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# REPRODUCTIVE SYNCHRONY, PARENTAL INVESTMENT, AND THE EVOLUTIONARY DYNAMICS OF SEXUAL SELECTION

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**Abstract.** Computer simulations showed that reproductive synchrony in the greater investing sex can evolve as a strategy for increasing the investment of mates. The potential for synchrony to increase in frequency for this reason decreased with (a) increasing population size, (b) decreasing importance of synchrony-enforced investment, (c) increasing variance in quality among members of the lesser investing sex, and (d) decreasing male : female sex ratio. By reducing the payoffs to desertion, synchrony may result in the evolution of uniquely effective forms of parental care by the lesser investing sex, making desertion unprofitable regardless of the availability of potential mates. Thus relative levels of optimal parental investment are subject to change through the action of sexual selection itself.

The theory of sexual selection has been a controversial subject since Darwin's full treatment of it in 1871 (for example Wallace 1889). Although it has received considerable attention since then (recently, Campbell 1972; Ghiselin 1974; Warner et al. 1975; Thornhill 1976b; Dawkins 1976; Dawkins & Carlisle 1976; Burley 1977; Cox & Le Boeuf 1977; Emlen & Oring 1977; Maynard Smith 1977; Ralls 1977; Zahavi 1977; O'Donald 1977, 1978; Blum & Blum 1978; Grafen & Sibly 1978), our understanding of the phenomenon remains essentially Darwinian, namely a process resulting in the spread of characteristics which aid in the acquisition of large numbers of and/or high quality mates. As Darwin emphasized, sexual selection often results in combat between males for the elimination of rivals and displays by males for the attraction of coy females.

Recent work has concentrated on the reasons for these 'typical' sex roles. Bateman (1948), Williams (1966) and particularly Trivers (1972) have focused on the importance of differences between the sexes in the degree to which they invest in the offspring. Emlen (1976), Emlen & Oring (1977) and Ralls (1977) have discussed the influence of spatial and temporal patterns of reproduction on the effective strength of sexual selection. Even with these modifications sexual selection, so viewed, acts unilaterally with respect to sex and always results in the evolution of sexual dimorphism by favouring characters in the lesser investing sex which increase success in competition for additional matings. The strength of selection may be measured by the difference between the sexes in potential rates of reproduction, or equivalently, by the potential for some members of the lesser investing sex to acquire a disproportionate share of the matings (Bateman 1948; Trivers 1972; Ralls 1977; Emlen & Oring 1977). When one or both parents tend the eggs or offspring, the sex providing the most behavioural care may or may not be the greater investing sex when the energetic investment in the eggs by the female is accounted for. Thus extensive parental care by males is sometimes (e.g. many polyandrous birds; Jenni 1974) but not always (e.g. many fish; Loiselle & Barlow 1978) associated with dimorphically conspicuous and aggressive females. As expected, complete role reversal in behaviour and morphology occurs when parental males do not have the opportunity to obtain multiple matings (i.e. species with monogynous mating systems; Ridley 1978).

In contrast to the above, competition for high quality mates need not act unilaterally with respect to sex. Although traditionally its effects on the lesser investing sex have been emphasized (primarily in the discussions by Darwin (1871), Fisher (1930) and O'Donald (1972a, 1972b, 1973, 1974) of competition among males for early breeding females), it is clear that members of the higher investing sex may also be in competition for high quality mates. Thus sexual selection for high quality mates does not necessarily result in the evolution of sexual dimorphism. The extent of sexual dimorphism in the development of characters related to competition for high quality mates depends on the degree to which variance in quality among mates differs between the sexes.

The factors which control the strength of sexual selection (discrepancies between the sexes in parental investment and the degree to which

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individuals vary in quality as mates) have generally been viewed as entities fixed by ecological conditions. The work of Fisher (1930) and O'Donald (1973), however, shows that both can be increased through the action of mate choice. When members of the greater investing sex (referred to for convenience as females for the remainder of this paper) prefer males which are superior mates for ecological reasons, then the genes governing choice on this basis can spread. If these preferred traits are to some extent heritable, then the degree to which males vary in quality as mates increases because females mating with the best males gain both the original, ecologically based advantages (heritable and non-heritable) and the new advantage of producing sons whose reproductive success, like their father's, stems in part from the preference patterns of females. This process can lead to an exaggeration of the traits which females prefer and thus to an increase in male energy devoted to attracting mates at the expense of that devoted to parental investment.

Thus sexual selection can be an evolutionarily dynamic process, influencing the factors which in turn control it. To date, however, the evolutionary dynamics of sexual selection have only been carefully explored in the direction of increasing the disparity between the sexes in the degree to which they invest in the offspring. The purpose of this paper is to show how a related process can act in the opposite direction and decrease this disparity.

Consider a species in which females invest more in the offspring than males. Females, to improve their reproductive success, might insist on the performance of some display or the possession of some characteristic by males useful to females in judging male quality (Zahavi 1975; Trivers 1976). Alexander (1975) and Emlen & Oring (1977) imply this kind of process when they discuss the advantages to females in male lekking behaviour. Alternatively, females might demand additional investment by the males in the offspring. For example, they might require some sort of premating 'present' before permitting copulation (Thornhill 1976b). A more general example of this is female preference for unmated males, a phenomenon which limits the potential for polygyny in many birds (Orians 1969; Altmann et al. 1977). This type of strategy does not necessarily prevent subsequent male desertion or eviction, however, and males may even attempt to repossess precopulatory offerings following mating (Thornhill 1976a).

Another possible strategy, avoiding these (but not all) pitfalls, is female reproductive synchrony. As Maynard Smith (1977), Ralls (1977), and Emlen & Oring (1977) have noted, female reproductive synchrony arising for any reason should generally decrease the likelihood of male desertion or eviction by the male of the female from his territory, because the probability of the male's finding another mate before his original mate is ready to reproduce again is reduced. The potential for female reproductive synchrony to evolve as a sexual strategy in its own right was preliminarily explored by Knowlton (1978) and mentioned as a possibility by Halliday (quoted in Krebs 1978). Alexander (1975) discussed the advantages to males and females of male reproductive synchrony. A more detailed and rigorous analysis of female synchrony, particularly as its frequency increases, is provided below. For the purposes of this paper, synchrony will be defined as the timing of reproduction among females such that one male is unable to mate with more than one of the synchronized females.

The benefits associated with reduced male desertion would be to some extent offset if: (1) the mechanisms for achieving synchrony were energetically expensive or risky, (2) it increased the probability of predation or interference through increased predictability, search image formation or predator aggregation or population growth rate, (3) it increased competition among mating adults or their young (Orians 1961), (4) it resulted in the loss or delay of opportunities for mating, and/or (5) it reduced mate choice (Wells 1977). These last two costs are clearly a function of the degree to which competition for mates (i.e. sexual selection) affects females.

## Computer Simulations

### Methods

To explore the interplay of these sexually selected costs and benefits, a computer program was written by Jerome Smith and myself which simulated mating in a finite population. Males were continuously available as mates, except during a period of specified, uniform length, following any mating. Females also had a characteristic refractory period. All information on the reproductive activities and success of individuals was stored using three two-dimensional matrices—one for males, one for females

and one for the clutches produced with mating. At the end of each simulation the numbers of offspring surviving from the clutches of synchronously and asynchronously reproducing females were compared. The period of time simulated (a series of discrete time units) may be thought of as one mating season, or as a segment in time from a continuously reproductive population. A series of 13 simulations (in which females reproduced in varying degrees of synchrony) was performed for each set of starting conditions. The three main parts of the program are described in order of execution below.

**Assignment of starting conditions.** (1) The optimal amounts of parental investment provided by males and females. These were expressed as the lengths of the refractory periods following each mating, and were assumed to be the evolutionarily stable strategies (or ESS's; Maynard Smith & Price 1973) in the absence of sexual selection for synchrony. For all simulations the female refractory period was 25 time units in length.

(2) The number of males and females. Within each sex all individuals were linearly ranked in terms of their ability to acquire high-ranking mates.

(3) Male quality. Each male was assigned a 'quality value' between zero and one. Higher-ranking males had quality values greater than or equal to those of lower-ranking males (with one exception noted below). A male's quality was an index incorporating all heritable and non-heritable characteristics, other than the actual amount of parental investment provided, affecting the survival and reproductive success of its offspring.

(4) The timing of the initial period of receptivity to mating. Males always became fertile at the onset of the simulation. For females the timing of the initial period of receptivity was used to control the extent of female reproductive synchrony. In all simulations females had their first opportunity to mate within the first 25 time units of the simulation (the length of the female refractory period). In the maximally asynchronous simulations female starting times were evenly dispersed throughout this initial time span. Synchrony was increased by increasing the percentage of females whose first reproductive periods occurred centrally within this span, while retaining the even spread of the first reproductive periods of the remaining asynchronous females (Fig. 1). In the maximally synchronous simulations all females first became reproductive at the central time unit within this time span.

In most simulations the synchronous females were higher-ranking than asynchronous females. The actual relationship between female rank and synchrony was irrelevant whenever the sex ratio was 1:1 because synchronous and asynchronous females never reproduced at the same time and thus never competed directly for mates. Ten sets of 13 simulations in which the females to be synchronized were chosed randomly with respect to rank gave identical results.

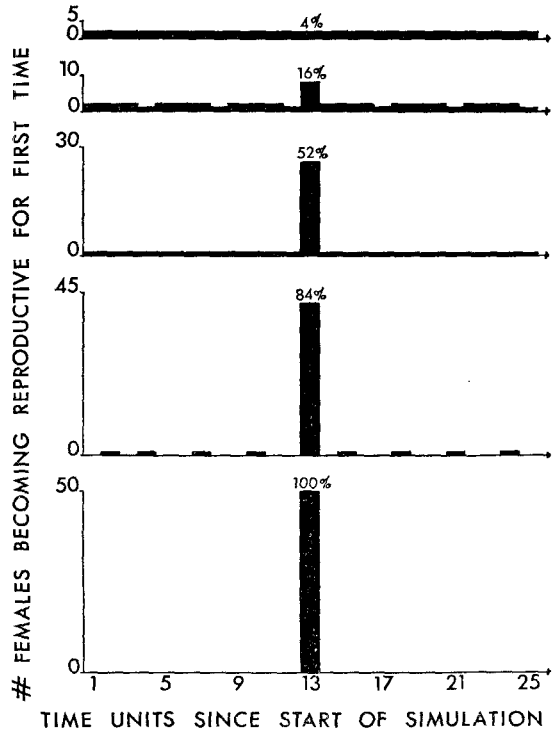


Fig. 1. Five examples of the timing of initial reproductive periods used to obtain varying degrees of reproductive synchrony (percentage females at synchrony mode) within a group of 50 females. Central placement of the synchrony mode allowed synchrony to be increased without changing the average amount of time available for reproduction to synchronous and asynchronous females. Whenever a perfectly even distribution of asynchronous females was impossible (as in 16% and 84% above), the exact form of the maximally even distribution was randomly determined, within the subset of possibilities slightly biased towards the desertion of synchronous females. Synchrony in populations of other sizes was controlled using the same patterns. See text for further details.

(5) The relative effectiveness of any extra male parental care provided. This was set by a fraction, constant for any set of simulations, which reduced integer units of extra male parental care (provided when the male was unable to find a new mate following the passage of his refractory period) to a fraction between 0 and (1 − maximum male quality). Thus the relative importance of male quality and care to the survival probability of offspring in any clutch was determined by the relative magnitude of these two fractions.

(6) The total number of time units (iterations) in the simulation. In all cases this was set at 100, allowing each female the opportunity to mate four times.

**Steps in each iteration.** (1) Recalculation of running total of extra male parental care for each clutch. An additional time unit was added to the total number of extra units for all clutches with males still caring after their refractory periods had elapsed.

(2) Identification of all potentially reproductive individuals. These consisted of (a) all unmated males, and any previously mated male whose refractory period from the most recent mating had elapsed; (b) any unmated female who had reached the onset of her first reproductive period, and those previously mated females as above for mated males.

(3) New matings. These were made between the highest-ranking individuals on down the line, until all members of the sex with the smallest number of potentially reproductive individuals had been mated. Remaining individuals of the other sex were returned to the clutches from the most recent mating if such existed; if no such clutch existed they 'waited' at no cost for an opportunity to mate at the next iteration. Each new mating was accompanied by the start of a new clutch. Newly mated individuals abandoned any clutches under their care from previous matings.

**Calculation of the success of each clutch.** At the end of the iterations, the number of offspring surviving from each clutch was calculated as $(100) \times (Q_m + aC_m)$, where $Q_m$ is male quality, $C_m$ is the number of extra units of male parental care provided, and $a$ is the constant controlling the effectiveness of the units of extra care $(0 \leqslant Q_m + aC_m \leqslant 1)$.

In summary, the important parameters manipulated in the simulations were (1) the numbers of males and females, (2) the optimal amounts of parental investment provided by each sex in the absence of synchrony, (3) the relative importance of male quality and extra male parental care, and (4) the timing of female reproductive periods. For various degrees of synchronization, the potential for the further spread of synchrony was determined by comparing the reproductive success of synchronous and asynchronous females. Reproductive success was measured by the mean number of surviving offspring produced per reproductive cycle (four cycles per female per simulation).

## Results

Figure 2 illustrates the basic patterns of reproductive success shown by synchronous and asynchronous females when the sex ratio was 1:1, when the male's refractory period was one fifth the length of the female's (5 versus 25 units), and when the ratio of maximum male quality to maximum effective parental care was 0·6: 0·186 (or 1: 0·31). Within a given population size, the advantages of synchrony were smaller when the trait was rare because the proportion of synchronous females receiving the maximal amounts of male parental care was lower (the number of females in the synchronous group who were deserted early, i.e. those with high quality mates, was roughly constant for synchronous groups of all sizes). The mean reproductive success of synchronizers who represented a given percentage of the total population was generally higher

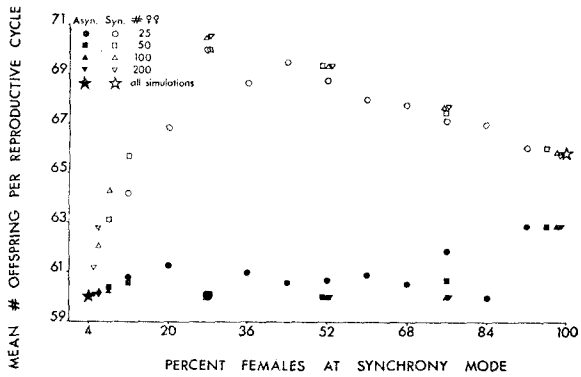


Fig. 2. Reproductive success of synchronous and asynchronous females as a function of percent females synchronized. All populations had a 1: 1 sex ratio. Populations with 4% and 100% of the females at the synchrony mode were defined as completely asynchronous and synchronous respectively. The males were divided into five groups of equal size in order of descending rank; their quality values were 0·60, 0·55, 0·50, 0·45, 0·40 respectively. The maximum contribution of extra male care to any clutch (see text) was 0·186. Minor fluctuations in these and other curves were the result of the use of integers and consequent cyclic interactions.

for larger populations. This was because the number of females deserted early often increased by a factor less than that by which the size of the synchronous group increased. The potential for synchrony to spread when rare, however, would be largely determined by the relative success of the initial synchronizers. This decreased with increasing population size because only the last two females in the initial group of synchronizers obtained any extra male care (the initial synchronizers consisted of those females at the synchrony mode when the population was maximally asynchronous plus two).

The underlying components of the changes in reproductive success are shown in Fig. 3. The costs of synchrony, namely the participation of lower quality males in the mating, increased steadily as synchrony increased in frequency (Fig. 3A); this particular pattern was caused by the step-wise, linear relationship between male quality and rank. In contrast, the benefits of synchrony (extra male parental care) rose at a decreasing rate as the percentage of females synchronized increased (Fig. 3B)—hence the initially rising and later falling success of synchronous females. If males were uniform in quality, no decline in the reproductive success of synchronous females with increasing frequency of synchrony would be observed. Asynchronous females also obtained extra male parental care as a consequence of synchronization once the spacing between their reproductive periods increased beyond the minimum spacing needed for one male to mate with all asynchronous females (all but two females at the synchrony mode for these simulations).

In this first set of simulations the success of synchronous females never fell below that of asynchronous females, implying that synchrony should spread throughout the population. When the relative costs and benefits of synchrony were changed, however, the reproductive success of asynchronous females sometimes exceeded that of synchronous females before synchrony became completely established (Figs. 4, 5 and 6). Under such conditions one would expect the evolution of a balanced polymorphism between synchronous and asynchronous strategies at the point where they were equally successful.

Benefits were lowered by decreasing the maximum potential influence of extra male parental care (Fig. 4). In nature these benefits would initially be related to the effectiveness of any investment the male might provide while simultaneously searching for reproductive females. This would depend on (1) the likelihood of a male being able to return to a deserted female following an unsuccessful attempt to find a new mate, (2) preadaptations in male behaviour making his presence of value to the female, and (3) a life history such that the benefits a male receives from current parental investment outweigh the costs (e.g. reduced life span) in terms of future ability to obtain additional matings. If males, for example, were unable to census fully their local populations for reproduc-

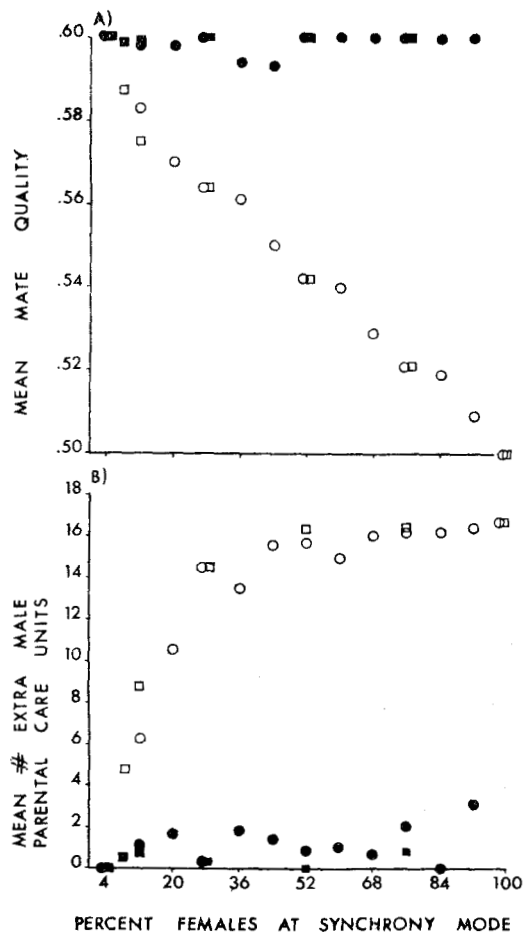


Fig. 3. Mean mate quality and mean amount of extra male parental care provided for the clutches of synchronous and asynchronous females. Symbols and simulation starting conditions were as for Fig. 2. The maximum value of the mean amount of extra male parental care was lower than the difference between the refractory periods of males and females because care of the last clutch produced by all females was cut short by the end of the simulation.

tive females between the time when their refractory periods elapsed and time when their mates' refractory periods elapsed, then males would be likely to search throughout this period if synchrony were not established, thus eliminating any advantage to rare synchronizing mutants. Even if males did stop searching after failure to find a new mate within a specified period, they still would retain the option of witholding extra parental care, thereby thwarting the synchrony strategy. Synchrony, of course, would never be advantageous if the presence of the male were for the female of no advantage or actually harmful (e.g. through competition for food or attraction of predators).

Costs to synchronizing females were increased by biasing the sex ratio to produce a shortage of males (Fig. 5) and by increasing the difference in quality between low- and high-ranking males (Fig. 6A). The effects of the two are essentially similar, as a female's lack of a mate is equivalent to her having a mate of infinitely low quality. The effect of increased variance in male quality was weakened when male quality was less than perfectly correlated with male rank (Fig. 6B). Such a situation might arise whenever adaptations used in intrasexual competition among

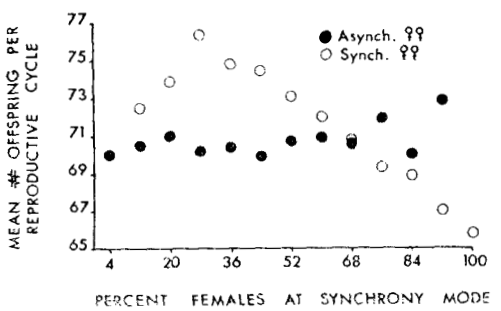


Fig. 4. The consequences of reducing the effectiveness of extra male parental care. Values for the simulation were the same as those for the 25 females–25 males simulation of Fig. 2, except that the maximum contribution of extra male care was reduced from 0·186 to 0·093.

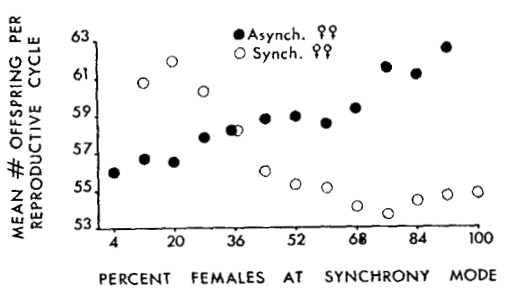


Fig. 5. The effect of a shortage of males. Simulation values were as in the 25 females–25 males simulation of Fig. 2, except that the number of males was reduced from 25 to 10. Also, points represent average figures for one simulation in which the highest ranking females were synchronized first and one in which the lowest ranking females were synchronized first. This was necessary because an absolute shortage of males resulted in direct competition between synchronous and asynchronous females for mates.

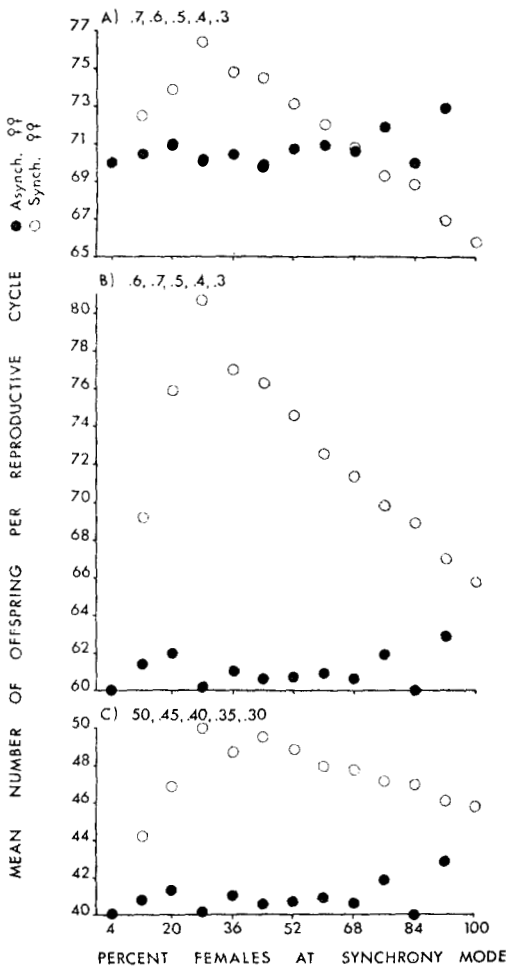


Fig. 6. The effects of male quality: (A) increased variance in male quality; (B) increased variance in male quality with rank imperfectly correlated with quality; and (C) male quality decreased by a constant amount. Simulation values were as in the 25 females–25 males simulation of Fig. 2, except that quality values of the five ranked-male groups were modified from 0·60, 0·55, 0·50, 0·45, 0·40 as indicated.

males lowered the fitness of their mates (Parker 1978). Simply shifting the absolute values of male quality by a constant amount had no effect on the potential for synchrony to evolve (Fig. 6C).

Until now no account has been taken of those costs and benefits which do not relate directly to sexual selection. Potential benefits of female reproductive synchrony, aside from increased male parental care, include: (1) an increase in the likelihood of either sex encountering a mate (Alexander 1975; Reaka 1976), (2) a reduction in the efficiency of predation through communal defence, or in the probability of predation through the 'swamping' of predators (Darling 1938, and many others), (3) an increase in the survival of young through group-dependent efficiencies in feeding (Bertram 1975; Emlen & Demong 1975), (4) a decrease in the side-effects of intramale competition (Bertram 1975) or other negative aspects of social interactions (Yomtov 1975), and (5) the focusing of reproduction at a time which is optimal for environmental reasons (Sadleir 1969; Reaka 1976; Wells 1977).

The evolutionary influence of these benefits and the costs mentioned earlier depends on both their magnitude and whether or not their magnitude is a function of the proportion of females synchronized. Most of these ancillary costs and benefits are likely to be frequency-dependent in their effects. Thus although they might shift the equilibrium point of a potentially polymorphic population (Fig. 7A), their ability to stop the early spread of synchrony would be more limited because their magnitude at low levels of synchrony would be small. In contrast, costs independent of the proportion of females synchronized, for example some costs associated with the means of achieving synchrony, might often be able to prevent the early spread of synchrony (Fig. 7B). The effects of frequency-independent costs would be particularly important if the initial benefits were quite low, as they would be in any large population. Note, however, that the asynchrony equilibrium would not be a stable one; if synchrony were to increase in frequency above a threshold level, then a higher, stable equilibrium level of synchrony would be reached. Frequency-independent benefits, for example those stemming from reproducing at an optimal time, would oppose the action of frequency-independent costs.

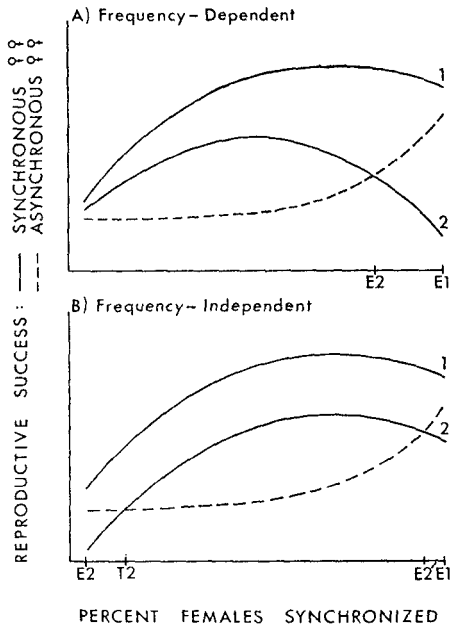


Fig. 7. The effects of frequency-dependent (A) and frequency-independent (B) ancillary costs and benefits on the evolution of synchrony. The equilibrium synchrony percentages when synchrony has associated benefits (E1) and costs (E2) are shown for both. A population subjected to frequency-independent costs which started from a point of synchrony above the threshold T2 would escape the E2 equilibrium and evolve towards the E2′ polymorphic state.

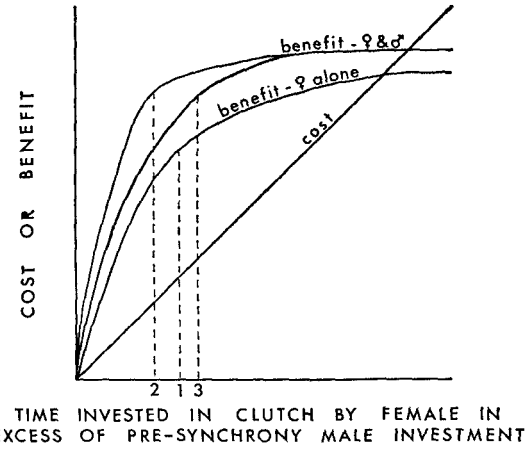


Fig. 8. The effect of differing returns to enforced male investment through synchrony on optimal female investment levels. The optimal level could decrease (2) or increase (3) compared to the level prevailing before synchrony evolved (1). The maximum difference between cost ($C(t)$) and benefit ($B(t)$) functions of this type occurs at the point where $dB(t)/dt = dC(t)/dt$ (Parker 1978).

I would now like to consider the long term consequences of the establishment of reproductive synchrony among the females of a population. First, should the resulting higher levels of male parental care change the ESS for the amount or kind of reproductive investment made by females? The method of life history analysis used by Gadgil & Bossert (1970) suggests that the total amount reproductively invested by any female during a particular period might change if the enforced male investment altered the shape of the curve relating total investment to reproductive success (Fig. 8). A shift by some females in investment, however, would initially throw the population out of synchrony, as well as changing the degree of sexual dimorphism in investment and hence the selective forces acting on synchronization (see below). A more detailed analysis of the evolutionary dynamics is needed to resolve this problem.

Even if the level of female reproductive investment remains constant, the kind of reproductive investment a female makes following mating might well change, particularly if an increase in the number of eggs is more effective than the addition of a second parent to the care of the clutch (Maynard Smith 1977). In such cases a female should benefit by a shift of some effort from the clutch being cared for by the male to the eggs to be fertilized at her next mating. From the male's perspective this represents a shift of investment from his offspring to future offspring of uncertain paternity. If synchrony has made desertion disadvantageous, two options remain for males: acquiesce to the shift or prevent it by witholding additional parental investment. Which will be selected for depends upon the balance between the male's loss of opportunities to mate in the future as a consequence of parental investment in the present and the increase in reproductive success of the offspring resulting from the male's care.

The spread of female synchrony is likely to increase the ESS for male parental investment because the payoffs to searching for new mates are reduced. The long term evolutionary consequences of changes in male strategy depend on whether the changes are superficial (advantage of new strategy dependent on level of female synchrony) or fundamental (advantage independent of female synchrony). Superficial increases in male parental investment are likely to be the initial response to female synchrony, and will usually involve male behaviours drawn from the pre-synchrony repertoire. With time, however, increasingly complex forms of male parental investment may evolve, eventually becoming so effective as to make desertion unprofitable regardless of the availability of unmated females.

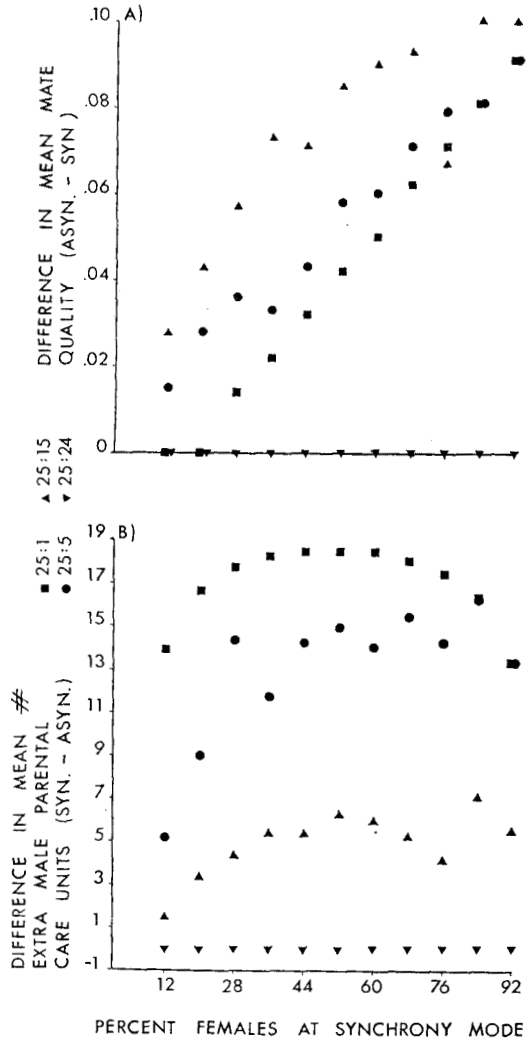


Fig. 9. The difference between synchronous and asynchronous females in mean mate quality and amount of extra male parental care provided as a function of female: male investment (i.e. refractory period) ratios. Simulation starting conditions, other than the investment ratios, were as for Fig. 2.

Superficial increases in male investment levels will not change the selective pressures maintaining female synchrony; any reduction in synchrony will lead to an increase in desertion and a return to the higher synchrony level. Fundamental changes in male investment patterns have more interesting evolutionary consquences which depend on the degree to which the disparity between the sexes in parental investment is reduced. A decrease in this disparity has several conflicting effects: (1) Reduction in the precision of synchrony needed to prevent desertion. Synchrony is fully effective if the time interval between the mating of the first and last of the synchronous females is less than the length of the male refractory period. Thus an increase in the male refractory period may allow a loosening of synchronization, particularly if the reduction in ancillary costs exceeds the reduction in ancillary benefits. (2) Creation of a shortage of males if males opt for a risky form of effective parental investment. As shown above (Fig. 5), a shortage of males will lower the relative success of synchronizing females. (3) Changes in the difference between asynchronous and synchronous females in the quality of their mates (Fig. 9A). As the male's refractory period approaches that of the female, the advantage in mate quality which asynchronous females have over synchronous females first increases and then decreases. (4) Decline in the benefits to synchronous females achievable through the elimination of all desertion by males (Fig. 9B).

The combined action of these last three effects will tend to make synchrony less favourable as the disparity between the sexes in parental investment is fundamentally reduced. Simulations to explore the influence of the latter two (Fig. 10) showed that synchrony would be selected against if a female:male investment ratio of 25:15 were reached (Fig. 10B; conditions otherwise as in the original series of simulations). Thus the point at which synchrony will be lost from a population will depend to some extent on the size of the evolutionary steps by which male investment levels change. If, for example, male brooding becomes fundamentally advantageous, and if offspring must be brooded for a fixed minimum period, then the male refractory period will jump from its original level to at least that of the minimum brooding period. If this increase is substantial, then continued 'use' of synchrony by females as a strategy to increase male parental investment further is unlikely.

## Tests of the Model

Evidence for the evolution of synchrony by the mechanism described above is not readily available. There is the additional problem of the potential for the loss of synchrony following fundamental changes in male parental care strategies. Even in those situations in which selection for synchrony is still occurring, one cannot use a simple correlation between synchrony and extensive male parental care as support for the model. Many species show such an association (for example Russell 1971; Kleiman 1977; Warham et al. 1977; Woodruff 1977), including man (McClintock 1971), but these

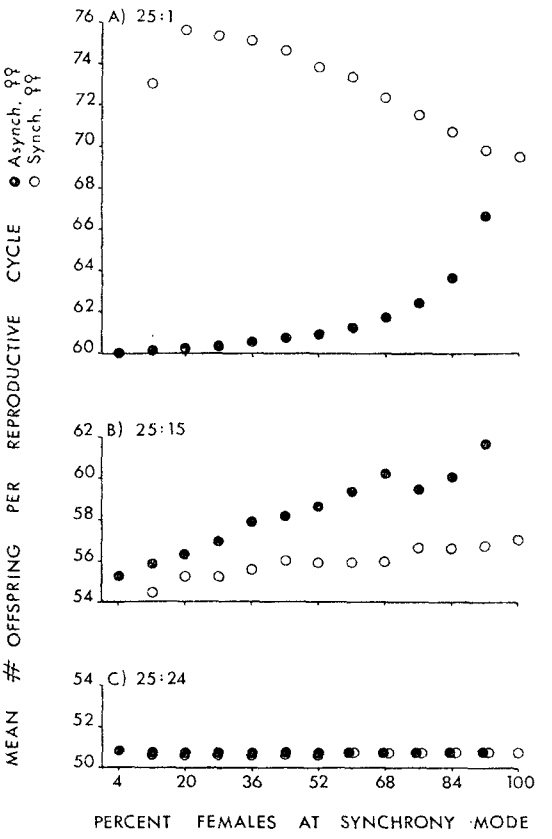


Fig. 10. Reproductive success of synchronous and asynchronous females for three female:male ratios of parental energy investment. Figure 2 shows simulation results with a 25:5 investment ratio in an otherwise identical population of 25 females and 25 males.

cases do not tell us whether the observed synchrony became established because of its usefulness as a sexual strategy. As Maynard Smith (1977), Ralls (1977), and Emlen & Oring (1977) have pointed out, the evolution of extensive male parental investment is more likely when females become reproductive synchronously, whatever the initial reason for synchrony (although for man, it should be noted, no alternative evolutionary reason has been proposed).

What are therefore needed are data on separate populations in similar areas or closely related species in one area showing comparable levels of male parental care but differing degrees of female reproductive synchrony. One would then predict that populations or species with more synchronous females would be characterized by ecological situations which would make it easier for males to desert or to expel the female and offspring if females did not mate in synchrony. Differences in the potential for successful mate abandonment could arise from differences in density, predation on individuals moving between mates, the extent to which an abandoned territory is replaceable or recapturable, the timing of availability of critical resources, or the vulnerability of offspring when cared for by the female alone. The usefulness of these predictions is increased by the fact that they are often contrary to those based on other explanations for reproductive synchrony. For example, predator swamping (Darling 1938) and mating efficiency (Reaka 1976) arguments for synchrony predict increased synchrony in species in which predation on the offspring is intense, or species in which rareness of or high predation rates on moving adults results in infrequent encounters between males and females. The model proposed above would predict decreased synchrony under such conditions because desertion would be less advantageous to males.

Species most likely to provide evidence for sexually selected synchrony will be those in which males can efficiently determine the reproductive readiness of available females, with the ability to return to their mates (or to have their mates return to them) should opportunities for mating be lacking. Site-attached species which nevertheless remain in relatively close contact with their surrounding conspecifics are most likely to satisfy these requirements. The potential for males to contribute to female reproductive success in behaviourally and morphologically flexible ways would also be expected in species retaining female synchrony as a sexual strategy (female synchrony will often have been lost where highly elaborate and fixed forms of male investment have evolved, as explained above). Coral reef damselfishes (Pomacentridae) meet these conditions and may provide good tests of the model's predictions; males guard the eggs in territories, and reproductive synchrony varies considerably in this species-rich group (L. Fishelson, J. Moyer, pers. comm.).

## Concluding Remarks

This model for the evolution of synchrony as a sexual strategy must be viewed as a preliminary effort in our understanding of the dynamics of sexual selection. Attention to genetics, more realistic behavioural details (such as the costs of searching for mates), and a more analytic approach are clearly needed. The evolutionary fate of strategies whose expression is rank dependent (for example, Burley 1977) must be explored further. In this model, low-ranking females have the most to lose in synchronization, and the potential for and effects of asynchronous cheating among such individuals should be more explicitly considered. The role of male counter-strategies (such as refusal to mate with synchronizing females) has been neglected entirely. These probably also involve the complications of rank-dependency, for even if high quality males prefer to mate with asynchronous females, it will never pay all males to do so as long as females invest more than males and thus constitute a limiting resource. Our understanding of the dynamics of sexual selection as investment levels in the two sexes approach equality, and of the influence of mate quality and biased sex ratios in such situations remains sketchy. We need to determine how female preference for males willing to invest prior to copulation and synchrony-enforced postcopulatory male investment differ in their short term and long term evolutionary consequences.

Even with these limitations, the model for synchrony illustrates how sexual selection can decrease the disparity between the sexes in parental investment and thus reduce the cost of sex (Maynard Smith 1971). The key factor defining the threshold between this process and the opposite one described by Fisher (1930) is variability in quality among members of the lesser investing sex. The two do not act symmetrically around this threshold, however. Preference for high quality males leads to a positive feedback loop. increasing male traits originally

correlated with quality (at the expense of parental investment) and female preference for these traits. This process is slowed down only later by other costs arising from the exaggeration of male traits (O'Donald 1973). Any fundamental increase in male parental investment through synchrony, in contrast, immediately generates a negative feedback loop by decreasing the intensity of selection for further synchronization. This difference between the two processes may help to explain why the parental investments of males and females are so rarely equal.

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