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UNIDIRECTIONALITY IN THE PHYLOGENY OF SOCIAL ORGANIZATION, WITH SPECIAL REFERENCE TO BIRDS

by

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(With 2 Figures)
(Acc. 5-II-1990)

Introduction

In a number of papers (van RHIJN, 1984, 1985, 1991, in press) I have argued that pure male parental care is probably the ancestral parental care pattern in birds. This seems to be contradictory to the finding that pure male parental care is extremely rare in recent birds, and absent in most families. Yet such a finding cannot be used as proof against the view of male parental care as a primitive condition. The reason for this is that primitive characters may get lost in the course of evolution. For instance, adult mammals, birds, and reptiles have no gills, although their foetuses do possess them, and their early ancestors had gills during their whole life cycle. As soon as these ancestors left the water they had to evolve lungs. By that time their gills became useless. A secondary return to the water, such as in turtles, penguins, auks, and whales, has in no case led to the maintenance of gills in adult individuals. This may be related to the continuing partial dependence on landlife present in most of these groups (sea-turtles, all birds, and seals). This factor, however, can hardly be considered as a cause of their inability to develop gills in adult individuals, but mainly as a consequence of it. A main cause of the con-

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tinuation of lung respiration is their very high demand for oxygen (to an extent that cannot be supplied by gills) to maintain their increased metabolism (*e.g.* SCHMIDT-NIELSEN, 1975). Thus the transition from gills towards lungs seems to be possible because it creates new perspectives for the animal, but a transition in the opposite direction seems to be very unlikely because it severely restricts several of the animal's potentialities.

The phenomenon that certain evolutionary processes tend to proceed in one direction, but not (or very rarely) in the opposite one, has been recognized by a large number of investigators (*e.g.* RENSCH, 1947; SIMPSON, 1953; ELDREDGE & GOULD, 1972; GOULD & ELDREDGE, 1977; MAYNARD SMITH *et al.*, 1985). Its importance in the evolution of morphological and physiological traits is widely accepted, but in the study of the evolution of behavioural properties this possibility is generally ignored. Only a small number of modest attempts have been made to consider it (*e.g.* GITTLEMAN, 1981; RIDLEY, 1983).

In this article I want to present arguments for the importance of unidirectionality in the evolution of behavioural traits, especially in the evolution of parental care and social organization. I shall develop my hypotheses from the diversity in social organization in waders and related groups (order Charadriiformes) and on the basis of earlier theoretical work. To test these hypotheses I shall consider whether they are compatible with the existing ideas about phylogenetic relations between various taxa of arctic sandpipers (subfamily Calidridinae), waders and related groups, and birds in general.

Diversity among Charadriiformes

A review of the diversity of social systems is presented in Table 1. In most species monogamous pair-bonds are established, usually associated with biparental care of the offspring. In many of these monogamous species the male performs most care after hatching of the eggs, in some species from the start of incubation onwards. In a few species sex-roles are completely reversed. In a few others the female typically produces two clutches of eggs, of which the first one is incubated and cared for by the male, and the second by the female (double clutching). In several waders social relationships between males and females are even more complex. Polyandrous relationships are fairly common, especially among species with sex-role reversal. Polygynous relationships also seem to occur in some species. Promiscuous relationships have been found in only a few species of waders. In some of the latter species males display lek behaviour.

TABLE 1. Social organization in recent Charadriiformes

(sub)family		num	mon	dcl	srr	pan	pgy	pmc	lek
Alcidea	auks	22	us						
Dromadidae	crabplovers	1	pr						
Stercorariidae	skuas	4	us						
Rhynchopidae	skimmers	3	us						
Laridae	gulls	82	us				oc	oc	
Chionididae	sheathbills	2	us						
Thinocoridae	seedsnipes	4	pr				pr		
Burhinidae	thick-knees	9	us						
Haematopodidae	oystercatchers	6	us						
Recurvirostridae	avocets	7	us						
Glareolidae	pratincoles	17	us						
Vanellidae	lapwings	24	us				oc		
Charadriidae	plovers	40	us	≥1	≥2	≥2	oc		
Jacanidae	jacanas	8	1?		us	us			
Rostratulidae	painted snipes	2	1?		1	1			
Scolopacidae	sandpipers	84	us	≥3	≥4	≥3	±5	±5	≥3
Calidridinae	arctic sandpip.	24	us	≥3	tt	oc	±2	±4	≥2
Gallinagininae	snipes, etc.	18	us				1?	≥1	≥1
Scolopacinae	woodstocks	6					pr		
Tringinae	godwits, etc.	31	us		≥1	≥1	oc		
Arenariinae	turnstones	2	us						
Phalaropodinae	phalaropes	3	us		3	≥2			

Key: num = number of species in family, mon = monogamy, dcl = double clutching, srr = sex-role reversal, pan = polyandry, pgy = polygyny, pmc = promiscuity, lek = lekking, us = usual pattern in most species, pr = pehaps usual in these species, tt = many species tend towards it, oc = occasionally in one or a few species. Numbers refer to number of species which usually display the type of social organization indicated.

Classification according to CRACRAFT (1981). Details on social organization after VAN TYNE & BERGER (1975), RIDLEY (1978), ORING (1982, 1986), CRAMP & SIMMONS (1983), JEHL & MURRAY (1986).

I wondered why the variety among waders is much greater than among most other groups of mutually related species. Two possibilities may be considered. Firstly, during the evolution of this group, selective forces might have been highly variable. This possibility is not unlikely, since the ancestral representatives of this group had to invade cold and very cold breeding areas during their evolution. A further investigation of this possibility, however, is almost impossible by the lack of sufficient biogeographic and climatic data from the past (but see LARSON, 1957). The second possibility, which may be analysed in more detail, implies that the common ancestor of this group might have displayed a very primitive type of social organization with the potential for evolving many types of derived patterns. In contrast, the common ancestors of most other groups would have derived types of social organization with fewer options for further specialization. I want to stress that this implies that certain types of social organization can easily be modified by natural selection (low phylogenetic inertia), whereas other types can hardly be modified (high inertia; see also Wilson, 1975). Thus, species of the former types can readily adapt to changing environmental conditions, but species in the second category may be doomed to extinction after environmental changes. Species with a large variety of properties which can easily be re-arranged to new combinations, represent the former types. Species with a limited array of properties, and which have to evolve combinations of new traits to survive environmental change, represent the latter types. I shall try to explain this with the help of some examples.

The most common monogamous system includes female parental care, male parental care, and the ability to establish a pair-bond. If the environment were to change in such a way that one parent became able to combine full incubation duties with foraging for its own needs, the species could evolve a pure male-care system or a pure female-care system, with or without competition among the members of the non-caring sex. Thus, monogamous biparental care systems seem to leave a considerable number of options for future evolution.

The double clutch system, such as displayed by Temminck's stint *Calidris temminckii* (*e.g.* Breiehagen, 1989), includes female parental care, male parental care, the ability to care alone for a clutch, elements of monogamy during a short-lasting pair-bond until completion of the first clutch, and elements of promiscuity preceding to the second clutch. If the environment were to change in such a way that the parent became unable to combine full incubation duties with foraging for self-maintenance, the species could readily evolve a system with biparental care. If the environment no longer allowed the production of two clutches of eggs, the species could evolve a pure male-care system, or a pure-female care system with competition among males for mates (polygyny, promiscuity, or lekking). If, on the other hand, the environment did allow the production of more than two clutches, the species could evolve a pure male parental care system with competition among females for mates (polyandry). Double clutching therefore seems to leave a very large number of options for future evolution.

The lekking system, such as displayed by the ruff *Philomachus pugnax* (*e.g.* van Rhijn, 1991) includes the ability of the female parent to combine full incubation duties with foraging for her own needs, but no clear ability to establish a lasting bond with a member of the other sex. If the environment of this species changed in such a way that the female parent became unable to combine full incubation duties with self-maintenance, the species could not readily evolve a monogamous system with biparental incubation, because this requires that at least two new traits evolve: the establishement of a pair-bond and of male parental care. The species would probably be doomed to extinction. If the environment made the production of more than one clutch possible, the species again could not adequately react to such a change, and would possibly lose out in competition with other species. Consequently, lekking systems seem to be highly derived, leaving almost no other options for future evolution.

In view of these examples, it is highly improbable that the social system of the common ancestor of the waders was something like a lekking system. It is more likely that it resembled (but was not necessarily identical to) the monogamous biparental care system, or even the double clutching system. The latter two might be considered as transitional states from the primitive pattern of parental care in waders and other birds to the more extreme derived patterns in some recent shorebirds.

Phylogenetic pathways

Fig. 1 summarizes the most probable pathways for the evolution of parental care and social organization in waders and related groups emerging from my analysis (see also van RHIJN, 1984, 1991, in press). From an initial stage with pure male parental care (see also ELZANOWSKI, 1985) and a short lasting pair-bond (mate guarding), the lineage towards modern wader birds first evolved a uniparental care system, in which the male usually cared, but the female took over all parental duties in case of desertion by her mate.

Pure male parental care may be considered as an essential step in the evolutionary pathway to a stage in which male and female use the same set of parental abilities: both participating in the incubation of eggs, distraction of predators, brooding of chicks and tending them to the suitable feeding grounds. Biparental care with similar roles and double clutching represent such a stage. The reason why pure male parental care (and not pure female parental care) is so important in this evolutionary pathway in internally fertilizing species, is that male parental care is not fully reliable and thus necessitates subsequent evolutionary steps. The male parent has the opportunity to desert his mate and offspring before

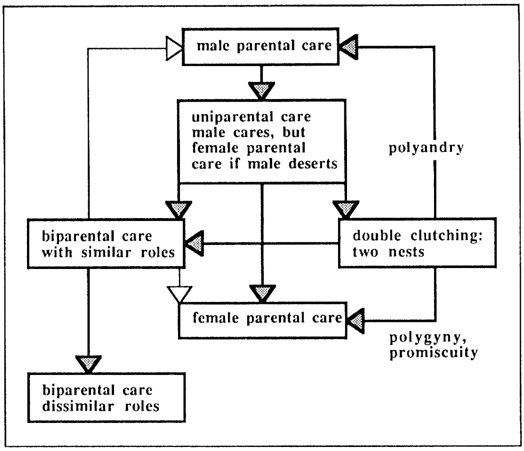

Fig. 1. Probable pathways in the evolution of parental care and social organization in waders and related groups. Grey arrows: high probability transitions. Blank arrows: low probability transitions.

laying, because he does not need to be present when and where the eggs are laid (see Maynard Smith, 1977). In contrast, the female is not able to desert her offspring before laying. Thus, male parental care has to evolve via a stage of mate guarding. This guarding behaviour may be profitable if the minority of the males in a population perform this strategy, but is, under a wide variety of natural conditions, not to the advantage of the male if the majority of the males in the population perform it (van Rhijn, 1984, in press). Thus, it may be adaptive to evolve female parental care to replace male parental care in case of desertion, but there seems to be no logical basis for the alternative: an evolution of male parental care to replace female parental care. It is also unlikely that an asymmetric stage of pure female parental care (role differentiation) evolves to a stage in which both parents stay with the offspring and the male acquires the same set of parental abilities as the female (uniformity of roles).

As soon as female parental care evolved from a stage of pure male parental care, the ability of the male to care alone for his offspring was easily lost. The most important factor for such easy loss is probably the delicate equilibrium between guarding and non-guarding strategies in males. Male parental care does not seem to be very stable in evolution, but female parental care is!

The uniparental care system includes male care or female care if the male deserts (both parents use the same set of parental abilities), and mate guarding (preceding to male parental care). This guarding behaviour may be considered as the beginning of a long-lasting pair-bond. Uniparental care can easily evolve in three directions. Firstly, it may gradually change into biparental care with similar roles, when one parent cannot do the whole job with sufficient success. Secondly, the uniparental care system may evolve towards double clutching under favourable conditions for egg-production, and thirdly, when inter-male competition becomes important, it may evolve into pure female parental care.

Biparental care with similar roles may evolve in various directions, such as biparental care with role differentiation, and, should one parent be capable of the whole job, into male care or female care. I doubt whether these latter two possibilities are very likely from a stage in which both parents incubate, and thus are able to control egg temperature very precisely. It would require considerable physiological adaptation, both in the parents and the egg: the parent has to deal with tight time-budgets for foraging and the egg needs to endure longer pauses in the incubation. Yet, it is generally believed that most or all recent mating systems in birds have been evolved from a monogamous system with shared parental care. In contrast to many others, for instance PIENKOWSKI & GREENWOOD (1979) and ERCKMANN (1983), I also doubt whether biparental care evolved into double clutching. Such a process requires the simultaneous evolution of several properties, such as the ability of a single parent to do the whole job, and the ability of the female to lay two clutches in quick succession. I consider this an extremely unlikely possibility.

Double clutching can easily evolve in three different directions. Firstly, females may become specialists in laying eggs for different males during successive short-lasting pair-bonds (polyandry). This is incompatible with prolonged female care, and thus the males have to fulfil all parental duties (male parental care). Since such a change may be associated with the loss of the female's ability to care, a reversal in the evolutionary process from polyandry to double clutching is unlikely. Secondly, it may evolve into biparental care with similar roles, when successful breeding requires more care than a single parent can give. The most probable explanation for this evolution is a substantial increase in the ability to control egg-temperature and thus to increase hatching success. One parent has to leave its clutch repeatedly for foraging, but two parents are able to incubate their eggs without marked interruptions. The advantages of such a change in harsh tundra areas are self-explanatory. Thirdly, it may also evolve into a system in which only the female cares for the offspring (female parental care). Such a situation may occur when inter-male competition becomes important. It may lead to polygyny, promiscuity, and lekking.

Whereas biparental care with similar roles and double clutching may evolve in various directions, female parental care seems to be a dead end, especially when (as in promiscuity and lekking) parents do not maintain any kind of pair-bonding.

Predictions from the model

Above I postulated the pathways in the evolution of parental care and social organization purely on theoretical grounds. I now want to consider whether these pathways are consistent with the ideas about the phylogeny of taxonomic groups by formulating the consequences of the pedigree of behavioural traits for the phylogenetic tree of species. These include two main predictions and an additional one.

Prediction 1.

My suggestion that male parental care or its derivative uniparental care is the primitive pattern in waders implies that male parental care, uniparental care, and double clutching, may be preserved in various, only distantly related, branches of the lineage. All occurrences of these patterns probably come from the same origin. Since double clutching easily evolves to other patterns, the probability that such other patterns occur in the same branch of the pedigree is relatively high.

Prediciton 2.

My suggestion that pure female care can hardly evolve into another parental care pattern, implies that any species in which pure female parental care evolved may become extinct, or lead to a lineage in which all or almost all species display this parental care pattern. Not every incidence of female parental care in a lineage refers necessarily to the same origin.

Prediction 3.

An additional prediction can be made that species with biparental care with similar roles are usually unrelated to species with pure male or pure female parental care, unless the same lineage also encloses species with uniparental care or double clutching.

Testing the model

Arctic sandpipers.

Both main predictions hold for the Calidridinae. This may be concluded from a close examination of Fig. 2, a probable representation of the phylogenetic tree (van Rhijn, 1991). Double clutching, which is characteristic for Temminck's stint, sanderling and little stint (Oring, 1986), occurs in different lineages of the group (prediction 1). Temminck's stint is probably not very closely related to the other small sandpipers, where double clutching only occurs in the little stint. Besides, in the long-toed stint the male seems to perform all parental duties (Myers *et al.*, 1982). The sanderling clearly belongs to the sub-family, but is

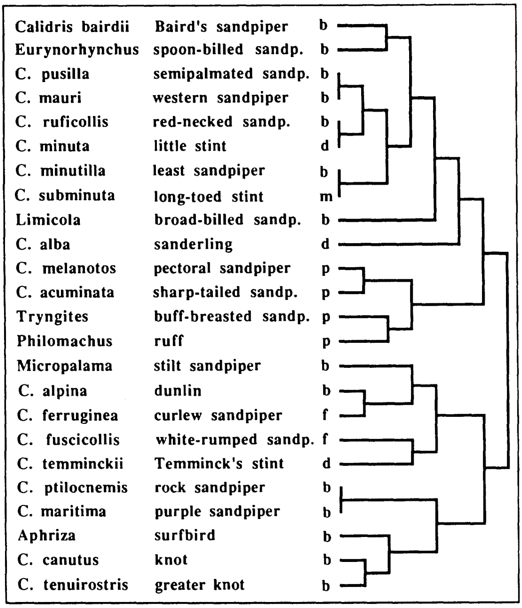

Fig. 2. Probable phylogenetic tree of arctic sandpipers and the divergence of parental care and social organization: d = double clutching, b = biparental care with roughly similar roles, m = strongly male biased biparental care, f = female parental care with polygyny, p = female parental care with promiscuity. Mutual relatedness between species or groups of species indicated by the position of the vertical line between them, decreasing from left to right.

probably not closely related to any particular other species of the group.

Pure female parental care (prediction 2) is shown by all four species within one and the same branch: pectoral sandpiper, sharp-tailed sandpiper, buff-breasted sandpiper, and ruff. All these species have complex promiscuous social systems without lasting bonds between the sexes (reviewed by van RHIJN, 1991). Besides, female parental care is also shown by two single species in another branch: curlew sandpiper and white-rumped sandpiper (reviewed by PITELKA *et al.*, 1974). These may represent separate instances of evolution of pure female care. The finding that males and females of both these species maintain lasting bonds provides additional support for the idea that they recently evolved pure female parental care. That pattern seems to be evolved from a stage with double clutching because one of the other three species (Temminck's stint) in the same lineage displays such a pattern. The remaining two species in the same lineage (stilt sandpiper and dunlin) display biparental care with roughly similar roles, a pattern which can also easily be derived from double clutching.

Waders and related groups.

The predictions also hold for the complete order Charadriiformes. This may be deduced from a comparison between Table 1, which summarizes the diversity in social organization, and Table 2, illustrating to what extent the different families are related to one another.

Sex-role reversal occurs in several distantly related groups (prediction 1), such as all three families of the suborder Scolopaci, and one family of the suborder Charadriomorpha. It may be characteristic for a whole group, such as the Jacanidae and Phalaropodinae (JENNI & BETTS, 1978; KOMEDA, 1983; and reviewed by ORING, 1986). Moreover, in most species of Calidridinae the male parent performs more parental care after egg-laying than the female (reviewed by PITELKA *et al.*, 1974; MYERS, 1981; CRAMP & SIMMONS, 1983), and thus these species display a slight tendency towards sex-role reversal. Pure male parental care may also be restricted to one or a few species of a group, such as the Charadriidae.

Pure female parental care occurs among several representatives of the suborder Scolopacidae (prediction 2). It seems to be the usual pattern among all woodcocks, it occurs in at least one species of the Gallinagininae, probably more, perhaps all but the dowitchers, and in at least six species of the Calidridinae (reviewed by JEHL & MURRAY, 1986). According to STRAUCH (1978) woodcocks and part of the Gallinagininae

TABLE 2. Phylogenetic classification of recent Charadriiformes after CRACRAFT (1981)

suborder Alcae	
family Alcidae	auks
suborder Charadriomorpha	
infraorder Dromae	
family Dromadidae	crabplovers
infraorder Lari	
superfamily Stercorarioidea	
family Stercorariidae	skuas
superfamily Laroidea	
family Rhynchopidae	skimmers
family Laridae	gulls
infraorder Chionae	
family Chionididae	sheathbills
family Thinocoridae	seedsnipes
infraorder Burhirni	
family Burhinidae	thick-knees
infraorder Charadrii	
superfamily Haematopodoidea	
family Haematopodidae	oystercatchers
family Recurvirostridae	avocets
superfamily Charadrioidea	
family Glareolidae	pratincoles
family Vanellidae	lapwings
family Charadriidae	plovers
suborder Scolopaci	
superfamily Jacanoidea	
family Jacanidae	jacanas
family Rostratulidae	painted snipes
superfamily Scolopacoidea	
family Scolopacidae	sandpipers
subfamily Calidridinae	arctic sandpipers
subfamily Gallinagininae	snipes and dowitche
subfamily Scolopacinae	woodcocks
subfamily Tringinae	godwits and curlews
subfamily Arenariinae	turnstones
subfamily Phalaropodinae	phalaropes

Phylogenetic relationship is closest in species of the same subfamily and becomes progressively looser in species belonging to the same family, superfamily, infraorder, suborder, and order.

(without the dowitchers) represent a group which is derived from the same common ancestor. This could imply that pure female care evolved only once in this group. Pure female care probably evolved three times in the Calidridinae (see above). The occurrence of pure female parental care in the suborder Charadriomorpha is open to question. The occasional incidence of polygyny and promiscuity in gulls (reviewed by van RHIJN & GROOTHUIS, 1985) and some plovers (CRAMP & SIMMONS, 1983) is, in all species concerned, an exception to the normal system of biparental care and a monogamous pair-bond. Pure female parental care certainly occurs in the seedsnipes (MACLEAN, 1969). However, one might question CRACRAFT's suggestion (1981) on the position of seedsnipes. STRAUCH (1978) presented evidence that seedsnipes are more related to the Scolopaci. Thus, pure female care might be restricted to only one suborder. This could imply that the common ancestor of this group had particular properties which enabled the evolution of pure female care, whereas the common ancestors of the other suborders probably did not have such properties.

Almost all species of these Alcae and Charadriomorpha, but also of several groups of the Scolopaci have biparental care (prediction 3) with roughly similar roles by males and females (CRAMP & SIMMONS, 1983; JEHL & MURRAY, 1986).

The three predictions imply that close relatives of species with double clutching and pure male parental care are not so likely to have a similar parental care system as relatives of species with pure female parental care and biparental care. Table 3 shows that this seems to be the case in this order (8/17 or 47% have a similar system in the former group and 97/108 or 90% in the latter).

Birds in general.

Fossil remains of the first representatives of the Charadriiformes are from about eighty million years ago (BRODKORB, 1967). Most modern orders of birds must have originated also around that time, or perhaps somewhat earlier. If we assume that double clutching or uniparental care was the early pattern of care in waders, the early pattern in the other orders was either the same, or the pattern from which uniparental care has been derived: pure male parental care.

At present pure male parental care (prediction 1) is shown in only a few groups (RIDLEY, 1978). Table 4 summarizes the main families in which only males tend broods. They occur in only four orders, or three divisions in the sense of CRACRAFT (1981). Besides Charadriiformes, these enclose Gruiformes, Galliformes, and Palaeognathiformes.

In two families of the Gruiformes (mesites family from Madagascar, Mesitornithidae, and the button quails, Turnicidae) sex-role reversal,

TABLE 3. Parental care in closely related species of Charadriiformes

Parental care of close relatives	Double clutch	Only male	Only female	Male + female	total
Double clutching	0	0	1	3	4
Only male parental care	0	8	0	5	13
Only female parental care	1	0	11	1	13
Biparental incubation	3	5	1	86	95

The sample includes 125 species: 6 auks, 4 skuas, 34 larids, 2 sheathbills, 2 seedsnipes, 2 thick-knees, 1 oystercatcher, 2 avocets, 4 pratincoles, 5 lapwings, 10 plovers, 5 jacanas, 2 painted snipes, 24 arctic sandpipers, 3 snipes, 2 woodcocks, 12 Tringinae, 2 turnstones, and 3 phalaropes. Each of these species is compared with its closest relative in the sample. Details on parental care after VAN TYNE & BERGER (1975), RIDLEY (1978), ORING (1982, 1986), CRAMP & SIMMONS (1983, 1985), JEHL & MURRAY (1986).

polyandry, and pure male parental care is common. In the mesites family pure male parental care is displayed by at least one species. In another species of the same family the parental role of the female seems to be most important (RAND, 1951). In button quail pure male parental care occurs in all species which have been studied (reviewed by LACK, 1968; RIDLEY, 1978). Parental care consists of incubation, accompanying the young, probably defending them against predators, and—in button quails, especially during the first days after hatching—bill to bill feeding of the young (HOESCH, 1959, 1960). The occurrence of pure male parental care in the Gruiformes is extremely interesting because this order seems to be related to the Charadriiformes (Table 4). Most other species of the Gruiformes have biparental care with approximately similar roles (prediction 3), but there is at least one family (the bustards Otididae) in which pure female care (prediction 2) is displayed by all, or almost all species (CRAMP & SIMMONS, 1980).

In the order Galliformes pure male parental care is common in the megapodes, but in that family it remains restricted to the regulation of temperature in the breeding mound. The young, who are fully independent after hatching, are not accompanied by any parent (reviewed by LACK, 1968). In this family all species display approximately the same pattern. In contrast, there is considerable diversity in mating systems in another family, the Phasianidae. This family includes a few species of partridges displaying male parental care, but also several monogamous species with biparental care, several polygynous species with female parental care, and a few species with occasional polyandrous relationships, double clutching, and male parental care (CRAMP & SIMMONS,

TABLE 4. Birds in which only males care for offspring

Order family		Species with pure male parental care	Number of species in family
Palaeognathiformes (6 families)			
Tinamidae	tinamous	most or all	± 45
Apterygidae	kiwi	all	3
Casuariidae	cassowary	all	3
Dromiceiidae	emu	at least one	2
Rheidae	rhea	at least one	2
Galliformes (5 families)			
Megapodiidae	megapodes	many or all	10
Phasianidae	pheasants	small proportion	± 200
Gruiformes (11 families)			
Mesitornithidae	mesites family	at least one	3
Turnicidae	buttonquails	many or all	16
Charadriiformes (16 families)			
Charadriidae	plovers	small proportion	± 50
Jacanidae	jacanas	most or all	7
Rostratulidae	painted snipes	one	2
Scolopacidae	waders	several	± 85

Classification according to CRACRAFT (1981). Details on parental care after VAN TYNE & BERGER (1975), RIDLEY (1978), and ORING (1982).

1980). Apparently, the adaptive radiation of parental care in this family occurred in a similar way as in the Scolopacidae. There are at least three taxa in the Galliformes—grouse, turkeys, and curassows—in which pure female care is displayed by all or almost all species (prediction 2). Biparental care with similar roles seems to be rare in this order (VAN TYNE & BERGER, 1976).

Pure male parental care is most common among the ratite birds and the Tinamidae (order Palaeognathiformes). Almost all species of this group display this pattern (LACK, 1968). The male incubates quite often the combined clutch of a number of females (*e.g.* BRUNING, 1974). In such species (*e.g.* the common rhea *Rhea americana*, common emu *Dromiceus novaehollandiae*, and various tinamous) females assemble in groups which may associate with different males in succession. In some other species (*e.g.* the kiwi *Apteryx*, cassowary *Casuarius*, and some other species of Tinamidae) male and female maintain monogamous relationships. The male accompanies the young, and defends his offspring against predators. The young feed independently. In the ostrich *Struthio camelus* females also assemble in groups, but social roles differ because parental care is shared between male and dominant female in the harem group (BERTRAM, 1980).

These data suggest that prediction 1 holds: pure male parental care seems to occur in lineages with various patterns of social organization. In three orders (Charadriiformes, Gruiformes, and Galliformes) male parental care is clearly associated with a large number of other parental care patterns, even at the level of families (Scolopacidae, Mesitornithidae, and Phasianidae) and genera. This variability of parental patterns is less clear within the order Palaeognathiformes, although the range of mating patterns in this order is considerable. It may be suggested that this order displays the primitive state of pure male parental care. No evolutionary trend towards the stage of uniparental care (Fig. 1), and the consequent adaptive radiation of parental care patterns, seems to have occurred in this group. The parental care pattern displayed by the ostrich may be considered as an extension of an original pattern (such as displayed by the rhea) by the evolution of supplementary female parental care.

Prediction 2 that many species with pure female parental care are not closely related to species with other parental care patterns seems to be partly met in the groups considered. To investigate this prediction somewhat better I want to consider the occurrence of female parental care among the remaining groups of birds.

In most families parental care is shared by both parents, quite often almost equally shared (LACK, 1968). In many of these groups there are no exceptions to this usual pattern. This supports prediction 3 that biparental care cannot easily evolve into care by one parent. Yet, it has been suggested by KEAR (1970) that pure female care, in almost all species of ducks, evolved from a stage in which both parents cared and maintained a long lasting pair-bond. Indeed, the occurrence of prolonged mate-guarding in all these species supports this idea. It must be stressed, however, that in most related groups, in which both parents care, parental tasks are unequally distributed between male and female. Most parental duties are performed by the females. Thus the evolution of pure female parental care in the Anseriformes from a stage with biparental care seems to be a very slow process.

Pure female parental care is further displayed by many species of hummingbirds. It is also common in at least five groups of the Passeriformes: (1) the cotingas, manakins, and tyrant-flycatchers, which are closely related to each other, (2) the lyrebirds and their allied scrub birds, (3) the bowerbirds and birds of paradise, (4) the weaverbirds, and (5) the oropendolas. In most of these groups pure female parental care is not universal (VAN TYNE & BERGER, 1976). In these cases the only alternative is biparental care, usually with highly differing roles of both sexes. Incubation, for instance, is a pure female affair in a large majority of these species. Besides, in a considerable number of other families, in which almost all species have biparental care, but unequally shared, a few species display pure female care. Thus, prediction 2 is not fully met, except if one accepts the possibility of a transition between pure female parental care and biparental care in which most care is performed by the female. Since there is no theoretical argument against such a transition in any of the two alternative directions, I consider this a probable explanation.

Discussion

The value of the model has been investigated by considering whether its main predictions were met. Their fit, however, does not prove the correctness of the model, but only that is a fair possibility. To investigate the likelihood of the model I want to consider to what extent predictions by alternative models overlap with the predictions by the present model. Four alternatives will be discussed. Two of them represent the adaptationist's point of view: evolution of parental care and social organization is primarily a response to environmental conditions, which is hardly constrained by phylogenetic factors. One of these two emphasizes the importance of resources and predation in the evolution of parental care, the other one emphasizes the importance of social organization as an isolating mechanism between species. The other two models recognize the importance of phylogenetic factors (without denying the role of ecological factors), but depart from different ancestral stages: one from biparental care with similar roles by the two sexes—the traditional view (*e.g.* LACK, 1968; ORING, 1982)—and the other from pure female parental care.

Resources and predation.

Evolution of parental care patterns and social organization might hardly be influenced by phylogenetic factors, but mainly by the ecological factors met by the species, such as food and predation. This hypothesis generates a main prediction that similarities between species in parental care patterns and social organization should be associated with similarities in ecological conditions. Within certain taxonomic groups (some genera and families) this prediction is entirely or partly met (see for instance LACK, 1968; PITELKA *et al.*, 1974; ORING, 1982), but the association becomes rather poor in a comparison between species of higher taxonomic units (orders and classes). Moreover, part of the variability in parental care patterns and social organization in the lower taxonomic units (for instance in the arctic sandpipers) is not explained by the hypothesis.

This hypothesis also generates predictions for the distribution of parental care patterns and mating systems in phylogenetic trees of species. Firstly, aberrant patterns in a certain lineage should be associated with diverging ecological conditions of the species. To investigate this possibility, habitat descriptions were compared with the accounts on parental care of various species of Charadriiformes and Phasianidae compiled by CRAMP & SIMMONS (1980, 1983). However, I failed to detect distinct associations of the kind in this material. Secondly, there should be a relation between ecological diversity between members of a group and diversity in parental care and mating patterns. I also failed to find clear evidence for this prediction. For instance, in the suborder Charadriomorpha parental care and mating patterns are fairly uniform but the ecological range is considerable, whereas in the family Scolopacidae the diversity in parental care and mating patterns is very large, but the ecological range is restricted. Thirdly, different taxonomic groups with similar ecological ranges should display almost the same variety of parental care and mating patterns. Since it is extremely difficult to select groups with similar ecological ranges, I shall not try to test this, but, intuitively, I do not think that this prediction will be met.

Isolating mechanisms.

Evolution of parental care patterns and social organization might hardly be influenced by phylogenetic factors, but mainly by the danger to produce bad quality offspring by interbreeding with related species. This hypothesis predicts considerable diversity in parental care and mating patterns in closely related species, especially when breeding close together. Although there is substantial diversity between closely related species in the separate courtship behaviour patterns (*e.g.* TINBERGEN, 1959), cases in which the diversity in parental care and mating patterns could be attributed to ethological isolation are scarce. For instance, the diversity in parental care patterns and social organization among colonially breeding seabird species is extremely small, although they often breed in mixed colonies (*e.g.* VEEN, 1977). On the other hand, ethological isolation cannot be excluded as a factor in the diversity of mating patterns in the arctic sandpipers.

Resources, predation and isolating mechanisms.

The hypothesis that mating pattern diversity evolved to prevent interbreeding between species, may be combined with the hypothesis emphasizing the importance of resources and predation. Such combination of hypotheses does not permit to make very precise predictions about the variability between closely related species, since the predictions of both original hypotheses may slightly contradict. For the more distantly related species this combination of hypotheses predicts similar relationships as the first of these two (resources and predation), but less strongly.

Biparental care as the ancestral pattern.

Parental care patterns and social organization in all birds might have evolved from a stage with biparental care with similar roles in their common ancestor, constrained by phylogenetic factors. This hypothesis predicts that pure male parental care is most likely to occur in lineages with biparental care with strongly dissimilar roles and most care performed by the male. On the other hand, pure female parental care is most likely to occur in lineages with biparental care with strongly dissimilar roles and most care performed by the female. Indeed, many species with pure female parental care are closely related to species with biparental care in which the female performs the major part of the job, but the biparental relatives of species with pure male parental care have at most slight asymmetries in the parental roles of the sexes. Moreover, this hypothesis does not explain the occurrence of both pure male and pure female parental care in the same lineage, and requires rather complex reasoning to explain the evolution of double clutching (see ERCKMANN, 1983).

Pure female parental care as the ancestral pattern.

Parental care patterns and social organization in all birds might have evolved from a stage with pure female parental care in their common ancestor, constrained by phylogenetic factors. This hypothesis offers no reasonable explanation for the evolution of biparental care with similar roles, which is widely distributed among birds. Besides, in view of the relative commonness of pure female parental care in birds, the hypothesis would predict the existence of higher taxonomic groups (*e.g.* orders) in which the pattern was universally distributed. This prediction is not met.

Conclusions.

The main implications of my model were (1) the various parental care patterns in birds have been evolved from a primitive stage of male parental care, (2) male parental care, and especially uniparental care (male parent cares alone, but female parent cares alone if male deserts) offers a firm basis for the adaptive radiation of parental care patterns and social organization, (3) biparental care with similar roles can hardly be considered as an ancestral stage in the evolution of double clutching, and (4) pure female parental care offers a very poor basis for an adaptive response to changing environmental conditions. This model seems to be feasible because its main predictions are met. It is also rather likely because predictions by alternative models, either by ignoring phylogenetic constraints, or by departing from another ancestral stage, do not seem to fit.

Summary

Ecological explanations for the diversity in parental care patterns and social organization in certain taxonomic groups of birds are not fully satisfactory. They need to be supplemented by phylogenetic explanations. In this article I discussed some aspects of the latter type of explanations, especially the difference between probabilities of certain evolutionary transitions occurring in the one and in the opposite direction.

To explain the diversity in parental care and mating patterns in waders and related groups, I presented a model on the phylogenetic pathways in the evolution of parental care and social organization in birds. It departs from an ancestral state with pure male parental care which may evolve via "uniparental care" (male cares, but female cares if male deserts) and "double clutching" towards biparental care with similar roles, polyandry and pure female parental care (polygyny, promiscuity). I have argued that certain transitions in this model (especially those from uniparental care and double clutching towards biparental care with similar roles and towards pure female parental care) may easily occur in the given direction, but not in the opposite one.

The model predicts that pure male parental care and related patterns may be preserved in various lineages and may be associated with several other patterns in related species. It also predicts that pure female parental care is, in many instances, a final stage in the evolution, and hence quite often combined with pure female parental care in related species. To investigate the value of the model I tested its predictions for the phylogenetic trees of (1) arctic sandpipers, (2) the complete order of Charadriiformes, and (3) birds in general. All predictions were met. To investigate the likelihood of the model I considered to what extent predictions by alternative models were met. These models either

ignored the effect of phylogenetic factors, or departed from alternative ancestral stages. The fit of the data seemed to be bad with the predictions of all of these models. Thus, the original model presented in this article must be considered as a probable reflection of the phylogeny of parental care and social organization in birds.

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Zusammenfassung

Ökologische Deutungen allein reichen nicht aus, um die Vielgestaltigkeit der Brutpflegetypen und Sozialstrukturen bei bestimmten taxonomischen Vogelgruppen zu erklären. So bedarf es darüberhinaus einer phylogenetischen Auslegung.

In diesem Beitrag werden verschiedene stammesgeschichtliche Ansätze diskutiert. Insbesondere wird der Frage nachgegangen, welcher evolutive Entwicklungsverlauf der wahrscheinlichste ist.

Um die Verschiedenheit des Paarungsverhaltens sowie der Brutpflege bei Watvögeln und verwandten Vogelgruppen zu erklären, wurde ein Modell auf der Grundlage evolutiver Vorgänge bezügich Brutpflege und Sozialstruktur bei Vögeln entwickelt.

Es wird davon ausgegangen, dass im Urstadium die Brutpflege ausschliesslich vom Männchen wahrgenommen wurde (Vaterpflege). Über ein Stadium von Einelternpflege (d.h. Brutpflege vom Männchen oder vom Weibchen, wenn das Weibchen vom Männchen verlassen wurde) und "Doppelbrut" könnte sich eine Elternpflege mit gleicher Rollenverteilung, Polyandrie und Brutpflege ausschliesslich durch das Weibchen (Polygynie, Promiskuität) entwickelt haben. Es wird mit diesem Modell dargelegt, dass die Übergänge in der beschriebenen Richtung leicht ablaufen, jedoch nicht in entgegengesetzter Richtung. Dies betrifft besonders die Umformung von Zweielternpflege mit gleicher Rollenverteilung sowie zur weiblichen Brutpflege.

Das Modell postuliert, dass reine Vaterpflege und ähnliche Strukturen bei wenig verwandten Arten überdauert haben können und dass ihre nahe verwandten Arten ziemlich häufig andere Brutpflegetypen aufweisen. Das Modell fordert ferner, dass in den meisten Fällen die ausschliessliche Mutterpflege ein evolutives Endstadium darstellt, das relativ stabil ist. Dies zeigt sich auch darin, dass bei ihren nahe verwandten Arten ziemlich selten andere Brutpflegetypen vorkommen.

Die Annahmen des Modells wurden bei 1) Strandläufern, 2) der Ordnung der Charadriiformes und 3) der Klasse der Vögel im allgemeinen überprüft. Alle Voraussagen des Modells erwiesen sich dabei als richtig. Daraufhin wurde untersucht, inwiefern die Vorausagen alternativer Modelle zutreffen könnten. Diese Modelle übersahen entweder die Bedeutung phylogenetischer Aspekte, oder sie gingen von einem anderen Urstadium aus. Viele Voraussagen dieser alternativen Modelle erwiesen sich als falsch.

Darum kann das in diesem Beitrag vorgestellte ursprüngliche Modell den Anspruch erheben, die Phylogenie von Brutpflege und Sozialstrukturen bei Vögeln widerzuspiegeln.