

PHYLOGENETICAL CONSTRAINTS IN THE EVOLUTION OF PARENTAL CARE STRATEGIES IN BIRDS

by

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SUMMARY

In species with internal fertilization, but without parental care, an evolution of 'maternal care' is fundamentally different from an evolution of 'paternal care'. Maternal care should be a pure ESS. Paternal care should always be superimposed on a mixed ESS to stay (or not to stay) and to establish some kind of a pair-bond with the female from copulation until egg-laying. This implies that paternal care is less reliable than maternal care. This could have led to the evolution of female strategies and properties which raise the chances for male care.

The above considerations offer a framework for the evolutionary pathways between the various parental care strategies and between their associated mating systems. Both paternal and maternal care might directly evolve towards biparental care. For the evolution from paternal towards biparental care it is more likely, however, that a transitional stage of 'uniparental care' will be passed. That stage is characterized by paternal care in most cases, but by maternal care if the male deserts. It is probable that the biparental care system with similar roles for both sexes evolved along this route. Since such similar role systems are widely distributed among birds, and since monogamous paternal care systems can easily evolve towards all recent mating systems in birds, it is advocated that the evolution of parental care in birds was primarily based on a monogamous paternal care system.

INTRODUCTION

Recent theories on the evolution of avian mating systems emphasize the role of ecological variables (SELANDER, 1965; LACK, 1968; ORIAN, 1969; JENNI, 1974; EMLEN & ORING, 1977; GRAUL *et al.*, 1977; WITTENBERGER, 1979; ORING, 1982). Related theories concerning the evolution of parental investment patterns mainly stress their evolutionary stability (TRIVERS, 1972; DAWKINS & CARLISLE, 1976; MAYNARD SMITH, 1977; GRAFEN & SIBLEY, 1978; PIENKOWSKI & GREENWOOD, 1979). Most authors, however, neglect to consider within which framework of phylogenetical constraints mating systems of birds may have evolved. Yet, such a framework could have a great influence on further thought about evolution. The purpose of this paper is to discuss some basic phylogenetical constraints in the evolu-

tion of parental care strategies in birds, and their consequences for avian mating systems.

Those studies which distantly take up the line of phylogeny of mating systems in birds, generally accept that most or all recent systems have been derived from a monogamous system with shared parental care (*e.g.* JENNI, 1974: 131; EMLÉN & ORING, 1977: 220; KREBS & DAVIES, 1981: 138; ERCKMANN, 1983). This hypothesis is merely based on the physiology of bird reproduction and on the fact that in recent birds the monogamous biparental care system prevails (LACK, 1968). In a number of systematic groups, such as the *Anseriformes* (ducks and geese), this view gives indeed more insight in the process of evolution (KEAR, 1970). In other groups, however, such as the *Charadriiformes* (waders and gulls), this representation is unsatisfactory (VAN RHIJN, *in press*; but see also ERCKMANN, 1983). In fact all recent social systems in waders can be understood to be derived from a primitive system in which the male cared for offspring after the eggs were laid.

A broader theory about the phylogeny of avian parental care and mating systems should incorporate knowledge about the evolution of the class *Aves* and related vertebrates. It is important to note that representatives from the other two amniote classes, either do not perform any parental care after egg-laying (most recent reptiles), or are characterized by a strongly developed maternal care (all recent mammals). The substantial role of males in caring for offspring is typical for birds and not for the other two classes.

Because of their poikilothermy recent reptiles have limited abilities to control the temperature and, hence, the speed of development of their eggs. Consequently the period between egg-fertilization and hatching may be fairly long. This seems to be one of the main factors opposed to the evolution of parental care in most recent reptiles. Nevertheless where egg-predation became an impressive cause of mortality, trends in the direction of egg-guarding (crocodiles) and delayed oviposition, finally resulting in ovoviviparity (some snakes and lizards), became possible. After hatching, however, prolonged parental care is rare among the recent reptiles.

Birds and mammals differ from reptiles by their constant and high body temperature (but see MARX, 1978). In the ancestors of the recent representatives of these two classes such high body temperatures suited parents for a shortening of the development of their embryonic descendants. Consequently the cost of parental care, measured in time, became lower. This could favour the evolution of prolonged parental investment after the formation of an egg. In birds this has resulted in the process of incubation: after laying the eggs are still

warmed by the body heat of the parent (see DRENT, 1975; DRENT & DAAN, 1980 for review). In mammals its consequence was pregnancy: implantation of the embryo in the mother's uterus. The finding that male mammals rarely care for offspring may be related to the long interval between copulation and parturition, which is a suitable condition for the evolution of mate desertion by males (DAWKINS & CARLISLE, 1976). In birds, where the interval between copulation and egg-laying is considerably shorter, the evolution of such trait is less likely.

FEMALE CARE OR MALE CARE?

The evolution of parental care must have been preceded by a stage without prolonged care after egg-laying. For the present argument it is important that this stage existed, but it is unimportant whether it occurred in an early bird, a birdlike reptile or an even earlier reptile. In such species without parental care after egg-laying, but with internal fertilization, females could evolve prolonged parental investment, simply by staying with the eggs. All extra investments would benefit their own offspring. This development could start when females were able to afford the extra investment after egg-laying. The only condition for it was that by prolonged parental care the reproductive success was increased. Let B_u and B_n be the benefits per clutch of uniparental care and no parental care respectively, and C_m , C_e , and C_p the costs per clutch of mate selection, egg-laying, and parental care. If:

$$B_u/B_n > (C_m + C_e + C_p) / (C_m + C_e) \quad (1)$$

then female care will readily spread through the population until all females possess this property.

If parental care is restricted to activities improving survival of eggs or young, then evolution of male care in species without parental care after egg-laying, but with internal fertilization, cannot be understood so easily as the evolution of female care. The male is not necessarily present at the moment of oviposition, because it occurs a certain amount of time after copulation. Yet, just as in females, the evolution of male care also requires a positive relation between the tendency to care and reproductive success. Two possibilities for the establishment of this positive relationship will be discussed. First, females might select caring males for copulation, which does not necessarily imply that these males care for their own offspring. Second, males might stay with the eggs of their copulation partners, provided that the extra investments after copulation benefit their own offspring or relatives.

The first possibility, evolution of male care by female preference, could only have taken place if females were able to make reliable

judgements about the male's caring qualities. For that purpose a female could follow three different strategies: first she might repeatedly check the male's caring efforts, second she might rely on the result of the male's previous investments (e.g. the number of surviving young), or third she might assess the care given to her by prospective mates. This third strategy can be brought in relation with the evolution of courtship feeding (LACK, 1940; KREBS, 1970; NISBET, 1973, 1977; NIEBUHR, 1981). These three different strategies all pose complicated assessment problems to the females. Therefore it is likely that such strategies did not easily arise during evolution. On the other hand, once they did originate they could easily be consolidated by the accidental circumstance that in many cases the investment of the male after that he had been selected as a copulation partner did benefit his own offspring.

The second possibility, evolution of male care through the male's propensity to stay with the eggs of his mate, could be initiated only when copulation partners already tended to accompany each other until egg-laying. Why should male and female stay together during that period? For the male it could pay to guard his copulation partner if females would accept succeeding copulations by other males (TRIVERS, 1972; PARKER, 1974; MCKINNEY *et al.*, 1983b). Mate guarding may ensure that the eggs will be fertilized by the male's own sperm (BEECHER & BEECHER, 1979; BIRKHEAD, 1979, 1982; ZENONE *et al.*, 1979; FUJIOKA & YAMAGISHI, 1981; POWER *et al.*, 1981; LUMPKIN *et al.*, 1982). For the female it could pay to stay with her copulation partner if males possessed territories (RIDLEY, 1978) with indispensable resources for the female. In an earlier stage of evolution the establishment of such territories could give selective advantages for males because it improved female attraction.

PURE AND MIXED STRATEGIES

While conditions for the evolution of female care could easily be mathematically formulated, such representation of the conditions for the development of male care is far more complex. This is due to the fact that the most profitable strategy for a male seems to depend on the strategies adopted by the other males. If a male could obtain more copulations by defending resources for females, then, the first male who developed this property would have only small costs. However, the more males possess this property of territory defence, the higher the costs to defend a similar portion of female resources because of increased inter-male competition, and the less profitable it will be to adopt the same strategy. Similarly, if a male could secure his paternity

by guarding the female inseminated with his sperm, then, the first male who developed this property should have high benefits, because many other males can be held away from the female. However, the more males are guarding, the less males are trying to copulate with unguarded females. Hence, the benefits of guarding decreases with the number of guarding males. While the costs of guarding in units of time remains similar, the profitability of guarding decreases as it spreads through a population.

Male strategies which result in an association between male and female in the period from copulation up to egg-laying, may thus only occur in combination with strategies which do not result in such an association. They may then be considered as mixed ESSs or perhaps in some cases as sets of pure conditional strategies (MAYNARD SMITH, 1974, 1979, 1982; MAYNARD SMITH & PARKER, 1976; PARKER, 1978; DAWKINS, 1980). The most important consequence for females of such frequency dependent pay-offs for males, is that at the time of egg-laying some of them would be attended by males, while others would be unattended. The evolution of male care must be influenced by this phenomenon because the incidence of male care is unlikely in the case where a female was unattended by a male between copulation and egg-laying.

It has been noticed already that under certain conditions female care will readily spread through a population until all females possess this property. Consequently female care may be considered as a pure ESS. Similarly, male care would also readily spread through a population of males which are present at the time of egg-laying if:

$$B_u/B_n > (C_m + C_f + C_p) / (C_m + C_f) \quad (2)$$

in which C_f is the cost per clutch of fertilization, while the other parameters are explained in connection with expression (1). However, since the primary condition to stay with the female until egg-laying can not be considered as a pure ESS, one should expect that male care will not spread as readily as female care through a population. The incidence of male care might be viewed as a conditional strategy: care if still present when female lays eggs and if expression (2) is fulfilled. It may also be viewed as a component of a complex mixed ESS: desert after copulation, or stay with female and care for offspring. I want to stress that this mixed strategy is not equivalent to the 'mixed strategy' mentioned by TRIVERS (1972: 145) and quoted by MCKINNEY *et al.* (1983b). The latter strategy implies that each male stays with one single female and cares for their joint offspring, but additionally uses the opportunities to mate (but not to care) with other females. In fact TRIVERS refers to a set of conditional strategies.

FEMALE STRATEGIES TO SECURE MALE PARENTAL CARE

If care by one parent results in a higher reproductive success than no parental care, but the female would be unable to care, or if biparental care would result in a higher reproductive success than care by the female alone, then, the female should develop properties or should adopt strategies to enlarge the probability that the male will be present at the time of egg-laying. There are several properties and strategies of female birds which may be considered from this point of view.

I want to consider the development of the male's propensity to stay with the female from copulation up to egg-laying as one of the main steps in the evolution of male parental care in birds. This development could be possible only under conditions where the pay-off to a male when staying was higher than the pay-off when deserting and resuming courtship with other females. This implies that the male's costs required to stay should not be too high in comparison with his costs required for a successful copulation with another female after deserting the first. The duration of the period between copulation and egg-laying is a factor influencing these costs, and could therefore be limiting in the evolution of male care. It is very likely that this interval is limiting in some reptiles, which may copulate several months before they lay eggs. For the female such long periods of fertility after one copulation offer the advantage of reserving the most suitable circumstances for each of two different actions: mate-selection and egg-production, which might counterbalance the disadvantage of no male care. In birds the interval between copulation and egg-laying is considerably shorter. It rarely lasts longer than ten days, although in some species longer periods have been reported (*e.g.* LAKE, 1975; MCKINNEY *et al.*, 1983b; HATCH, 1983). One might conclude now, that preceding the evolution of male parental care, females should have evolved the property of accepting copulations only shortly before egg-laying and females should not store and maintain viable sperm for long periods. However, a shortening of the period of sperm viability might lower the proportion of fertilized eggs.

A second possibility for raising the pay-off to a male when staying with the female, relative to the pay-off when deserting and resuming courtship, would be to increase the male's costs required for copulation. If all females would accept copulation only after a long period of courtship by the male, then, mate desertion would not be a very profitable strategy to males. However, such a long period of precopulatory courtship might also impose costs on the female. Her reproductive cycle would last longer, and consequently, her lifetime production of eggs might decrease. Hence, it is difficult to imagine

how this trait could have evolved, unless the costs were counterbalanced by particular benefits. Such benefits could arise from opportunities during courtship for females to select the best available mate (see TRIVERS, 1972; BURLEY, 1977, 1981b).

A long period of precopulatory courtship might entail other disadvantages. Males and females that lose partners near the end of the mating season would probably copulate too late with a new partner for a successful breeding attempt. Thus, in the end of the season courtship periods may become shorter. This is not necessarily associated with a decrease in the tendency of males to care for offspring, because at the end of the season desertion offers almost no opportunities for successful copulations with other females. A long precopulatory courtship period may also be a waste of time because it cannot give much information about the likelihood that both partners are able to cooperate for the difficult copulation act. Finally, in those species where male success may be strongly influenced by forced extra pair copulations (GLADSTONE, 1979; MCKINNEY *et al.*, 1983a), male sexual competence may be an important property for the female to evaluate in an early stage of the courtship, because it may influence the fitness of her sons. Thus, there may be selection pressures promoting the occurrence of copulations, and in some cases also the transfer of sperm, from the beginning of the courtship season. However, it is unlikely that the occurrence of ovulations in the female will be affected by the same factors. Early copulations may thus not be interpreted as fertilizations. This distinction between copulation and fertilization may be an ultimate factor for males to stay with the female. In fact the female holds all the trumps. She determines the moment of ovulation. The male might be unable to detect it until she is laying her first egg. Since the next ovulation occurs shortly after egg-laying (STURKIE, 1976), the best strategy for the male is to copulate and to guard his mate now. Again it is the female who determines the number of eggs. The male might be unable to detect whether the female is laying her last egg. Consequently, the female may be able to desert her mate when the male is still expecting the following egg. By this sequence of events the male could be brought into a situation in which male parental care is the best strategy for future reproductive success.

A final possibility for females to secure male parental care is appropriate only for species with short breeding seasons, in which a female can normally lay only one clutch of eggs and a male or a pair can normally raise only one brood of young. If the females of those species synchronize their reproductive efforts, then, males should not desert their mates, because usually they will be too late for successful copulations with other females. It is not difficult to imagine how this

reproductive synchrony could arise during evolution. Any female who postponed ovulation until the end of the mating season would increase the probability of male parental care for her offspring. When the survival of such offspring became higher in comparison with chicks which were not tended by males, an evolutionary trend towards synchronized breeding close to the end of the season could be established. Reproductive synchrony has been described for a large number of bird species which mainly breed in colonies. Its functional significance has been interpreted in relation to predation and the availability of food (DARLING, 1938; KRUUK, 1964; EMLLEN & DEMONG, 1975; VEEN, 1977; GOCHFELD, 1980). This additional idea of reproductive synchrony, as a female strategy for selecting males which care for offspring, predicts a peak of reproductive activities just after the most suitable ecological conditions. This should be a reason for a re-examination of data on reproductive synchrony.

WHICH EVOLUTIONARY PATHWAYS ARE POSSIBLE?

On the basis of the above considerations the alternative pathways may be indicated along which parental care and related social systems could have been evolved in birds (fig. 1). Each step in the diagram refers to either the development of a simple character based on elementary mutations (solid lines, black arrows), or the loss of such characters (solid lines, open arrows), or the loss of a complex character (broken lines, open arrows) which may be considered as an 'irreversible' step in the evolution. In this paper irreversibility only implies that the initial stage cannot be reached through the same pathway vice versa, but it does not exclude that the initial stage may be reached again through a longer pathway. A wider application of the concept 'irreversibility' goes beyond the scope of this study. It may be noticed, however, that for many pathways the alternative directions do not seem to be equally likely. One might question, for instance, whether an evolution towards a decrease of parental care per offspring is very realistic.

No Care at All

In the primitive case of 'no parental care' (the box in the upper left corner) at least three different types of mating systems can be distinguished. A promiscuous system may evolve towards monogamy (1) when it pays for a male to guard the female inseminated by him until egg-laying. However, as pointed out above, such monogamous system can never become a pure *ess*. Consequently promiscuous

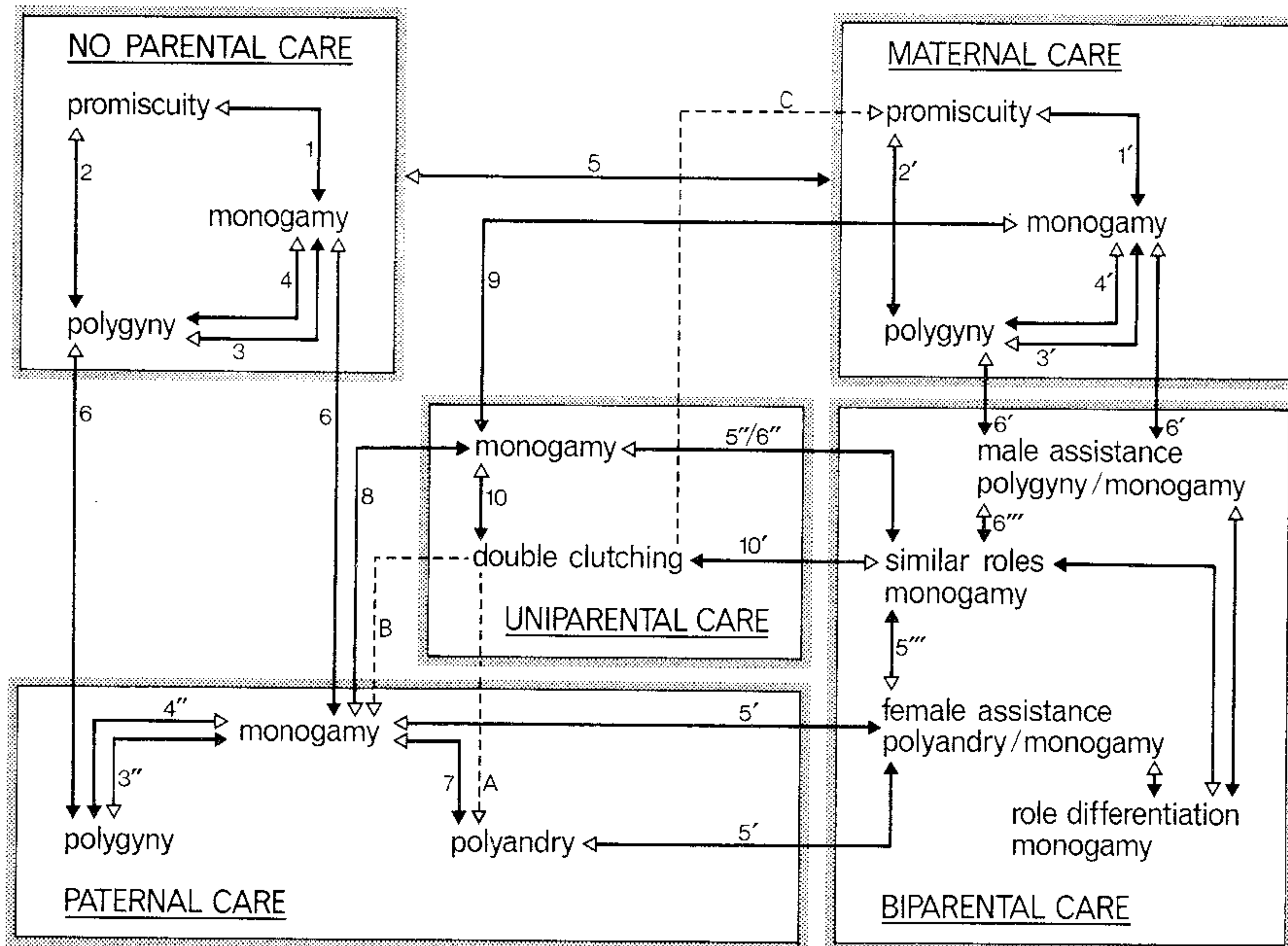


Fig. 1. Evolutionary pathways between the various parental care strategies, represented as five boxes: and their associated mating systems. *Solid line with black arrow*: development of a simple character (elementary mutations). *Solid line with open arrow*: loss of much simple character. *Broken line with open arrow*: loss of a complex character (irreversible step). 1-1': male stays with female until egg-laying. 2-2': female stays in male's territory. 3-3'': female intolerant towards other females. 4-4'': male defends females or female resources. 5-5''': female stays with eggs. 6-6'': male stays with egg. 7: female defends males or male resources. 8: female stays with eggs if male deserts or dies. 9: male stays with eggs if female dies (or deserts). 10-10': female continues with a new cycle. A: female loses ability to care for a clutch, but develops ability to defend males or male resources (irreversible). B: female loses abilities to lay successive clutches and to care for a clutch of eggs (irreversible). C: female loses ability to lay successive clutches and male loses ability to care for a clutch of eggs (irreversible).

matings will continue to occur. Conversely such monogamous systems may change to complete promiscuity when it does not pay any longer for males to guard. If a male would be able to attract females by defending a territory with female resources, the promiscuous system may also evolve towards polygyny (2) when it pays for females to stay in such territories. Again the defence of these territories must be considered as part of a mixed ESS. When staying in a territory no longer pays for females the polygynous mating system may revert to promiscuity. Monogamous and polygynous systems may also directly

change into each other. When it pays for a female to become intolerant towards other females visiting the same male territory, polygyny may evolve towards monogamy (3), so that all resources in a particular territory become available for only one female. When it pays for a guarding male to defend more females or to defend female resources, monogamy may evolve towards polygyny (4).

Care by Only One Sex

The evolution of 'maternal care' (the box in the upper right corner) from a stage without parental care requires only that it pays for a female to stay with the eggs and to proceed after egg-laying with parental care (5). On the other hand, maternal care may revert to no parental care when it no longer pays females to stay with the eggs. Since the female must always be present during egg-laying, maternal care may evolve from the complete set of social systems which are possible in the primitive case of no parental care. The same set (viz. monogamy, polygyny and promiscuity) is applicable to maternal care and their mutual derivations are also similar (1'-4').

The evolution of 'paternal care' (the box in the lower left corner) from a stage without parental care requires that it pays for a male to stay with the eggs and to engage in parental care (6). On the other hand, paternal care may revert to no paternal care when it no longer pays males to stay with the eggs. Since the male may accompany his egg-laying mate in a limited number of social systems, paternal care could evolve only from monogamous or polygynous social systems without parental care. In the case of paternal care at least three different types of mating systems can be distinguished. Two of them (viz. monogamy and polygyny) can be derived from each other in the same way as in the cases of no parental care and maternal care (3"-4"). Paternal care may also be characterized by the occurrence of polyandry. This social system may evolve from monogamy when it pays for the female to defend males or a territory with male resources (7).

Care by One Parent, Both Sexes Able to Care

When either maternal or paternal care became established, conditions had been created potentially favouring the production of eggs unable to develop without parental care. The only disadvantage of this evolutionary step was that there was no survival of the clutches which were by some reason not tended by an adult. The caring adult could disappear because it died or deserted its mate or clutch. Mortality among adults during the laying season may be substantial because reproduc-

tion makes high demands on the birds. It may occur in both sexes. Desertion should be mainly confined to males because their property to stay with eggs was superimposed on a mixed ESS to stay with the female up to egg-laying, while the property of females to stay with eggs should be considered as a pure ESS. It may thus be suggested that the probability of disappearance by the caring adult is higher in species with paternal care than in species in which the mother cares.

If the probability of disappearance by the caring sex is high, it could pay for the non-caring sex to stay with the eggs if its partner died or deserted. Consequently a monogamous 'uniparental care' system (central box) can be derived from the monogamous paternal care system (8) and from the monogamous maternal care system (9). The first derivation leads to a system in which in most cases the male cares, but in some cases the female if the male disappears. The second derivation leads to a system in which in most cases the female cares, but in some cases the male if the female disappears. Because the probability of disappearance of the male is highest, the first derivation is most likely. When food conditions are good, the system in which mainly males are caring may further evolve towards a 'double clutch' system in which the male usually cares for the first clutch and the female produces a second clutch which will mostly be cared by herself because most males are already engaged in the care for a nest (10).

The double clutch system, which may be found in some *Galliformes* and *Charadriiformes* (see ORING, 1982 for review), is possibly characterized by a unique combination of features. First of all females lay several clutches in quick succession (PARMELEE & PAYNE, 1973; HILDÉN, 1975) and, second, it has been suggested that the criteria for selecting a mate by the female may be different between the successive clutches (VAN RHIJN, *in press*). For the first clutch a male with good parental qualities seems to be the best choice for a female; for the second clutch the female should prefer superior males in inter-male competition, who may be expected to possess good genes. This combination of features of the double clutch system opens a large number of possible directions for further evolution. The ability to lay several clutches may develop in combination with a new characteristic of the female, namely the defence of males or male resources. This may result in a polyandrous system with paternal care (A). Since such processes will also be associated with the loss of a character, namely the ability of the female to care for a clutch of eggs, it may be considered as an irreversible step. There are at least two other irreversible trends which can also be derived from the double clutch system when ecological conditions permit only one clutch per female per season. The first trend refers to a consolidation of the first clutch of the original

system, resulting in a monogamous system with paternal care (B). The ability of the female to care for a clutch of eggs will become lost, just as in step A. The second trend refers to a consolidation of the last clutch of the original system, resulting in a promiscuous system with maternal care and strong inter-male competition (C). In this case the ability of the male to care for a clutch of eggs will become lost.

Origin of Care by Both Parents

If maternal, or paternal, or uniparental care becomes established, it could pay for the non-caring parent also to stay with the eggs. Incubation may make high demands on one parent because, with low and moderate ambient temperatures, it can not leave the clutch alone for a long period. Owing to this, the single parent may be unable to collect food for itself. The help of the other parent could reduce the probability of nest desertion under stressful conditions. Similarly, when young, during their first weeks of life, are unable to collect their own food, two adults may raise more offspring than only one adult.

Biparental care in birds could have evolved from various directions. Both monogamous and polygynous maternal care systems may evolve towards a situation in which the male assists the female when it pays for the male also to stay with the eggs (6'). Similarly, monogamous and polyandrous paternal care systems may evolve towards a situation in which the female assists the male when it pays for the female also to stay with the eggs (5'). The monogamous uniparental care system may evolve towards a biparental care system with similar roles for both sexes when it pays for each sex to stay with the eggs irrespective of the presence of the other sex (5"/6"). A biparental care system with similar roles may also arise from the double clutch system when it becomes more profitable for the parents to care together for only one clutch of eggs than to tend one clutch each, in spite of a 50% decrease of the number of offspring. This last development will be associated with the loss of the ability to lay more clutches in a quick succession. The reversed trend for a similar role biparental care system towards the double clutch system (10') may occur when it is more profitable for the parents to tend one clutch each than to care together for only one clutch of eggs, because of a 100% increase of the number of offspring. The appropriate scheme for this development has been described by PIENKOWSKI & GREENWOOD (1979).

Further Evolution of Care by Both Parents

The great majority of recent bird species are monogamous, and both parents to some extent care for their joint offspring after egg-laying.

Yet, in a few monogamous species, among which are several ducks (KEAR, 1970), the pair separates immediately after egg-laying and the female cares alone for the offspring. In species expressing resource-defence polygyny (EMLEN & ORING, 1977) the role of males in parental care is always smallest, but may vary considerably (ORING, 1982). In species with male-dominance polygyny and with a high degree of promiscuity, male care is generally thought to be absent, although certain behaviour patterns of the males may sometimes be interpreted as contributing to the survival of the offspring (*e.g.*, FEEKES, 1982). In species with role reversal between the sexes, among them several polyandrous species, the female may fulfill a non-negligible role in the care for offspring (JENNI & BETTS, 1978; MAXSON & ORING, 1980). Yet, in many ratite birds, in which sequential polyandry is combined with a harem-defence polygyny, the incidence of parental care seems to be restricted to males (*e.g.*, BRUNING, 1974).

It is generally believed that most or all recent mating systems in birds have been derived from a monogamous system with shared parental care. The present paper proposes alternative routes. To compare the likelihoods of these different possibilities, more understanding is needed about the evolutionary pathways among the various biparental care systems. To obtain more insight a distinction will be made between systems in which the disappearance of one parent after egg-laying is not necessarily associated with the complete loss of a clutch, and systems in which one parent is unable to raise any offspring. The word system may be used here for the whole parental care period of a particular species, but also for a restricted phase within that period, such as incubation.

Those biparental care systems in which one parent is able to raise some offspring may evolve towards a system with similar roles by both parents. This trend is most likely when the number of offspring which can be raised by one parent is not much lower than in the case of two parents and when the probability of disappearance of a parent (*e.g.* by predation) is considerable. Thus, both a maternal care system with male assistance and a paternal care system with female assistance may evolve towards a biparental care system with similar roles (fig. 1:5'' and 6'').

Those biparental care systems in which one parent is unable to raise any offspring may evolve towards a system with role differentiation between the sexes, such as found in many raptors (*e.g.*, NEWTON, 1979). The rationale behind this evolutionary trend bears on the economical consideration that two parents specializing on different sets of tasks from the whole set to be done during the parental care period may spend less effort for the same result, or reach a better result

with the same effort, than two parents which equally share the whole set of tasks. This trend implies that each sex may improve its performance of particular tasks if the other sex is less suited to do so. Conversely, each sex may lose the ability to perform particular tasks which are required for the survival of the offspring, if the other sex is better suited for these tasks. Thus, again both a maternal care system with male assistance and a paternal care system with female assistance may evolve towards a biparental care system with role differentiation. Additionally, a biparental care system with similar roles may also evolve towards a biparental care system with role differentiation. The roots for role differentiation between sexes may be detected across the various evolutionary lineages. Asymmetries between sexes clearly exist in the maternal care system with male assistance and in the paternal care system with female assistance. In the biparental care system with similar roles asymmetries may be associated with egg-laying by females, postcopulatory mate guarding and territorial behaviour by males, and the mixed ESS basis for male parental care.

Finally, it may be questioned to what extent the different routes are reversible. A biparental care system with similar roles may evolve towards systems with either male or female assistance when the probability of disappearance becomes different for the two sexes. The sex most likely to be present should develop the most elaborate parental care behaviour. Trends from biparental care systems with role differentiation towards systems with male or female assistance may occur when less parental care is needed for a similar number of surviving descendants, or when an equally shared quantity of parental care becomes unequally shared between sexes because of an asymmetry in the quality of parental care. A direct trend from a biparental care system with role differentiation towards a biparental care system with similar roles does not seem to be very likely because this development must be associated with increased efforts by both sexes or with reduced results (economy argument). Under certain conditions, however, it might pay for both sexes to conceal sexual identity (BURLEY, 1981a; VAN RHIJN, *ms*). It is conceivable that such conditions may also lead to the evolution of similar parental roles of both sexes.

WHICH EVOLUTIONARY PATHWAYS ARE MOST LIKELY?

This paper offers a comprehensive, perhaps still incomplete set of possibilities for the evolution of parental care in birds. It is plausible that parental care systems in different unrelated recent bird species may have evolved along strongly differing evolutionary pathways. It is also plausible, however, that for most or all recent bird species the in-

initial steps in the evolution of parental care were similar. It is generally believed that these common initial steps have led to a monogamous system with shared parental care. It can indeed be deduced from figure 1 that theoretically all conceivable social systems in birds can be derived from such biparental care system with similar roles. It may be questioned, however, whether this is the most probable solution. This concluding section is intended to speculate about the likelihoods of different possibilities for common initial steps in the evolution of parental care and mating systems in birds.

In recent birds biparental care with similar or almost similar roles is one of the most frequently practised systems. It occurs in many nidifugous species, such as sandpipers (PITELKA *et al.*, 1974) and plovers (WALTERS, 1982), in which one parent might be able to raise some offspring when the other disappears (but see ERCKMANN, 1983). It also occurs in seminidicolous species, such as gulls (HUNT, 1980), and in many nidicolous species, in which one parent is rarely able to raise any offspring. In fact biparental care with similar roles occupies a central position among the various parental care systems. It may therefore be helpful to determine the most probable route for the evolution of that system.

It has been mentioned already that a 'similar role' system can be derived from each of the other three biparental care systems, but that the derivation from a system with role differentiation is not very likely (economy argument) unless it pays to conceal sexual identity. Derivations from the system with male or female assistance are possible if one parent is able to raise at least some offspring when the other disappears, and if the probability of disappearance of a parent is fairly high but independent of sex. This last condition, the probability of disappearance of a parent being independent of sex, seems to be very hard to reach. It has been pointed out that the tendency of females to stay with and care for their eggs may be a pure ESS. The tendency of males to stay with eggs, however, seems to be superimposed on a mixed ESS to stay (or not to stay) with the female after copulation. Consequently, the probability that males stay with eggs will mostly be smaller than the probability that females stay with eggs. Similarly, in a biparental care system with male assistance the probability that a female will be assisted by her mate will mostly be smaller than the probability that a male will be assisted by his mate in a biparental care system with female assistance. The derivation of a similar role biparental care system from a system with male assistance seems to be unlikely for that reason. Derivation from a system with female assistance is more likely, unless female mortality after egg-laying is high. The likelihood that this route represents the origin of a similar role biparental care system

is related to the chances for an evolution of a system with female assistance from exclusively paternal care systems.

A 'similar role' system can also be derived from uniparental care systems, double clutching included. For such evolutionary step it must pay for each sex to stay with the eggs irrespective of the presence of the other sex. This condition is not unlikely because an increase of predation, food shortage, or extreme ambient temperatures may require the attendance of the two parents in order to maintain the same reproductive success. Consequently, the route from uniparental care towards a similar role system may also be considered as a serious candidate for the origin of that system.

To weigh the likelihoods of the two remaining possibilities against each other, namely the biparental care system with female assistance versus the uniparental care system, their origins must be further examined. The uniparental care system could be derived from monogamous maternal and monogamous paternal care systems. It has been discussed already that the derivation from a paternal care system is most likely. The biparental care system with female assistance can be derived only from the paternal care systems with monogamy and polyandry. Since the polyandrous paternal care system must also be derived from the monogamous one, the monogamous paternal care system might occupy a key-position in the phylogeny of parental care in birds. That system can be derived from a monogamous system without paternal care but with postcopulatory mate-guarding by the male. It can also be derived from a polygynous paternal care system. Since the origin of paternal care seems to be less complex in a monogamous relation than in a polygynous relation, the monogamous paternal care system must be considered as the most likely candidate for the common ancestral parental care system in birds. Since parental care is based on a mixed ESS, a monogamous paternal care system does not ensure that all clutches to be laid will be actually tended. For that reason an evolutionary trend towards uniparental care seems to be more likely than a trend towards biparental care with female assistance.

To summarize, the various parental care systems in recent birds seem to have evolved from a monogamous paternal care system, which originated after a stage of postcopulatory mate-guarding by the male. It is possible (and, building on that starting point, certainly the most parsimonious solution) that polygynous paternal care systems, such as in many ratite birds, evolved directly from this primitive state. Monogamous paternal care systems, such as found in a few orders of birds (*Galliformes*: megapodes; *Charadriiformes*: phalaropes) might represent fairly unchanged strategies with respect to the common

ancestral system. Uniparental care systems, such as found in the same orders (*Galliformes*: some partridges; *Charadriiformes*: some sandpipers and plovers) may be considered as transitional stages to biparental care systems. Finally, the maternal care system may have evolved from uniparental care in some species (particularly from double clutching: some or all female caring *Galliformes* and *Charadriiformes*), while in the other species it is more likely that the biparental care system with male assistance is its ancestral state (all female caring *Anseriformes* and *Passeriformes*).

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