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THE CHARACTERISTICS AND OCCURRENCE OF COOPERATIVE POLYANDRY

JOHN FAABORG & CINDY B. PATTERSON*

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The occurrence of multiple-male breeding groups in the Galapagos Hawk *Buteo galapagoensis* was first detailed by de Vries (1973, 1975, 1976). We have recently begun a new study on the evolutionary conditions leading to this system (Faaborg *et al.* 1980). Because all males in a territorial group copulate with a single female throughout the breeding process, the Galapagos Hawk should be considered polyandrous. Yet the help of several adults at one nest also classifies this species as a cooperative breeder. Recent models for the evolution of avian polyandry (Jenni 1974, Emlen & Oring 1977, Graul *et al.* 1977, Maynard Smith 1977) are difficult to apply to cooperative breeders for reasons discussed below. Likewise, recent reviews of cooperative breeding refer to the Galapagos Hawk but fail to note its distinctive mating characteristics (Brown 1978, Emlen 1978). Thus, it seems appropriate to synthesize the evolutionary theories concerning polyandry and cooperative breeding in order to explain more distinctly the system of 'cooperative polyandry'.

FORMS OF AVIAN POLYANDRY

Mating systems have generally been classified according to the type and number of pair-bonds in individual forms. Jenni (1974) pointed out the problems with defining a pair-bond, since intensity of the bond can vary temporally and by sex. Tempting definitions involving genetic contributions to the next generation, eliminating the necessity of defining a pair-bond, have recently been proposed (Ralls 1977, Symons 1979). However, these definitions have the problem of equating functionally different mating systems, i.e., promiscuous systems with monogamous ones or, more importantly for this paper, cooperative polyandry with monogamy (variance of male reproductive success equals variance of female reproductive success). While sex differences in variance of reproductive success may often be the outcome of non-monogamous systems (Payne 1979), it is not a necessary outcome and thus does not suffice as a definition.

In their simplest sense, mating systems can be defined on the basis of sex differences in the number of partners with whom is made a simultaneous attempt to raise a brood (*sensu* Emlen & Oring 1977). Here we are concerned only with polyandry and consider only those species where females regularly attempt to raise a brood(s) with multiple males while males contribute to the brood of only one female. Contributions by males or females can range from simple production of gametes to extensive or exclusive parental care. This excludes those species (primarily from the Rheidae and Tinamidae) where males are simultaneously polygynous and females are sequentially polyandrous and those species exhibiting 'rapid multiple clutch polygamy' (Emlen & Oring 1977). It also excludes species where monogamous individuals change mates after the successful completion of a brood.

This leaves the following three general classifications of avian polyandry:

(1) SEQUENTIAL (SERIAL) POLYANDRY

A female will copulate with, and lay a clutch of eggs for, two or more males in succession. In most cases the female does not maintain close association with males after egg-laying—

* Deceased

although the female may return to provide replacement clutches—but moves on to another male should one be available. Females generally do not defend males or territories or provide parental care, although these behaviours can be variable depending on the species. [Female Spotted Sandpipers *Actitis macularia* maintain territories but may desert them to pursue extra males (L. W. Oring, pers. comm.).] Sequential polyandry has been reported for the Northern Phalarope *Lobipes lobatus* (Hilden & Vuolante 1972), the Red Phalarope *Phalaropus fulicarius* (Schamel & Tracy 1977, Mayfield 1978), the Spotted Sandpiper (Hays 1972, Oring & Knudson 1972), the Dotterel *Eudromias morinellus* and the Pheasant-tailed Jacana *Hydrophasianus chirurgus* (both reviewed in Jenni 1974).

(2) SIMULTANEOUS POLYANDRY

A female copulates with and forms a stable association with several males simultaneously through the breeding attempt. Females generally hold large territories superimposed over territories of several males. Females may copulate with all males within a short period of time (one day) and lay a separate clutch of eggs for each male. Although females do not generally aid in incubation or provide parental care, they do defend both males and broods against conspecific males and predators. The classic example of simultaneous polyandry is the American Jacana *Jacana spinosa* (Jenni & Collier 1972, Jenni 1974), although it has also been reported for the Spotted Sandpiper (Oring & Maxson 1978).

(3) COOPERATIVE POLYANDRY

A female has simultaneous pair-bonds with several males and all adult birds in a group contribute equally to the raising of a single clutch of eggs. All males are at least potential fathers of each young. This is distinctly different from the above forms of polyandry in that there is an increase in the amount (or at least the potential amount) of parental care and no role reversal occurs.

Cooperative polyandry was first reported in the Tasmanian Native Hen *Tribonyx mortierii* (Ridpath 1972) and since has been studied in two species of hawk. Harris' Hawk *Parabuteo unicinctus* populations in southern Arizona have regular trios (2 males, 1 female) (Mader 1975a, b, 1977, 1979), although such trios are rare in the west Texas population of this species (Griffin 1976). [Mader (1979) has referred to the Harris' Hawk as being simultaneously polyandrous but because all males contribute to a single nest, we feel it is cooperatively polyandrous.] As many as four male Galapagos Hawks *Buteo galapagoensis* have been found mated to one female (de Vries 1973, Faaborg *et al.* 1980) and on some islands 85% of the territories possess polyandrous groups.

EVOLUTION OF POLYANDRY

The obvious preadaptation for the evolution of simultaneous and sequential polyandry is sex role reversal or female emancipation from parental care. It has been suggested that a male might take over incubation and subsequent parental care in order to ensure the health and well-being of his mate with regard to reproduction (Oring & Knudson 1972, Parmelee & Payne 1973, Jenni 1974, Emlen & Oring 1977, Graul *et al.* 1977). If the female is unable energetically to provide subsequent care or is required to provide rapid replacement clutches after nest failure, male incubation would maintain the first clutch. Female emancipation then might result from extreme and unpredictable, fluctuations in food supply, a variable but generally short breeding season and a rigorous climate [characteristics faced by the tundra species and, at least in terms of food supply, by the Mountain Plover *Eupoda montana* (Graul 1973)]. Conversely, female emancipation might result in populations facing long seasons and abundant food supply but high egg predation, as is true for the American Jacana (Jenni & Collier 1972) and Spotted Sandpiper (Oring & Maxson 1978).

In either case, in times of food abundance or if nest failure does not occur, the emancipated female then has the opportunity to double clutch, incubating the second clutch herself (this could be termed double clutch monogamy). This would double the reproductive effort of both the male and female. If females remate before the second clutch, the system becomes polyandrous. Remating might be adaptive if females switched to better territories or better males or if the original mate is unavailable due to incubation demands or other factors. This sex role reversal would be further enhanced by selection for larger size in females to increase reproductive capacity, a condition necessary for reproducing under limited food conditions or for providing many clutches. Large size in females increases the difficulty for a male attempting to prevent his female from mating with another partner.

Thus, polyandrous species might have followed an evolutionary pathway from monogamy to 'double clutch' monogamy, to sequential polyandry. From sequential polyandry, a species might have two evolutionary options, rapid multiple clutch polygamy or simultaneous polyandry. If, after desertion by the female, the male is able to delay incubation (because of benign climatic conditions and low nest predation) and remain sexually active, he might attract a second mate and become polygynous while the female is polyandrous. This is rapid multiple clutch polygamy as described by Emlen & Oring (1977). If the male is unable to leave the eggs, polygyny is generally prevented and the species would be strictly polyandrous. If nest mortality is extremely high, then a close association of male and female through simultaneous polyandry might be necessary to ease rapid egg replacement. In addition, the extent and value of male parental care in preventing predation makes him a valuable resource for the female and worthy of defence. Females thus would superimpose territories over those of their males and remain in close contact. It is not surprising, then, that Spotted Sandpipers can also be simultaneously polyandrous. That the evolutionary gap between simultaneous and sequential polyandry is a small one is further evidenced by the occasional occurrence of sequential polyandry in American Jacanas (L. W. Oring, pers. comm.). Whether you have sequential or simultaneous polyandry might depend on the feasibility of territoriality and the local and seasonal levels of predation.

The evolutionary gap between these two forms of polyandry and cooperative polyandry is much larger. Many traits of cooperative polyandry are in sharp contrast to those shared by sequential and simultaneous polyandry. Nests and young of cooperatively polyandrous species are cared for by more than two adults, while the nests and young of other polyandrous species usually have one parent providing all the care. Sequential and simultaneous polyandry are characterized by extreme role reversal while the sexual roles of cooperatively polyandrous individuals are essentially identical to those of their monogamous relatives. In terms of confidence of paternity, a sequentially polyandrous male who vigorously defends his mate through the egg-laying period can be fairly sure he is incubating eggs carrying his genes. A simultaneously polyandrous female may copulate with all males in one day (Jenni 1974) but if males nest at all asynchronously, a male could monopolize the female's sexual activity and increase his confidence in the paternity of the eggs. Even without asynchrony, males could have equal representation in all nests and if females defend mates equally, have the same potential reproductive success. In cooperatively polyandrous species (barring sperm competition or some other subtle variation in copulation capabilities that has not been described), the male's confidence in paternity has been reduced to a probability related to the relative amounts of sexual activity between the female and each male. In the Galapagos Hawk the reproductive chances of each male appear equal (Galapagos Hawk males copulate with the female in sequence throughout the breeding period) while in the Tasmanian Native Hen they are apparently unequal—one sexually dominant male often attains significantly more copulations than the other male (Maynard Smith & Ridpath 1972).

With multiple male copulations, it is not surprising that concepts of inclusive fitness and relatedness (Hamilton 1964) have been discussed with regard to reproductive success in cooperatively polyandrous species (Maynard Smith & Ridpath 1972, Emlen 1978). A male would gain indirect genetic representation in the brood if eggs he did not father were fertilized by a closely related male. While trios of Tasmanian Native Hens regularly consist of pairs of brothers, such that each male has a significant genetic investment in each egg, pairs of non-related males do occur. In the Galapagos Hawk there is no evidence suggesting any relatedness among cooperating males (Faaborg *et al.* 1980). Certainly, if the female jacana regularly copulates with several males before laying eggs, confidence in paternity for each male is lost, fatherhood may be related to proportion of sexual activity and inclusive fitness-relatedness factors could be beneficial. More data are needed on this.

Because of the extensive variation in the forms of avian polyandry, we feel that a single model accounting for their evolution is impossible. While progression from monogamy to sequential polyandry to, perhaps, simultaneous polyandry seems logical given the proper set of resource conditions and preadaptations, the communal traits of cooperatively polyandrous species are not the end of this gradient. Rather, cooperatively polyandrous species share more ecological and evolutionary traits with cooperatively breeding (communal) species and models explaining the gradient from monogamy to group breeding to cooperative polyandry seem more appropriate (see below). This does not make cooperative polyandry any less a form of polyandry; a female still gains by monopolizing the reproductive potential of more than one male. Whether the gain is a second clutch or additional young produced from one clutch is irrelevant in terms of defining the system. It does, however, make cooperative polyandry distinct in its evolutionary roots from the other forms of polyandry, a distinction which we feel has not been appropriately made.

COOPERATIVE BREEDING SYSTEMS

Cooperative or communal breeding describes the situation where more than two adults provide some care for a single set of young. A cooperative unit usually consists of a monogamous pair and a variable number of subordinate, non-breeding helpers (Brown 1978). In many species, however, females lay in communal nests attended by a variable number of potential breeders. In this case all adults obtain copulations, although their genetic contributions to the nest vary. Communal nests may be formed by groups of monogamous pairs, as in the Groove-billed Ani *Crotophaga sulcirostris* (Vehrencamp 1977); by groups of promiscuous individuals, as in the Noisy Miner *Manorina melanocephala* (Dow 1977), the Pukeko *Porphyrio porphyrio* (Craig 1975) and possibly several bee-eater *Merops* species (Fry 1972, Emlen 1978); and by single polygamous groups, as in the cooperatively polyandrous species mentioned earlier. Thus there is tremendous variation even within the rather narrow definition of cooperative breeding. It is not our intent here to review fully cooperative systems, as that has recently been done (Brown 1978, Emlen 1978, Gaston 1978). Rather, we hope to show how the various characteristics of cooperative polyandry fit within the ecological and evolutionary framework of these cooperative systems.

Explanations for the evolution of cooperative behaviour generally suggest that it is adaptive as a long-term reproductive strategy for populations living in saturated habitats (Brown 1974). However, single explanations for any complex behaviour generally prove unsatisfactory and that appears to be the case with cooperative breeding (Fry 1972, Ricklefs 1975, Brown 1978, Emlen 1978). Cooperative breeding seems to occur most regularly in either stable habitats with severely limited conditions or in highly unstable habitats. The first condition results in limited and predictable (but unchanging) breeding space and low adult mortality, such that a juvenile is unable to move into the breeding population immediately. Becoming a helper allows an individual to stay on a territory (where survivorship is often high), establish a dominant position in the social structure

of the group and eventually move into or inherit a vacant territory. These populations generally exhibit so called 'K-selected' characteristics (low fecundity, high adult survival, and low dispersal). These conditions could then produce breeding by a monogamous pair and helping by (often related) subordinates [see Woolfenden (1975) and Parry (1974) for examples]. In highly unstable habitats, severely fluctuating climatic conditions and/or food resources can result in highly variable juvenile mortality and 'bet-hedging' life history traits similar to those of K-selection (late maturity, long life, low fecundity) (Stearns 1976, Horn 1978). Under such conditions, communal breeding might enhance adult survival and allow reproduction under lowered resource conditions. Population saturation is not a necessary correlate of cooperative breeding in these unstable conditions. For example, bee-eaters and the Noisy Miner are colonial rather than territorial and do not appear to be breeding site limited (Dow 1977, Emlen 1978).

Most of the cooperative units consisting of potentially breeding adults appear to occur in such unstable habitats (marshes, savannahs and arid or semi-arid regions) and utilize ephemeral food resources (see Brown 1978). The bee-eaters, for example, are savannah species and face unpredictable periods of drought (a problem for an aerial insectivore). The Noisy Miner breeds in dry sclerophyll woodland that has varying rainfall patterns (Dow 1977). All three of the polyandrous species live in arid or semi-arid habitats and face erratic rainfall and spatially or temporally unpredictable food resources which affect reproductive success [see Mader (1979) for the Harris' Hawk and Ridpath (1972) for the Tasmanian Native Hen]. In the Galapagos, rainfall is extremely erratic both seasonally and annually (Grant & Boag 1980) and nestling survival in the Galapagos Hawk varied greatly among years depending on the dryness (Faaborg *et al.* 1980). The possibility exists, though, that for long-lived species with fairly stable populations (like the hawks), these seasonal fluctuations are relatively unimportant and the environment, although extremely harsh, may effectively be considered stable.

For virtually all cooperative species, cooperation results in higher survival of adults and generally higher reproductive success per nest (Fry 1972, Ridpath 1972, Vehrencamp 1977, Dow 1978, Stallcup & Woolfenden 1978, Mader 1979; but see Zahavi 1974). In the Galapagos Hawk, territorial birds have higher survivorship than non-territorial birds and polyandrous groups have higher reproductive success per nest than do pairs. However, polyandrous males have lower reproductive success per individual than do monogamous males and it has been suggested that a polyandrous male may be trading the higher yearly fitness of a monogamous male for increased chances of survival on a territory with lower year-to-year fitness but equal or greater life-time fitness.

Despite general correlations between demographic conditions and cooperative breeding behaviour, these conditions are not absolute predictors of the type of cooperative breeding displayed. If you assume group living is advantageous for individuals in most cooperative species, the question still remains of why in some species all birds in a group are potentially allowed to breed and in others they are not. The answer to this may lie in the ability of birds to establish breeding dominance or the costs of subordination in terms of life-time fitness (see below). In species with related helpers, it is easy to see how parents could dominate offspring and refuse to allow copulations or extra nests on the territory. [When offspring get older, this parent-offspring dominance may break down, such as when males bud-off part of the parental territory in the Florida Scrub Jay *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1978).] Where groups are composed of siblings, as in the Tasmanian Native Hen, partial dominance is established by one brother over another and the number of copulations by each corresponds to that relationship (Ridpath 1972). In groups of unrelated adults, dominance relationships are generally more subtle and multiple matings may occur. In many of these cases, number of copulations may differ among males based on status or age but significant numbers of copulations by other males in the group are not prevented (Dow 1978, Emlen 1978, Fry 1972).

In these cases of cooperative promiscuity, competition among males for copulations is made more severe by an apparent skew in the sex ratio favouring males.

In the Galapagos Hawk, groups are formed by apparently unrelated full adults and any dominance relationships among males are extremely subtle (de Vries 1973, Faaborg *et al.* 1980). Young birds are excluded from territories within a few months after fledging and spend the next three years (minimum) in non-territorial areas (de Vries 1973). However, available breeding habitat is limited and many females are excluded from breeding. As is true for many hawks, females are the larger and more competitive sex; thus female exclusion from established territories is possible and polyandry rather than promiscuity occurs.

The need to establish dominance over breeding attempts may also be affected by kin selection. Young birds might accept subordinate, non-breeding status more readily if they have some genetic representation in the nest, even though that representation is indirect. For the Tasmanian Native Hen, the subordinate brother gains as much through inclusive fitness as he would by breeding alone (Emlen 1978). This is not to say, however, that kin selection is the driving force for the evolution of cooperative breeding. Most studies have adequately shown individual selective advantages for cooperation to both breeders and non-breeders (Emlen 1978, Ligon & Ligon 1978, Woolfenden 1981). For most species with related helpers, the short-term gain through inclusive fitness does not equal that of individual breeding [see Emlen (1978) for specific examples]. However, kin selection may reinforce the dominance relationship by reducing the need for competition for copulations, given the constraints mentioned above. Thus we would expect that a male Galapagos Hawk, with no apparent kinship within the group, should compete strongly for an equal number of copulations with the other males in his group. It is also not surprising that parental investment in many of these species is related to probable proportion of eggs fertilized or degree of genetic relatedness to the brood (Dow 1977, Vehrencamp 1977). In the Galapagos Hawk, male investment is apparently equal but with equal copulations males share equal chances of being each offspring's father. [The relationship between genetic investment and parental investment apparently does not always hold for females. In the Ani, older females who end up with more eggs in the nest do the least caring for eggs and young (Vehrencamp 1977).]

Two major problems with a purely dominance approach to explaining specific traits of these systems remain. The first is why Anis remain monogamous rather than having become promiscuous. It appears that these birds have evolved a strategy of aggression toward nest-mates (through egg-rolling) that replaces extra copulations as a way of increasing their genetic investment in the nest (Vehrencamp 1977). The result is the same but the evolutionary pathway is obviously different. The second problem is why in groups containing unrelated helpers, as occurs in the Green Woodhoopoe *Phoeniculus purpureus* (Ligon & Ligon 1978), unrelated birds do not attempt copulations. Although the percentage of unrelated helpers is apparently small, we would have predicted that matings by more than one pair would occur. An answer may be found in apparently significant differences between the breeders and the helpers (which are usually sub-adults) such that strong age dominance occurs to prevent such copulations. Additionally, in some cooperative species single-pair bonding predominates but is not found in 100% of the population (Zahavi 1974). Thus some competition can occur even in those species characterized as singular breeding. In many other species copulations are so rarely seen that we cannot be sure of the exact situation.

While the above material is necessarily speculative, it shows the relative position of the cooperatively polyandrous species within the wide array of cooperative breeding behaviours. It suggests that the Galapagos Hawk has evolved cooperative breeding in an isolated and saturated habitat to increase the length of an individual's reproductive life despite concomitant reduction in average yearly production. Formation of groups of

unrelated males may be the reason males share copulations equally. Because these males are all sexually active, the system must be considered a mating system and not just a helping system. The past tendency to approach mating system evolution as one topic and cooperative breeding systems as another has lead to the exclusion of important species in both areas. Future syntheses of reproductive strategies should include the conditions that result in maximum fitness when a female shares a male in a high quality territory (polygyny), a male shares a female on a hard-to-find territory (cooperative polyandry) or because of energetic constraints (simultaneous or sequential polyandry), or a young bird shares a territory until it establishes its reproductive position in the community (cooperative breeding). In all these cases individual birds are attempting to maximize fitness by adopting the reproductive strategy most appropriate to the prevailing environmental conditions.

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SUMMARY

This paper discusses the relative position of cooperative polyandry among models for the evolution of both polyandry and cooperative breeding. Cooperative polyandry is described as the situation where more than one male and one female breed as a group with males sharing equally in copulations and the care of one set of young. Sequential and simultaneous polyandry are defined to show how they differ from cooperative polyandry. These systems generally are characterized by the care of only one parent for each set of young, a trait which is in sharp contrast to cooperative polyandry. An argument is made that the present models for the evolution of polyandry cannot be expanded to include the cooperatively polyandrous species. Instead, the cooperative traits of cooperative polyandry fit within the array of characteristics of cooperative (communal) breeding. General characteristics of all cooperative species (monogamous, promiscuous and polyandrous) are reviewed and possible reasons for the evolution of equal-status males are discussed. A plea is made for the unification of evolutionary models dealing with mating systems and cooperative systems.

REFERENCES

- BROWN, J. L. 1974. Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. *Am. Zool.* 14: 63–80.
- BROWN, J. L. 1978. Avian communal breeding systems. *Annu. Rev. Ecol. Syst.* 9: 123–155.
- CRAIG, J. L. 1975. Cooperative breeding of pukeko. *Emu* 74: 308.
- DE VRIES, T. J. 1973. *The Galapagos Hawk*. Amsterdam: Free University Press.
- DE VRIES, T. J. 1975. The breeding biology of the Galapagos Hawk, *Buteo galapagoensis*. *Le Géfaut* 65: 29–54.
- DE VRIES, T. J. 1976. Prey selection and hunting methods of the Galapagos Hawk, *Buteo galapagoensis*. *Le Géfaut* 66: 3–43.
- DOW, D. D. 1977. Reproductive behavior of the Noisy Miner, a communally breeding honeyeater. *Living Bird* 16: 163–186.
- DOW, D. D. 1978. Breeding biology and development of the young of *Manorina melanocephala*, a communally breeding honeyeater. *Emu* 78: 207–222.
- EMLEN, S. T. 1978. The evolution of cooperative breeding in birds. In Krebs, J. & Davies, N. B. (eds), *Behavioural ecology, an evolutionary approach*. London: Blackwell Scientific Publications.
- EMLEN, S. T. & ORING, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215–223.
- FAABORG, J., DE VRIES, T. J., PATTERSON, C. B., & GRIFFIN, C. R. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galapagos Hawk (*Buteo galapagoensis*). *Auk* 97: 581–590.
- FRY, C. H. 1972. The social organization of bee-eaters (Meropidae) and co-operative breeding in hot-climate birds. *Ibis* 114: 1–14.
- GASTON, A. J. 1978. The evolution of group territorial behavior and cooperative breeding. *Am. Nat.* 112: 1091–1100.
- GRANT, P. R. & BOAG, P. T. 1980. Rainfall on the Galapagos and the demography of Darwin's Finches. *Auk* 97: 227–244.
- GRAUL, W. D. 1973. Adaptive aspects of the Mountain Plover social system. *Living Bird* 12: 69–94.
- GRAUL, W. D., DERRICKSON, S. R., & MOCK, D. W. 1977. The evolution of avian polyandry. *Am. Nat.* 111: 812–816.
- GRIFFIN, C. R. 1976. A preliminary comparison of Texas and Arizona Harris' Hawk (*Parabuteo unicinctus*) populations. *Raptor Res.* 10: 50–54.
- HAMILTON, W. D. 1964. The genetical evolution of social behavior. I and II. *J. Theor. Biol.* 7: 1–52,

- HAYS, H. 1972. Polyandry in the Spotted Sandpiper. *Living Bird* 11: 43-57.
- HILDEN, O. & VUOLANTE, S. 1972. Breeding biology of the Red-necked Phalarope (*Phalaropus lobatus*) in Finland. *Ornis Fenn.* 49: 57-85.
- HORN, H. S. 1978. Optimal tactics of reproduction and life-history. In Krebs, J. & Davies, N. B. (eds), *Behavioural ecology, an evolutionary approach*. London: Blackwood Scientific Publications.
- JENNI, D. A. 1974. The evolution of polyandry in birds. *Am. Zool.* 14: 129-144.
- JENNI, D. A. & COLLIER, G. 1972. Polyandry in the American Jacana (*Jacana spinosa*). *Auk* 89: 743-765.
- LIGON, J. D. & LIGON, S. H. 1978. Communal breeding in Green Woodhoopoes as a case for reciprocity. *Nature* 276: 496-498.
- MADER, W. J. 1975a. Biology of the Harris' Hawk in southern Arizona. *Living Bird* 14: 59-85.
- MADER, W. J. 1975b. Extra adults at Harris' Hawk nest. *Condor* 77: 482-485.
- MADER, W. J. 1978. A comparative nesting study of Red-tailed Hawks and Harris' Hawks in southern Arizona. *Auk* 95: 327-337.
- MADER, W. J. 1979. Breeding behavior of a polyandrous trio of Harris' Hawks in southern Arizona. *Auk* 96: 776-788.
- MAYFIELD, H. P. 1978. Undependable breeding conditions in the Red Phalarope. *Auk* 95: 590-592.
- MAYNARD SMITH, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25: 1-9.
- MAYNARD SMITH, J. & RIDPATH, M. G. 1972. Wife-sharing in the Tasmanian Native Hen, *Tribonyx mortierii*: a case of kin selection? *Am. Nat.* 106: 447-452.
- ORING, L. W. & KNUDSON, M. L. 1972. Monogamy and polyandry in the Spotted Sandpiper. *Living Bird* 11: 59-73.
- ORING, L. W. & MAXSON, S. J. 1978. Instances of simultaneous polyandry by a Spotted Sandpiper *Actitis macularia*. *Ibis* 120: 349-353.
- PARMELEE, D. F. & PAYNE, R. B. 1973. On multiple broods and the breeding strategy of arctic Sanderlings. *Ibis* 115: 218-226.
- PARRY, V. 1973. The auxiliary social system and its effect on territory and breeding in kookaburras. *Emu* 73: 81-100.
- PAYNE, R. B. 1979. Sexual selection and intersexual differences in variance of breeding success. *Am. Nat.* 114: 447-452.
- RALLS, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.* 111: 917-938.
- RICKLEFS, R. E. 1975. The evolution of cooperative breeding in birds. *Ibis* 117: 531-534.
- RIDPATH, M. G. 1972. The Tasmanian Native Hen, *Tribonyx mortierii*. I, II, & III. CSIRO Wildl. Res. 17: 1-118.
- SCHAMEL, D. & TRACY, D. 1977. Polyandry, replacement clutches, and site tenacity in the Red Phalarope at Barrow Alaska. *Bird-Banding* 48: 314-324.
- STALLCUP, J. A. & WOOLFENDEN, G. E. 1978. Family status and contributions to breeding in Florida Scrub Jays. *Anim. Behav.* 26: 1144-1156.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51: 3-47.
- SYMONS, D. 1979. The evolution of human sexuality. Oxford: Oxford University Press.
- VEHRENCAMP, S. L. 1977. Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris*. *Science* 197: 403-405.
- WOOLFENDEN, G. E. 1975. Florida Scrub Jay helpers at the nest. *Auk* 92: 1-15.
- WOOLFENDEN, G. E. 1981. The selfish behavior of avian altruists. Proc. XVIIth Int. Ornithol. Congr. (in press).
- WOOLFENDEN, G. E. & FITZPATRICK, J. W. 1978. The inheritance of territory in group-breeding birds. *BioScience* 28: 104-108.
- ZAHAVI, A. 1974. Communal nesting in the Arabian Babbler, a case of individual selection. *Ibis* 116: 84-87.

*Division of Biological Sciences, University of Missouri-Columbia, Columbia, Missouri 65211,
U.S.A.*