

SECTION V

CO-OPERATIVE BREEDING

CARE OF YOUNG PIÑON JAYS AND THEIR INTEGRATION INTO THE FLOCK

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Pinon Jays *Gymnorhinus cyanocephalus* live as a tightly knit social unit all year. The means by which the young of the year are accepted and integrated into the flock was investigated by observing which individuals fed tethered young and how the young were socially accepted into the flock after fledging. Young responded positively to the vocalizations of their parents by begging from them. Foster young begged primarily in response to the begging calls of the natural young. Because only begging young were fed, natural young were fed first and more often than foster young. Adult males fed foster young in about 22 per cent of all their feedings whereas adult females fed foster young only in about 3 per cent of their total feedings. Adult females preened and cared for foster young and natural young equally.

After fledging, young joined the flock and fed in close association with all members. At a feeding station observations of aggressive behaviour of all cohorts indicated that yearlings enjoyed a special status and were dominated by no cohort during their first three months and thereafter by only the dominant males. Yearlings also engage in far fewer aggressive encounters than other cohorts because other cohorts actively avoid conflicts with the yearlings even though they are aggressive and bold at the supply of food. Integration of young is accomplished by communal care and feeding and by permissive acceptance of the young at concentrations of food.

MULTI-MALE CO-OPERATION IN THE NESTING BEHAVIOUR OF MALIMBUS (PLOCEIDS OF THE FOREST OF WEST AFRICA)

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The very variable social structures of the African Ploceidae have been described as a good example of ecological adaptations, gregariousness and polygamy being the social structure of savanna species, rather solitary life and monogamy being the social structure of rainforest species.

A three-year study has been made in Gabon on the reproduction of the strictly forest species *Malimbus coronatus*, *M. racheliae* and *M. cassini*. The results show some facts that to some extent do not confirm the basis of the theoretical conclusion on the relations between social life and ecology in the ploceine group. During the breeding season, the social structure of these *Malimbus* is a multi-male group with a single female. The multi-male groups participate in nest-building, the female being the leader of the group. Building of the nest, one of the most elaborate among birds' nests, in *Malimbus cassini* takes two weeks, all males working, displaying and courting in the same manner. After the completion of the nest, a single male remains and shares incubation with the female.

ARE HELPERS ALTRUISTS ?

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The evolution of altruism is an important problem in evolutionary biology. In Hamilton's (1964:1) discussion an altruist by definition is required to suffer a loss

in fitness relative to the recipient, where 'fitness is based, as it should be, on the number of adult offspring'. This concept of altruism can be referred to as *offspring altruism*. In practice, gains and losses in fitness stemming from certain types of behaviour seem to be virtually impossible to estimate, hence the need for an operational definition. Altruistic behaviour can be defined operationally as behaviour that aids other individuals who are not offspring or mates of the performer without giving any immediate benefit to the performer, where aid and benefit are assessed in observable ways, such as the giving of food. This will be referred to as *operational altruism* to distinguish it from other definitions of altruism.

The following questions relevant to the evolutionary problem of altruism will be discussed using data from jays and other birds: Do recipients raise more young than altruists? Do helpers affect breeding success? Do helpers sacrifice or profit? What similarities with social insects are shown by communal birds?

RECENT OBSERVATIONS ON THE FAMILY GRALLINIDAE AND COMMENTS ON ITS TAXONOMY

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The family Grallinidae as arranged by Peters (1960) brings together two dissimilar groups of birds on the basis that they all build bowl-shaped nests consisting largely of mud. The present arrangement of four genera, each with a single species, virtually admits defeat. Rowley (1970) in a review of the use of mud in nest-building clearly demonstrated that its value as a taxonomic character is doubtful. He suggested that both *Corcorax* and *Struthidea* (subfamily Corcoraciinae) are quite timaliid-like and bear no resemblance to *Grallina* and *Pomareopsis* (subfamily Grallininae). The morphological resemblance of *Grallina* to the wagtails (Motacillidae) has long been known (Mathews 1919) and field observations by the author together with the scanty published knowledge of *Pomareopsis* support this view.

This paper contrasts the morphology and behaviour of all four species. Recent field studies of *Corcorax* (Rowley 1974) and *Struthidea* (Chapman unpubl.) point out the very similar communal life of both species. Communal nesting has not been reported either for *Grallina* or *Pomareopsis*. Many other characters such as general morphology (including nestlings), nests and eggs, calls, flight, tail-wagging and feeding patterns clearly divide the four species into two dissimilar groups resembling babblers on the one hand and wagtails on the other.

So similar are *Corcorax* and *Struthidea* that I suggest that two genera are unnecessary for two species. As suggested by Rowley, their affinity is with babblers; in fact they have much in common with the Australian *Pomatostomus*. They would best be regarded as a single genus *Corcorax* with two species within the subfamily Timaliinae. The Grallininae, however, though their affinities are clearly with wagtails, are more distinctive and would best be retained as a subfamily, but in the family Motacillidae.

TIME-ACTIVITY BUDGETS OF A COMMUNAL BREEDING BIRD POMATOSTOMUS TEMPORALIS

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Activity budgets and nesting behaviour of the Grey-crowned Babbler *Pomatostomus temporalis* are being studied at two localities in Queensland. Only data on total budgets of both populations are presented here.

I recognized eighty-four activities in five categories: foraging, social behaviour, maintenance, interactions with other species and reproduction. Comparing budgets for 1973, the population at Laidley, eighty kilometres west of Brisbane, spent more time foraging (66 versus 59%) and interacting with other species (3 versus 2%) and less time in social behaviour (10 versus 12%) and maintenance (16 versus 22%) than the population on Boningar Station, 400 kilometres west of Brisbane. Reproduction

was 5 per cent of the yearly budget at both sites. These differences were not attributable to weather or to size or age-structure of groups. Percentage of time foraging and number of activities per hour at Laidley correlated with abundance of some arthropods on foliage and in litter. This was not true at Boningar, which had more of these arthropods. Also, average bouts of foraging were much longer and flights were fewer at Laidley. The large amount of time Babblers spend hunting suggests that food is a strong influence on their social system.

CO-OPERATIVE BREEDING OF PUKEKO

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Pukeko *Porphyrio porphyrio melanotus* breed in pairs or groups. The number of permanent members (adults and yearlings) of a communal group varied from three to six with an even sex ratio except in those groups formed seasonally from flocking birds. The proportion of group- to pair-territories varied with habitat. In each group a linear social hierarchy existed with status related to sex, age and size. Well-defined boundary zones were defended with the proportion of defence undertaken related to status and sex. Courtship (allopreening and symbolic feeding) involved all birds in a territory but only adults copulated, which was a group event with most copulation observed involving more than two birds. Homosexual mountings were common and the frequency of copulation was related to status. In groups, one or more adult females laid in the same nest at the same time, the number of eggs deposited varying with status and age. All adults helped with incubation with the proportion done related to status. Proportion of care of the precocial chicks depended on status and age with all birds in the territory participating. Other chicks even fed younger chicks, especially in pair-territories.

BREEDING BIOLOGY AND BEHAVIOUR OF MANORINA (MYZANTHA) MELANOCEPHALA, A COMMUNALLY NESTING HONEYEATER

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The Noisy Miner *Manorina (Myzantha) melanocephala*, an insectivorous honeyeater, was studied in dry sclerophyll woodland in south-eastern Queensland. The female alone builds the nest. Sites vary widely and range in height from one to eighteen metres. The clutch numbers two to five and averages 2.7. Only the female incubates. The incubation period is about fifteen days, nestling period fourteen to sixteen. Up to twelve birds feed the young of one nest. No nests were found with only two birds in attendance and all visitors were males. The incubating female is also visited by males, who direct displays at the eggs. Considerable aggression occurs at nests and incubation is frequently interrupted. Males generally do not confine their activities to one nest, but some do when feeding nestlings. A female's successive nests do not necessarily attract the same visitors; this relates partly to the distance of the second site from the first. The interactions of different birds at different nests is described in detail. One female, nesting several times in one breeding season, had nestlings fed by more than twenty males. Despite vigorous feeding visits, up to seventy per hour, nesting success is very low. Only 13 per cent of all nests started fledged young.

CO-OPERATIVE BREEDING IN BEE-EATERS AND LONGEVITY AS AN ATTRIBUTE OF GROUP-BREEDING BIRDS

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The African bee-eater *Merops bulcocki* nests in small compact colonies in wooded savannas. Helpers, one to three per nest, are found in about one third of nests and are

generally progeny from a previous season of the pair that they assist. Among helpers, males outnumber females by between two and four to one (Fry 1972). Population studies have been resumed and data on synchrony of laying within and between colonies are given. First indications are that survival of adults is high and that (contrary to the view held previously) more than a single female may lay in one nest. Clutches of second females can be regarded as parasitic. Small tropical and Australian landbirds are not, in general, exposed to severe seasons or hostile environments and do not have to migrate overseas. Consequently their adult survival is remarkably good (as population studies are currently demonstrating). In many species pre-breeders associate with breeders for years until the opportunity to reproduce themselves arises, i.e. there is perennial flocking and involvement of pre-breeders with breeding activity. In such long-lived birds group-breeding is one of the aspects of the life history that tends to prevent maximum reproductive output.

THE RELATION OF HABITAT TO SIZE OF GROUP IN THE GENUS TURDOIDES

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A population of the Jungle Babbler *Turdoides striatus* was studied from July 1971 to the present time in an area of mixed scrub and dry deciduous woodland on the outskirts of Delhi, North India. *Turdoides striatus* occurs most often in the closed-canopy woodland. The species lives in stable groups of 3-16 individuals, which defend common territories. Only one pair of each group attempts to nest. The foraging area of a group is divided into two zones: an inner, vigorously defended core and an outer home-range, which is only loosely defended.

Groups of *T. striatus* can be classified into three types on the basis of the territories they occupy. In Type 1, all of the core and most of the home-range is closed canopy woodland. In Types 2 and 3 there is proportionately more scrub. Sixteen groups were followed. Breeding success and size of group was compared with the type of territory occupied. Groups holding territories of Type 1 had a larger mean size than other groups, nested earlier and more often, fledged more young in the year and had more surviving young in December than other groups. They did not produce more young per nest. Birds leaving their natal group to join another usually did so at more than two years old. A higher proportion of birds leaving territories of Type 1 succeeded in establishing themselves in other groups than did birds from other territorial types.

It is suggested that size of group in *Turdoides* is largest in habitats where the population is most dense and that the mean size of groups is determined by a balance between the rate of reproduction and the age of females leaving the group.

CO-OPERATIVE BREEDING BEHAVIOUR AND FAMILY RELATIONSHIP WITHIN GROUPS OF THE LONG-TAILED SHRIKE CORVINELLA CORVINA

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Since the beginning of the study in 1970 only co-operative breeding has been recorded at Legon (5.63°N, 0.19°W). The study area is 500 hectares, within which there are at least twenty-three breeding groups. The number of birds per group is usually in the range of ten to fifteen, the lowest recorded being four and the greatest twenty-three. In addition to the breeding pair each group may contain surviving offspring, of both sexes and age up to at least four years, and other non-breeding adults from other groups. During the life history of a group the ratio of males to females may be greater or less than one.

Three successful clutches (young leaving nest) appear to be the maximum possible for a group during a breeding period from December (dry season) through the main wet season (May and June) into August. The breeding female may continue her role within a group for at least two years and may switch groups and continue to be the breeding female in the new group.

Co-operative behaviour includes territorial defence, attack on predators, feeding of incubating female and feeding of nestlings and fledgelings. All independent members of a group participate and there is participation by some members in construction of nests.

COMMUNAL NESTING BY THE GREY-CROWNED BABBLER *POMATOSTOMUS TEMPORALIS*

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Pomatostomus temporalis lives in small flocks composed of a primary pair of adults with a varying number of auxiliaries, who are mostly offspring from previous broods. Adult birds may occasionally join a flock from outside. Vagrants live a solitary nomadic existence outside the established flocks. These may join existing flocks or combine to form the nuclei of new ones. Each flock defends a large territory from neighbouring flocks and vagrants by means of a territorial group display. A flock moves as a group and roosts at night in one nest. All members of a flock co-operate in nest-building at any time of the year. Nests are used for roosting as well as breeding. Breeding occurs from mid-July to February. More than a single brood may be raised in a season. The primary pair alone are believed to be responsible for the production of eggs. The primary female almost always lays and incubates alone, but all members of the flock participate in rearing the brood. The age dominance of an individual was related directly to its role in group activities. The primary pair played a major role in such activities as display, nest-building and rearing of young; participation by other members of the flocks increased with age.

SOCIAL ORGANIZATION OF ACORN WOODPECKERS *MELANERPES FORMICIVORUS*

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The Acorn Woodpecker *Melanerpes formicivorus* has long been suspected to live in groups and to breed co-operatively. This paper will report some of the results of a three-year study of this species at the Francis Simes Hastings Natural History Reservation, Monterey Co., California. The results indicate that Acorn Woodpeckers live all year in groups of between two and fifteen individuals (average six), which consist of both sexes in equal numbers. The members of each group defend an all-purpose territory from members of other groups. There are no floating or solitary individuals. Each group breeds co-operatively and may have two nests in a season, but a group has never been known to have had two nests simultaneously. The second nest is begun only after the first clutch is fledged or lost. Most individuals in the group aid in incubation and in feeding the nestlings and fledgelings. The parentage of clutches is usually not known because obvious pairing does not occur. The birds that aid in the nesting effort are both yearlings and older birds, the older birds doing the greater part of the work. Recruitment to the group is both by non-dispersal of young and by immigration. The feeding habits of this species are atypical for Picidae. Over half the diet is acorns, which are stored in prepared holes for winter use. Sap and insects form

the rest of the diet. The ecological conditions leading to sociality in this species appear to be similar to those suggested for some other group-living birds: a surplus of individuals, a limited amount of suitable habitat and the particular requirements (e.g. feeding habits) of the species, which favour non-dispersal from the home territory.

CO-OPERATIVE BREEDING IN THE JAPANESE LONG-TAILED TIT

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The Long-tailed Tit *Aegithalos caudatus* has a flock-territory of about 20 hectares. The size of flock averages nine. The flock-territory is maintained through winter and is communally defended by the members of the flock, especially males. In the breeding season, a flock-territory is divided into some pair-territories. This process occurs gradually through the stage of one or two pair-flocks. The pairs separate completely from the winter flock and winter communal roost when the outer part of the nest is completed. The direction of antagonism changes from the members of other flocks to all other individuals. The highest frequency of such fighting coincides with the lining of the nest. Helpers are never present during nest-building, laying and incubation. Then, solitary birds are instead chased by each mated member from near the nesting site. Thus, helpers are allowed in only during periods of nestling and fledging.

There are two problems in co-operative breeding of the Long-tailed Tit. One is that the pair-flock has a communally defended area. One or two pair-flocks bud off from a winter flock. No member of a winter flock, although they may divide into pairs or pair-flocks, go out of their winter home-range. Secondly, helpers take part only in feeding of nestlings and fledgelings. There is no proof that the quality and quantity of food brought by helpers is useful for the growth of nestlings. There is no communal behaviour in nest-building, laying and incubation. I think that the function of helpers in the Long-tailed Tit is to promote sociability.

THE AUXILIARY SOCIAL SYSTEM AND ITS EFFECT ON TERRITORY AND BREEDING IN KOOKABURRAS

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Kookaburras are social and live in territories with either a single permanent mate or a family consisting of a mate and one or more auxiliary members. Auxiliaries form one third of the adult population; they are non-breeding birds, the progeny of previous seasons that remain round the year and aid in defence, nest attendance and provision of young. The auxiliary social system operates because of uniform plumage and a strict territorial regime.

Size of territory was correlated with the number of birds present at the time when boundary adjustments were made. It is determined by the amount of space the birds can successfully defend. Auxiliaries occupy the same space in the same habitat as breeders, so reducing the breeding potential of the population by about one third.

The auxiliary system appears to be a long-term adaptation for reducing fertility in accord with longevity incurred from living in the equitable Bassian Region. But short-term regulation of the population appears to be achieved through mortality from asynchronous hatching and the ability of families to rear two broods. A cybernetic approach is being taken to test the validity of this hypothesis.

ADAPTIVE ADVANTAGE OF COMMUNAL NESTING IN GROOVE-BILLED ANIS

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Breeding groups of Groove-billed Anis *Crotophaga sulcirostris* consist of one, two, three or rarely four co-operating pairs. The females lay their eggs in a communally constructed nest and all individuals contribute towards incubation and care of the young. For such a system to evolve, groups must gain some advantage that enables them to produce more young per pair than single breeding pairs. About fifty groups of Anis were observed through two breeding seasons and one dry season. The aim was to identify those factors that accounted for the reproductive superiority of groups over pairs. Particular attention was devoted to evidence for increased foraging efficiency or feeding rates per nestling by larger groups, evidence for more effective defence of the nest from predators by large groups, evidence for relatedness among group members, which would increase fitness via kin selection, evidence for greater longevity of birds in large groups, evidence for skew of clutch-size and parental effort among the pairs in a group and any useful variations of the above parameters between habitats.

FLORIDA SCRUB JAY HELPERS

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Florida Scrub Jays *Aphelocoma c. coerulescens* are stenoecic, sedentary, long-lived, monogamous, single-brooded and defend a permanent territory. First breeding occurs after two or more years; meanwhile young stay in their natal territory and participate in many breeding activities. Various measures of reproduction show that pairs with helpers produce more young than those without. Defence against predators may be the most important help given by helpers. Helpers are nearly always close relatives of the breeders. The sex ratio at one year appears to be 1:1, but shifts to a 15 per cent majority of males. Females probably die younger than males because they disperse farther and earlier.

COMMUNAL NESTING IN THE ARABIAN BABBLER

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The Arabian Babbler *Turdoides squamiceps* is a bird that holds group territories. The entire group in various combinations of adult males, females and young of earlier broods defends the territory and cares for the one communal nest and nestlings. Usually only one female lays and probably only one male fathers the clutch. The occurrence of a few potential breeders calls for a conflict as to which bird will breed and which will help. Sometimes more than one female lays. This is evidence for conflict and breeding success is not improved, probably the reverse. A population of a few hundred birds has been followed for the last three years. Males tend to stay in the group and females to disperse. Larger groups do not reproduce better than small groups. Although Babblers co-operate to defend their territory they probably try to further their own reproductive chances even by destroying those of their fellow group members.

The social pressures inherent in such a system result in special adaptations such as the colour of eggs, laying, sexual display, allopreening, etc. The social organization of Babblers will be considered also as a consequence of the niche they occupy.