



Sex Ratio Strategies After Perturbation of the Stable Age Distribution

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(Received on 29 March 1996, Accepted in revised form on 6 December 1996)

Animals with overlapping generations may be selected to change their sex ratios after perturbation of the stable age distribution. Specifically, Werren and Taylor have shown that in a tightly regulated population with normally constant recruitment, sex ratios are biased at times of exceptional recruitment towards the sex with the most even distribution of reproductive value over its adult life. It is shown that an episode of exceptional recruitment also affects the optimal sex ratios of cohorts born subsequently, although the sex ratio adjustment is typically in the opposite direction. It is also shown that the expected sex ratio depends critically on female mating behaviour: whether females mate throughout their reproductive life or, as in many insects, once after emergence. Perturbation of the stable age distribution by an episode of exceptional mortality may also lead to selection for biased sex ratios, even if the mortality affects both sexes equally.

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Introduction

The study of sex allocation is one of the most successful areas of evolutionary ecology (Charnov, 1982; Leigh *et al.*, 1985; Herre *et al.*, 1987). Frequency dependent selection in favour of the production of the rarer sex results in equal allocation of resources to sons and daughters which translates, when sons and daughters are equally costly to produce, into a sex ratio of equality (Fisher, 1930; Leigh, 1970). This argument, however, assumes that the fitness returns from the production of sons and daughters are linear, or if not linear then identical (Frank, 1990). Many different biological mechanisms break this assumption and in these cases biased sex ratios are predicted. The classes of mechanisms that have received the most attention are sex-specific competition in structured populations (Hamilton, 1967) and the differential effects of the environment

on male and female fitness (Trivers & Willard, 1973; Charnov, 1979). In these and other areas there is a very rich experimental literature exploring the predictions of many theoretical models (Charnov, 1982).

One aspect of sex ratio theory that has received comparative little attention is disruption of the stable age distribution by a period of exceptional recruitment or mortality in populations with some degree of generation overlap. The first workers to consider such effects were Werren & Charnov (1978) who showed that a temporary episode of strong mortality that killed more of one sex than the other could lead to selection for increased production of the rarer sex. For this to happen, generations must overlap and the developmental period of the young must be relatively short compared with the adult reproductive lifespan.

More recently, Werren & Taylor (1984) have shown that a temporary change in population recruitment can also favour facultative adjustment of the sex ratio in populations with overlapping generations. They considered a species in which recruitment is normally constant, but where the reproductive values of

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individuals of the two sexes are distributed in different ways across adult age classes. [Throughout this paper we use reproductive value to mean reproductive value at birth, defined in the standard way and measured in a constant-sized population at the stable age distribution, see e.g. Caswell (1989)]. For example, if one sex suffers higher rates of mortality than the other, its reproductive value is concentrated in earlier age classes. Werren & Taylor (1984) asked what a female's optimal sex ratio should be during periods of exceptional recruitment. They showed that above average recruitment favours the production of the sex that has its reproductive value distributed more evenly over the adult age-classes, and below average recruitment favours production of the other sex. In their model, males compete for mates and females for opportunities for their young to enter the breeding classes (recall that recruitment is normally constant). Above average recruitment results in the exceptional cohort facing increased reproductive competition. However, the increase will be less in the sex whose reproductive value is most evenly spread out over the adult age classes and a bias towards this sex is thus favoured by natural selection.

The possibility that disruption of the stable age distribution leads to selection for biased sex ratios has not yet stimulated much experimental work. Our aim here is to develop some of the ideas described above, in particularly incorporating biological processes that may make the theory more amenable to testing. We begin with the Werren & Taylor (1984) model and relax two of its assumptions. First, we allow sex ratios to evolve not only during the period of exceptional recruitment but subsequently. We show that the effects of increased recruitment on optimum sex ratio can continue over a number of time periods. Second, we relax the assumption that females mate continuously through out their life. While a reasonable assumption for many animals, a large number of other species mate only once, soon after reaching maturity. If females are able to store a male's sperm, this effectively prolongs his reproductive life, possibly beyond his death. Finally, we explore the consequences of a period not of increased recruitment but of increased mortality. Unlike the situation considered by Werren & Charnov (1978), we assume mortality affects both sexes equally. We show that increased mortality can lead to selection for sex ratio adjustment when, as in the Werren & Taylor (1984) model, generations overlap and the distribution across age classes of male and female reproductive value is different. In the Discussion, we suggest the systems to which the theory developed here may best apply.

We first describe the model developed by Werren & Taylor (1984) which forms the basis of our subsequent models.

Werren & Taylor Model

Assume that the lifespan of the animal can be divided into a series of discrete periods, perhaps days (for insects) or years (for larger organisms). Under normal conditions, N individuals are born each time unit except at times of exceptional recruitment when $(1 + a)N$ individuals are born. An individual born at time 0 matures at time 1 and continues reproducing until time ϕ , its maximum age. Define $p_{m(i)}$ and $p_{f(i)}$ to be the relative contribution of age class i to the total reproductive value of males and females respectively under normal conditions. Thus, $\sum_{i=1}^{\phi} p_{m(i)} = \sum_{i=1}^{\phi} p_{f(i)} = 1$. Assume also that females have to remate each time unit before reproduction.

The relative reproductive success of a male or female at any particular age is its reproductive value divided by the number of competitors alive at that time. Males compete for opportunities to mate and females for opportunities to reproduce. Let $c_{m(i)}$ and $c_{f(i)}$ be the relative numbers of competitors at time i experienced by males and females respectively. If there has been no exceptional recruitment then the population will be at the stable age distribution and so $c_{m(i)} = \sum_{k=1}^{\phi} p_{m(k)} = 1$ and $c_{f(i)} = \sum_{k=1}^{\phi} p_{m(k)} = 1$ and relative reproductive success and reproductive value are identical. Individuals in the exceptional cohort experience altered levels of competition at each age. Specifically, when the exceptional cohort is aged j , the competitive environment experienced by males will be

$$c_{m(j)} = 1 + p_{m(j)}(2x_1(a + 1) - 1), \quad (1)$$

where x_1 is the sex ratio (proportion males) of the exceptional cohort. The quantity $2x_1(a + 1) - 1$ represents the extent to which the exceptional cohort differs from normal. The cohort is larger leading to greater competition when recruitment is increased ($a > 1$) and the reverse when recruitment is decreased ($a < 1$); the parent can modulate the effect of recruitment by biasing the sex ratio towards males ($2x_1 > 1$) or towards females ($2x_1 < 1$). Note that if recruitment is unexceptional ($a = 0$) and the sex ratio unbiased ($2x_1 = 1$), the competitive environment returns to normal, $c_{m(j)} = 1$. An expression for the competitive environment experienced by females is obtained in the same way

$$c_{f(j)} = 1 + p_{f(j)}(2(1 - x_1)(a + 1) - 1). \quad (2)$$

The expected reproductive success of males born in the period of exceptional recruitment ($W_{m(1)}$) is obtained by summing over all age classes and a similar expression can be written down for female reproductive success ($W_{f(1)}$).

$$W_{m(1)} = \sum_{j=1}^{\phi} \frac{P_{m(j)}}{C_{m(j)}} \quad (3)$$

$$W_{f(1)} = \sum_{j=1}^{\phi} \frac{P_{f(j)}}{C_{f(j)}} \quad (4)$$

The ESS sex ratio is that which satisfies the condition $W_{m(1)} = W_{f(1)}$.

Throughout this paper we follow Werren & Taylor and consider an animal with four adult age classes ($\phi = 4$). Similarly, we assume

$$P_{m(i)} = \frac{M^i}{\sum_{i=1}^{\phi} M^i}, \quad (5)$$

$$P_{f(i)} = \frac{F^i}{\sum_{i=1}^{\phi} F^i}. \quad (6)$$

where M and F are constants. Values of M or F greater than one (not considered by Werren & Taylor) indicate greater reproductive success later in life, perhaps due to growth and increasing prowess or experience; M or F equal to one represent equal reproductive success throughout life; while values less than one indicate reduced expected reproductive value late in life, perhaps due to mortality. If mortality is the only factor influencing the schedule of reproductive value, then M and F can be interpreted as sex-specific survival probabilities.

Figure 1 shows the optimal sex ratio predicted by the Werren & Taylor model for different values of the relative size of the exceptional cohort (a) and for different values of M and F . As described above, higher than average recruitment favours the production of the sex with the more even distribution of reproductive value (M or F nearest to one). Below average recruitment has the opposite effect. Note that in this model, if one sex has a less even distribution of reproductive value than the other, it makes no difference whether its reproduc-

tive value is concentrated in early or late age classes (thus the optimal sex ratio when $F = 1$ is the same for $M = 0.5$ and $M = 2$).

ESS Sex Ratio at Different Times

We now relax the assumption that females produce a sex ratio of 0.5 at all times following the perturbation. We number the cohorts so that 1 is the exceptional cohort, 2 that born in the following time unit and so on. The aim is to find the ESS set of sex ratios $\{x_1, x_2, \dots\}$ where x_j is the sex ratio of the cohort that attains maturity at time j . Note, we assume that the exceptional episode of recruitment cannot be predicted. If it could, selection would lead to females adjusting their sex ratio in anticipation of the event.

The extent of competition experienced by males and females at different times depends both on the magnitude of the change in recruitment (a) and the sex ratio strategy adopted by females at different times. As before, define $c_{m(j)}$ and $c_{f(j)}$ to be the magnitude of competition experienced at time j after the perturbation by males and females respectively.

$$c_{m(j)} = 1 + (p_{m(j)}(2x_1(a+1) - 1)) + \left(\sum_{k=1}^{j-1} p_{m(k)}(2x_{j-k+1} - 1) \right), \quad (7)$$

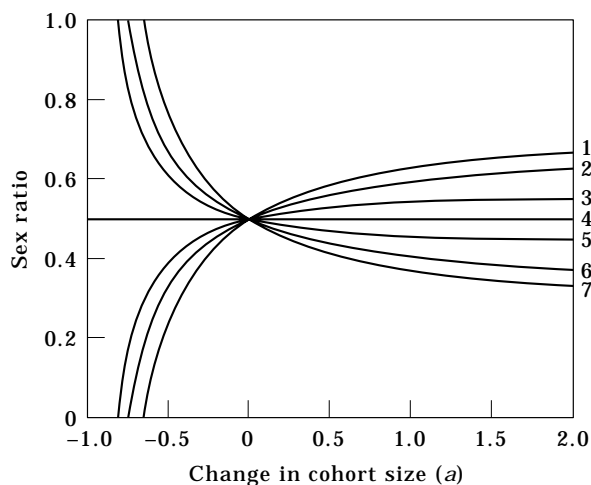


FIG. 1. The optimal offspring sex ratio to produce in a period of exceptional recruitment. The numbered lines represent different values of M & F : (1) $F = 0.1$, $M = 1$; (2) $F = 0.1$, $M = 0.5$; (3) $F = 0.5$, $M = 1$; (4) $F = M$; (5) $F = 1$, $M = 0.5$; (6) $F = 0.5$, $M = 0.1$; (7) $F = 1$, $M = 0.1$.

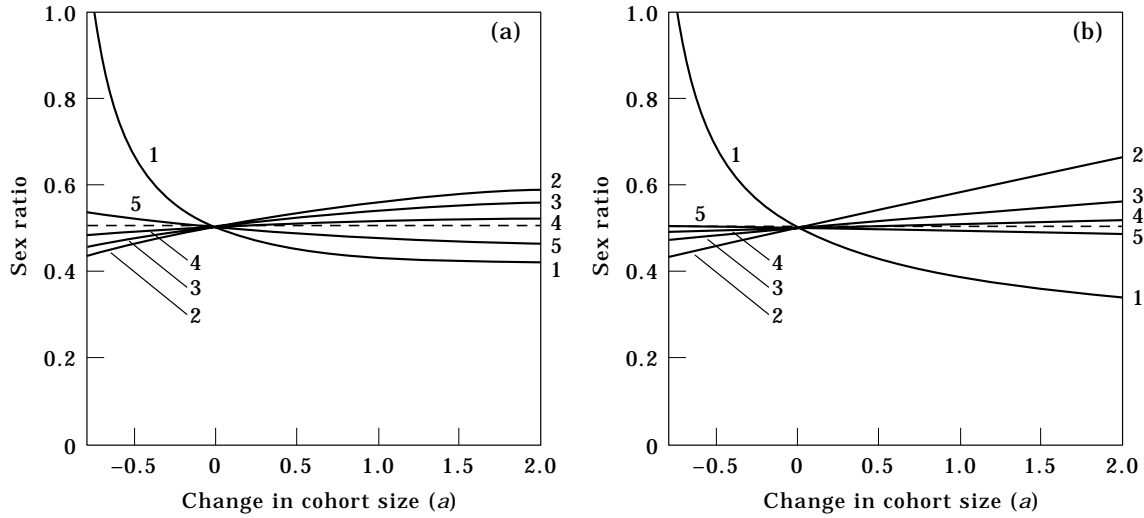


FIG. 2. The optimal offspring sex ratio to produce in a period of exceptional recruitment and in following time periods. Values of M and F for the two graphs are: (a) $F = 1$, $M = 0.5$; (b) $F = 0.5$, $M = 0.1$. The cohorts are numbered so that 1 is the exceptional cohort, 2 that born in the following time period and so on.

$$c_{f(j)} = 1 + (p_{f(j)}(2(1 - x_1)(a + 1) - 1)) + \left(\sum_{k=1}^{j-1} p_{f(k)}(2(1 - x_{j-k+1}) - 1) \right). \quad (8)$$

In both equations, the first term in parentheses represents the change in the competitive environment brought about by the exceptional recruitment event and any change in the sex ratio produced at this time. This term is identical to that in the Werren & Taylor model [eqns (1) and (2)]. The second term in parentheses represents changes in the competitive environment caused by females adjusting the sex ratio of cohorts 2, 3 etc. The fitnesses of males and females in cohort j are

$$W_{m(j)} = \sum_{i=1}^{\phi} \frac{p_{m(i)}}{c_{m(i+j-1)}}, \quad (9)$$

$$W_{f(j)} = \sum_{i=1}^{\phi} \frac{p_{f(i)}}{c_{f(i+j-1)}}. \quad (10)$$

The ESS sex ratio is found by solving $W_{f(j)} = W_{m(j)}$ simultaneously for all j by numerical iteration. We first set $x_j = 0.5$ for all j and then calculated x_1 . Using this value for x_1 we then calculated x_2 and so on for a predetermined number of steps (in the results presented below we stopped at $j = 5$). The process was then repeated 100 times by which time stable solutions of x_i had been obtained (convergence to

three decimal places normally required just 10 iterations). The same solution was obtained if the sex ratios were calculated in decreasing rather than increasing order.

Examples of the ESS sex ratio predicted by the model are shown in Fig. 2. As before, the cohort produced during a period of increased recruitment is biased towards the sex with the more evenly spread reproductive value and the reverse in periods of reduced recruitment. However, compared with the Werren & Taylor model, the bias is now slightly stronger (compare Fig. 1 and Fig. 2). In the following three time periods, a biased sex ratio is also found, but in the opposite direction and of steadily declining magnitude. The sex ratio bias in time periods 2–3 is relatively more marked for increased ($a > 0$) compared with decreased ($a < 0$) recruitment. In the fifth time period (the final period considered) the sex ratio was weakly biased in the same direction as in the period of exceptional recruitment).

As before, females producing offspring during times of exceptional recruitment adjust their sex ratio to minimise the competition experienced by their offspring. This sets a competitive environment that favours a counter-adjustment by females in the following time periods. The reason for this is that after a period of above average recruitment, the following cohorts experience low recruitment relative to their competitors. This counter-adjustment decreases the competition experienced by the favoured

sex in the exceptional cohort (in all but the first time period). Consequently, females will evolve to anticipate the counter-adjustment by producing an even more biased sex ratio during the first period. The initial cohort, with the most biased sex ratio, are all dead by time period 5, although the subsequent cohorts whose sex ratio are biased in the opposite direction are still alive. In consequence, the cohort produced at this time has a sex ratio biased in the same direction as the initial cohort, although the deviation from a sex ratio of 0.5 is relatively small. To a certain extent, however, the bias in cohort 5 arises because of our assumption of a strict upper age limit of four time units.

Females Mate Once

In many animals, females mate only once soon after they emerge and this will alter the distribution of male reproductive success after a period of exceptional recruitment. Here we calculate the ESS sex ratio in the Werren & Taylor model but assuming single mating. We only calculate the ESS sex ratio of the exceptional cohort, although the methods used in the last section could be applied here as well.

In the Werren & Taylor model, males compete each time unit for access to females. In their model, the number of females present each time

unit does not influence male fitness: because female reproductive success is assumed constant each time period, only the proportion and not the absolute number of matings obtained by a male is important. If females mate only once, a mating achieved now will provide offspring for a male as long as that female lives. To assess male reproductive success, we need to know the relative number of females available for mating now and their future reproductive success. Define Q_j to be the relative size of the female cohort that becomes reproductively competent at time j . For the exceptional cohort $j = 1$, $Q_1 = (2(1 - x_1)(1 + a))$ and for all other cohorts $Q_j = 1$. The fitness of a male born in cohort 1 is thus

$$W_{m(1)} = \sum_{j=1}^{\phi} \left(\frac{p_{m(j)}}{c_{m(j)}} Q_j \sum_{i=1}^{\phi} \frac{p_{f(i)}}{c_{f(i+j-1)}} \right), \quad (11)$$

where $c_{m(i)}$ and $c_{f(i)}$ are defined in eqns (1) and (2). The fitness consists of the sum over all age classes of a quantity that is the product of three factors: (i) the male's expected reproductive success at each age; (ii) the relative numbers of unmated females at that age, Q_j , and (iii) the future reproductive success of a female mating at that time (the embedded summation). Female fitness, $W_{f(1)}$ is the same as in the Werren & Taylor model and the ESS sex ratio is achieved as before by setting $W_{m(1)} = W_{f(1)}$ and solving for x_1 .

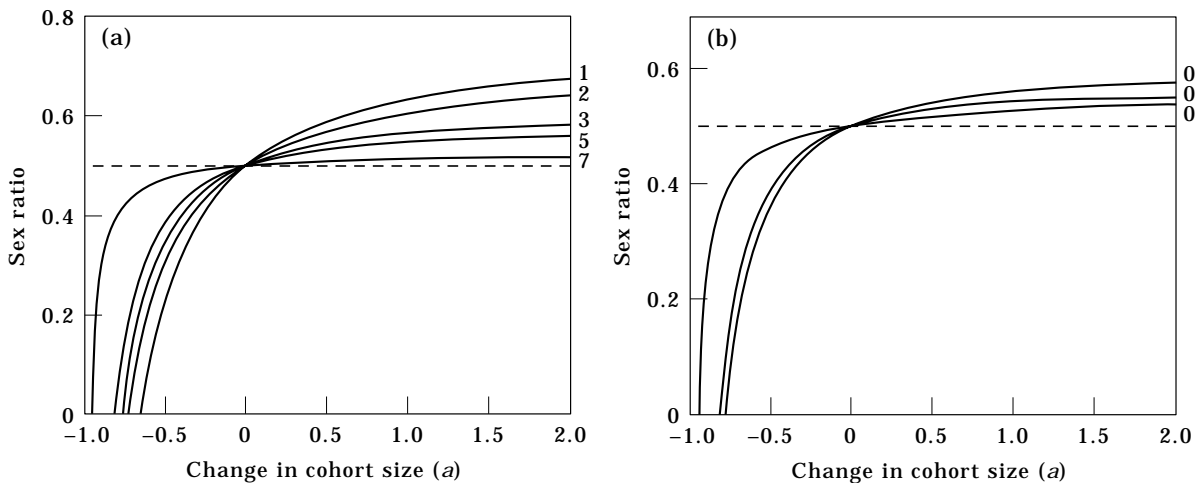


FIG. 3. The optimal offspring sex ratio to produce in a period of exceptional recruitment when females only mate once on attaining maturity. (a) Values of M and F for the different lines are the same as those used in Fig. 1. (b) The case of $M = F$. The three lines represent $M = F = 0.1, 0.5, \& 0.8$.

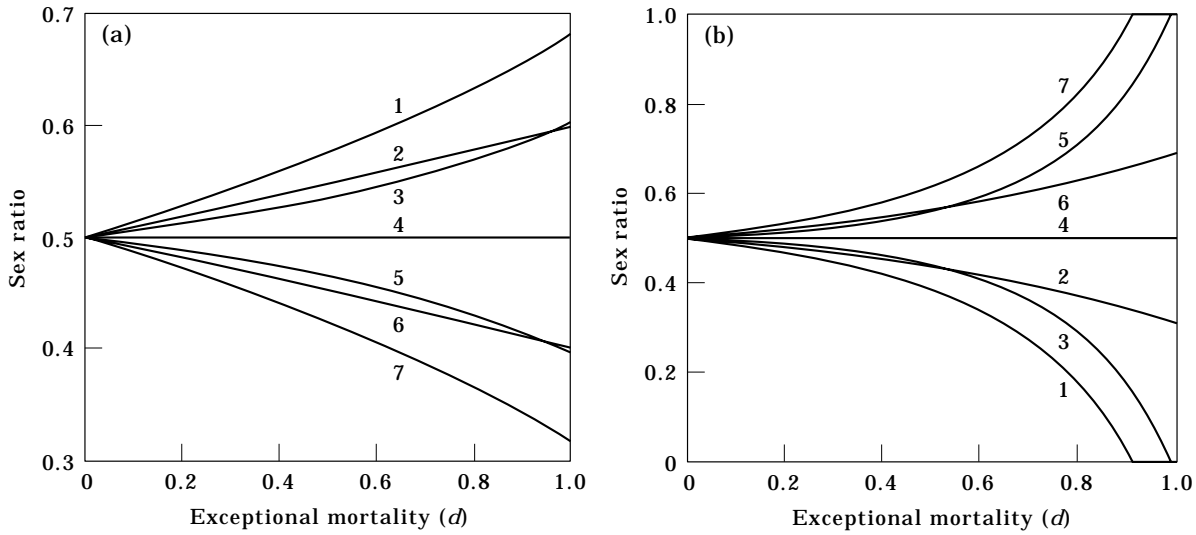


FIG. 4. The optimal offspring sex ratio to produce before and following a period of exceptional mortality. In (a) mortality occurs before ($d_1 = 0$) the production of the focal cohort while in (b) mortality affects the focal cohort ($d_1 = d$). The numbered lines refer to the values of M & F given in the legend of Fig. 1.

When females mate only once, we always found a male biased sex ratio during a period of above-average recruitment and a female biased sex ratio during a period of below average recruitment (Fig. 3). This occurs because a male's reproductive life is extended through sperm storage by the female. For all but the most extreme differences in M and F , the actual spread and evenness of reproductive value is greater for males than females and the sex ratio bias is always in the same direction. Biased sex ratios are even found when $M = F$. These predictions are markedly different from those of the Werren & Taylor model where females mate every time period.

Exceptional Mortality

Consider now the consequences of a period of exceptional mortality rather than exceptional recruitment. The exceptional mortality will decrease competition until the members of the youngest age class affected by the mortality have all died. We ask what is the ESS sex ratio for a female to produce at the time of exceptional mortality (x_1). As before we could also calculate the effects of the exceptional mortality on the ESS sex ratio for subsequent cohorts but here we concentrate solely on x_1 where the effects will be most extreme. For $j = \{1 \dots \phi\}$ time units following the episode of mortality, the relative competition experienced by

males and females are

$$c_{m(j)} = 1 + p_{m(j)}(2x_1 - 1)(1 - d_j) - \sum_{k=j}^{\phi} p_{m(k)}d_{k-j+1}, \quad (12)$$

$$c_{f(j)} = 1 + p_{f(j)}(2(1 - x_1)(1 - d_j) - 1) - \sum_{k=j}^{\phi} p_{f(k)}d_{k-j+1}, \quad (13)$$

where d_j is fraction of age class j killed by the exceptional mortality. Note that we assume mortality affects males and females identically. In what follows we shall assume d_j is a constant, d , for age classes 2–4 but examine the two cases of mortality acting before reproduction so that current offspring are not affected ($d_1 = 0$), and mortality acting after reproduction and influencing current offspring ($d_1 = d$). The ESS sex ratio is found by substituting eqns (12) and (13) into eqns (3) and (4).

Consider first the case of $d_1 = 0$: mortality occurs before the production of the focal cohort. Figure 4(a) shows the ESS sex ratio for different values of M and F when both are less than one; in other words when expected reproductive value declines monotonically throughout adult life. Selection favours a switch to a male biased sex ratio when $M > F$ and a female biased sex ratio when the inequality is reversed. Thus,

the sex ratio is biased towards the sex which has more of its reproductive value in the older age classes. The period of exceptional mortality decreases competition from the older age classes. This competition is greatest, and hence its reduction most valuable, for the sex that has relatively more of its reproductive value in the older age classes. Natural selection favours a bias towards the sex that gains most from the perturbation.

Now consider the case when the mortality acts after the production of the focal cohort ($d_1 = d$); the direction of selection is reversed and the sex whose reproductive value is concentrated in the youngest age classes are favoured [Fig. 4(b)]. The focal cohort is reduced in size and will thus suffer severe competition from cohorts of normal size produced in the future but reduced competition from cohorts already alive and that have also experienced the exceptional mortality. The sex whose reproductive value is most strongly concentrated in young age classes suffers least from competition from future cohorts (the majority of their reproductive output occurs before these future cohorts are born) and is thus favoured by natural selection.

In the Werren & Taylor model, sex ratio was influenced by the variance in reproductive value but not by whether the youngest or oldest age classes were most productive. In the present case, with an episode of exceptional mortality rather than recruitment, this is no longer true. The difference occurs because an episode of exceptional recruitment affects only one cohort while exceptional mortality affects several. Figure 5 shows the optimal sex ratio for the cohort produced immediately following mortality ($d_1 = 0$) when the reproductive value of one sex increases with time (in this case male reproductive value). The sex ratio is biased towards females except when the exceptional mortality is very severe. Two processes are at work here. The mortality affects cohorts born in the past and so leads to a reduction in competition that wanes as new cohorts are born. This acts against the sex with reproductive value concentrated late in life which benefits relatively little from the reduced competition. However, if the older age classes exert the strongest competitive effects on other age classes, then by reducing the numbers of old individuals the exceptional mortality may favour the production of this sex. Figure 5 suggests that the former process determines the optimal sex ratio unless the mortality is very severe when the latter predominates.

Discussion

The evolution of sex ratios is normally studied using models that assume discrete, non-overlapping generations. As Werren & Charnov (1978), Werren & Taylor (1984) and our results demonstrate, there is much scope for facultative adjustment of the sex ratio in response to perturbation of the stable age distribution in populations with overlapping generations. Our results extend those of Werren & Taylor to show how the effect of a perturbation and the consequent adaptive changes in sex ratio can propagate through successive cohorts, exerting an effect even after the death of all individuals alive at the time of perturbation. We also show that the predicted sex ratio can depend quite critically on female reproductive strategy, specifically whether she mates once on becoming reproductively active or continuously throughout her reproductive life. Finally we show that an episode of mortality, even if it affects both sexes equally, can lead to selection for sex ratio adjustment. For this to occur, male and female reproductive value must be distributed non-identically across age classes. These results emphasise the point that factors which have no effect on sex ratio evolution when generations are discrete may have large effects on sex allocation strategies in populations with overlapping generations.

In developing the models described here we have made a series of simplifying assumptions. Perhaps the most important are those of (i) perfectly compensating density dependence acting only on recruitment;

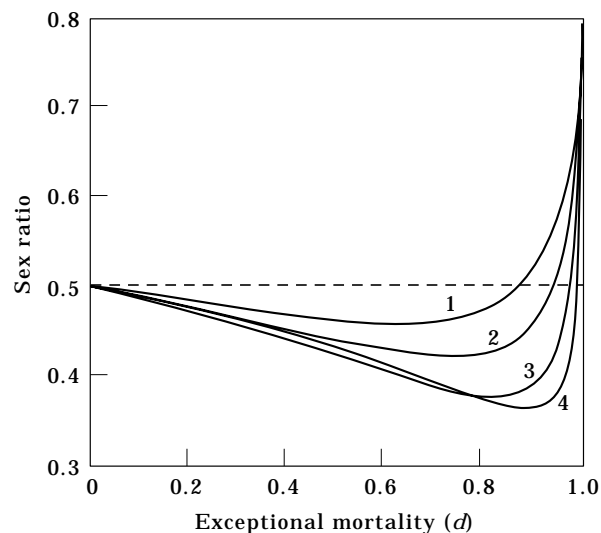


FIG. 5. The optimal offspring sex ratio to produce following a period of exceptional mortality ($d_1 = 0$). The lines represent different values of M & F : (1) $F = 1$, $M = 3$; (2) $F = 1$, $M = 5$; (3) $F = 1$, $M = 10$; (4) $F = 1.5$, $M = 10$.

(ii) the absence of any complicating factors such as population structure or conditional sex expression that might affect the optimal sex ratio; and (iii) the absence of any spatial or temporal stochasticity affecting the model's parameters. Any of these assumptions could be relaxed, although obviously at the cost of a more complex model. We have also assumed a particular population structure and form of perturbation, although there is a very large number of other possibilities.

Observations of natural systems may suggest which of these other possibilities are most profitable to investigate. For example, sex ratio with partial bivoltinism (species with two generations a year with some individuals of one sex surviving from the first generation to the second) has attracted considerable attention (Werren & Charnov, 1978; Seger, 1983; Stubblefield & Charnov, 1985; Grafen, 1986; Brockmann & Grafen, 1992) because of its implications for the evolution of hymenopteran eusociality. Interesting sex ratio patterns are also found in other organisms with highly seasonal dynamics where there are a number of overlapping generations each year, for example in littoral gammerids (Crustacea) (Watt & Adams, 1993; McCabe & Dunn, 1994). We also believe that a study of optimal sex ratios following colony foundation, especially before a stable age distribution is attained, may be valuable in explaining sex ratio patterns in groups such as mites (Acari) (Wrensch, 1993).

To what type of organisms might the theory developed here be most applicable? For facultative sex ratio adjustment to occur, females must have some means of influencing the sex ratio of their offspring. Haplodiploid organisms, particularly Hymenoptera, have proved extremely good models for testing sex ratio theory. The female controls the sex of her offspring by choosing whether or not to fertilise her eggs, and natural selection has been shown to act on this decision to produce a wide range of locally adaptive sex ratio strategies (Werren, 1987; King, 1987; Godfray, 1994). There are a number of cases where parasitoid wasps have been shown to alter their sex ratios in response to environmental stress and one possible explanation is that they are using the environmental cue as an indicator of a population perturbation. However, there are alternative hypotheses and as yet no system has been studied in sufficient detail to provide evidence for (or against) the processes discussed here.

Species with environmental sex determination can often also influence the sex ratio of their progeny. The sex of many reptiles is determined by the temperature at which their eggs develop which can be at least

partially controlled by the mother through choice of nest site. Our models provide a possible explanation for the observed increased female bias in the offspring sex ratio of crocodile populations following a period of exceptional mortality (Ferguson & Joanen, 1982, 1983; Deeming & Ferguson, 1989). The distribution of male and female reproductive value across age class appears to differ in crocodiles. Large males guard harems of females, and so male reproductive success is likely to increase enormously with body size (Ferguson, 1985; Deeming & Ferguson, 1989). If large body size reflects old age then male reproductive value would be concentrated in the older age-classes. The models developed in this paper suggest that under these circumstances a female biased sex ratio should be favoured following a period of relatively high (although not extreme) mortality.

We thank Austin Burt, James Cook, Jenny McCabe, Dan Racey and Jack Werren for helpful discussion. SAW was supported by a NERC studentship.

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