competition with lethal male combat: effects of competitive asymmetry and information availability on a sex ratio game. Journal of Evolutionary Biology 16, 607-613.

Bulmer, M., 1986. Sex ratio theory in geographically structured populations. Heredity 56, 69-73.

Bulmer, M.G., and Taylor, P.D., 1980. Dispersal and the sex ratio.

Burton□Chellew, M.N., Koevoets, T., Grillenberger, B.K., Sykes, E.M., Underwood, S.L., Bijlsma, K., Gadau, J., van de Zande, L., Beukeboom, L.W., and West, S.A., 2008. Facultative sex ratio adjustment in natural populations of wasps: cues of local mate competition and the precision of adaptation. The American Naturalist 172, 393-404.

Charnov, E.L., 1982. The theory of sex allocation. Princeton University Press.

Charnov, E.L., 1987. On sex allocation and selfing in higher plants. Evolutionary Ecology 1, 30-36.

Clark, A.B., 1978. Sex ratio and local resource competition in a prosimian primate. Science 201, 163-165.

Coney, N.S., and Mackey, W., 1998. The woman as final arbiter: A case for the facultative character of the human sex ratio. Journal of Sex Research 35, 169-175.

Courteau, J., and Lessard, S., 1999. Stochastic effects in LMC models. Theoretical population biology 55, 127-136.

Courteau, J., and Lessard, S., 2000. Optimal sex ratios in structured populations. Journal of theoretical biology 207, 159-175.

Cremer, S., and Heinze, J., 2002. Adaptive production of fighter males: queens of the ant Cardiocondyla adjust the sex ratio under local mate competition. Proceedings of the Royal Society of London. Series B: Biological Sciences 269, 417-422.

Darwin, C., and Beer, G., 1951. The origin of species. Oxford University Press.

Edwards, A., 2000. Carl Düsing (1884) on The Regulation of the Sex-Ratio. Theoretical population biology 58, 255-257.

Fisher, R.A., 1930. The genetical theory of natural selection. The Clarendon press, Oxford,.

Frank, R.H., and Bernanke, B., 2007. Principles of economics.

Gardner, A., and Ross, L., 2013. Haplodiploidy, sex-ratio adjustment, and eusociality. The American Naturalist 181, E60-E67.

Ghana, S., Suleman, N., and Compton, S.G., 2012. Factors influencing realized sex ratios in fig wasps: double oviposition and larval mortalities. Journal of Insect Behavior 25, 254-263.

Godfray, H.C.J., 1994. Parasitoids: behavioral and evolutionary ecology. Princeton University Press.

Greeff, J., 1996. Alternative mating strategies, partial sibmating and split sex ratios in haplodiploid species. Journal of Evolutionary Biology 9, 855-869.

Greeff, J.M., van Noort, S., Rasplus, J.-Y., and Kjellberg, F., 2003. Dispersal and fighting in male pollinating fig wasps. Comptes rendus biologies 326, 121-130.

Hamilton, W., 1979. Wingless and fighting males in fig wasps amd other insects. Sexual selection and reproductive competition in insects, 167.

Hamilton, W.D., 1967. Extraordinary sex ratios. Science 156, 477-488.

Hardy, I., 2002. Sex ratios: concepts and research methods. Cambridge University Press.

Hardy, I.C., 1994. Sex ratio and mating structure in the parasitoid Hymenoptera. Oikos, 3-20.

Herre, E.A., 1985. Sex ratio adjustment in fig wasps. Science 228, 896-898.

Jordal, B.H., Beaver, R.A., Normark, B.B., and Farrell, B.D., 2002. Extraordinary sex ratios and the evolution of male neoteny in sib□mating Ozopemon beetles. Biological Journal of the Linnean Society 75, 353-360.

Kazmer, D., and Luck, R., 1991. The genetic-mating structure of natural and agricultural populations of Trichogramma. Colloques de l'INRA.

Mabry, K.E., Shelley, E.L., Davis, K.E., Blumstein, D.T., and Van Vuren, D.H., 2013. Social Mating System and Sex-Biased Dispersal in Mammals and Birds: A Phylogenetic Analysis. Plos One 8, e57980.

MacArthur, R.H., 1965. Ecological consequences of natural selection. Theoretical and mathematical biology. Blaisdell, New York, 388-397.

Nunney, L., and Luck, R.F., 1988. Factors influencing the optimum sex ratio in a structured population. Theoretical population biology 33, 1-30.

Reece, S., Shuker, D., Pen, I., Duncan, A., Choudhary, A., Batchelor, C., and West, S., 2004. Kin discrimination and sex ratios in a parasitoid wasp. Journal of Evolutionary Biology 17, 208-216.

Rodrigues AMM, Gardner A. 2015. Simultaneous failure of two sex-allocation invariants: implications for sex-ratio variation within and between populations. Proceedings of the Royal Society B Biological Sciences 282.

Shuker, D.M., and West, S.A., 2004. Information constraints and the precision of adaptation: sex ratio manipulation in wasps. Proceedings of the National Academy of Sciences of the United States of America 101, 10363-10367.

Shuker, D.M., Pen, I., Duncan, A.B., Reece, S.E., and West, S.A., 2005. Sex ratios under asymmetrical local mate competition: theory and a test with parasitoid wasps. The American Naturalist 166, 301-316.

Sundström, L., 1994. Sex ratio bias, relatedness asymmetry and queen mating frequency in ants. Nature 367, 266-268.

Suzuki, Y., and Iwasa, Y., 1980. A sex ratio theory of gregarious parasitoids. Researches on Population Ecology 22, 366-382.

Tagawa, J., 2000. Sex allocation and clutch size in the gregarious larval endoparasitoid wasp, Cotesia glomerata. Entomologia Experimentalis Et Applicata 97, 193-202.

Taylor, J.B., and Weerapana, A., 2011. Principles of economics. Cengage Learning.

Taylor, P.D., 1993. Female-biased sex ratios under local mate competition: an experimental confirmation. Evolutionary Ecology 7, 306-308.

Wang, R.-W., Wang, Y.-Q., He, J.-Z., and Li, Y.-T., 2013. Resource Elasticity of Offspring Survival and the Optimal Evolution of Sex Ratios. PloS one 8, e53904.

Werren, J.H., 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. Science 208, 1157-1159.

West, S., 2009. Sex allocation. Princeton University Press.

West, S.A., Shuker, D.M., and Sheldon, B.C., 2005. Sex□ratio adjustment when relatives interact: a test of constraints on adaptation. Evolution 59, 1211-1228.

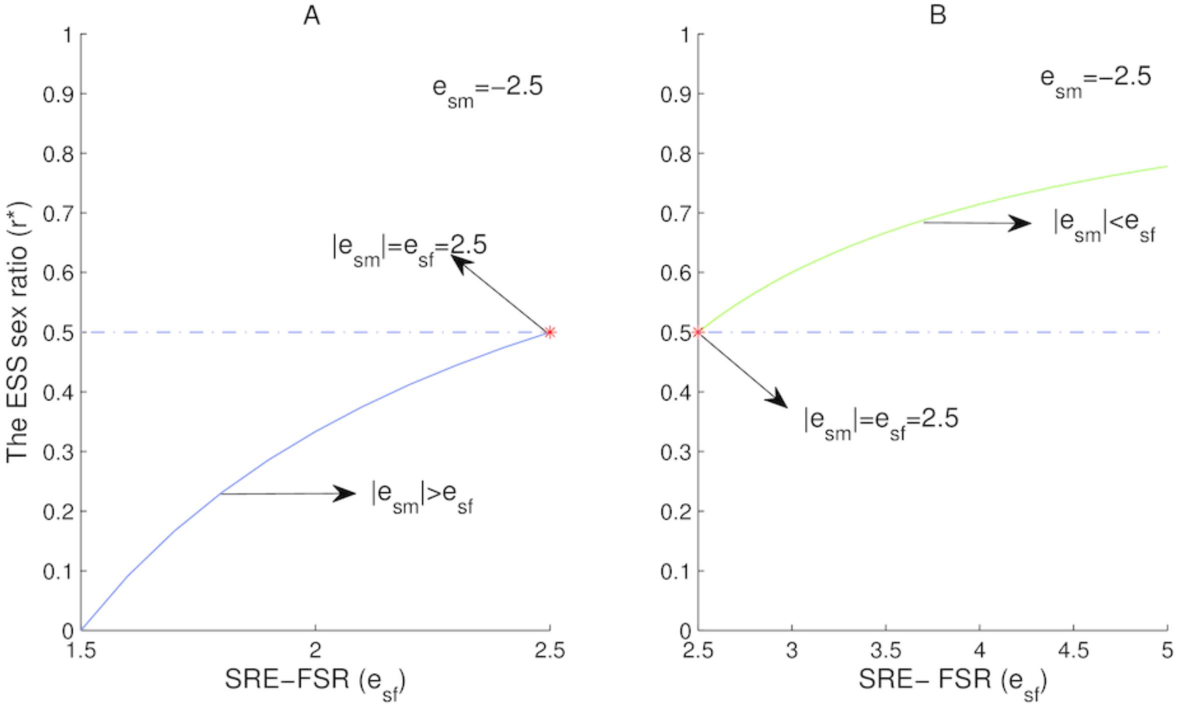
Wilson, D.S., and Colwell, R.K., 1981. Evolution of sex ratio in structured demes. Evolution, 882-897.

Wylie, H., 1965. Discrimination between parasitized and unparasitized house fly pupae by females of Nasonia vitripennis (Walk.)(Hymenoptera: Pteromalidae). The Canadian Entomologist 97, 279-286.

Figure 1

Figure 1

Sex ratio elasticity influences the selection of sex ratio strategy Figure 1. The relationship between the SRE-FSR and ESS sex ratio when the male survival rate is elastic



PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2166v1 | CC BY 4.0 Open Access | rec: 27 Jun 2016, publ: 27 Jun 2016

Figure 2

Figure 2

Sex ratio elasticity influences the selection of sex ratio strategy The relationship between the SRE-FSR and ESS sex ratio when the male survival rate is unitary elastic.

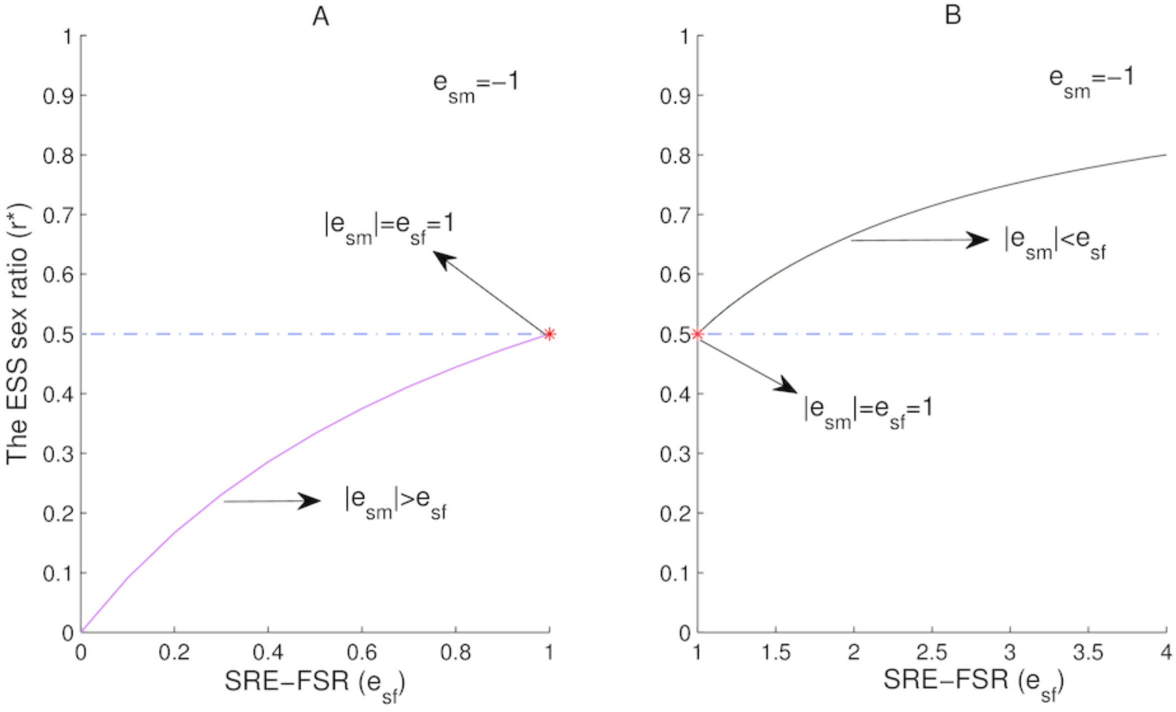
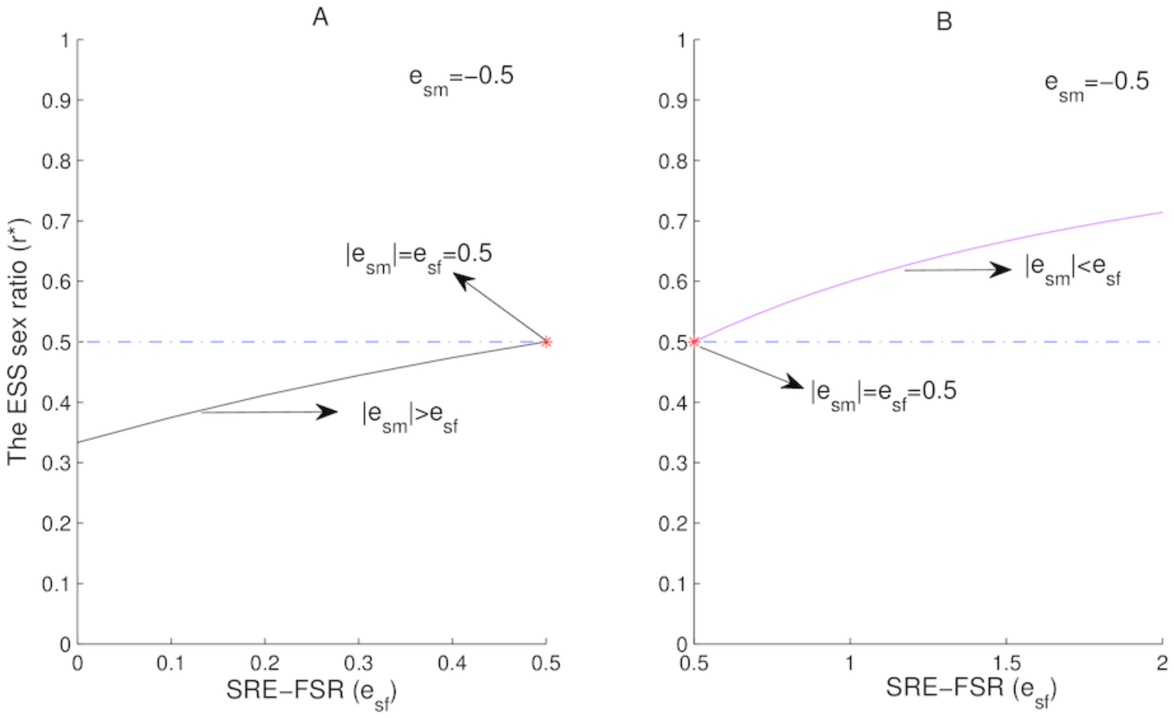


Figure 3

Figure 3

Figure 3. The relationship between the SRE-FSR and the ESS sex ratio when the male survival rate is inelastic.



PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.2166v1 | CC BY 4.0 Open Access | rec: 27 Jun 2016, publ: 27 Jun 2016