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1985-67

PRE-NESTING COOPERATION IN BIRDS: ANOTHER FORM OF HELPING BEHAVIOR

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ABSTRACT. Reports of cooperative behavior among promiscuous species and cooperative performance of pre-nest reproductive activities such as mate attraction, courtship, and copulation are rare. Factors that influence the likelihood of helping behavior occurring in promiscuous species are considered. The occurrence of pre-nest helping behavior and factors that may have selected against its presence in most species and favored its evolution in the groups in which it is found are discussed. It is argued that help with pre-nest activities should be detrimental to both the helper and recipient in species with lasting pair bonds.

RESUMEN. Son raros los informes sobre comportamiento cooperativo entre especies promiscuas y sobre el desempeño cooperativo de actividades reproductivas pre-anidadoras, tales como atracción de pareja, cortejo y copulación. Se consideran los factores que influyen en la probabilidad de comportamiento de ayuda que se presenta en especies promiscuas. Se discute la presencia de comportamiento de ayuda pre-anidadora y los factores que pueden haber sido seleccionados en contra de su presencia en la mayoría de las especies y los que pueden haber favorecido su evolución en los grupos en que se presenta dicho comportamiento. Se discute que la ayuda en las actividades pre-anidadoras debe ser detrimento para ambos, el ayudante y el ayudado, en especies con vínculos de pareja perdurables.

The literature on cooperative breeding suggests that cooperation occurs much more frequently at some stages of the reproductive cycle than at others. In an overwhelming majority of species, the help provided involves feeding and care of the young, although in some, help with nest building, nest defense, nest sanitation, incubation, and territory defense is reported also. At the same time, the distribution of helping behavior among species with different types of mating systems is not uniform. So far, cooperative breeding has been reported primarily for monogamous species with Type A territories (i.e., those in which courtship, copulation, nesting, and feeding occur, Nice 1941), although helping in colonial nesters (e.g., Fry 1975; Dow 1977; Balda and Balda 1978; Emlen 1982) and polyandrous species (e.g., Maynard Smith and Ridpath 1972; Ridpath 1972; Mader 1979; Birkhead 1981) is also known. In all of these species males and females share duties at the nest.

It is not surprising that most help reported involves nest-related activities. When Skutch (1935) first reported the phenomenon, he dealt only with "helpers at the nest." In fact, there is no *a priori* reason why help could not be rendered with any reproductive process, including pre-nest activities, or in species with any type of mating system, yet, reports of cooperative behavior among promiscuous species, and cooperation with mate attraction, courtship, and copulation, are rare. Interestingly, help with these particular pre-nest activities has been reported only from promiscuous species, and promiscuous species (with one exception, Dow 1977) have been reported to exhibit only this type of help. In fact, the primary basis of this relationship may not be the type of mating system, *per se*, but rather, the associated characteristic of pair-bond length, or length of the male-female association.

In the present paper, I consider factors that influence the likelihood of various types of helping behavior occurring in promiscuous species as well as the likelihood of help with mate attraction, courtship, and copulation occurring in species with different types of mating systems. I argue that selection should favor help with pre-nest activities among forms with transient bonds (most promiscuous species), but that its occurrence should be detrimental to both the helper and recipient in species with lasting pair bonds (most bird species).

DEFINITIONS

I use Verner and Willson's (1966:143) definition of promiscuous species as "those in which a member of one sex copulates with more than one member of the other [sex] but no lasting

[pair] bond is formed." In birds with lasting pair bonds males and females are associated through at least one nesting cycle. In those with transient bonds the association persists for a few hours or a few days, the sexes being associated only during the period of copulation; one sex assumes all responsibility for incubation and rearing of the young.

I use cooperative breeding to refer to situations in which one individual assists another who is neither offspring nor mate with some activity directly related to reproduction, and in which the help provided is not simply a coincidental result of normal, non-cooperative behavior. Thus, assistance with the defense of a breeding site may be considered help; defense of a separate feeding site is not. Likewise lek males displaying simultaneously, but independently, on different courts are not considered to cooperate, since at any given time, each may display or not regardless of the activities of the other males. Any benefit accruing to a male as a result of activities in which a second male is engaged are an incidental consequence of the second male's activities. In contrast, males that engage in reproductive activities at the same court, particularly joint, simultaneous, coordinated displays, and in which the behavior of one male directly influences that of the other, are considered to cooperate.

THE POTENTIAL AMONG PROMISCUOUS SPECIES FOR COOPERATION WITH REPRODUCTIVE ACTIVITIES

Generally, females of promiscuous species are solely responsible for rearing the young, and male-female contact is limited to copulation. Characteristically, females breed their first year and so are unavailable to serve as helpers (e.g., Wiley 1974; Foster 1976). Even if environmental factors prevented females from breeding, however, it is unlikely that they would help with nest-related activities. If helpers could enhance nest success, then it is hard to imagine how selection would have favored male emancipation from nest-related duties in the first place. Likewise, it has been suggested for some species that the separation of the parents is necessary to minimize activity around the nest in order to decrease predation (D. W. Snow 1962; B. K. Snow 1970; Wrangham 1980). Helpers at the nest would negate this advantage.

Males of promiscuous species, in contrast, often delay breeding for one to several years and, thus, are potential helpers (e.g., Snow 1962; Wiley 1974; Lill 1976; Foster 1977). Selection would not be expected to favor males that help at the nest, for the same reasons given for females. Another factor with regard to male helpers is that they would be in a position to commit infanticide and thereby increase their probability of fathering the female's next brood. Such behavior would be more likely to occur in promiscuous species than in those with persistent pair bonds because helpers in the former species would be less likely to be closely related to the young in the nest. This would be extremely detrimental to the female who already has invested substantially in the nest, eggs, and incubation. Thus, selection should favor breeding females that do not tolerate helper males at the nest.

In addition, as adults, males will not contribute to the rearing of the young, so they are not apt to benefit from learning aspects of nestling or fledgling care. Nor is such behavior likely to improve their future abilities to obtain mating territories (which are separated from nesting areas), to obtain high positions in a dominance hierarchy, or to attract females for copulation. Virtually the only means by which benefit would accrue to helping males would be through kin selection, although potential benefits would be less than if the males, themselves, bred. If males of one brood were to stay with their mother and help to rear young of a subsequent brood, they would be assured only of helping either full or half sibs. Thus, their average relatedness, r , to the young helped would be $\frac{1}{2} \geq r \geq \frac{1}{4}$, less than the relatedness of helpers to their own offspring.

The only other way for non-breeding males to cooperate with reproduction would be to assist breeding males with pre-nest activities.

OCCURRENCE OF PRE-NESTING COOPERATION

Help can be provided with three types of pre-nesting behavior—mate attraction, courtship, and protection of the courting or copulating pair from disruption by rivals (Foster 1983). I have found five species, representing three families, for which such cooperative activities have been reported and four more in which it is likely to occur. Because the number of species is small and this type of help is poorly known, a brief summary of the activities of each species and the contexts in which they occur is in order.

MANAKINS

Three of the 51 species of Pipridae are known to exhibit such behavior, and it is suspected to occur in four others. As the behavior and mating systems of only a small number of manakin species are known well, it seems likely that such behavior will be found in other piprids, as well.

In the Long-tailed Manakin, *Chiroxiphia linearis*, pairs (or occasionally trios) of males establish bonds that persist throughout a reproductive season, and often from year to year (data for this species from Foster 1977, unpubl. data). Each pair occupies a court on an exploded lek (one on which males maintain auditory rather than visual contact; Gilliard 1963) where the males advertise for and court females. One male of a pair is dominant and performs all copulations. Within trios, the dominance hierarchy is linear. If the dominant male disappears, the beta male apparently assumes his place and acquires a new subordinate male partner. Females of this species and all other members of the genus are solely responsible for nest-building and rearing of the young (Foster 1976).

The males of a Long-tailed Manakin pair cooperate to attract females and advertise their readiness to display and copulate. They do this by means of a call that they give in synchrony continuously through the day and breeding season. It almost never is given by a single male. Because the calls are essentially synchronous, the area over which they are detectable, their active space (sensu Bradbury 1981), increases in direct proportion to the number of males calling (theoretically, doubles). The expansion of the active space around the two calling males, as opposed to one, increases the area from which they can draw females. If a female arrives, the males move with her to a display perch and perform a cooperative courtship display that cannot be performed by one male alone, but requires the participation of at least two individuals. When the display ends, the subordinate male moves to nearby vegetation while the dominant completes an additional precopulatory display for the female, and copulates. The cooperative display serves to excite the female and probably increases the likelihood that copulation will occur, but only by the dominant male who performs all copulations.

The calling and dance activities of the subordinate should benefit the dominant by increasing the number of females that he may court and enhancing his success at copulation. These activities incur some cost to the subordinate in terms of time and energy expended and, perhaps, in terms of increased vulnerability to predators. The subordinate has little or no opportunity to mate and accrues no immediate benefit.

Cooperative courtship also is found in the Swallow-tailed Manakin, *Chiroxiphia caudata* (data for this species from Foster 1981, unpubl. data), in which four to six males occupy a series of communal display courts. As in *C. linearis*, the male associations persist throughout a breeding season and between years. A linear dominance hierarchy exists among the males, each moving up a step with the elimination of a higher-ranking male. Only the dominant male advertises for females in this species. When one arrives at the court, however, the alpha and beta males perform a cooperative, precopulatory display like that of the Long-tailed Manakin. This requires participation by two individuals and, again, serves to excite the female, increasing the probability that copulation will occur. Should the alpha or beta male be absent when a female visits, the gamma male takes his place in the display, and so on down the length of the hierarchy. However, the alpha male was always observed to return before copulation occurred and was responsible for all copulations, which are preceded by a solo display as in the Long-tail. The subordinates, at some cost, benefit the dominant with their actions, but without the opportunity for any immediate benefit to themselves.

Although the mating systems of the other two *Chiroxiphia*, *C. pareola* and *C. lanceolata*, are not known, these species exhibit the same cooperative, coordinated displays described for *C. caudata* and *C. linearis* (Aldrich and Bole 1937; Friedmann and Smith 1955; Gilliard 1959; Snow 1963a). Thus, cooperative courtship display and cooperative mate attraction may exist in these species as well.

In the Band-tailed Manakin (*Pipra fasciicauda*) each territory on an arena is owned by a single male (data for this species from Robbins 1983, in press, pers. comm.). Closely associated with him is a subordinate or beta individual who spends less time on the territory and occasionally visits alpha males on adjacent territories. Below them in the dominance hierarchy are non-territorial males that make brief visits to many territories. The alpha and beta males, and sometimes the non-territorial birds, display on the courts, sometimes simultaneously, but usually independently. If a female arrives, the alpha male chases the beta male away from

the main display perches and displays for the female alone. However, if a female has visited and displayed with the alpha male and then left without copulating, the male may perform a coordinated, joint display in an attempt to lure her back. If she does return, then the actions of the beta male have benefitted the alpha by providing another opportunity for him to copulate, but since again the alpha alone will display with her, the beta receives no immediate benefit from his presumably costly actions.

Also of benefit to the alpha male may be the presence and activity of the beta male at the court. Robbins (in press, pers. comm.) suggested that females may prefer territories with increased display activity as has been found for other lek species (e.g., Kruijt and Hogan 1967). The beta males seem analogous to the satellite males of the Ruff (*Philomachus pugnax*; discussed later), although whether or not the beta males have the opportunity to copulate has not been determined. Unlike the satellite males of the Ruff, beta male *P. fasciicauda* inherit dominance on a territory with the disappearance of the alpha male, and competition among non-territorial males for the alpha position is intense (Robbins, in press).

Males of both the Crimson-headed (*Pipra aureola*; Snow 1963b; Haverschmidt 1968) and Wire-tailed (*P. filicauda*; Schwartz and Snow 1979) Manakins, closely related members of a zoogeographical superspecies (Haffer 1970; Schwartz and Snow 1979) with *P. fasciicauda*, engage in coordinated, joint displays very similar to those of *P. fasciicauda*. The contexts in which the displays are given, their function, and the relationships of the males that perform them remain unknown, but also may turn out to be pre-nest stage helping.

TURKEY

In the Rio Grande subspecies of the Wild Turkey (*Meleagris gallopavo*, Phasianidae; data for this species from Watts 1968, Watts and Stokes 1971) males occur in groups consisting of individuals that were reared by the same hen, but are not necessarily kin related (Balph et al. 1980). Because some brood mixing occurs after hatching, and broods may combine to form large flocks, genetic relatedness of males in a group is not clear. In the late winter or early spring, both males and females visit the mating grounds where for about a month males court and copulate with females. The males continue to associate in their brood groups, a hierarchy existing both within groups and among them. Males of the most dominant group move about and display among the females at the arena, while those of subordinate groups display at the periphery. The males of each group display close together and in synchrony, which apparently provides for more rapid and intense stimulation of the female and increases the probability that copulation will occur. Usually, only the dominant male of the dominant group mates, disrupting attempts by subordinates of his own or other groups to copulate. Thus, synchronous display activities of subordinates contribute to the success of the dominant.

Copulation generally persists for four minutes or more, during which time members of the dominant's brood group fend off males from other groups, protecting him from disruption so that copulation proceeds undisturbed. Whether this last activity truly represents cooperation, however, has been questioned by Balph et al. (1980) who suggested that the "protection" provided by brood mates may be nothing more than a coincidental consequence of their defense of their own individual spaces.

During the latter months of the breeding season, male groups visit small groups of females occupying nesting sites. Because nesting sites are far more numerous than display grounds, some groups of females may be attended by only a single brood group. Thus, male groups that were subordinate on the display ground may be dominant at a nesting site, and the dominant males of many more groups may copulate. Again, subordinate members of the group display with the dominant and may protect him from disruption while he copulates.

Apparently, males never change brood groups, even when group size is reduced to one or two. With an average annual mortality of 40 percent among adult male turkeys, turnover in dominance position must be fairly rapid so that many males of a brood group may have the opportunity to copulate during their lives. However, among groups, dominance seems to be positively correlated with group size, so most males will have the opportunity to mate only on the nesting grounds and not at the display grounds. The dominance hierarchy that exists among the males of the brood group presumably determines the sequence of inheritance of the dominant position.

RUFFS

Males of the Ruff (Scolopacidae) occupy small territories grouped together on arenas where they court and copulate with females (data for this species from Hogan-Warburg 1966, van

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Rhijn 1973). These males fall into three categories based on a variety of criteria, including differences in behavior. Resident males own and defend territories on the arena. Marginal males, who will not concern us, attempt to establish territories (usually at the margin of the arena) and sometimes succeed in becoming residents. Satellite males do not own territories but use those of resident males, often becoming associated with one (or a few) male(s) and persistently visiting his territory. Both males display on the territory, often simultaneously, but always independently.

The success of a resident male in achieving copulations is influenced significantly by the number of females that visit his residence in the absence of a satellite male. Females, however, preferentially visit territories where satellites are displaying, which means that a high incidence of satellite males on a territory results in a high number of female visits to that territory. Thus, it is advantageous to residents to tolerate, or even attract, satellites. Once females are present on a territory, however, the owner attacks the satellite(s) and attempts to drive him (them) out (satellites never respond aggressively toward residents). Females generally do not copulate when satellite males are present, so the departure of the satellite increases the probability that copulation will occur. In addition, the aggressive resident-satellite interaction increases the receptivity of females for copulation. With copulation completed and/or the females gone, the owner male again allows satellites onto his territory as a means of increasing his chances of attracting more females.

The activities of the satellites on the court of a resident contribute directly to the reproductive success of the resident by increasing the number of females that visit and by increasing the likelihood that copulation will occur once the females are there. If a resident male disappears, the satellite attaches himself to another territorial male. He does not become the owner of the territory and, so far as is known, remains a satellite throughout his life. Satellites benefit by visiting and, thus, intermittently sharing good territories on the lek, which sometimes provides them with an opportunity to display for females and copulate.

DISCUSSION

COSTS, BENEFITS, AND THE LENGTH OF THE PAIR BOND

All of the cases reviewed involve species with transient pair bonds in which male helpers assist with pre-nest reproductive activities. Benefits accruing to recipients of this help seem fairly straight forward. Benefits to helpers are more difficult to ascertain, perhaps because they usually are delayed. Nevertheless, they are basically the same as those accruing to birds helping at any point in the reproductive cycle (i.e., increased survival, learning, acquisition of a display site or dominant position in a hierarchy, stolen copulations, increased inclusive fitness through kin selection). Why, then, does help at pre-nest stages appear to be confined to lek species, or, at least, to those with brief, transient, pair bonds? To answer this question, it is necessary to review the benefits and costs to both the donors and the recipients of the helping behavior and the ways in which these factors may be influenced by the length of the pair bond or male-female association.

Benefits to the recipient.—As a result of cooperative mate attraction, male advertising signals are broadcast over a greater area and, thus, should draw more females to the display ground. Females attracted to the arena and exposed to a cooperative courtship display are apparently more likely to mate. Likewise, if auxiliary males protect the mating pair from disruption by rival males, then copulation is more likely to succeed. All of these factors should directly increase the fitness of the breeding males. However, the magnitude of these benefits should decrease as the length of the pair bond increases (Fig. 1), for several reasons:

(1) When pair bonds are very short, they must be made rapidly and the female must be excited quickly for copulation. In conjunction with this, males of promiscuous species rank among those with the most elaborate and brightly colored plumages and the most elaborate displays (Sibley 1957). Addition of help by a subordinate can be considered an extension of this, analagous, perhaps, to the acquisition of an additional set of plumes or crests or to a functional increase in size of the displaying male. As the bonding/courtship period lengthens, the premium on speed of bonding decreases since the process may occur over a period of several days or weeks instead of just a few minutes. Thus, the addition of a second, helping male may not be favored by selection.

(2) As the length of the pair bond increases from mating systems of promiscuity to polygyny, and then to monogamy, the proportion of males who mate with only a single female will increase. Even in polygynous species, males generally have only a few mates. As females of

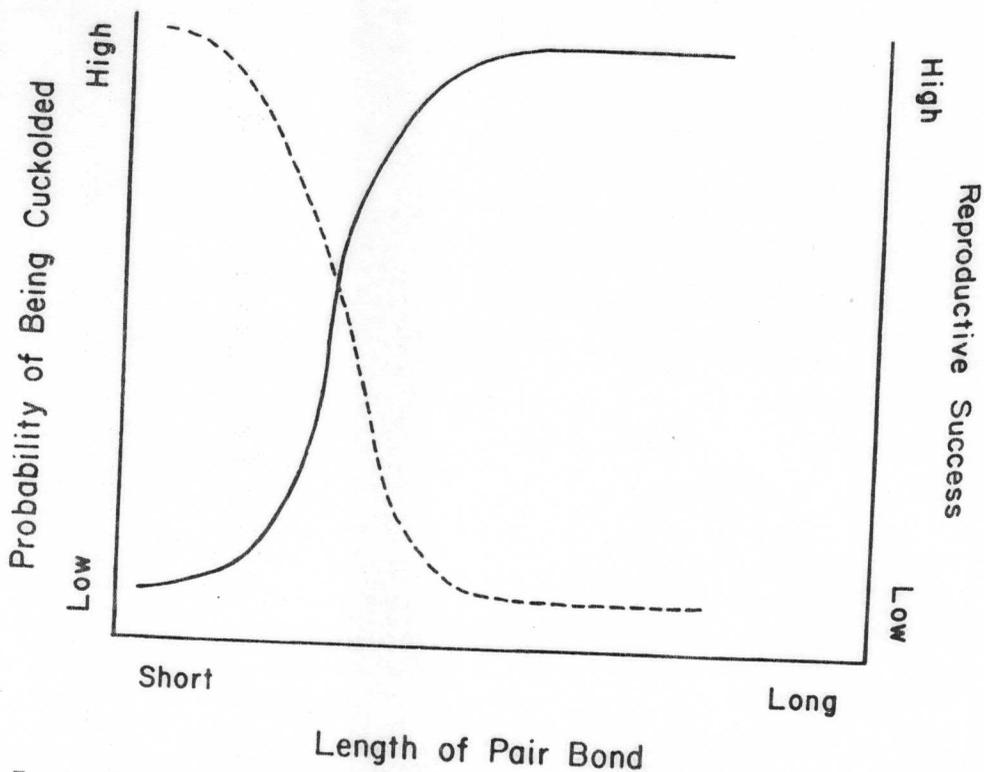


FIG. 1. The costs (probability of being cuckolded; solid line) and benefits (increased reproductive success through enhancement of mate attraction, more rapid mate excitation, and protection from disruption; dashed line) to male breeders of pre-nest cooperation with auxiliary males according to the length of the male-female bond.

promiscuous species are mated, the operational sex ratio (i.e., the ratio of fertilizable females to sexually active, potentially "eligible" males; Emlen and Oring 1977) will decrease. Thus, competition among males for females will increase continuously through the breeding season. In monogamous species, in contrast, the operational sex ratio should remain fixed as females become mated. In polygynous species, competition for females will increase, but at a slower rate than in promiscuous forms, while the operational sex ratio will show periodic, stepwise, decreases. In monogamous species with equal sex ratios, each male has a high probability of mating. In a promiscuous species with equal sex ratios, a few males will have a very high probability of mating, and most males will have a very low probability of mating. Thus, competition among males for mates will be intense, and anything that enhances a male's attractiveness to females, such as a helper, will be favored.

(3) Finally, the need for protection from disruption by rival males during copulation should be more common in birds with arena mating systems and associated short pair bonds because males of these species are usually closely grouped and in visual contact, and, thus, aware of visits by females to their rivals who are readily accessible for disruption. Birds with lasting pair bonds, on the other hand, tend to occupy large, Type A territories; neighbors are widely spaced and, perhaps, unaware when copulation occurs on an adjacent territory. Unmated males lacking territories should be more apt to disrupt, but the probability of their being present at the right moment for this should be very small.

Overall, a benefit curve should follow a sigmoid path (Fig. 1). Benefits should be very high during a brief courtship period and then drop rapidly to zero when the premium on rapid excitation of the female no longer exists and competition among males is less, as in mating systems with long pair bonds.

Costs to the recipient.—The costs to the recipient of helping behavior also will vary with

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the length of the pair bond, but now, directly as opposed to inversely (Fig. 1). Costs such as use of food or other resources that might be needed by the monogamous breeding pair or its offspring, or attraction of additional predators to the area, if anything, should increase because more birds will be occupying the territory, i.e., mate and young. In most promiscuous species, the birds do not feed on the mating territory, nor do females nest there, so attraction of predators to a nest is impossible. If helpers enhance activity at the mating site, however, they could attract more predators there.

The really significant cost to the recipient is the probability of being cuckolded. In species in which the male-female association is brief, a male can guard the female until she leaves the mating site. As the length of the courtship/mating period increases from a few minutes to a few days, however, the difficulty the dominant male will have guarding his mate will increase steeply as, therefore, will the probability of stolen copulation by a subordinate (Fig. 1). Although a male may stick with his mate closely throughout her receptive period, it is unlikely that he can be with her every instant. Important in conjunction with this is the proximity of a helping male to the mating site. A helper at courtship has access to that site; helper males at other stages do not.

If we consider these costs graphically, we see that the cost curve follows a sigmoid path (Fig. 1). Presumably, as long as courtship and copulation occur within a short period, the dominant male can be reasonably assured of protecting his mate from copulation with rivals. As the length of this period increases, the probability of his being cuckolded should rise steeply. At some point, however, his efficiency and the amount of time he spends with his mate per day should be constant, regardless of the length of the receptive period, and probability of being cuckolded should level.

A combination of high benefits and low costs for male recipients of pre-nest help would be expected only when the courtship/breeding period is very short, as in promiscuous (including arena-mating) species (to the left of the graph, Fig. 1). Because the slopes of both curves change steeply, the transition from net benefit to net loss should be relatively sharp. This means that males of non-promiscuous species should not tolerate the presence of helper males during the courtship/mating period and should actively drive them from the mating area or keep them away from the receptive female. This is what occurs in territorial males without help, and even in those species in which helping behavior occurs in post-copulatory stages (e.g., Andrews and Naik 1970; Woolfenden 1975; Zahavi 1976; Woolfenden and Fitzpatrick 1977).

Costs and benefits to the donors.—We also may consider the relative costs and benefits of pre-nesting help to the donor of the action, and the ways in which these factors may be influenced by the length of the pair bond. Benefits to helpers fall into five categories:

(1) Increased survival. Certain benefits associated with group living may enhance the survival of group members as opposed to solitary individuals (e.g., Stallcup and Woolfenden 1978). These should apply to birds with any social system. That they may be affected by stage in the life cycle or length of the breeding period is not evident.

(2) Increased experience or learning. In those species in which the pair bond is short, in which competition for mates is extreme, and in which speed and intensity of female excitation are at a premium (as in manakins), courtship behavior should be elaborate and intense. Thus, learning may be important, not necessarily with regard to performance of particular display elements, although this may occur, but with regard to tactics (i.e., use of particular display elements in response to particular female behaviors, as in Black Grouse [Kruijt and Hogan 1967]). If participation through helping is a form of learning, then one would expect to see this type of behavior. As the courtship period lengthens, and especially as courtship shifts from predominantly visual to predominantly auditory stimuli, the premium on learning should decrease. Thus, one would expect learning of courtship techniques to be most important in lek-displaying forms (Fig. 2).

(3) Increased probability of taking over a good display site or territory, or assuming the dominant position in a hierarchy, and (4) Increased probability of stealing copulations. Assumption of the dominant position in a hierarchy seems important in both manakins and turkeys. In those species for which data on marked individuals are available, dominance position on good sites is inherited in a linear sequence. Presumably, by helping, a male retains the opportunity to be present on the territory and to improve his status as males above him are eliminated. And, though position in a hierarchy and, thus, inheritance may be correlated with age, prior occupancy also may bestow an advantage in contests for dominance (e.g., Foster 1981). An auxiliary male also could enhance the quality of the territory in the eyes of

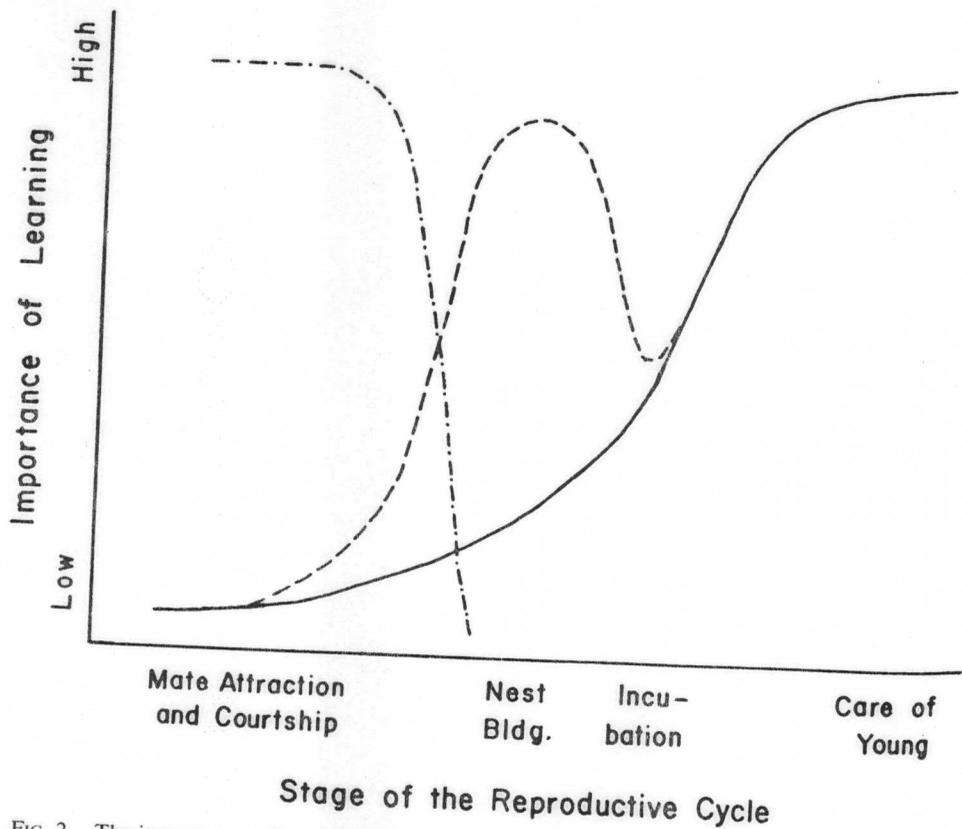


FIG. 2. The importance of learning at different stages of the reproductive cycle for species with brief, transient pair bonds (dot-dash line), or extended, persistent pair bonds (solid line). For species with extended bonds, an additional period of learning (dashed line) may be important in those species with elaborate nests.

females who might return in subsequent years (when he is the dominant) to breed. Stolen copulations may occur among species with all types of mating systems (e.g., Bray et al. 1975; Fujioka and Yamagashi 1981), yet the closer and more frequently a male is at the site of copulation (e.g., Power and Doner 1980), the greater the probability that he will be able to take advantage of the opportunity should it arise. This surely must be a factor in both manakins and Ruffs and, perhaps, turkeys.

Increased opportunities for stolen copulation, and enhanced probability of taking over a good territory or assuming a dominant position in a hierarchy would seem to accrue to helpers regardless of the length of the pair bond. Thus, one would expect helpers to assist with courtship activities and, thereby, to increase their proximity to receptive females and the mating site, and, perhaps, to enhance their status, whenever the opportunity arose. That they do not in species with extended pair bonds probably results, at least in part, from the intolerance of the breeding males.

(5) Increased inclusive fitness through kin selection. Enhancement of inclusive fitness through kin selection requires first that the relatedness of helpers and recipients be greater than the relatedness of helpers and the general population. Second, it requires that the helpers be able in some way to insure that the probability that the individuals they help will be kin is greater than random. Very few data on the kin relationships of the species considered here are available. Various lines of evidence argue, however, that males of several of these species are not kin-related (Foster 1977; Balph et al. 1980) and that this factor is not important. Even so, from a theoretical point of view, especially since the sample of species so far reported to

TABLE I
 EXPECTED OCCURRENCE OF NET BENEFITS (+) OR COSTS (-) TO BREEDERS AND HELPERS AS A RESULT OF COOPERATION WITH DIFFERENT REPRODUCTIVE ACTIVITIES, AS A FUNCTION OF PAIR-BOND LENGTH

Reproductive activity	Pair-bond length			
	Long ¹		Short ²	
	Breeder	Helper	Breeder	Helper
Territory defense	+	+	+	+
Mate attraction	-	-	+	+
Courtship	-	-	+	+
Copulation	-	-	+	+
Nest-building	-/+	-/+	-	-
Incubation	-	-	-	-
Care of young ³	+	+	-	-

¹ Monogamous and polygamous forms.

² Promiscuous forms.

³ Includes nest defense, nest sanitation, brooding and feeding of young.

show pre-nest help is so small, it is useful to consider how the factor may be influenced by pair-bond length.

As indicated earlier, helpers at pre-nest stages may assist their fathers, to whom they are related by 1/2, brothers or half-brothers, to whom they are related on average by 1/2 or 1/4, respectively, or various individuals of lesser kinship. Degree of relatedness should not be influenced by pair-bond length. The likelihood of association with related individuals, on the otherhand, definitely may be influenced by the persistence of the relationship between the helper's parents.

In monogamous species, the helpers most often are offspring of previous broods. From the time they hatch until they leave to breed on their own, they remain in the family territory or home range, associated with family members. Thus, the probability that the recipients of their help will be parents or sibs, as closely related to them as their own offspring, is high.

In promiscuous species, on the other hand, females alone rear young, usually in areas away from the display grounds where they copulated. Young males that delay breeding often undergo a period of pre-reproductive dispersal and may not become associated with a male as a helper until they are several years old (e.g., Foster 1977; Graves et al. 1983). These factors should greatly decrease the probability of a male becoming associated with close kin when he begins to help. The only other alternative would be for male sibs from the same brood to remain associated until they breed and then to assist one another. There is no evidence of this for any species so far described (Balph et al. 1980), and in some species, small clutch size, low reproductive success, and advanced age at which males begin helping (Foster 1976, 1977) argue against it.

Thus, one must conclude that kin selection is not likely to be a driving force in the evolution of pre-nest helping behavior in promiscuous species. In those species in which helpers and breeders share a close kin relationship, however, it may reinforce selective advantages that accrue for other reasons.

ARENA VERSUS NON-ARENA FORMS

Males of species with promiscuous mating systems may be clumped on arenas or leks, loosely grouped on exploded leks, or uniformly dispersed throughout the habitat. Thus far, all reports of pre-nest helping behavior, as I have defined it, are for arena-occupying forms. This is not unexpected since the opportunity for the evolution of cooperative displays is greater in these species. Such displays often appear to have originated from male-male aggressive interactions related to disputes over display sites (Foster 1977, 1981) or territory ownership (satellite males). Such disputes would be expected to occur more frequently if males were closely grouped in a small area with a finite number of display perches than if they were widely dispersed through a habitat. The same argument applies to disruptions of copulations by rival males (Foster 1983).

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OCCURRENCE OF HELP WITH OTHER REPRODUCTIVE ACTIVITIES

The arguments developed in an attempt to explain the rarity of pre-nest helping behavior and its apparent restriction to promiscuous species can be applied equally to help provided at other stages of reproduction. In Table 1, the major reproductive activities are listed along with the expected occurrence of net benefits or costs accruing as a result of cooperation with these activities among species having mating systems with long or short pair bonds. I will briefly consider the rationale behind these designations.

If acquisition of a territory or dominance in an area is one of the benefits accruing to helpers, then they should be expected to assist with territory defense. Territory owners, on the other hand, should welcome such help, even though it means that more individuals will occupy the territory, as long as the help ensures control of a larger and/or better quality area. These benefits should operate for both the donor and recipient of the help regardless of the length of the pair bond. Defense of territories by all members of a group has been reported for many monogamous species (e.g., Woolfenden and Fitzpatrick 1978; Grant and Grant 1979) and the promiscuous noisy miner (Dow 1979), although in the latter, unlike the situation in most promiscuous forms, males and females remain associated throughout the reproductive period.

For the reasons given above, promiscuous forms would be expected to cooperate with pre-nest stage but not nest-related activities (Table 1). In contrast, I have argued that in species with persistent pair bonds, individuals should not have pre-nest stage help (Table 1), but may be expected to cooperate with nest-related activities.

The major nest-oriented activities with which helpers of such species can cooperate are nest-building, incubation, and care of young (nest defense, nest sanitation, incubation, and feeding). As indicated earlier, helpers should maximize the likelihood of return on the help invested by helping at the latest reproductive stage possible and/or by helping at the most crucial stage. Nest-building does not fit either category except, perhaps, among species with complex nests, the building of which requires considerable effort or practice (e.g., Rowley 1978). In addition, male help with nest building generally should not be tolerated by breeding males if the helpers are sexually mature, since females usually are receptive during this period.

Cooperative incubation also should occur only rarely (Table 1) and involve species in which more than one female lays in a particular nest or in which more than one male mates with the laying female (Frith and Davies 1961; Ridpath 1972; Vehrencamp 1978; Koenig and Pitelka 1979; Mader 1979). All birds sharing in incubation would be parents (or potential parents). It is not likely that non-breeding helpers would practice infanticide if associated with a nest (at any stage) because of a high probability that the young would be full sibs. Breeders, however, might not welcome incubation by inexperienced helpers because exposure of eggs to temperatures outside the optimum range may be fatal or lead to developmental abnormalities (Drent 1975). It also may be that non-breeders are not physiologically equipped to incubate successfully (Vehrencamp 1982).

Finally, it would appear advantageous to both the donor and the recipient of help for birds to cooperate in feeding nestlings (Table 1). Inexperienced helpers may benefit from learning (Lawton and Guidon 1981), but, unlike the situation with incubation, an error (e.g., bringing too large a food item or eating it oneself) causes no direct damage to the nestling. Helpers also may benefit through kin selection because in most instances, their average relatedness to the nestlings they feed is $\frac{1}{2}$. The breeders benefit from the help provided by producing more young (e.g., Rowley 1965; Woolfenden 1975), or by producing the average number of offspring, but at less cost to themselves (e.g., Krekorian 1978; Rowley 1978).

ACKNOWLEDGMENTS

The development of my ideas was enhanced by discussion with many colleagues, several of whom also read an early draft of the manuscript. For their helpful comments I thank B. Beehler, R. P. Balda, R. W. McDiarmid, E. S. Morton, M. B. Robbins, D. E. Wilson, and R. L. Zusi. I also thank G. Graves and M. Robbins, who kindly supplied copies of unpublished manuscripts for my use, and C. W. Angle, who prepared the figures.

LITERATURE CITED

- ALDRICH, J. W., AND B. P. BOLE, JR. 1937. The birds and mammals of the western slope of the Azuero Peninsula [Republic of Panama]. *Sci. Publ. Cleveland Mus. Nat. Hist.* VII.
 ANDREWS, M. I., AND R. M. NAIK. 1970. The biology of the Jungle Babbler. *Pavo* 8:1-34.

- BALDA, R. P., AND J. H. BALDA. 1978. The care of young Piñon Jays (*Gymnorhinus cyanocephalus*) and their integration into the flock. *J. Ornithol.* 119:146-171.
- BALPH, D. F., G. S. INNIS, AND M. H. BALPH. 1980. Kin selection in Rio Grande turkeys: a critical assessment. *Auk* 97:854-860.
- BIRKHEAD, M. E. 1981. The social behaviour of the dunnock, *Prunella modularis*. *Ibis* 123:75-84.
- BRADBURY, J. W. 1981. The evolution of leks. Pp. 138-169, *In* R. D. Alexander and D. W. Tinkle (eds.), *Natural Selection and Social Behavior*. Chiron Press, New York.
- BRAY, O. E., J. J. KENNELLY, AND J. L. GUARINO. 1975. Fertility of eggs produced on territories of vasectomized Red-winged Blackbirds. *Wilson Bull.* 87:187-195.
- DOW, D. D. 1977. Reproductive behavior of the Noisy Miner, a communally breeding honeyeater. *Living Bird* 16:163-185.
- DOW, D. D. 1979. Agonistic and spacing behaviour of the Noisy Miner *Manorina melanocephala*, a communally breeding honeyeater. *Ibis* 121:423-436.
- DRENT, R. 1975. Incubation. Pp. 333-420, *In* D. S. Farner and J. R. King (eds.), *Avian Biology V*. Academic Press, New York.
- EMLEN, S. T. 1982. The evolution of helping. I. An ecological constraints model. *Am. Nat.* 119:29-39.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- FOSTER, M. S. 1976. Nesting biology of the Long-tailed Manakin. *Wilson Bull.* 88:400-420.
- FOSTER, M. S. 1977. Odd couples in manakins: a study of social organization and cooperative breeding in *Chiroxiphia linearis*. *Am. Nat.* 111:845-853.
- FOSTER, M. S. 1981. Cooperative behavior and social organization of the Swallow-tailed Manakin (*Chiroxiphia caudata*). *Behav. Ecol. Sociobiol.* 9:167-177.
- FOSTER, M. S. 1983. Disruption, dispersion, and dominance in lek-breeding birds. *Am. Nat.* 122:53-72.
- FRIEDMANN, H., AND F. D. SMITH. 1955. A further contribution to the ornithology of northeastern Venezuela. *Proc. U.S. Natl. Mus.* 104:463-524.
- FRITH, H. J., AND S. J. F. DAVIS. 1961. The ecology of the Magpie Goose. *CSIRO Wildl. Res.* 6:91-141.
- FRY, C. H. 1975. Cooperative breeding in bee-eaters and longevity as an attribute of group-breeding birds. *Emu* 74 Suppl., pp. 308-309.
- FUJIOKA, M., AND S. YAMAGISHI. 1981. Extramarital and pair copulations in the Cattle Egret. *Auk* 98:134-144.
- GILLIARD, E. T. 1959. Notes on the courtship behavior of the Blue-backed Manakin (*Chiroxiphia pareola*). *Am. Mus. Novit.* No. 1942.
- GILLIARD, E. T. 1963. The evolution of bowerbirds. *Sci. Am.* 209(2):38-46.
- GRANT, P. R., AND N. GRANT. 1979. Breeding and feeding of Galapagos Mockingbirds, *Nesomimus parvulus*. *Auk* 96:723-736.
- GRAVES, G. R., M. B. ROBBINS, AND J. V. REMSEN, JR. 1983. Age and sexual difference in spatial distribution and mobility in manakins (Pipridae): inferences from mist-netting. *J. Field Ornithol.* 54:407-412.
- HAFFER, J. 1970. Art-Entstehung bei einiger Waldvogeln Amazoniens. *J. Ornithol.* 111:285-331.
- HAVERSCHMIDT, F. 1968. Birds of Surinam. Oliver and Boyd, Edinburgh.
- HOGAN-WARBURG, A. J. 1966. Social behavior of the Ruff, *Philomachus pugnax* (L.). *Ardea* 54:109-229.
- KOENIG, W. D., AND F. A. PITELKA. 1979. Relatedness and inbreeding avoidance: counterplays in the communally nesting acorn woodpecker. *Science* 206:1103-1105.
- KREKORIAN, C. O. 1978. Alloparental care in the Purple Gallinule. *Condor* 80:382-390.
- KRUIJT, J. P., AND J. A. HOGAN. 1967. Social behavior on the lek in Black Grouse, *Lyrurus tetrix tetrix* (L.). *Ardea* 55:203-240.
- LAWTON, M. F., AND C. F. GUINDON. 1981. Flock composition, breeding success, and learning in the Brown Jay. *Condor* 83:27-33.
- LILL, A. 1976. Lek behavior in the Golden-headed Manakin, *Pipra erythrocephala* in Trinidad (West Indies). *J. Ethol. Suppl.* 18:1-84.
- MADER, W. J. 1979. Breeding behavior of a polyandrous trio of Harris' Hawks in southern Arizona. *Auk* 96:776-788.
- MAYNARD SMITH, J., AND M. G. RIDPATH. 1972. Wife sharing in the Tasmanian Native Hen, *Tribonyx mortierii*: a case of kin selection? *Am. Nat.* 106:447-452.
- NICE, M. M. 1941. The role of territory in bird life. *Am. Midl. Nat.* 26:441-487.
- POWER, H. W., AND C. G. P. DONER. 1980. Experiments on cuckoldry in the Mountain Bluebird. *Am. Nat.* 116:689-704.
- RIDPATH, M. G. 1972. The Tasmanian Native Hen, *Tribonyx mortierii* II. The individual, the group, and the population. *CSIRO Wildl. Res.* 17:53-90.
- ROBBINS, M. B. 1983. The display repertoire of the Band-tailed Manakin (*Pipra fasciicauda*). *Wilson Bull.* 95:321-342.

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