Evolution of Polyandry in Birds

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SYNOPSIS. Polyandry in which one female forms either simultaneous or sequential pair bonds with more than one male is a rare vertebrate mateship system. Prior to 1972 only two cases were known with certainty among birds. All other reports of polyandry were based on inadequate information. Recently, polyandry has been demonstrated in several additional species. Surprisingly, they all belong to the avian order Charadriiformes. Comparisons of the existing polyandrous systems suggest that they can be arranged in a sequence that leads through a series of relatively minor differences from monogamy to simultaneous polyandry.

Polyandrous species differ from species with other mateship systems in the following ways: females large, females more aggressive, egg or clutch size reduced, production of multiple clutches. Except in some sequential systems, the small, subordinate males perform all incubation behavior and provide all parental care for the chicks. In the Charadriiformes, polyandry has evolved in conjunction with sex role reversal and with assumption of incubation and parental behavior by the male. It is not clear why role reversal and parental behavior are related. The simplest forms of polyandry are in high-latitude birds, but the best developed forms are found in tropical species.

INTRODUCTION

Polyandry has long been considered one of the basic avian mateship systems. However, careful search of the literature prior to 1972 provides only two documented examples of polyandry in birds in the wild. One of these was a preliminary report of simultaneous polyandry in a flightless gallinule (Ridpath, 1964) which also has a disparate sex ratio. There was also a report of sequential polyandry by three of five females studied in one species of jacana (Hoffmann, 1949). All other reported cases of polyandry in birds were based on observations made of birds in captivity, or were based on indirect or circumstantial evidence. However, in 1972 there appeared

carefully documented reports of polyandry in several more species (Hays, 1972; Jenni and Collier, 1972; Oring and Knudson, 1972; Raner, 1972) as well as a detailed sequel to Ridpath's earlier report (Ridpath, 1972). Additional reports are in preparation or in press.

The purpose of this paper is (i) to review the occurrence of polyandry in birds; (ii) to compare in some detail the documented examples of polyandry, all but one of which are in the order Charadriiformes; and (iii) to attempt to hypothesize the way in which these polyandrous systems could have evolved from a monogamous system. The paper thus attempts to review polyandry and to describe how polyandry might have evolved; the factors responsible for its evolution are considered briefly.

MATESHIP SYSTEMS

Most zoologists agree that vertebrate mating systems can be classified as monogamous, polygamous, and promiscuous. These categories are defined in terms of the number of individuals with which one individual forms pair-bonds. The extent to

which copulation and other social behavior is limited to the other member of the pair and the absolute amount of these behaviors varies widely among different species. For these reasons, it is difficult to define the term pair-bond precisely. In this paper, pair-bond is used to mean that a male and a female copulate with one another. Duration of pair-bond is not usually considered an essential part of the definition. The bond may vary in length from one copulation and the preliminary behavior to the entire adult life of the birds. Typically, the individuals consort with one another for some variable number of days, usually well in excess of the duration necessary to fertilize one clutch. In many species, individuals that have formed such bonds consort with one another more or less to the exclusion of other conspecifics.

In monogamous systems, usually considered the avian archetypal system, a pair-bond is formed between one male and one female. During the breeding season the members of a monogamous pair usually consort with one another exclusively, but they may spend much time feeding or interacting aggressively with other conspecifics.

In polygamous systems one individual forms pair-bonds and copulates with more than one individual of the opposite sex during a single breeding season. The relationships between the various individuals may be simultaneous or they may be arranged sequentially in a series of relationships that resemble monogamous bonding. The most common polygamous system is polygyny in which individual males form pair-bonds with two or more females. Less common is polyandry in which the females form pair-bonds with two or more males.

In promiscuous systems, no pair-bonds are formed. It is often implied that in promiscuous species each individual copulates with more than one individual of the opposite sex, but this is not an essential part of the definition. However, in some species such as many grouse, the female may copulate with only one male.

This simple scheme for classifying mating systems appears adequate. Unfortunately, as pointed out by Wiley (1973), the application of these terms has been based on the separable features of genic contributions to the next generation and the length of association between breeding adults. Because the length of time the adults stay together directly affects their availability for care of eggs and young, often the additional feature of parental care is included as part of the definition of these mating systems. Sometimes these terms are applied to populations and at other times to individuals. In Sage Grouse (*Centrocercus urophasianus*), for example, fewer males than females contribute genic material to the next generation and on the basis of this criterion, the species can be called polygynous. However, one male copulated with 159 hens in 13 mornings (Hartzler, 1972) and using this criterion, the behavior of a male can be considered promiscuous. Each hen apparently copulates only once in a given breeding season although she may come to the male's territory for several mornings before she mates with him. Thus, the female behaves as if she were monogamous, but it seems improbable that 159 hens can have the kinds of relationships we call pair-bonds with the same male during less than 2 or 3 weeks. However, one might regard the female's behavior as a weak, one-sided sort of pair-bonding.

Selander (1972) has attempted to sort out the temporal aspects by restricting the terms monogamy, polygamy, polygyny, and polyandry to pair-bonds of considerable duration. For a very brief pair-bond or in its absence, he proposed the terms monobrachygamy, polybrachygamy (which includes relationships we now call promiscuous), polybrachygyny, and polybrachyandry.

It is essential to recognize that different authors use these terms in different ways. It also appears that mating systems among bird species may be more variable than this artificial system of classification now allows. At the very least, it is imperative that each writer make clear the sense in which he uses the terms.

POLYANDRY AND ROLE REVERSAL

There are two radically different ways in which polyandry can function. The males can cooperate with one another and share the role played by a single male in a monogamous system. Territory defense, nest construction, incubation, and care of the young can all be shared by the males and by the female in what amounts to an expanded family group. In the alternative form of polyandry, behavior of each male can be independent of the other males and each male can interact with the female as if the relationship were monogamous. This relationship must be accompanied by reversal of the typical reproductive behavioral roles. The males must perform all or a large portion of post-ovipositional reproductive behavior, thus freeing the female to interact with another male and produce a clutch for him. In mammals, dependence of young on their mothers for milk appears to have precluded the evolution of polyandry. In a very few human cultures, polyandry of the expanded family type in which the males share a single female is maintained by cultural traditions which, in some cases, includes female infanticide (Ford and Beach, 1951; Peter, 1963).

In the second kind of polyandry described above, the male must perform most of the post-ovipositional reproductive behavior. This is sometimes called sex role reversal. However, in the avian literature, the term sex role reversal usually means that the female is more aggressive than the male and also that she initiates courtship behavior. We think that the primitive pattern is for parents to share the parental responsibilities, and in most bird species, they do share them. However, in some species the females perform all or most of this behavior and in others the male performs this behavior. Both patterns are apparently derived from the pattern of shared behavior. Therefore, it is somewhat misleading to consider exclusive male care of the eggs and young as role reversal. But the significant point is that sex role reversal and exclusive male incubation and parental care tend to appear together and are often accompanied by large female size. Often this indirect evidence has been accepted as *prima facie* evidence of polyandry.

REPORTED CASES OF POLYANDRY IN BIRDS

Polyandry has been reported in 6 of the 28 orders of birds, 11 of the 98 families in these 6 orders, and in 31 of the 1440 species in these families. Thus, polyandry has been reported in substantially less than 1% of the 8500 species of birds. Of course, social systems are not known in all birds, but it is clear that polyandry is extremely rare. The species of birds reported to be polyandrous except for the cuckoos are listed in Table 1 along with a brief description of the evidence for polyandry and the literature citations.

The bizarre social system of the American or Greater Rhea (*Rhea americana*) first described for captive birds, has recently been described for a natural population of rheas in Argentina. The males are simultaneously polygynous, but the females are sequentially polyandrous. It is clear that this is an unusual system and the species cannot be characterized as simply polyandrous. In the tinamous, three of the five species studied have complex mateship systems that appear to be essentially like that described for the rhea. In the other two tinamous studied there is indirect evidence for simple sequential polyandry in which a female produces a clutch for one male and moves on to another. However, these systems have not been adequately studied and the evidence is indirect.

Although at least one of the mesites (order Gruiformes) has been described as polyandrous (Rand, 1936), the evidence is so limited and circumstantial that any statement concerning their social organization is probably premature. Sequential polyandry has been demonstrated in captivity in one species of button-quail (Turnicidae). The button-quail has long been considered polyandrous on the basis of sex role reversal, but polyandry has not been confirmed in the wild. In the rails (Rallidae) simultaneous polyandry has been intensively studied by Ridpath (1972) in the Tas-

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TABLE 1. *The species of birds for which evidence of polyandry has been reported.*

Order Family Species	Cage or wild	Extent of polyandry	Reference
Rheiformes			
Rheidae			
Rhea americana	Cage	♂ ♂ are simultaneously	Steinbacher (1951)
	Wild	polygynous; ♀ ♀ are sequentially polyandrous	Bruning (1973)
Tinamiformes			
Tinamidae			
Nothocercus bonapartei	Wild	As for Rhea	Shäfer (1954)
Nothoprocta cinerascens	Wild	As for Rhea	Lancaster (1964a)
Crypturellus boucardi	Wild	As for Rhea	Lancaster (1964b)
Crypturus variegatus	Wild	Good indirect evidence for sequential polyandry, disparate ratio, role reversal	Beebe (1925)
Nothoprocta ornata	Wild	". . . some possibility of sequential polyandry"	Pearson and Pearson (1955)
Gruiformes			
Mesoenatidae			
Monias benschi	Wild	"Some evidence of polyandry," role reversal, disparate sex ratio	Rand (1936)
Turnicidae			
Turnix sylvatica	Cage	Unequivocal sequential polyandry	Hoesch (1960)
Turnix suscitator and others	Wild	Polyandry based on role reversal	Baker (1928)
Rallidae			
Tribonyx mortierii	Wild	Simultaneous polyandry with cooperative breeding and group territories	Ridpath (1972)
Charadriiformes			
Jacanidae			
Jacana spinosa	Wild	"Classic" simultaneous polyandry with role reversal	Jenni and Collier (1972)
Metopidius indicus	Wild	Colony of 1 ♀, 2 ♂ ♂	Mathew (1964)
Hydrophasianus chirurgus	Wild	Sequential polyandry, role reversal	Hoffman (1949, 1950)
Actophilornis africana	Wild	Colony of 1 ♀, 2 ♂ ♂	Vernon (1973)
Rostratulidae			
Rostratula benghalensis	Wild	Disparate ratio, role reversal	Baker (1929) Henry (1955)
Charadriidae			
Eudromias morinellus	Wild	Sequential polyandry	Nethersole-Thompson (1973)
Eupoda montana	Wild	"Some evidence of sequential polyandry"	Graul (personal communication)
Scolopacidae			
Actitis macularia	Wild	Sequential polyandry at least in some populations	Hays (1972) Oring and Knudson (1972)
Tringa erythropus	Wild	One case of sequential polyandry reported	Raner (1972)
Calidris alba	Wild	Double-clutching with possibility of sequential polyandry	Parmalee and Payne (1973)
Calidris temminckii	Wild	Double-clutching, sequential polyandry described, not documented	Hilden (1965)
Phalaropodidae			
Lobipes lobatus	Wild	Sequential polyandry in 2 of 4 ♀ ♀ in a colony	Raner (1972)
Phalaropus fulicarius	Wild	Role reversal	Höhn (1971[a])
Steganopus tricolor	Wild	Role reversal	Johns (1969[a])

Passeriformes			
Troglodytidae			
Troglodytes aedon	Wild	Change mates between broods	Kendeigh (1941)
Turdidae			
Sialia sialia	Wild	One anomalous case of simultaneous polyandry	Laskey (1947)
Parulidae			
Dendroica kirtlandii	Wild	One anomalous case of sequential polyandry	Radabaugh (1972)
Seiurus aurocapillus	Wild	One anomalous case of simultaneous polyandry	Hahn (1940)
Icteridae			
Molothrus badius	Wild	One case of sequential polyandry	Fraga (1972)
Fringillidae			
Calamospiza melanocorys	Wild	One abnormal case	Verner and Willson (1969)
Sporophila aurita	Wild	One case of simultaneous polyandry	Gross (1952)

[a] Höhn (1971) and Johns (1969) argue against polyandry in phalaropes. Their papers review the pertinent literature.

manian Native Hen (*Tribonyx mortierii*); this system is described in the next section.

In the shorebirds (Charadriiformes) simultaneous polyandry has been conclusively demonstrated in the American Jacana (*Jacana spinosa*), and sequential polyandry has been reported in one other jacana. Sequential polyandry has been demonstrated conclusively in three of the other four shorebird families reported as polyandrous. In the fourth family the primary evidence is sex role reversal.

Cuckoos (Cuculiformes) are often reported as polyandrous (e.g., Sokolov et al., 1969; Molnar, 1950). The evidence for polyandry, when cited, is either that there is an apparent disparate sex ratio or that females are known to mate with more than one male, which suggests promiscuity as well as polyandry. The evidence for polyandry in this order is so slim that I have not listed it in Table 1.

All of the songbirds (Passeriformes) reported as polyandrous are basically monogamous (mateship systems in passerines are reviewed in great depth by Verner and Willson, 1969). In one species of Troglodytidae the female often moves on to a second male after the first reproductive effort of the season, but the first male just as often acquires a new female. This system appears to be basically sequential monogamy. The other passerine species listed are basically monogamous and the one or two cases of

polyandry reported all appear atypical.

This brief review (Table 1) shows that polyandry has been demonstrated unequivocally in only a few of the species reported as having polyandrous social systems. The American Rhea is polygynous-polyandrous. In some of the tinamous and in the buttonquail the circumstantial evidence for polyandry is particularly strong. Polyandry has been demonstrated conclusively in the Tasmanian Native Hen. Every other bird species in which polyandry appears to occur regularly belongs to the order Charadriiformes: American Jacana, Pheasant-tailed Jacana (*Hydrophasianus chirurgus*), Dotterel (*Eudromias morinellus*), and Spotted Sandpiper (*Actitis macularia*). In five additional charadriiform species there is strong evidence suggesting at least occasional polyandry (Table 1). Furthermore, at least one of the rostratulids is probably polyandrous, but the mateship system has not yet been studied. Polyandry is thus most common in the Charadriiformes and has been conclusively demonstrated in only two species outside the order.

The phalaropes (Phalaropodidae) have been cited as the best example of polyandry for so long that they have become almost the classic example. Careful search of the literature prior to 1972 reveals that the evidence for polyandry has been reversal of the behavioral roles of the sexes prior to egg-laying and assumption of all incubation and

parental behavior by the male. However, in 1972 an ornithologist in Sweden described sequential polyandry in a small population of marked Northern Phalaropes (*Lobipes lobatus*) (Raner, 1972). Biologists who have looked closely at the other two phalarope species (Johns, 1969; Höhn, 1971) are skeptical that they are polyandrous. They consider them monogamous or possibly promiscuous. The unfortunate assumption that species with sex role reversal must also therefore be polyandrous has been the cause of much confusion in the literature.

ORGANIZATION OF POLYANDROUS SYSTEMS

Polyandry is known in detail in only five of the species in which it has been reported. Polyandry is different in each of them and they are reviewed below. Polyandry has also been reported in seven additional shorebirds, and these are also discussed below.

American Rhea

On the pampas of northern Argentina the seasonally breeding American Rhea has what must be one of the most unusual breeding systems in birds (Bruning, 1973). As spring progresses, the males establish dominance relationships amongst themselves and the dominant males begin acquiring harems that range from 2 to 15 females. As the season progresses the male copulates with each of his females at least once every 2 or 3 days. The male builds the nest and females lay at the rate of every other day for a period of 7 to 10 days when the clutch numbers 20 to 50 eggs. The male begins incubation a few days after the first egg is laid and becomes increasingly aggressive toward the females. At about this time the females stop returning to the nest of the first male. He performs all incubation and parental behavior. The male is simultaneously polygynous. The females, however, begin to consort and copulate with another male. They produce a clutch for this second male and move on to yet another male. The females are sequentially polyandrous with as many as seven males in a single season. Nest loss is very high and so

is chick loss. Apparently the unique polygynous-polyandrous system and exclusive male incubation and parental behavior are all adaptations that allow females to produce a great many eggs per season and to reduce to a minimum the time necessary to provide each male with a large clutch (Bruning, 1973).

Tasmanian Native Hen

Simultaneous polyandry has been described in only two species: the Tasmanian Native Hen (Ridpath, 1972) and the American Jacana (Jenni and Collier, 1972). In the Native Hen, females often form bonds with two brothers, but sometimes larger groups are formed (Table 2). Each polyandrous group forms a single cooperative breeding unit with all individuals sharing copulation, nest-construction, incubation, care of the young, and defense of a single territory. In two-male groups, one of the males performs twice as much copulation as the other. Reversal of the roles of the sexes which occurs in all other species reported to be polyandrous does not occur in the Native Hen. The female produces a single clutch; she does not produce a clutch for each male. However, polyandrous females do produce larger clutches and raise more young than monogamous females. The number of adults in the breeding habitat is increased beyond the typical two per nest. In all of these ways this system of simultaneous polyandry differs from that in the American Jacana. The Native Hen is flightless and has very specific habitat requirements. This makes it possible to determine with certainty that there is an excess of males in the population. Maynard Smith

TABLE 2. *Composition of polyandrous groups in the Tasmanian Native hen,* Tribonyx mortierii *(from Ridpath, 1972).*

	Total	Group size			
		2	3	4	5
No. of groups	51	26	19	5	1
No. w/2 ♀ ♀	3	0	2	1	0

Average number of ♂ ♂ per ♀ = 1.6

and Ridpath (1972) have interpreted this system as an example of kinship selection. It is not known whether there is a cause-effect relationship between the disparate sex ratio and polyandry. In its functional aspects the system resembles the situation known as helpers at the nest more than it resembles the other systems of polyandry. Helpers have been documented for many species including other members of the Rallidae (Skutch, 1961). In the Tasmanian Hen, polyandry appears to be a unique form of cooperative breeding.

American Jacana

The American Jacana was first found to have a polyandrous social organization near Turrialba, Costa Rica, in 1963 (Jenni and Collier, 1972). Since then this population has been studied during parts of six additional years. The birds have been mist-netted or trapped and color-ringed.

The species breeds year-round at Turrialba. The overall composition of the population remains fairly stable, but individuals are replaced from time to time. Courtship appears to be quite different from what we consider typical for birds and consists primarily of female aggression followed by male appeasement, and then by female invitations to mount. Sex role reversal in the conventional sense appears to be essentially complete. The male also performs almost all nest-building behavior. All females show some nest-building behavior, but it is usually restricted to periods of overt sexual behavior. Female nest-building behavior appears to have little to do with nest construction and may be functionally similar to nest cup displays by female Western Sandpipers and other arctic sandpipers (Holmes, 1973). The male also performs all incubation and all parental care of the precocial young.

Each breeding male defends a small territory. Almost all breeding females defend much larger territories which are superimposed on the male territories (Fig. 1). A few females are monogamous and defend only the area of one male's territory. Males

generally succeed in excluding other males from their territories, but are unable to exclude persistent female invaders. Females succeed in excluding all other Jacanas except their mates from their large territories. Females also help each male defend his small territory against his male neighbors, even when they have pair-bonds with those male neighbors. Such polyandrous females may copulate with a male a few minutes after driving him from his neighbor's territory.

The pair-bonds between any one female American Jacana and her males are simultaneous rather than sequential. Individual females often copulate with all their males on the same day. Copulation with any one male is suspended only during the period of incubation and until the chicks are about 6 weeks old. However, the bond between the female and the male persists through this time and the female continues to occupy the male's territory, to assist him in territorial defense, and to attack potential predators. Copulation with a male resumes several weeks before he is ready to start nesting again. If a clutch is lost, copulation may resume by the end of the following day, and a new clutch is laid within a very few days. Females start laying 7 to 10 days after completing earlier clutches. Although comparative data are scant, female American Jacanas appear to exhibit an exceptional amount of overt sexual behavior. Most pre-copulatory invitations to mount never lead to mounting and only one out of four mounts leads to copulation. Mounting time in successful copulations averages more than 60 sec. A female often

TABLE 3. Composition of 25 mateship groups in the American Jacana, Jacana spinosa.

Year	No. of groups	No. of ♂ ♂ per group				Average no of ♂ ♂ per ♀
		1	2	3	4	
1963	3		1	1	1	3.0
1964	3		2	1		2.3
1969	4		3	1		2.3
1970	5	2	2	1		1.7
1971	4	1	2	1		2.0
1972	3	1	1	1		2.0
1973	3	1	1	–	1	2.3
Totals	25	5	12	6	2	2.2
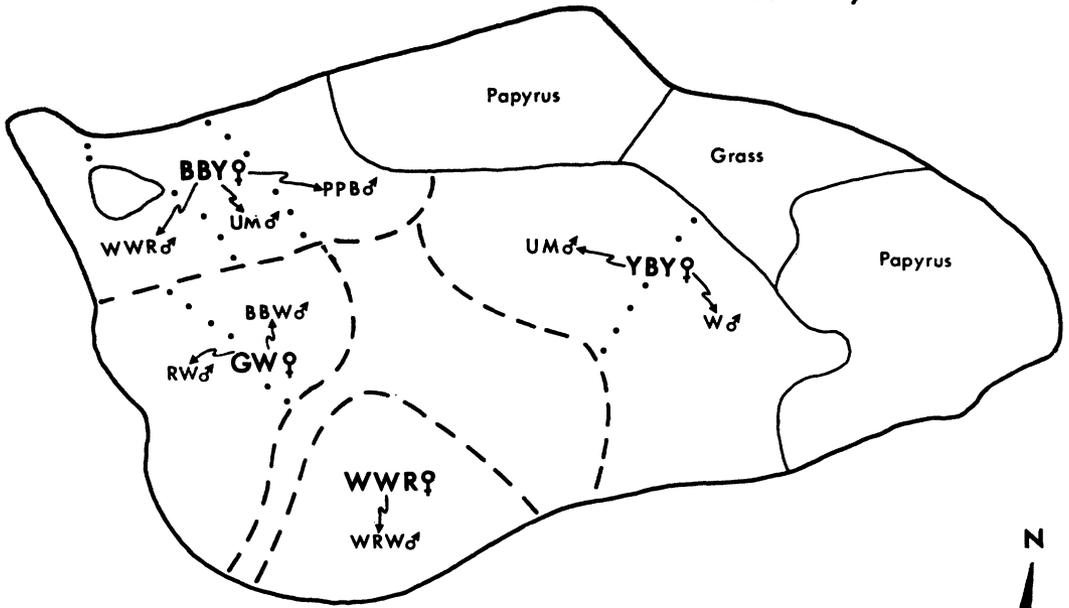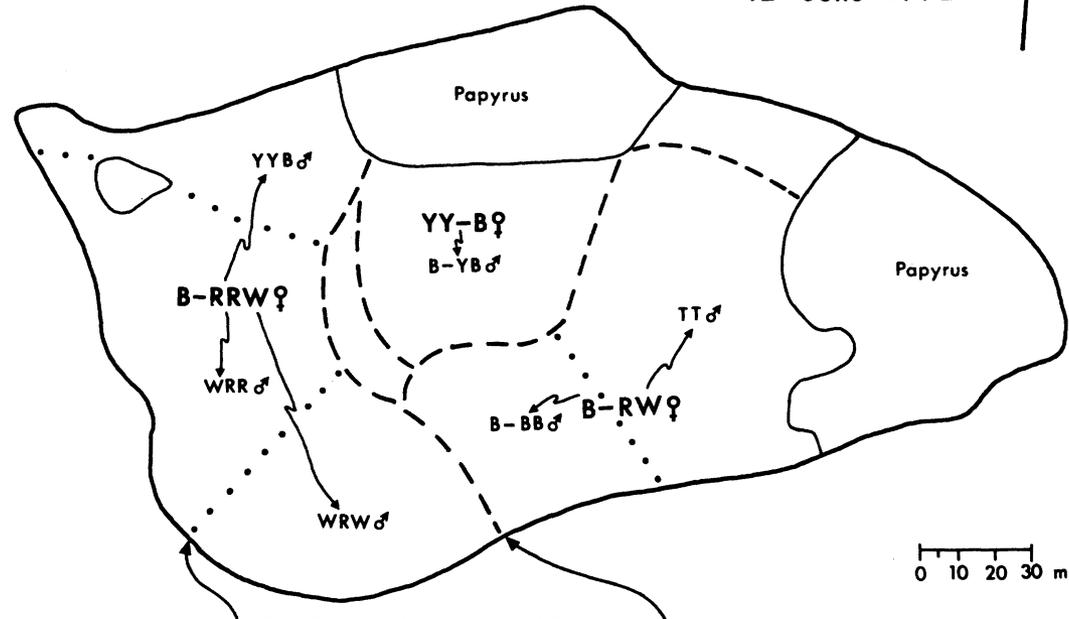
FIG. 1. Distribution of male and female American Jacana territories on the marsh at Turrialba, Costa Rica, during two seasons.

copulates with all of her males on the same day.

Over 7 years, a total of 25 breeding units have been identified (Table 3). Four of the females were monogamous; the 18 polyandrous females averaged 2.4 males each.

Breeding females weigh almost 75% more

than the males (Jenni and Collier, 1972) and are able to dominate males in all situations. Males show strong territorial fidelity and form pair-bonds with any female who succeeds in excluding other females from his territory. The distribution of the female territories and hence, the polyandrous system itself, is based on female-female intractions. The males have no adaptive alternative but must accept the female if they are to breed at all.

Three different sources of evidence suggest that the American Jacana is subjected to heavy predator pressure. The nesting success is extremely low, probably less than 50% of the clutches are successful. Secondly, the birds spend much time threatening, attacking, and distracting potential reptilian and avian egg and chick predators. If the potential predator is toward the middle of the territory, both the male and the female attack; if it is near the edge of the territory or in undefended areas, the neighboring birds also join in the attack. Finally, although the male neither feeds them nor leads them to food, the precocial chicks depend on social facilitation of their feeding behavior. This suggests that feeding in the absence of the male is so fraught with danger that it has been selected against.

Pheasant-tailed Jacana

The best documented case of polyandry before the recent reports on the Tasmanian Native Hen and the American Jacana was a description of sequential polyandry in the Pheasant-tailed Jacana by Hoffmann (1949, 1950). Although the birds were unmarked, the data few, and the bird studied mostly at the geographic limit of its range,

it is clear that the species is polyandrous (Table 4). Hoffmann describes the female as forming sequential pair-bonds with different males. Egg losses were considerable and the female formed, or reformed, pair-bonds with males who lost clutches. Females began laying as soon as 9 to 12 days after completing an earlier clutch. Only one male succeeded in raising a first brood and in obtaining a second clutch (which it lost). Many of the behavioral details described by Hoffmann (1949) bear strong resemblance to similar behavior in the American Jacana. However, he did not describe copulation with more than one male between completion of one clutch and initiation of another. Both he and others (e.g., Lack, 1968) interpret the system as sequential polyandry. Hoffmann observed only three polyandrous groups. It therefore remains possible that a more extensive study will show that the Pheasant-tailed Jacana also has simultaneous polyandry.

Spotted Sandpiper

Polyandry was reported in the Spotted Sandpiper in 1972 by Hays (1972) who worked in New York and by Oring and Knudson (1972) who worked in Minnesota. Both of these studies were of relatively small, isolated populations in which the number of males exceeded the number of females (Table 4). In the New York population there were many more males than females. At Lake Itasca in Minnesota the sex ratio was more nearly equal and the species was essentially monogamous, but at least two females produced clutches for two different males. In both populations the relationships appear to be sequential, but

TABLE 4. *Size of polyandrous "groups" in various species.*

	Total no. of groups	No. of ♂ ♂ per female				Average no. of ♂ ♂ per ♀	
		1	2	3	4		
Tasmanian Native Hen	51	28	18	4	1	1.6	Ridpath (1972)
American Jacana	22	4	11	6	1	2.2	this study
Pheasant-tailed Jacana	5	2	2	1		1.8	Hoffman (1949)
Spotted Sandpiper (NY)	10	4	4	1	1	1.9	Hays (1972)
Spotted Sandpiper (MN)	12	10	2			1.2	Oring and Knudson (1972)
Northern Phalarope	4	2	2			1.5	Raner (1972)

females do replace clutches lost by earlier males. After producing a clutch for one male the female abandons him and moves on to a new male, if one is available, and produces a clutch for him. The female stays with the last male for whom she produces a clutch and assists him in incubation and care of the chicks.

Other species

Other Jacanas. Small breeding colonies consisting of one female and two males have been described for both the Bronze-winged Jacana (*Metopidius indicus*) and the Greater African Jacana (*Actophilornis africana*) (Mathew, 1964; Vernon, 1973). Although copulation by the single female with both males was not observed in either species, the descriptions of the activities of these birds leave little doubt that these populations were polyandrous. Whether the polyandrous relations in these small populations were typical of the species is unknown.

Dotterel. Nethersole-Thompson (1973) describes in detail one example of sequential polyandry in the Dotterel and reviews several other less well-documented examples.

Mountain Plover. In the Mountain Plover (*Eupoda montana*), males take over the first clutch and perform all incubation and brood care behavior (Graul, personal communication). The females typically take over the second clutch, and Graul has some evidence that the females may mate with a second male. The system appears to be very similar to that in the Temminck's Stint described below.

Temminck's Stint. Male Temminck's Stints (*Calidris temminckii*) take over the first clutch and apparently perform all incubation and subsequent parental behavior (Hilden, 1965). Males typically delay the initiation of incubation for a few days. Presumably this allows them to continue to associate with their mate or, perhaps, other females. The females lay second clutches, usually far from where they laid the first clutch. Hilden (1965) states that during the interval between clutches, at least some females were known to mate with second males. Unfortunately, he does not give any details, and it is not clear how commonly the female associates with a second male. One gets the impression that laying the second clutch far from the first one is considered as part of the evidence for mate changes. Apparently the second clutch is incubated by the female exclusively.

Sanderling. Female Sanderlings (*Calidris alba*) are also capable of double-clutching (Parmalee and Payne, 1973). In this species, as in the Temminck's Stint and the Mountain Plover, the male takes over the first clutch and the female incubates the second. There appears to be a high probability that polyandry occurs at least occasionally in this species too.

Northern Phalarope. Although polyandry has been inferred in all the phalaropes, on the basis of circumstantial evidence, it has been demonstrated conclusively in only the Northern Phalarope. In a small color-banded colony of four female and six male Northern Phalaropes in Sweden, two of the females each produced clutches for two males (Raner, 1972). It will be interesting to see whether other workers will find polyandrous relationships in the Northern Phalarope or whether this will stand as an example of facultative polyandry.

DISCUSSION

The polygynous-polyandrous mateship system of the American Rhea appears to be an adaptation that allows each female to lay a maximum number of eggs during the relatively short breeding season. It also greatly reduces the time from initial laying to incubation. The system very much resembles harem polygyny, until the male takes over incubation and the females abandon him. This mateship system is very similar to that of some tinamous, but nothing resembling harem polygyny has been described in the other polyandrous birds.

The polyandrous system in Tasmanian

Native Hen appears to be a unique system of expanded family size in which the adult members cooperate in the care of a single clutch and brood. It appears to have little similarity to the forms of polyandry or incipient polyandry seen in the Charadriiformes and stands as a unique and isolated case.

In the Charadriiformes we find mateship systems ranging from monogamy through simultaneous polyandry. Although polygyny also occurs, its evolution does not interest us here. The most highly evolved polyandrous system appears to be that of the American Jacana.

The behavioral characteristics of the American Jacana that appear to be of critical importance in maintaining the polyandrous system include fidelity of the male to his relatively small territory and non-interference in the relationship between his mate and his male neighbors. These behaviors are reinforced by the females who defend the territories of each of their males against invasion by their other males. The small size of the male territories may make defense of more than one male territory energetically feasible for the female. The females are more aggressive than males and are able to dominate them in all situations. Female hyper-sexuality may be an important mechanism for maintaining polyandry. Reversal of the roles of sexes apparently occurs in courtship. Male assumption of incubation and parental behavior allows the female to maintain simultaneous, functionally effective relationships with more than one male. Large female body size and small egg size may both be related to the female's ability to produce many clutches. Large female body size may also be related to high levels of female aggression.

Sequential polyandry

If the ancestral shorebird mateship system was monogamous with shared parental responsibilities, one can envision simultaneous polyandry evolving through a series of relatively small changes in the social systems. Most of the intermediate steps between monogamy and sequential polyandry can be found in the social systems of different modern shorebirds. Some species such as the Spotted Sandpiper appear to have evolved extremely flexible mateship sys-
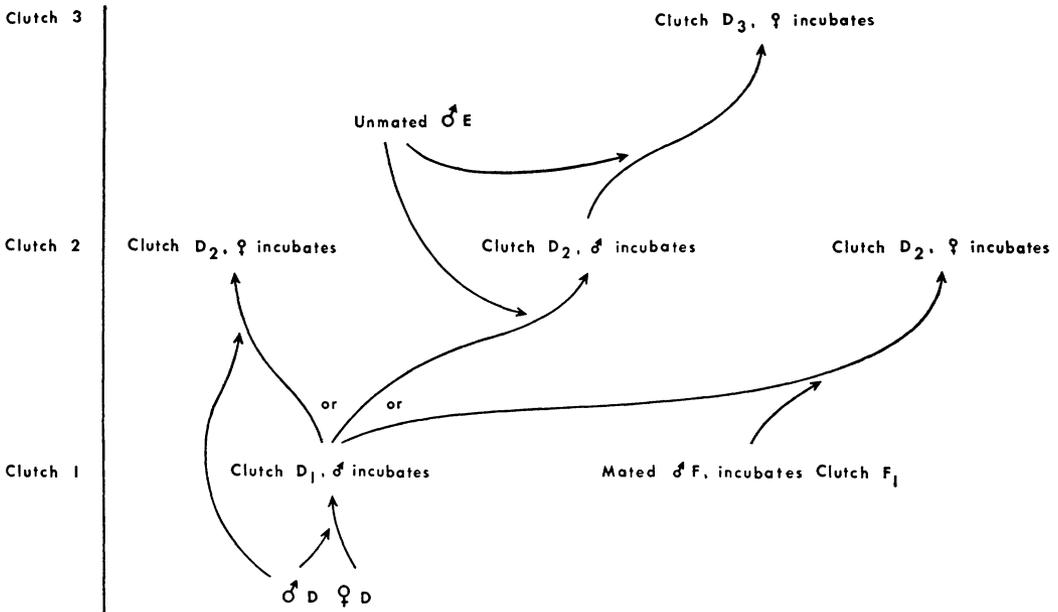

FIG. 2. Sequence of relationships between one female and one to three males. See text for explanation.

tems. During different seasons or at different places, individuals may be monogamous, polyandrous, or perhaps even polygynous.

Two basic requisites to any form of polyandry other than the expanded family type are the production of multiple clutches and the assumption of incubation and parental care by the male. Antecedents for both these traits exist in the typical monogamous system in which the male performs part of the incubation and parental chores and in which the female may produce a clutch to replace the first one if it is lost.

Double-clutching, in which the female leaves the first clutch to the care of the male and then produces a clutch she tends herself, is a system in which we find the critical components of polyandry. The female might continue to copulate with her first mate in which case she would presumably tend the second clutch herself. Rather than continue to copulate with her first mate she might form a pair-bond and copulate with a second male; the second male might already have a clutch produced by some other female, or he might be previously unmated, or he might have lost his first clutch. The female could then take over the second clutch herself, as in the Temminck's Stint and apparently the Sanderling, or she could stay with the second male and assist in incubation and brooding as do bigamous female Spotted Sandpipers, or she could turn this clutch over to the new male as female Spotted Sandpipers do with all but their last clutch of the season.

Most of the above relationships have been diagrammed in Figure 2. The interaction between female D and male D illustrates typical double-clutching. However, the second clutch could be fertilized by another male who is unmated (male E) or who already has a clutch produced by his first female (male F). In either of these alternative cases the female could proceed to incubate her second clutch as she would have had her first male fertilized it. However, if she did form a second pair-bond with an unmated male there are also a number of possible alternatives. Incubation and parental behavior could be shared or performed exclusively by one of them. If

the male took over the second clutch, the female would be in a position similar to when she turned her first clutch over to her first male. Potentially, the female could produce a third clutch.

The Dotterel, Mountain Plover, Spotted Sandpiper, Sanderling, Temminck's Stint, and Northern Phalarope differ in the degree to which the female is involved in incubation and subsequent brood care for her last clutch, but in all of them the first male can assume all such responsibilities. Whenever the female of such a species has adequate food resources and an additional male available, she has the potential for expressing sequential polyandry. It is significant, however, that none of these birds appear to have evolved sequential polyandry as a regular, annual phenomenon involving most of the females. Nevertheless, such complex, purely sequential polyandrous relationships occur at least occasionally in some of these species. Further detailed studies of these species promises to provide data useful in understanding the adaptiveness of polyandry. It is perhaps only a relatively minor step to evolve simultaneous polyandry from such a system.

Simultaneous polyandry

If additional males are limited in number, it would be of advantage to a sequentially polyandrous female to retain contact with her earlier male(s) and replace any clutches they lose. If clutch loss is appreciable it would be to the female's advantage to maintain the pair-bonds and to continue to monitor regularly the behavior of her earlier males. The males' time is occupied with egg and chick care. It would nonadaptive, unless food were short, for him to expand time and energy excluding any female from his territory, especially if she might mate or remate with him and produce a replacement clutch. Given such conditions, males become a valuable resource worthy of defense by the females.

Whatever the adaptive value of simultaneous polyandry, its evolution depends upon the prior or concommitant evolution of exclusive male incubation and parental

	COPULATION	PAIR BOND	PARENTAL BEHAVIOR	EXAMPLE
MONOGAMY	1♀:1♂	Persists	Shared	Western sandpiper
	"	Short	(Increased ♂ respon.) ♂ only	Wilson's phalarope
	"	"	♂ w/lst, ♀ w/2nd	Sanderling
SEQUENTIAL POLYANDRY	1♀:>1♂	"	♂♂ w/all but last, ♀ w/ last or shared	Spotted sandpiper
	"	"	♂♂ exclusively	Northern phalarope
	"	Short, but w/ replacement clutches	"	Pheasant-tailed jacana
SIMULTANEOUS POLYANDRY	"	Simultaneous & persistent	"	American jacana

FIG. 3. The relationship between the evolution of polyandry and the evolution of exclusive male incubation and parental behavior.

behavior. Sex role reversal, that is reversal of the roles in courtship and increased female aggressiveness toward the male, also occurs in polyandrous systems. It is not readily apparent why sex role reversal occurs in polyandrous systems, but it may be related to high aggressive levels that have evolved primarily as part of female-female competition for males. In an earlier paper, Collier and I did not differentiate between role reversal and incubation-parental behavior (Jenni and Collier, 1972), but I think the distinction is important. Reduction of egg size or clutch size occurs in species with polyandrous systems and appears to be an adaptation allowing for an increased number of clutches. Increase in female size with stable egg and clutch size would have the same effect. In Figure 3, I have attempted to arrange selected charadriiform mateship systems in a sequence that shows progressive steps toward simultaneous polyandry from a system with no

deviation from monogamy in spite of the wide geographic variation in density (Western Sandpiper, *Calidris mauri*) (Holmes, 1971). The Figure should not be interpreted as showing phylogenetic relationships; the species are listed solely to identify further the type of mateship system described.

Evolution of polyandry

More data are needed before we can postulate or identify the ecological conditions responsible for the evolution of polyandrous systems. We know, however, that social systems in birds in general appear to be adapted to, and we assume that they have evolved in response to, the spatial and temporal distribution and abundance of certain critical resources such as food and suitable nesting habitat (Verner and Willson, 1966; Lack, 1968; Orians, 1969). Predator pressures are also important and

though we see many examples of behaviors that appear to have evolved in response to predator pressures, it appears to be much more difficult to demonstrate the consequences of predation on the evolution of mateship systems. Polygamous systems might also evolve in response to disparate sex ratios. This notion has received much attention but does not appear to be a valid hypothesis (Willson and Pianka, 1963; Verner, 1964; Selander, 1972). Certainly, there is no evidence of disparate sex ratios being a significant factor in the evolution of polyandry in shorebirds. However, it is entirely possible that in a species with a flexible mateship system such as the Spotted Sandpiper, local variations in the sex ratio provide the females with the opportunity to acquire extra mates and that polyandry in such forms is facultative. In the Tasmanian Native Hen where there is a disparate sex ratio, the cause of which remains unknown, a form of polyandry has evolved that is completely unrelated to those found in the shorebirds.

In the American Jacana the suitable breeding habitat where the chicks are raised appears to be much less extensive than suitable feeding areas for adults (Jenni and Collier, 1972). Non-breeding adults do much of their feeding away from the marsh. Although breeding adults, especially the females do some of their feeding away from the marsh, they apparently do most of their feeding inside their territories. Males with eggs or young chicks spend essentially all of their time inside their territories.

If one parent acting alone can perform adequately the parental duties, and if there is selective pressure for reduction of the number of continually attentive adults, there appears to be no *a priori* reason why in birds the males cannot perform that behavior as readily as females. High probability of egg or chick loss to predators or some other factor would increase the demand for egg production. In any event, the female's time might be better spent in preparing herself to produce more eggs than in incubation behavior and tending chicks. It thus might be of advantage to both male

and female for the male to tend the eggs and chicks while the female prepares herself for production of additional clutches. In rich environments or in areas where food is available in relative abundance for protracted periods where the female can mobilize enough energy to produce multiple clutches, it would be of selective advantage to her to provide clutches for additional males. The acquisition of additional males would not be advantageous to the first male, nor would it necessarily be disadvantageous. It could be disadvantageous to the male if the female's ability for providing replacement and second clutches or her availability for defense against conspecific harassment or predators was reduced.

Even if polyandrous female behavior were of some selective disadvantage to the male, it might be of such selective advantage to the female that on balance it would still evolve. The likelihood that it might evolve under such circumstances would be greatly enhanced if the species had already evolved exclusive male incubation-parental behavior. In the American Jacana at Turrialba, the size of each female's territory, that is, the number of male territories, and therefore the number of males, is determined through female-female interactions and is simply imposed on the males. The males are a resource divided up amongst the females. Each male retains fidelity to his territory and forms a pair-bond with any female who excludes other females. He mates with this female and incubates her eggs. Because there is a good probability that he, rather than some other male, has fertilized them, it is clearly of advantage to him to cooperate. He is unable to exclude a polyandrous female in favor of a monogamous female. The only alternative open to these small, subordinate males is to desert. Because alternative territorial sites are not available to the males (Jenni and Collier, 1972) abandoning a territory because it is controlled by a polyandrous female is not a viable alternative. In this strongly matriarchal system, males appear able to maximize their reproductive potential only through successfully raising a max-

imum of young or managing to fertilize eggs that their females deposit in the nests of other males. (The problem of paternity and the relative reproductive success of polyandrous units of different sizes are currently under study.)

Hypotheses such as Orians' (1969) on the evolution of mating systems help focus our attention on potentially important and often testable questions. Such hypotheses must of necessity be based primarily on data on monogamous, polygynous, and promiscuous species. From these data and the meager data on polyandry, it is possible to construct models to help understand the evolution of polyandry. Critical factors for any such model appear to be distribution and abundance of food, both in space and time; the distribution and amount of suitable breeding habitat; and probably predator pressure. On the basis of his theory, Orians (1969) predicts that polyandry should be rare. The prediction that polygyny should be more prevalent among precocial than among altricial birds holds true for polyandry; all the polyandrous species so far known have precocial young. Orians' (1969) predictions that polygyny should be more common for species that nest in marshes and in early successional stage is supported at least partially. The prediction that polygyny should be more prevalent among species with widespread feeding but restricted breeding areas holds true for the polyandrous species to at least a limited extent, but the relationship is not so clear as in the polygynous species. The final prediction is based on feeding of altricial young and cannot be appropriately applied to polyandrous systems because the polyandrous species all have precocial young.

The most highly evolved polyandrous systems are found in the tropics (American Jacana and Pheasant-tailed Jacana). The tropics certainly provide the potential for protracted breeding seasons with potentially rich food resources or, at least, protracted availability of food at locally maximal levels. There is some evidence to support the idea that predator pressure on nests is greater in the tropics than at higher latitudes (MacArthur, 1972).

To improve our hypotheses on social systems and certainly in order to test them, more concrete data on polyandrous systems are needed. We need to know more about the present adaptiveness of polyandrous systems. It would be helpful to verify polyandry in other groups where it is only suspected. Unfortunately, most of these species are tropical; some of them are quite secretive and others dwell in marshes. Current research by many workers on several species of shorebirds promises to be of great help in understanding the adaptiveness of polyandry. Perhaps this new work will enable us to understand why polyandry has evolved in a few select species.

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