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Parental care and sex role reversal

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Parents do not send their descendants into the world as naked DNA. The unfertilized egg is rich in nutrients, and the zygote and developing offspring may be cared for in a number of ways. This care represents a commitment of time, energy, and risk.

It is generally the female who provides most or all of the nourishment which goes into the egg. This initial discrepancy between the sexes in parental commitment is often maintained or exaggerated by subsequent parental care by the female. As a result, the availability of females is generally rate limiting for reproduction within a population. This situation leads, through the process of sexual selection, to the well-known differences between the sexes in sex roles – namely, that males are typically more conspicuous and aggressive in courtship interactions than females (Darwin, 1871; Fisher, 1930; Bateman, 1948; O'Donald, 1962, 1973; Williams, 1966; Trivers, 1972; Dawkins & Carlisle, 1976; Emlen & Oring, 1977; Parker, 1974, 1979).

In some species, however, paternal care is substantial and maternal care slight or nonexistent (see review by Ridley, 1978). In a few of these there appears to be genuine sex role reversal, i.e. females show the typically male characteristics associated with competition for mates. This role reversal stems from a reversal from female to male in the sex which limits the population's reproductive rate (Williams, 1966; Trivers, 1972; Emlen & Oring, 1977).

Examples of such high levels of paternal commitment are extremely rare among animals. The purposes of this paper are to review the natural history patterns of extensive male parental care and the theory which attempts to explain them, and to present results of a computer simulation designed to explore conditions which favour increased paternal commitment. The

results suggest that high levels of male parental care evolve most readily when (1) a mutation in females gives males the option of providing care, (2) failure by males to provide care results in lower offspring survivorship, and (3) the frequency of males potentially willing to provide care is already high.

Natural history patterns

Sex role reversal is best documented in several species of birds, and jacanas represent the extreme case (Jenni, 1974). In *Jacana spinosa* (Jenni & Collier, 1972) the female defends a large territory which contains the smaller territories of her harem of males. The males build the nests, incubate the eggs and raise the young. Although the plumages of males and females are similar, the females are on average over one and a half times heavier than males. In other sex role-reversed birds such as the phalaropes, males provide most or all of the parental care, but polyandry is less well developed; females typically have a more conspicuous breeding plumage than males but differ less from them in size. In the majority of bird species, in contrast, parental care is provided jointly by males and females (Lack, 1968).

In mammals the presence of mammary glands restricts early feeding of the young to females. In only a few species do males provide large amounts of care (Kleiman, 1977), and there are no known examples of sex role reversal.

In both fishes and anuran amphibians, care by the male alone is more common than exclusively female or joint care, although most often neither sex cares for the young (Ridley, 1978). Among the fishes only the pipefish and seahorses (Syngnathidae) show clear evidence for sex role reversal. In all members of this family the males brood the eggs under the abdomen, sometimes in a brood pouch. In several species the females are bigger, more brightly coloured, and more aggressive in courtship (Fiedler, 1954; T. Lim, personal communication). Possible herpetological examples of sex role reversal (some of the dendrobatid frogs in which the male carries the young on his back) have not been rigorously confirmed (Ridley, 1978; Wells, 1981).

Among the invertebrates, species with parental care, particularly male care, are relatively rare (Ridley, 1978; Smith, 1980*b*). The best studied and most striking examples of paternal care are some of the giant water bugs (Belostomatidae) (Smith, 1976, 1979, 1980*a*). In the Belostomatidae, females lay the fertilized eggs on the backs of males, who brood them. Even here, however, there is no unambiguous evidence for sex role reversal,

although Smith (1980*a*) believes that the backs of males may limit the reproductive rate of populations he has studied during certain seasons. In a number of insects, males may contribute substantially to the energetic costs of egg production through courtship feeding (Thornhill, 1976), but in none of these do the sexes appear to be role reversed.

Sex role reversal is so rare that it is difficult to correlate it with ecological, behavioural or reproductive features. Looking more broadly at species with exclusively male parental care, there is a general tendency for such species to be externally fertilizing (Dawkins & Carlisle, 1976; Ridley, 1978). One may contrast, for example, fish and anuran amphibians with birds, mammals and insects, or note that the only salamanders with paternal care are found in the few families with external fertilization (Ridley, 1978). There is also a loose correlation between paternal care and male territoriality (Ridley, 1978).

Previous theoretical contributions

As Trivers (1972), Dawkins (1976) and Parker (1979) have argued, the members of a mating pair are often in conflict over how much each should invest in the offspring. Once fertilization has occurred, each would usually enjoy a higher reproductive success if the other would care for the offspring until further care would be ineffective. Thus one theoretical approach is to specify the conditions which permit or encourage sex role reversal as the evolutionary resolution of this conflict.

Females generally lack the ability to force males by physical means to care for the offspring. As the limiting sex, females can, however, use 'strategies' of timing (e.g. synchrony) to prevent male desertion when males would otherwise find it advantageous to desert. But the potential for the trait of reproductive synchrony to spread through the females of a population decreases as the male to female potential reproductive rate ratio approaches unity (Knowlton, 1979). Thus sex role reversal cannot be achieved through such a mechanism. There are probably similar constraints which limit the precopulatory demands (e.g. courtship feeding) which females can make.

Several verbal models have been suggested for the evolution of sex role reversal, particularly as associated with polyandry in birds (see Emlen & Oring, 1977). Jenni (1974) proposed an evolutionary sequence running from (1) monogamy with care of the offspring by both parents through (2) 'double clutching', in which the male cares for the first clutch his mate lays and the female cares for the second, to (3) systems in which females lay clutches for a number of males, never attending any of the offspring in the

most extreme case. Jenni hypothesized that males as well as females might benefit from female emancipation from care if it allowed females to lay additional clutches for their mates, or replacement clutches (should the original clutch fail).

Smith (1980*b*) suggested that paternal care in the giant water bugs might have evolved because females laying eggs on the backs of males avoided competition for oviposition sites and perhaps egg cannibalism. He noted that males were likely to be available and receptive because of their tendency to guard females to prevent sperm competition.

Ridley (1978) has reviewed a number of features which have been proposed to facilitate the evolution of paternal care: the potential for increasing female fecundity (described above), male territoriality, external fertilization, and female preference for caring males. He also suggested that the condition of 'isoinvestment' might be more susceptible to destabilizing evolutionary forces than conditions where the sexes differed greatly in parental investment (and thus potential reproductive rate). If the direction of destabilization were random, then sex role reversal would be the outcome in some cases. This idea, based on Parker, Baker & Smith's (1972) analysis of the evolution of anisogamy, has merit. The Fisher effect (Fisher, 1930), for example, is a kind of positive feedback loop which results in increasingly intense selection on one sex for characteristics which indicate ability to attract mates, potentially at the expense of ability to care for offspring.

Several analytic models for the evolution of paternal care have also been put forward. All of these have been based on the concept of the evolutionarily stable strategy (or ESS; Maynard Smith & Price, 1973) – a strategy which once established is stable against invasion by all other mutant strategies. Also assumed is that the ESS for each sex will be that which maximizes the number of surviving offspring produced per unit time given the ESS characteristic of the opposite sex.

Dawkins (1976) presented a simple analysis for the case when males can either desert or be faithful and females can either be coy or indiscriminate in their mating preferences. Drawing on this, Maynard Smith (1977) analysed the case when both males and females have the options of guarding or deserting, and offspring survival is a function of the number of parents guarding. The model assumes that if females do not care for the young then they are potentially able to lay more eggs, while if males desert they have a constant probability of obtaining a second mate. Male care and female desertion were found to be favoured when (1) the probability of the male's finding a second mate is low, (2) female fecundity increases with desertion,

and (3) care by one parent greatly increases offspring survival but the addition of a second parent has a much smaller positive effect. For some parameter values, both male care/female desertion and female care/male desertion are ESSs.

Although supportive of Jenni's (1974) verbal model, the analysis has several limitations. The probability of offspring survival with single parent care is not dependent on which sex provides the care (although this feature could be easily added to the model). More seriously, males have a constant probability of obtaining a second mate. This probability should be a function of the proportion of males which desert their mates (as in Rubenstein's (1980) model for the evolution of territoriality as a reproductive strategy). Females are also not given the option of mating again (an option which they clearly have in polyandrous species), so that males always directly benefit through the increased fecundity of their mates.

Later in the same paper, Maynard Smith escaped the latter two problems in a model for a continuously breeding population. The analysis specifies the ESS for the amount of time each sex should spend with the offspring (i.e. both males and females have an infinite number of potential strategies). He again reached the conclusion that there may sometimes be two ESSs for single parent care, even when one alternative would result in a higher average reproductive rate for the population than the other. He stressed that starting conditions would be expected to influence critically the outcome whenever two ESSs are theoretically possible.

The continuous strategy set model of Grafen & Sibly (1978) provides the most precise predictions for the evolution of parental care. They explored in detail the consequences of the following special assumption: 'The rate of increase of expected benefit from a brood at any one time depends only on the expected benefit from the brood at that time (in other words, the current state of development of the brood) and on whether the male, or the female, or neither has already been deserted'. With this assumption they were able to conclude that

$$\text{for } t_1 < t_2 \quad h(g)/h_2(g) = (1/r) + 1$$

and

$$\text{for } t_2 < t_1 \quad h(g)/h_1(g) = r + 1$$

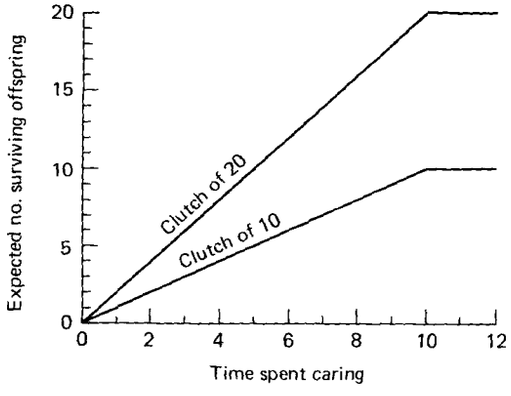
where t_1 and t_2 are the times when males and females desert the young, respectively; $h(g)$, $h_1(g)$ and $h_2(g)$ are the rates at which benefit from the brood increases with time spent caring, for joint care, male care, and female care, respectively; and r is the number of breeding males per breeding female.

These are powerful predictions. For a 1 : 1 sex ratio, for example, they

imply that desertion will first occur when for one member of the pair, the rate of benefit increase from joint parental care falls below twice that which would result from care by the mate alone. This suggests that the evolution of parental care is very conservative. Once one sex becomes parental, it is likely to be more efficient in providing care than the other sex and thus be the one to be deserted, since the less efficient sex is the one which will desert first unless the breeding sex ratio is strongly skewed towards an excess of the less-efficient sex. This would tend to make the evolution of sex role reversal extremely difficult, a finding not inconsistent with the rarity of the phenomenon.

It is important to examine the biological implications of their special assumption, however. Fig. 10.1 illustrates the relationship between benefit from the brood and time spent caring when benefit is a function of the number of eggs laid times the probability of the egg producing a surviving offspring, and when the probability of survival is directly related to the time for which they are cared. The differences in clutch size between the two cases presented are assumed to result from differences in the amount of care initially provided by the male. This example violates the special assumption of Grafen & Sibly (1978) because the rate of increase of benefit at any one time depends not only on the benefit achieved and who will provide the care, but also on the past history of caring for the brood through its effect

Fig. 10.1. The expected number of surviving offspring from a clutch as a function of the number of eggs laid times the probability (P) of each egg producing a surviving offspring. This number is assumed to be a function of the time (T) for which the eggs are cared. For $T \leq 10$, $P = T/10$; for $T > 10$, $P = 1$. The curves represent the hypothetical case of clutch size being doubled if males help in the caring during the early stages of clutch deposition.



on brood size. When an expected benefit of ten offspring has been achieved, for example, the first female may still expect a positive rate of benefit increase, while the second female can expect no further benefit. Thus their special assumption appears to exclude from consideration that feature which many believe to be the most potent force favouring the evolution of high levels of male parental care.

In summary, the available analytic ESS models for the evolution of parental care are of only partial value in understanding sex role reversal. In addition to their individual weaknesses, they also fail by definition to examine whether strategies, which though stable when established, can spread when rare.

A computer simulation

These limitations inspired the writing of a computer program capable of simulating changes in the frequencies of parental strategies. As in the first of the Maynard Smith (1977) models, each sex has only two behavioural options. Both sexes have the potential for multiple matings, however, and the simulation is also capable of examining the influence of starting conditions on the final outcome.

The original design was influenced by Smith's (1980*a*) scenario for the evolution of male parental care in the giant water bugs: a population consisting of normal females, who lay their eggs on vegetation; mutant females, who attempt to lay their eggs on the backs of males; tolerant males, who allow mutant females to lay eggs on their backs; and intolerant males, who refuse to accept the eggs of mutant females. Thus there are four types of matings, but only three different sets of consequences: normal female/tolerant or intolerant male (in either case the eggs receive the same treatment), mutant female/intolerant male, and mutant female/tolerant male. In more general terms, this model describes the fate of mutations which cause females to provide males with the opportunity to care for the offspring, and mutations in males which govern their response to this opportunity.

Each of the three mating types has associated with it three parameters: (1) the cost to the female (in terms of the percentage of her reproductive effort which the mating represents), (2) the cost to the male, and (3) the proportion of the offspring produced which survive. The simulations fell into two broad classes as a function of whether or not mutant females had lower reproductive costs than normal females. Other parameters were varied to determine the effects of (1) increasing the cost to tolerant males who mate with mutant females, (2) increasing the probability of survival of

eggs from tolerant male/mutant female matings, (3) decreasing the probability of survival of eggs from intolerant male/mutant female matings, and (4) changing the discrepancy between males and normal females in reproductive costs. For all simulations the starting frequency of mutant females was set at 2%. Two starting frequencies for tolerant males, 2 and 98%, were tried for all combinations of parameter values.

The bulk of the program consists of two nested, iterative loops. Each passage through the outer loop generates the numbers of the four adult types for the next generation from their relative proportions in the previous generation. This is done by standardizing these proportions against a population consisting of 100 females and 100 males.

The inner loop simulates mating and production of offspring within each generation. The loop repeats until the reproductive potential of the males or the females is exhausted. At each iteration, the number of matings between males and females of each type is equal to the proportion of females available of that type times the proportion of males available of that type times the number of available males or females, whichever is smaller. Thus there is no potential for random mating effects, and the population simulated is effectively infinite. The number of available individuals of each type for the next iteration is reduced by substracting the cost of each mating in which individuals of that type participated. The number of matings of each type is stored cumulatively.

After mating is completed, the total number of matings of each type is multiplied by the probability for that mating type of offspring survival. Half of this number are designated females of the mother's type and half males of the father's type. These numbers are then summed for each of the four types of individuals, and the sums standardized for the next generation as described above. The Appendix outlines the statements of the program.

Results

The results of the simulations are presented in a series of seven figures. In each, the left-hand (L) pair of graphs shows the outcome when tolerant males started out at 98%, and the right-hand (R) pair when they started out at 2%. In each graph, the effects of increasing costs for tolerant males mating with mutant females (from 0.1 to 0.5 and 0.9, except in Fig. 10.7) are represented as families of curves. The two sets of simulations (Figs. 10.2–10.5, Figs. 10.6–10.8) distinguish between situations when mutant females save nothing directly by leaving their eggs with males (as would be the case, perhaps, if they simply shifted their oviposition sites),

and situations when mutant females decrease their costs (by, for example, caring less for the offspring).

Mutant and normal female costs equal

If the offspring from matings between mutant females and tolerant males did not have a higher survivorship than offspring produced by normal females, then mutant females never increased in frequency. This was expected. Mutant and normal females had identical costs in these simulations, and thus mutant females could only do better than normal females if survivorship from some of their matings were higher.

Increasing tolerant male costs always lowered the rate of increase or increased the rate of decrease in the frequency of tolerant males and generally mutant females. Some of these rate alterations were very slight, however. The final equilibrium frequencies of tolerant males were also lowered in some simulations (especially Figs. 10.2, 10.3L, 10.4). Again, this

Fig. 10.2. Simulations when mutant female costs = 0.5, and the probability of their offspring surviving = 1.0 for matings with tolerant males and 0.5 for matings with intolerant males. Normal females have a reproductive cost of 0.5 and a probability of offspring survival of 0.5. Curves represent outcomes, from lowest to highest, when costs to tolerant males from matings with mutant females are 0.9, 0.5, and 0.1; the two upper curves or all three curves are sometimes indistinguishable. Costs to intolerant males and tolerant males mating with normal females = 0.1.

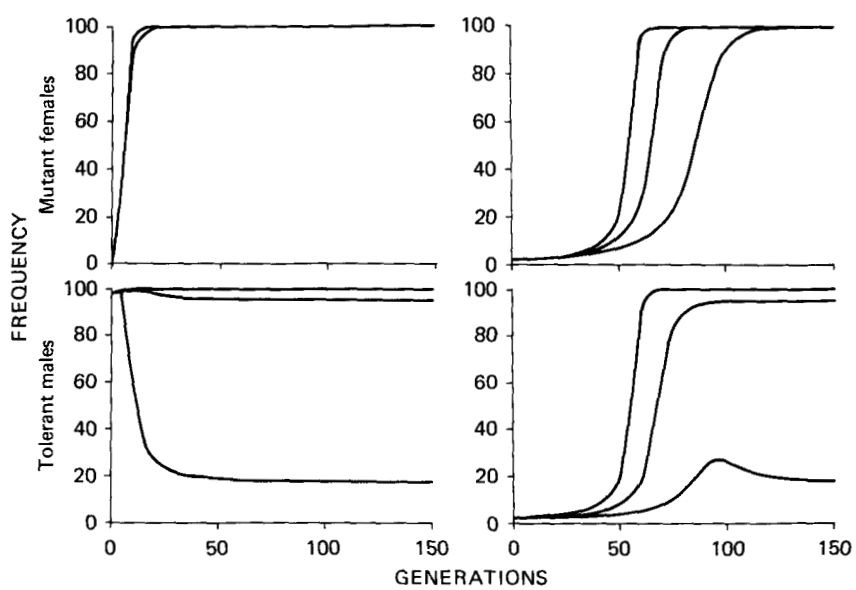


Fig. 10.3. Simulations as in Fig. 10.2, except that the probability of offspring surviving for mutant female/intolerant male matings was lowered to 0.25.

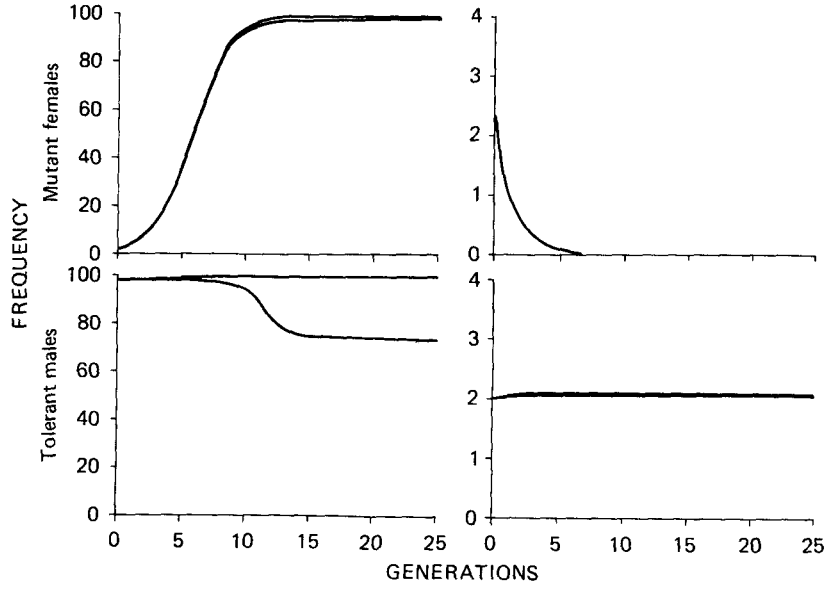
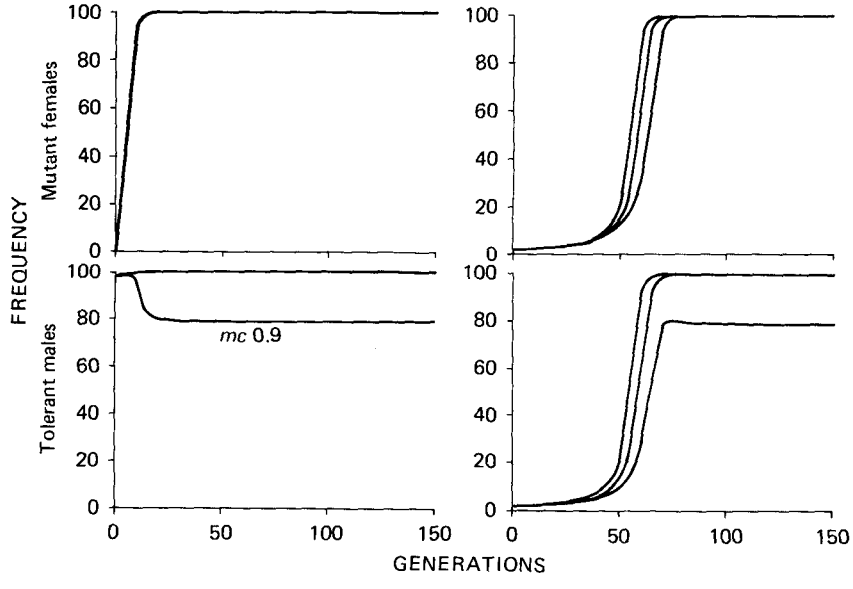


Fig. 10.4. Simulations as in Fig. 10.2, except that mutant and normal female costs were raised to 0.75.



was not unexpected. It should be noted that there appeared to be no evidence for boundary conditions surrounding the point where tolerant male costs equalled female costs. For example, in the simulations illustrated by Fig. 10.2, the point where tolerant males did not increase to fixation occurred when their costs, when mated with mutant females, were approximately 0.48.

Increasing the baseline level of female costs (from 0.5 to 0.75) increased the equilibrium frequency of tolerant males when the equilibrium frequency was originally less than 100% (compare Figs. 10.2 and 10.4, and Figs. 10.3L and 10.5L). Thus the greater the cost discrepancy between intolerant males and females, the more likely was the establishment of higher levels of paternal care.

The starting frequency of tolerant males sometimes, but not always, had an effect on the final outcome. This frequency dependence was established by lowering the probability of survival of the offspring produced from mutant female/intolerant male matings (from 0.5 to 0.25). For example, Figs. 10.2L and 10.2R show the same equilibrium results while those of Figs. 10.3L and 10.3R differ dramatically. A similar comparison can be made between Figs. 10.4 and 10.5. A low probability of survival of offspring from mutant female/intolerant male matings made a high starting frequency of tolerant males necessary for tolerant males to increase in frequency. Given a high starting frequency, however, the final equilibrium frequency of tolerant males was higher when survivorship of mutant female/intolerant male offspring was lower (compare Figs. 10.2L and 10.3L, Figs. 10.4L and 10.5L).

Mutant female costs lowered

In some respects this set of simulations resembled those described above. Increasing tolerant male costs, for example, lowered their final equilibrium frequency for at least some cost levels in all simulations. In one case mutant female equilibrium frequency was also lowered (Fig. 10.8L). Decreasing the probability of survival of offspring from mutant female/intolerant male matings again created an initial frequency dependence effect and raised the final equilibrium frequency of tolerant males when their starting frequency was high (compare Figs. 10.7 and 10.8).

There were important differences, however. First, it was no longer necessary for the probability of survival of mutant female/tolerant male offspring to exceed that of offspring produced by normal females. This was not surprising, for mutant females had lower reproductive costs than normal females in all cases. Second, raising the baseline cost level of normal

Fig. 10.5. Simulations as in Fig. 10.3, except that mutant and normal female costs were raised to 0.75.

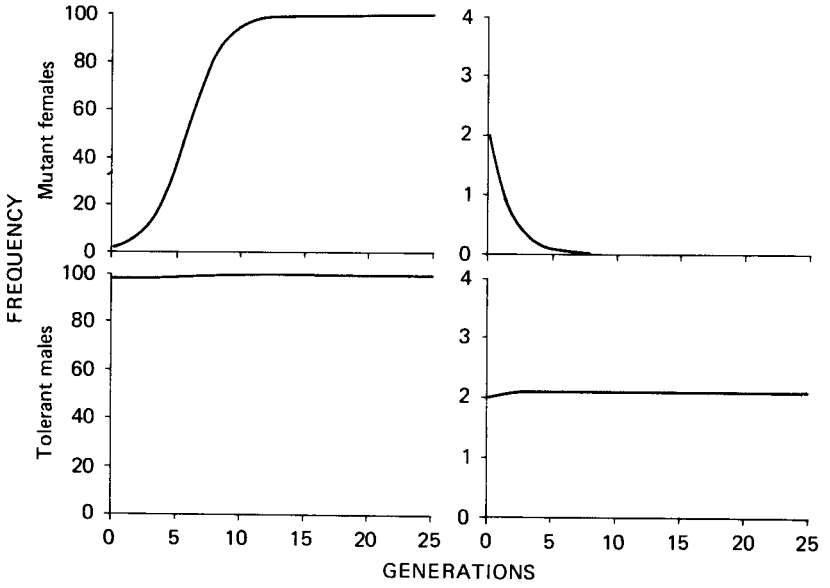
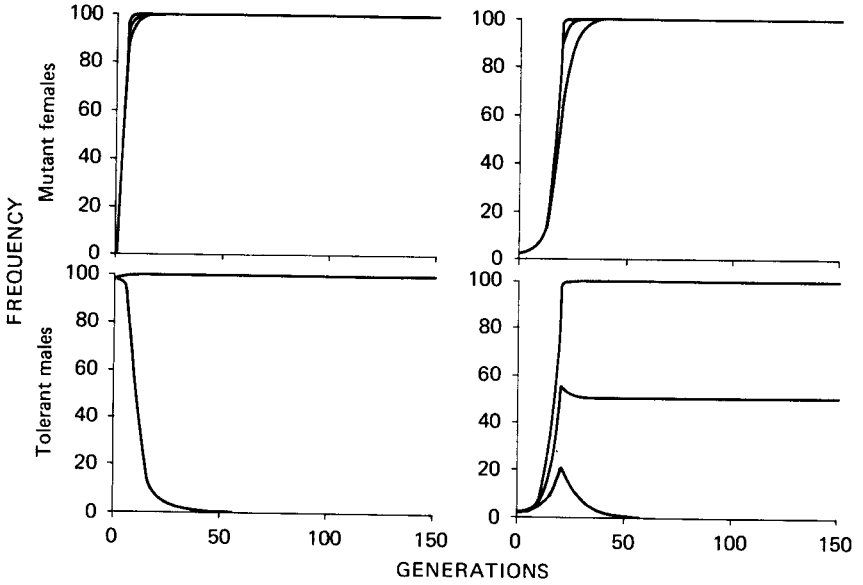


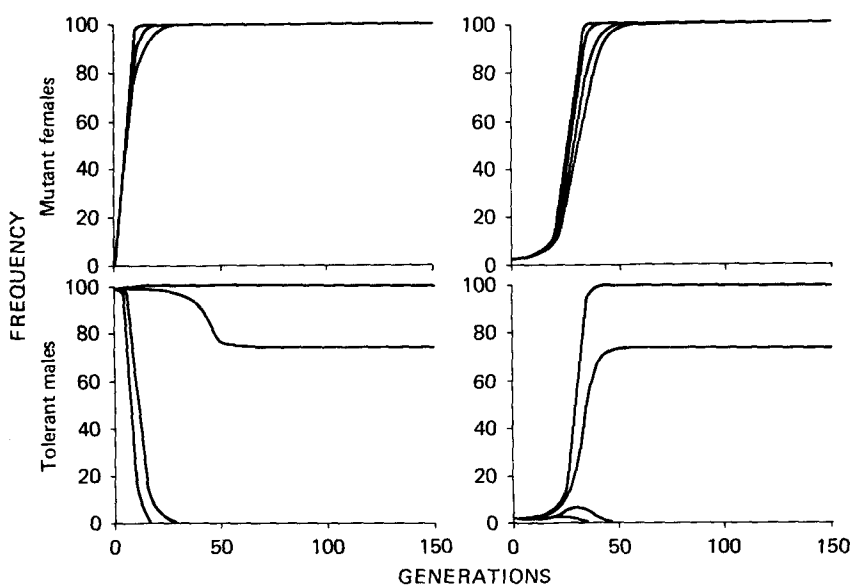
Fig. 10.6. Simulations as in Fig. 10.3, except that mutant female costs were lowered to 0.2.



females from 0.5 to 0.75 had little effect; when simulations were run with parameter values otherwise equal to those run for Fig. 10.7, results were very similar with identical equilibrium values. Finally, the equilibrium levels of tolerant males were changed in several ways. Fig. 10.6 can be compared to Fig. 10.3, where starting conditions were identical except for the mutant female costs. When starting frequencies of tolerant males were high, then costly forms of male care were less likely to evolve than they were when mutant female costs remained unchanged. When starting frequencies were low, mutant females increased instead of rapidly disappearing, and tolerant males as a consequence became established at levels determined by the cost of male care.

A more biologically realistic picture of the effects of a cost decrease for mutant females is presented in Figs. 10.7 and 10.8, however. In these simulations, there was no difference in offspring survivorship between matings involving normal females and those involving mutant females and tolerant males (i.e. tolerant males merely compensated for the effort not expended by mutant females). A comparison of Figs. 10.3 and 10.7 illustrates the difficulty in establishing male parental care under these con-

Fig. 10.7. Simulations as in Fig. 10.6, except that the probability of offspring surviving for mutant female/tolerant male matings was lowered to 0.5. The results when costs to tolerant males mating with mutant females = 0.25 are also shown (curve with second highest values).



ditions. Even moderate levels of paternal care seemed unlikely to evolve unless the probability of survival of offspring from mutant female/intolerant male matings was quite low and the starting frequency of tolerant males high (Fig. 10.8L).

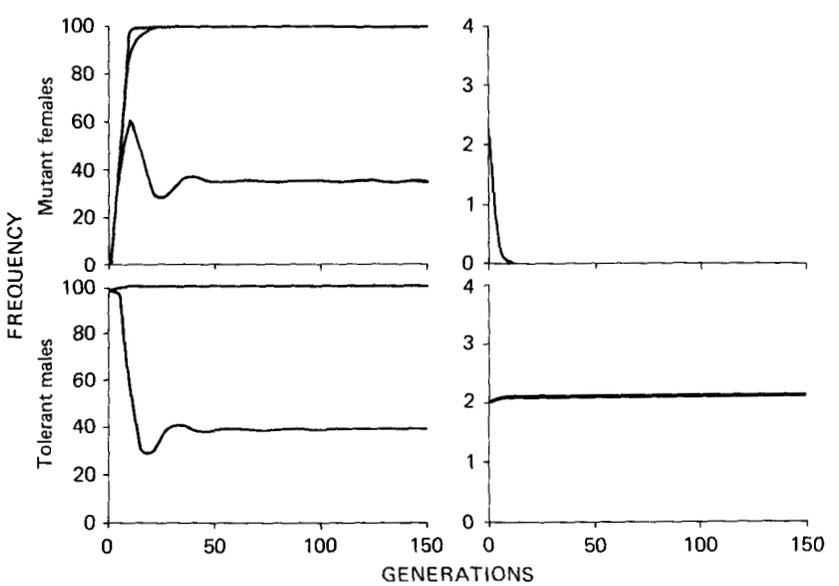
Discussion

The simulations presented here are limited in scope; a variety of assumptions (more complex modes of inheritance, variations in clutch size and sex ratio, etc.) and intermediate parameter values have yet to be tried. Within the context of these limitations, however, several results which were not derived from earlier models deserve mention.

First, a large initial discrepancy between the sexes in reproductive costs favours increases in male parental care if female care is not at the same time reduced. In essence, this feature tends to stabilize, or decrease up to a point, differences between the sexes in potential reproductive rate and hence the intensity of sexual selection. This tendency opposes the Fisher effect, which acts as a positive feedback loop in the sexual selection process.

The simulations in which females save nothing also show that mutations in females which give males the option of providing additional care can

Fig. 10.8. Simulations as in Fig. 10.6, except that the probabilities of offspring surviving for mutant females were lowered to 0.5 for matings with tolerant males and 0.125 for matings with intolerant males.



result in higher levels of paternal care than mutations in males alone. This is seen in the effect of lowering offspring survivorship from mutant female/intolerant male matings. When there is no lowering of survival, the situation is logically equivalent to one in which males simply vary in the amount of care they provide. (Logical equivalence was verified by a modified simulation.) Decreasing the survivorship of offspring from mutant female/intolerant male matings allowed higher levels of male care to evolve, provided the starting frequency of tolerant males was high.

Interestingly, Smith's (1980*b*) assessment of the conditions which led to the evolution of male care in giant water bugs parallels these simulation results. He stressed two features: (1) females changing their oviposition site from emergent vegetation to the backs of males (which would certainly involve the potential for poor survivorship if males discarded or otherwise mistreated the eggs), and (2) a high probability of male acceptance of these eggs because of their tendency to guard females in an effort to avoid sperm competition. His discussion also points up the need for simulations in which females test male willingness to care by a preliminary investment in a small number of eggs. This might reduce the starting frequency of tolerant males needed for the evolution of paternal care.

A parallel effect is seen in the simulations in which mutant females do save in reproductive costs (i.e. mutations in both sexes are by definition involved). If offspring survivorship is lowered, as is likely, when females provide less care and males provide no additional care, then the highest levels of male care occur when survivorship is considerably impaired and males willing to provide extra care occur at high frequency. This accords very well with Jenni's (1974) linking of double clutching and sex role reversal in birds. In all birds, offspring survivorship is very low if neither sex cares, but in species with a history of double clutching there is likely to be the necessary high starting frequency of males willing to care for the young without female help.

The relationship between territoriality and male parental care (Ridley, 1978) makes sense in light of these simulation results. As Ridley argued, the extra costs to males for guarding eggs on their territories might be low (provided defence against egg predators was not particularly costly). In addition, territoriality could be viewed as a preadaptation which results in a high starting frequency of tolerant males.

Interpreting the general relationship between external fertilization and care by the male alone is more complex. This complexity stems partly from the fact that costs to males vary widely within this category of parental care. In addition, internal fertilization can act in two ways with respect to the

parameters of these simulations. First, it would increase the baseline discrepancy between the sexes in reproductive costs if internal fertilization represented a more substantial commitment for females than external fertilization. Second, it might increase the potential for loss in offspring survivorship in matings between mutant females and intolerant males. This would be very likely if mutant females retained the fertilized eggs for a shorter time. The consequences of this might help to explain the apparent rarity of transitions from internal to external fertilization (in sessile invertebrates, Ghiselin, 1974, p. 120; in fishes, J. Gittelman, personal communication).

Even if mutant females simply changed their oviposition sites (i.e. no direct savings), the change might be more likely to affect adversely offspring survivorship in mutant female/intolerant male matings when fertilization is internal. Externally fertilizing females would be expected to leave their eggs in the vicinity of males in any case, because the male must fertilize them. Internally fertilizing females are not normally under this constraint, and thus a mutation for leaving eggs with males might involve a more radical change in oviposition site. For the parameter values tried, decreases in offspring survivorship necessitated high starting frequencies of tolerant males, even when the initial discrepancy between the sexes in reproductive cost was increased. This suggests that moderate increases in male parental care would be expected to evolve more readily in species with external fertilization, because there would be a less-stringent prerequisite for a high starting frequency of tolerant males.

Finally, it should be noted that the conditions which make the regular evolution of some male parental care probable (no decrease in female costs, or other features likely to require a high starting frequency of tolerant males) do not facilitate the evolution of the highest levels of paternal care. This may explain why a number of the extreme cases which approach or achieve sex role reversal (e.g. jacanas, giant water bugs) are found in groups where exclusively male paternal care is atypical.

While the details of these simulations may later be shown to be limited by their assumptions, the sensitivity of the outcome to the initial frequencies of the strategies is likely to be a general phenomenon in the evolution of parental care. Analyses based only on the concept of the ESS cannot examine this problem because they consider only the stability of strategies once they are established.

The theory for the evolution of mating and parental care strategies has many potential directions for growth. Analytic methods should be directed

at the situations examined here. More unusual forms of sex role reversal also need to be explored. Hatziolos (1979), for example, has demonstrated that in a species of mantis shrimp in which only the female cares for the eggs, males are coy and females actively court them. She suggested that matings are relatively risky for males (mantis shrimp are extremely aggressive and effective predators and females are generally larger than males), and thus that males should only mate with females of the highest quality (large females produce much larger clutches). It would be interesting to model the evolution of complex systems of this type.

All of the theoretical approaches outlined and used here share a common microevolutionary bias, based essentially on the principles (though not the elegant mathematics) of population genetics. The substantial developments in macroevolutionary theory (Gould, 1977; Stanley, 1979) have had almost no influence on sociobiological issues (the evolution of sex being a notable exception (Stanley, 1975)). The relationship between parental care strategies and speciation and extinction rates, for example, and the influence such a relationship might have on the patterns we observe (e.g. the rarity of male parental care) remain to be explored.

Ultimately, however, our theories are only as good as the assumptions on which we base them, and these assumptions are largely drawn from our knowledge of natural history. The diversity of male parental care types in tropical frogs, cichlids, and wading birds invites further careful study. Equally fascinating on a more fine-grained level, is the variation among pipefish in the degree to which females compete for males as mates (T. Lim, personal communication). Although the ancestral conditions for the situations studied will often have been obscured by subsequent evolutionary events, partial knowledge is clearly preferable to none.

Summary

1. The natural history of and earlier models for the evolution of paternal care and sex role reversal are reviewed.
2. The fate of mutations in females which give males the opportunity to care for the offspring (mutant *vs.* normal), and mutations in males which govern their response to that opportunity (tolerant *vs.* intolerant) are examined with computer simulations.
3. The evolution of modest amounts of male care can be expected to occur regularly when there is no loss in offspring survivorship for matings between mutant females and intolerant males.
4. The evolution of costly forms of male care typically requires the

more stringent conditions of a loss in offspring survivorship for mutant female/intolerant male matings, coupled with a high starting frequency of tolerant males.

5. These results are used to interpret previously documented natural-history patterns, including the associations between paternal care and territoriality, external fertilization, and double clutching.

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Appendix

Outline of computer program

I. Read in values for (1) numbers of mutant females, normal females, tolerant males, intolerant males; (2) the reproductive costs and probabilities of offspring survival for the mutant female/tolerant male, mutant female/intolerant male, and normal female matings; (3) the number of generations to be simulated. The total number of males and the total number of females always equalled 100.

II. Outer loop

  II 1. For each of the four mating types, set the total number achieved to zero.

  II 2. Set numbers of available mutant females, normal females, tolerant males, and intolerant males to their initial values.

  III. Inner loop

    III 1. Calculate the total number of available females and the total number of available males.

    III 2. If the number of available individuals of either sex is less than one, exit from inner loop and go to II3.

    III 3. Calculate the proportion each type represents of its sex (e.g. number of available normal females/total number of available females).

    III 4. Set the number of members of the limiting sex to the number of available males or the number of available females, whichever is smaller.

    III 5. Calculate for this passage through the loop the number of matings of the four types. Do this by multiplying the

proportion of males of a given type by the proportion of females of a given type by the number of members of the limiting sex.

III 6. Recalculate the numbers of the two types of available females and the two types of available males. Do this by subtracting from the current value for each, the product of the number of matings and their cost for each of the two relevant mating types.

III 7. Recalculate the total number of matings of each type achieved by adding to the current number the number achieved in this passage through the loop.

III 8. Return to III 1.

II 3. Calculate for each of the four mating types the number of offspring produced. Do this by multiplying the number achieved by the probability of survival.

II 4. Calculate the total number of offspring produced.

II 5. Recalculate the initial values for the number of mutant females, normal females, tolerant males and intolerant males. For each, (1) add the number of offspring produced from the two types of matings, (2) multiply this sum by 100, (3) divide this product by the total number of offspring produced.

II 6. If the desired number of generations has been reached, stop simulation.

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