Acta 19th Congressus Internationalis Ornithologici. 1986.
Ottawa, Canada pp. 420-227.

Mate Guarding in the Arabian Babbler, a Group-living Songbird

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Abstract
The Arabian Babbler (*Turdoides squamiceps*) breeds in groups in which several males and females may co-operate to defend a territory. Within groups, adults are usually not aggressive, but are instead altruistic toward their rivals. I interpret such altruistic acts as a display of social status. Any aggression between adult males or females always results in the eviction of the loser from the group. Reproduction, however, involves both competition and co-operation within any group. For example, males compete with one another to copulate with the alpha female even when the beta female is available. More than one male may copulate with the breeding female, and several females may, under some conditions, co-operate in laying at the same nest. Because babblers do not copulate when another babbler is watching, subordinate babblers may interfere with the copulations of dominants by following them. Babblers copulate not only to fertilize eggs but also with members of other groups and outside the breeding season. I suggest that the potential for gain through mate guarding may be high in group-breeding birds in which only a few adults actually breed. Thus, well-developed social hierarchies in a system involving both co-operation and conflict may result in a subtle form of mate guarding that replaces threat and physical conflict.

Introduction

Groups of birds that co-operate in breeding often consist of several adult males and females, some or all of which reproduce in a given season. It is reasonable to expect the reproducing individuals within a group to compete with one another, especially when the reproductive output of the group does not increase with an increase in the number of reproducing individuals (Zahavi 1974). Mate guarding is an obvious way to improve success in such reproductive competition.

Group-living birds may have one or more breeding males per group. In groups with a single breeding male, such as the White-fronted Bee-eater (*Merops*

bullockoides) (Emlen and Wrege 1986), mate-guarding behaviour is similar to that in species that do not live in groups (see other papers in this symposium). Groove-billed Anis (*Crotophaga sulcirostris*) form a group composed of several breeding pairs laying at the same nest (Vehrencamp *et al.* 1986). Both extra-pair copulations and the attention paid by males to females during egg laying suggest that mate guarding is also important in this social system. In Pukekos (*Porphyrio p. melanotus*) (Craig 1980), subordinate males succeed in copulating, but not in the presence of the dominant male. In Acorn Woodpeckers (*Melanerpes formicivorus*) (Mumme *et al.* 1983), on the other hand, mate guarding occurs only in groups with several breeding males.

In this paper, I discuss mate guarding in the Arabian Babbler (*Turdoides squamiceps*), a species that I have studied over the last 15 yr in Hatzeva, in the desert of the Rift Valley, Israel, 30 km south of the Dead Sea. These birds live and breed in groups of 2 to 22 individuals that are resident in their territories throughout the year. Groups are often composed of several adult breeding males and up to two or three breeding females all laying eggs in the same nest. During my study, there has never been more than one nest active in a group territory at any one time. A female normally lays 3 to 5 eggs, but we have had cases of two females laying 6 to 9 eggs, and, once, three females laid a total of 13 eggs in the same nest. Because large groups do not fledge more young than smaller groups, co-operation in breeding cannot be explained by either kin selection or reciprocity. Even when more than two individuals participate in breeding, never more than five fledglings have been reared from a nest.

In 1971, we ringed 20 groups (120 individuals), and we have followed the life histories of all of these marked individuals. We have also followed all babblers that were born or have come to reside in the study area since 1971: altogether, approximately 1500 individuals. Nearly all the birds in the study population are tame to the extent that we are able to watch them while standing among the members of a group. For example, we are able to watch a nest early in the morning when a female is laying, and we can follow the birds when they copulate.

It is obvious that group members have a conflict of interest with respect to breeding in the common territory while at the same time sharing an interest in defending that territory. I believe that this mixture of conflict and common interests in a breeding group of babblers is typical of group breeding in general (Zahavi 1976; Emlen 1978).

Breeding Groups

The simplest group of babblers is composed of a breeding pair and their offspring. There is no competition for breeding in such groups because babblers maintain a strict taboo on incest, i.e., a babbler never mates with another that was a nestling while it was a member of the same group. Thus, although babblers mature when they are 2 yr old, some offspring have attained the age of 6 yr within their parental territory without attempting to breed, apparently because both of their parents were still alive and present in the group.

More complex breeding relationships have occurred in groups in which the mother of some group members was replaced by an alien female (females tend to disperse and males tend to stay and breed in or near their parental group). In such groups, all sexually mature males court and may copulate with the breeding female.

The most complex groups are those in which a few adult males and several adult females begin to collaborate in breeding. Such associations occur when a new group is formed, either on a vacant territory (which is a rare event) or when more than one mature female joins a group. In such groups, the breeding males and females are initially always alien to one another.

Social Rank and Social Status

Adult babblers always dominate younger members of a parental group, and adult males dominate all females. A few days after they fledge, siblings from the same brood determine their social rank by fighting. Such aggression, however, declines with age so that, by the time they are sexually mature, male babblers do not display much overt aggression among themselves. For example, they fight higher-ranking individuals only once, because the loser in such a fight is either killed or chased from the group.

There is also much variation in the age differences between dominants and subordinates within a group. In one group, the dominant male may be 10 yr old and the beta male his 2-yr-old son, whereas in another group, the dominant male may be a 2-yr-old and the beta male its sibling from the same brood. As a result, the dominance relationship (i.e., the relative social status) between the alpha and beta male may be quite different in the two cases.

Because the rank of a babbler relative to any other babbler in its group does not change as long as they are both members of the same group, displays of dominance and subordination can change only the degree of dominance between two individuals. In simpler social systems, a higher social rank usually enables an individual to obtain whatever it wishes from a subordinate. In cooperative systems such as a group of babblers, group members often compromise, even in disputes over the right to copulate. As a consequence, the most dominant babbler in a group attains the most copulations; lower-ranking males attain copulations in relation to their rank and social status. Displays of social status by competing males enable them to reach such a compromise without overt aggression.

Mate Guarding and Copulations

From a few days preceding egg laying until the clutch is complete (or often until the day before clutch completion), the dominant male usually stays close to the laying female or acts as a sentinel and ensures that it can observe the female continuously. If the female disappears around a bush, a dominant male acting as a sentinel will move to another post or come down near her, especially if a competing male is nearby. In addition, the dominant male in a group often perches on the nest rim when the female is laying an egg and accompanies her when she leaves the nest after egg laying. The very close attendance of the domi-

nant male with the female at that time of day suggests that this is the best time for fertilization (see also Mace, this symposium). The male nearly always copulates with the female in the early morning after egg laying.

This behaviour of the dominant male stands in contrast to his relative lack of interest in the female a week or two before egg laying, when he may let the female out of his sight and may let her court subordinate males without interfering. The decline in the male's interest in the female on the morning on which the last egg is laid also suggests that the male may have a way of knowing when the female ovulates.

It is not easy, however, to determine the period during which copulations function to fertilize the eggs, as babblers seem to copulate for reasons other than fertilization. Thus, when a breeding female copulates with a subordinate male a few weeks (or even a week) before egg laying, it is difficult to know if such a copulation has any chance of fertilizing her eggs. Males also copulate outside the breeding season with new females joining the group and, occasionally, during border fights (when subordinate non-breeding males have been observed copulating with subordinate non-laying females from other groups). A dominant male was also observed copulating once with a refugee female.

In contrast, two to four males have been observed copulating early in the morning with a breeding female on days when she laid her eggs. Although copulations during the egg-laying period may occur throughout the day, they seem to be more common in the early morning. Subordinate males often follow the dominant pair waiting for their chance to find the female unattended. Subordinates invest less time in following the female later in the day, either because they have been discouraged earlier by the dominant male or because the probability of successful fertilization decreases during the day.

Babbler pairs do not copulate while another babbler is watching. Thus, copulation may not be an easy task, because the members of a group of babblers spend most of their day within a few metres of one another. In most cases, the male invites the female to copulate by taking a food item (or sometimes a stick) in his beak and leading the female away from the group. If the female follows and if they manage to be alone behind or under a bush, they copulate. Babbler pairs may copulate more than once at any one invitation, and they may copulate several times during a day. Copulations also occur without such an invitation by the male if a female crouches in the male's presence.

The arrival of any babbler within sight during copulation stops the proceedings, even if the intruder is a fledgling. Thus, when subordinate babblers follow the breeding pair, their presence interferes with copulation. As a rule, males do not threaten or act aggressively toward other babblers that interfere with their copulations; the conflict between rival males is resolved by more subtle means. The dominant male may walk toward a subordinate, cross its path, feed it, allopreen it on the back, or even reprimand it by circling while emitting the "reprimand call." Dominants usually do not chase subordinates in such an encounter, nor do they show any overt aggression such as they often display to mature males or to females during the breeding period.

Hence, to perform a successful copulation, a male babbler should be able to hinder the approach of other members of the group. I suggest that the ability of a male to control the approach of other individuals displays to the female his ability to control the group in general. This ability to control the group may, in turn, be correlated with the male's ability to defend the clutch from destruction by rival males.

Role of the Female in the Social Group

Because male babblers do not force copulations, they need the collaboration of the female. A female may follow a male to copulate with it, or it may vocalize to attract the attention of the group when courted by a male with which it does not desire to copulate. A female may also fly quickly from the nest to copulate with a subordinate male before the dominant male arrives.

A dominant male that is not satisfied with the behaviour of a female often attacks, chases, grabs, and pecks her. A dominant male finding a female courting or copulating with a subordinate attacks the female first and then approaches the male to reprimand him and allopreen. The subordinate usually acknowledges the arrival of the dominant by a display of subordination; a display of overt aggression is very rare.

Females court the dominant male early in the season by presenting food or a stick. The male often reacts with aggression. At that time, the female often courts and copulates with subordinate males and rejects the dominant male. I suggest that the female behaves in this way to tempt the dominant into displaying his status (i.e., to display his claim for his share in copulations). Later in the breeding cycle, the dominant male stays near the female, and the female tends to reject subordinate males. However, she often copulates with any subordinate that manages to follow the dominant male over long periods, even copulating with subordinates on the days she ovulates.

Mate Guarding in Complex Groups

The pattern of mate guarding in groups with two to three laying females and two or more breeding males is much more complex. For example, the behaviour of males, especially beta males, is very variable. Usually the alpha male guards the dominant female. The beta male may visit the nest frequently or only on rare occasions. When a beta male is allowed to perch on or near the rim of the nest along with the alpha male, he is aggressive towards the beta female and often follows the dominant pair as if the beta female did not exist. However, when an opportunity arises during the day, both males may copulate with the beta female.

The variation in these behaviours is as large as the number of such groups we have watched. Subordinate breeding males may copulate with females whenever opportunity arises. For example, when the alpha and beta males court the alpha female, the gamma male may copulate with the beta female. In another case, when the gamma male was being reprimanded by the beta male, the delta male copulated with the beta female. Thus, opportunities often arise for subordinate males to copulate, even with the alpha female.

Females usually collaborate in breeding (i.e., lay in the same nest) only in the first successful brood after forming a new group. Once they succeed in raising a brood, the dominant female either chases its rivals from the group or inhibits them from laying.

Mate Guarding, Social Status, and Altruism

Although the alpha male obtains more copulations than the beta, and so on, both the absolute number and the timing of copulations obtained by the beta male are very variable. Some subordinates obtain several copulations on days when the female lays an egg, and others may not copulate at all or may copulate only before egg laying when the alpha male is not yet closely guarding the laying female. An old male can easily control his son, who rarely interferes with his copulations. On the other hand, a subordinate may follow his dominant brother and the breeding female for many hours, interfering with copulations by his presence and often obtaining many more copulations than a 2-yr-old son in competition with his father. I suggest that the difference between these two cases is a consequence of the difference in the social status of the dominant males. The old father has a higher status in his group than the dominant brother in his own group. In some cases, one reprimand call early in the morning discourages the beta male from following the alpha male during courtship. In other cases, the beta male may follow the dominant pair closely for hours despite many interactions. A higher social status enables an individual to obtain copulations without resorting to aggression.

Because a higher social status provides a better chance for successful copulation, it is not surprising that babblers invest much time and energy in displaying their status. One of the methods babblers use to advertise their status is allofeeding, in which a dominant male feeds a subordinate. If a subordinate does not accept the food, the dominant may display other behaviours that reflect its status, such as allopreening the subordinate on the back. If a babbler attempts to feed a higher-ranking individual, the higher-ranking individual retaliates with aggression, which in mature babblers results in the exclusion of the loser from the group.

Babblers also display their social status by other apparently altruistic activities (Zahavi 1977), such as helping at the nest (Carlisle and Zahavi 1986). Sentinel activity also reflects the rank and status of the male. Dominant males act as sentinels more often than subordinates. Dominants also tend to interfere with the sentinel activity of their subordinates, especially when competing over copulations. This interference often involves allofeeding at the top of a tree and advertising by a trill that they are allofeeding (Zahavi, Larkman, and Faran, unpublished data). We interpret competition to act as sentinels, to allofeed, and to help at the nest as investment in advertising the male's claim for social status. Higher social status deters other males from interfering with copulations and possibly persuades the female to collaborate more with the higher-ranking male and less with his rival.

Discussion

The need to collaborate in the defence of the common territory presumably selects for a compromise that results in the sharing of copulations among males, even though this may conflict with their individual breeding interests. It is reasonable to assume that the particular compromise achieved during each breeding cycle reflects the motivation of males to collaborate and the importance of each individual to the collaboration.

The cost of aggression among collaborators is higher than that in less co-operative social systems because, in co-operating systems, the wounding of a rival is also the wounding of a collaborator. In addition, when a dominant is wounded, a subordinate observing his temporary weakness may take advantage of the situation. Thus, aggression is bad advertisement for an individual that wishes to attract collaborators.

In babblers, displays of social status replace aggression in most conflicts between rival adult males. These displays, such as helping at the nest, sentinel activity, and allofeeding, may be mistaken for altruistic activities when in fact they are an investment in the advertisement of social status. The gain from a higher social status (i.e., efficient mate guarding) compensates for the investment in apparently altruistic activities. This model for interpreting altruistic acts is the only model suggested so far that offers an explanation, on the basis of Darwinian fitness and simple individual selection, for helping among co-operative breeders.

A male may increase his social status by following and interfering with the copulations of a more dominant male. He may also increase his chances to copulate by being aggressive to the female or even by damaging the clutch, thus harming the interests of the female. The inhibition among males from attacking one another (a consequence of the need of males to co-operate) may reduce the ability of the dominant male to guard the female from rival males. Unlike relative social rank, which does not change, it is reasonable to assume that social status may easily change with pressure from an outside group or with temporary variation in physical strength or any other measure of ability.

Males often compete over the chance to copulate with the alpha female, even though the beta female may invite copulations at the same time. Subordinate males may even attack the beta female while they are courting, but are otherwise unable to copulate with, the alpha female. I believe that this behaviour of subordinates is a consequence of their motivation to display their status, because copulations with the alpha female provide a higher status. Such a display of status may also be of benefit in the future, resulting in more copulations with the alpha female in later breeding cycles.

Our observations of babblers manoeuvring to meet their mates away from the group, of the counter-manoeuvring of competing males to interfere, and of the subtle displays that stop such interference suggest that the birds are programmed to acquire a great deal of information on social relationships and to plan their movements in space and time accordingly.

Acknowledgments

Thanks are due to Naama Zahavi-Ely and Avishag Zahavi for many suggestions that improved the manuscript. R.D. Montgomerie was of much help in editing the final version. Many thanks are also due to the very many volunteers who helped me follow the breeding babblers over many hundreds of days to observe the pattern of mate guarding. This research was supported by a grant from the United States/Israel Binational Science Foundation (BSF), Jerusalem, Israel. Thanks are due also to the Society for the Protection of Nature in Israel, which provided accommodation during the study.