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Slightly male-biased sex ratios for the avoidance of extinction

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ABSTRACT

Background: Slightly male-biased sex ratios occur commonly in animals with a higher male juvenile mortality, including humans. R.A. Fisher's principle of equal sex ratios does not explain these slightly biased sex ratios. Tainaka *et al.* (2006) suggested that male juvenile mortality can cause a slight male bias.

Aim: To develop and analyse a model of sex ratio and extinction probabilities assuming sex-biased mortality.

Hypothesis: Slightly male-biased sex ratios reduce the probability of extinction of a population, leading to a shortage of one sex at maturity.

Mathematical method: Analyse the probability of extinction of a population exhibiting a shortage of one sex at maturity.

Key assumptions: Mothers give birth to a total of n children with sex ratio r at every generation on a small island. Males incur higher risks of mortality at the juvenile stage. The number of males and females at birth follows a binomial distribution.

Conclusions: A slightly male-biased ratio at birth is most persistent when higher rates of male-specific mortality apply. Male biases become larger with population size. Our results suggest that group selection helps to explain why slightly male-biased sex ratios are common in humans and other animal species.

Keywords: extinction probability, Fisher's principle, male mortality, optimal sex ratio.

INTRODUCTION

Sex ratio theory was first proposed by Fisher (1930), who advanced an explanation for equilibrium sex ratios. Since its publication, Fisher's verbal theory has been subject to criticism (Shaw and Mohler, 1953). But it has also been supported and expanded with genetic models (MacArthur, 1965; Leigh, 1970; Uyenoyama and Bengtsson, 1979, 1981; Karlin and Lessard, 1986) and evolutionarily

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stable strategies (Maynard Smith, 1989). Conceptually, Fisher's theory of sex ratio indicates that equal allocation of resources at birth to both sexes is optimal, irrespective of gender-specific differences in juvenile mortality and reproductive success at maturity (MacArthur, 1965; Karlin and Lessard, 1986).

Even though Fisher's theory seems to be powerful in explaining the optimality of equal sex ratios, it does not explain fully the sex ratios of humans and some other animals, where the sex ratios are biased towards the sex with higher juvenile mortality. Empirical data on these sex ratios depart consistently from equality (Cowgill and Hutchinson, 1963; Trivers, 1985). Thus we lack a complete explanation for the observed slightly biased sex ratios. In humans and some other animal species, observed slightly male-biased sex ratios are thought to be the result of higher male mortality rates during the juvenile stages (Cowgill and Hutchinson, 1963). However, to date we have no mathematical verification to show the effect of male juvenile mortality on male-biased sex ratios.

Meanwhile, many theoretical analyses have been advanced to explain biased sex ratios, such as local mate competition (Hamilton, 1967; Uyenoyama and Bengtsson, 1982), local resource competition (Clark, 1978), local resource enhancement (Trivers and Willard, 1973), and relatedness asymmetry (Sundström, 1994). These exceptional findings do not falsify Fisher's theory, but reinforce it (West, 2009). The optimality of sex ratios has been also considered in the context of group selection, i.e. the haystack model of dispersing mice (Bulmer and Taylor, 1980). However, most of the above models exhibit strong female biases, rather than slight male biases. Furthermore, sex ratio biases are not caused by male mortality, but by many other factors, such as inbreeding, coloniality, breeding structures, assortative mating, and haplodiploidy.

In the context of group selection, Tainaka *et al.* (2006) considered the effects of limited mating opportunities on the persistence of an equal sex ratio using lattice simulation models. These authors also suggested that male juvenile mortality can cause a slight male bias. Even though they presented a plausible explanation for a slight male bias in human populations, their argument is only verbal and no simulation results are shown. Instead of simulation approaches, here we develop an analytical model of sex ratio under sex-biased mortality in terms of extinction probabilities. We show that male-biased mortality results in male-biased sex ratio even in an extremely large population.

MODEL AND RESULTS

Consider a small island, where mothers (even in one pair) give birth to a total of n offspring with sex ratio r at every (discrete) generation. We evaluate the probability of extinction for all-male or all-female populations. Note that the number of males (x) and females ($n - x$) for each generation follows a binomial distribution:

$$f(x; n, r) = \binom{n}{x} r^x (1-r)^{n-x}. \tag{1}$$

Let m be the additional mortality of males and, for the sake of simplicity, ignore female mortality. The extinction probability at a given generation is written as

$$\begin{aligned} z_1(m, n, r) &= f(0; n, r) + f(n; n, r) + \sum_{i=1}^{n-1} f(i; n, r) m^i \\ &= r^n - m^n r^n + (1 - r(1-m))^n. \end{aligned} \tag{2}$$

The first and second terms in the right-hand side of equation (2) imply no male offspring and no female offspring, respectively, and the third term implies the death of all male offspring following birth. Since the survival probability within a generation becomes $s_1(m, n, r) = 1 - z_1(m, n, r)$, the probability of t generations surviving is $s_t(m, n, r) = (s_1(m, n, r))^t$. Therefore, the survival probability depends on sex ratio r and additional male mortality m (Fig. 1). The optimal sex ratio r^* is slightly biased towards males with additional male mortality m (Fig. 1a). Here r^* is solved analytically as

$$r^* = 1/\{[(1 - m^n)/(1 - m)]^{1/(n-1)} + (1 - m)\}. \tag{3}$$

Therefore, r^* increases with n (Fig. 1b) and $r^* = 1/(2 - m)$ when n goes to infinity. Here r^* also increases towards 1 with an increase in m (Fig. 1c). From the phase plane diagram of r^* on m and n, r^* depends on m and is nearly constant when $n = 20$ or more (Fig. 1d).

DISCUSSION

Unlike the classic Fisherian model for equal sex ratios (Fisher, 1930; MacArthur, 1965), our results demonstrate the effects of gender-specific mortality rates on optimal sex ratios. Tainaka *et al* . (2006) suggest verbally that excess male mortality incurs a slight male bias. However,

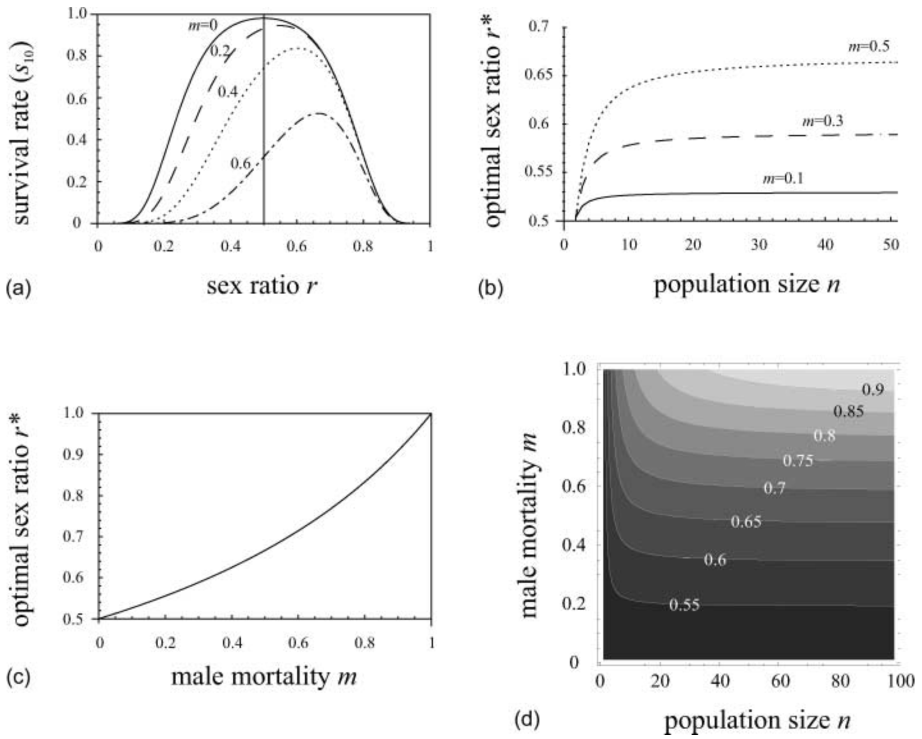

Fig. 1. Optimal sex ratios for a persistent population with male-biased mortality rates. (a) 10-generation survival rate (s_{10}) versus male ratios (r) for various mortalities ($m = 0.0$, 0.2, 0.4, and 0.6). (b) Optimal male ratios (r^*) versus population size (n) for various mortalities ($m = 0.1$, 0.2, and 0.5). (c) Optimal male ratios (r^*) versus male mortality (m) in an infinite population ($n = \infty$). (d) Phase plane diagram of optimal male ratios versus male mortality (m) and population size (n).

no simulation data are provided. Furthermore, the underlying mechanism biasing sex ratio was unknown, even if simulation results are obtained. Therefore, our results are not only a simple analytical solution, but also the first demonstration of a slightly male biased sex ratio.

In the context of group selection hypotheses, our model resembles a haystack model (Bulmer and Taylor, 1980). However, it does not require any spatial structure, as assumed in the haystack model. Furthermore, the haystack model does not assume additional male mortality. The conceptual similarity between the two models is the long-term growth rate (or geometric mean fitness) used as a fitness criterion (see Yoshimura and Clark, 1991). Note that the survival probability of a population (i.e. one minus extinction probability) correlates with the geometric mean fitness (population multiplicative growth rates) (Cohen, 1993). Also, unlike the haystack model (Bulmer and Taylor, 1980), which exhibits rather strong female biases, our model exhibits a slight male bias under various conditions. Under the effects of local mate competition, an increase in population size reduces the bias in predominantly female sex ratios (Hamilton, 1967). Likewise, in terms of mating opportunities (Tainaka *et al.*, 2006), increasing population size is expected to reduce male biases, since more mating pairs are formed. Contrary to these studies and to expectation (counter-intuitively), our model shows that male biases increase with increasing population size (Fig. 1b). The reason for this phenomenon is that an increase in population size decreases the proportion of the all-male and all-female binomial terms (the first two terms in equation 2).

We assume in our model that population size is constant as long as both sexes survive. However, in reality, a population is likely to decrease if one or only a few pairs remain from the previous generation. Our model does not include such quantitative effects of pair formations. If these uncertainties are added, more male biases may be expected. Simulation studies (Tainaka *et al.*, 2006) may be more suitable for evaluating such quantitative effects on sex ratio bias.

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APPENDIX

1. Derivation of $z_1 = z_1(m, n, r)$

$$z_1(m, n, r) = f(0; n, r) + f(n; n, r) + \sum_{i=1}^{n-1} f(i; n, r) m^i$$

$$= (1-r)^n + r^n + \sum_{k=1}^{n-1} \frac{n!}{k!(n-k)!} r^k (1-r)^{n-k} m^k$$

$$= (1-r)^n + r^n + \sum_{k=0}^{n} \frac{n!}{k!(n-k)!} r^k (1-r)^{n-k} m^k - (1-r)^n - (rm)^n$$

Using binomial theorem, we get equation (2) as:

$$z_1 = (rm + 1 - r)^n + r^n - (rm)^n$$

2. Derivation of the optimal male-sex ratio, $r^*(= r_{\text{opt}})$

Differentiating equation (2) with respect to r, we get

$$\frac{1}{n} \cdot \frac{dz_1}{dr} = (m-1)[(m-1)r + 1]^{n-1} + r^{n-1} - m^n r^{n-1}.$$

By setting $dz_1/dr = 0$, we get r_{opt} as follows:

$$r_{\mathrm{opt}}{}^{n-1} = (1-m)[(m-1)r_{\mathrm{opt}}+1]^{n-1} + m^n r_{\mathrm{opt}}{}^{n-1}$$

$$(1-m^n)r_{\mathrm{opt}}{}^{n-1} = (1-m)[(m-1)r_{\mathrm{opt}}+1]^{n-1}$$

$$1-m^n = (1-m)\left[\frac{(m-1)r_{\mathrm{opt}}+1}{r_{\mathrm{opt}}}\right]^{n-1}$$

$$\frac{1-m^n}{1-m} = \left[\frac{(m-1)r_{\mathrm{opt}}+1}{r_{\mathrm{opt}}}\right]^{n-1}$$

$$(m-1)r_{\mathrm{opt}}+1 = r_{\mathrm{opt}}\cdot\left[\frac{1-m^n}{1-m}\right]^{\frac{1}{n-1}}$$

$$\left\{(m-1)-\left[\frac{1-m^n}{1-m}\right]^{\frac{1}{n-1}}\right\}r_{\mathrm{opt}} = -1$$

$$r_{\mathrm{opt}} = \frac{1}{\left[\frac{1-m^n}{1-m}\right]^{\frac{1}{n-1}}-(m-1)}$$

The derivation of r_{opt} at $n=\infty$ is as follows:

$$r_{\mathrm{opt}} \xrightarrow{n\to\infty} \frac{1}{\left[\frac{1-m^\infty}{1-m}\right]^{\frac{1}{\infty}}-(m-1)}$$

$$= \frac{1}{\left[\frac{1-m^\infty}{1-m}\right]^{0}-(m-1)}$$

$$= \frac{1}{1-(m-1)}$$

Therefore, we get:

$$r_{\mathrm{opt}} \xrightarrow{n\to\infty} \frac{1}{2-m}$$

End of the derivations.