

## SOCIAL BEHAVIOUR WITHIN GROUPS OF JUNGLE BABBLERS (*TURDOIDES STRIATUS*)

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**Abstract.** Five aspects of intra-group behaviour among wild jungle babblers were analysed in relation to the age, sex and breeding status of the participants. The amount of participation in allopreening, sentinel behaviour, and movement initiation were found to be closely correlated with age and breeding status, resulting in a rough concordance between rankings based on these three activities. There was some difference between the sexes in the degree of participation in allopreening and sentinel behaviour and this may be explained by differences in their strategies for breeding. Changes in play and roosting behaviour with age are related to the establishment of dominance relations among birds of the year and possible connections between other aspects of behaviour and social status are also discussed.

Birds in which offspring remain in their parents' territory for several years after fledging, forming a family flock which feeds together, breeds co-operatively, and takes part in joint territorial defence, have been classed by Wilson (1975) as 'advanced subsocial' in their organization. This group territorial pattern of social organization was considered rare until recently, but is now known to be widespread among birds of warm-temperate and tropical climates (Skutch 1961; Lack 1968; Fry 1972 and several reviews in the *Proc. XVI Int. Orn. Cong.*). Despite their widespread occurrence, no detailed studies have so far been published on social relations within free-living groups of this type.

The present study sets out to analyse social relations within groups of jungle babblers (*Turdoides striatus*), small insectivorous passerine birds (weight about 65 g), living in tropical woodland and scrub over most of lowland India. The species is similar in general behaviour to several species of group territorial birds studied previously, such as the Florida scrub jay (*Aphelocoma c. coerulescens*) (Woolfenden 1974, 1975), the Arabian babbler (*Turdoides squamiceps*) (Zahavi 1974), the white-winged chough (*Corcorax melanorhamphus*) (Rowley 1965 and in preparation) and the long-tailed shrike (*Corvinella corvina*) (Grimes 1975). Jungle babblers live throughout the year in groups of 2 to 20 birds which defend a common territory. Young birds remain with the group in which they were reared for at least 18 months and dispersal after this is largely by females, many males remaining with their natal group for at least 4 years. A general introduction to the biology of the species is given by Andrews & Naik (1970).

Dominance is widely recognized to be important in birds (Wood-Gush 1955; Crook 1961; Wilson 1975) and this concept has been frequently used in the interpretation of their social behaviour. Dominance has also been widely studied among social mammals, particularly primates (Hall 1968; Rowell 1972; Richards 1974), which live in groups similar in size and composition to those of jungle babblers and other group territorial birds. Several authors have criticized the indiscriminate application of the dominance concept to situations other than those involving approach-retreat interactions however, (Rowell 1966; Bernstein & Sharpe 1966; Bernstein 1970) and Jolly (1972) points out that there appear to be consistent differences between primate species in the degree to which different measures of dominance are correlated. Bernstein & Sharpe suggest that analysis in terms of sex and age, as well as status, can be more meaningful than one based on the construction of a linear dominance hierarchy. This practice was followed in analysing the intra-group behaviour of jungle babblers.

Intra-group aggression among jungle babblers was very rarely seen. Because of this it did not prove possible to describe dominance within groups based on approach-retreat interactions. Even at artificial feeding sites, where food was very concentrated, no evidence of conflict over food was observed, except among first-year birds or between members of different groups.

In the absence of approach-retreat interactions, or any form of overt aggression, the following behaviour patterns were analysed in relation to the age, sex and breeding status of the participants in order to determine the

relationships between different group members: (1) Allopreening behaviour; (2) Sentinel behaviour; (3) Leadership behaviour; (4) Play; (5) Roosting behaviour.

### General Methods

#### Study Area

Jungle babblers were observed in an area of about 1 km<sup>2</sup> of dry deciduous woodland and tropical thorn scrub adjacent to New Delhi, N.W. India. The structure of the vegetation ranged from low scrub, less than 1 m high, to closed canopy woodland up to 15 m high, usually with an understory up to about 3 m. Jungle babblers were found mainly in the woodland, spending most of their time feeding among leaf-litter on the ground and sometimes searching the boles and larger branches of the trees.

Observations were made between July 1971 and June 1974 during an intensive study of the ecology of the species. Most observations on intra-group behaviour were made during the winter months (November to February) since work in the summer was concentrated on breeding ecology. More than 3000 hours were spent in the field, of which about half were devoted to watching jungle babblers. Sixty-two birds were trapped as post-juveniles and marked with coloured plastic leg-rings and a further seventy-seven were ringed as nestlings.

#### Collection of Data

Observations were made through 10×50 binoculars at ranges from 10 to 50 m, while following groups as they moved through the study area. Individual groups were followed for periods of up to 6 hr and observations during the winter spanned the whole daylight period although more were made in the morning than the afternoon. Every effort was made to minimize disturbance by the observer but some was inevitable. Groups which were followed regularly became habituated to the presence of the observer and sometimes allowed approach to within a few metres but catching one of the group in a mist net immediately destroyed this habituation.

All behaviour falling into the five categories specified above was noted, along with the time of day, the identity of the participants, the reactions of other group members and the presence of any relevant extra-group stimuli. The position of the group under observation was marked on a map of the study area at ½-hr

intervals and the positions of all important inter- or intra-group interactions were also recorded.

During periods when groups were under observation it was usually possible to keep some birds in view at all times, but rarely possible to see all members of the group at once. While feeding, birds were often out of sight in ground vegetation, but behaviour performed by birds which were perched in trees could usually be monitored continuously because the woodland canopy was fairly open, particularly in winter. Most allopreening and sentinel behaviour which took place during a period of observations was probably noted, although the identity of the participants could not always be seen. Leaders, however, could only be identified in a small proportion of group movements. Play behaviour was probably frequently overlooked.

Three groups were chosen for intensive study, and these were referred to by letters; L, P and M. The number of birds in each group in each of the three winters of the study is given in Table I, which also shows their age composition. Specific methods for recording different types of behaviour are dealt with separately when each behaviour is introduced, but before dealing with these the vocalizations of the jungle babbler need to be described so that reference can be made to them, where appropriate.

### Vocalizations

Andrews & Naik (1970) list eight vocalizations of the jungle babbler and describe the situations

Table I. The Size and Composition of Three Groups of Jungle Babblers Studied Intensively

		Group P	Group L	Group M
1971-72	1Y	5	2	3
	2Y and Adult	7	7	7
		12	9	10
1972-73	1Y	1	5	2
	2Y	4	2	2
	Adult	5	6	3
		10	13	7
1973-74	1Y	0	3	2
	2Y	1	5	2
	Adult	8	7	5
		9	15	9

Abbreviations used in Tables and Figures: 1Y, bird less than 1 year old; 2Y, bird more than 1 year and less than 2 years old; A, adult bird more than 2 years old; B, breeder; BB, breeding pair; NB, non-breeding adult.

in which they are used. A list made independently in the present study includes 11, of which three intergrade. Two of those described by Andrews & Naik are included here under one heading, while two which they do not distinguish are separated. Vocalizations distinguished in the present study are listed in Table II; names used by Andrews & Naik are given in parentheses.

The shriek call of the jungle babbler is similar to the calls given in similar circumstances by the common babbler *Turdoides caudatus* and the bulbuls *Pycnonotus* spp. which occupied the same habitat. The cackle calls, although distinct from the other vocalizations described, formed a continuum. The chack call was similar in form to the cuk call, but these two did not intergrade in volume, the chack call always being audible up to at least 50 m, the cuk call not usually being audible beyond 15 m. The latter may have been used more frequently than was apparent since only a few groups allowed prolonged approach to within 15 m. All the other vocalizations listed appeared to

constitute relatively discrete signals, with little variation in volume or duration, although calls seven and eight were heard only a few times.

Vocalizations two and three were the most frequently recorded. The intergradation of the three types of cackle call, all used quite frequently, probably allows greater flexibility in communication than would be the case if they were discrete (Struhsaker 1966), allowing quantitative as well as qualitative information to be transmitted (Konishi 1963). Frequent intergradation is characteristic of the calls of primates, compared with those of birds (Mulligan & Olsen 1969) and it is also true of the vocalizations of hyaenas *Crocuta crocuta* (Kruuk 1972) and lions *Felis leo* (Schaller 1972), both highly social species.

### Allopreening and Clumping

#### Methods Used to Record Allopreening Behaviour

An allopreening interaction was recorded whenever one bird was judged to be attempting to allopreen another, bringing its bill into firm contact with the feathers. When one bird pecked

**Table II. Vocalizations Recorded Among Jungle Babblers; the Names Used by Andrews & Naik (1970) are Given in Brackets**

Name	Description	Situations in which call was used
(1) Shriek call (danger call)	Short, high-pitched shriek	Given by any bird at the unexpected appearance of a predator. The group immediately seeks cover and may freeze.
(2) Cackle call, type (a) (exciting call)	Low volume, intermittent wheezing	Given by sentinel birds in the presence of potential danger, as yet remote. Often given at the approach of the observer. Usually no visible reaction by the group.
type (b) (2(b) and 2(c) included under mobbing call type (c))	Loud, wheezy cackle	Given by part or all of the group in the presence of a ground predator or perched raptor.
	As 2(b), but including a rattling, guttural noise, rising and falling slightly in pitch	Given by the entire group during inter-group confrontations.
(3) Chack call (contact call)	Short 'chack' given at irregular intervals	Given by birds detached from their group, or in reply to other chack calls. Sometimes given while sitting on the nest.
(4) Cuk call (feeding call)	Short, low 'cuk', given intermittently	Given by any bird while feeding, but not often heard.
(5) Cu-cu-cu call	Low, guttural 'cu-cu-cu', usually repeated several times	Given by adult birds just prior to moving to a new feeding site. Frequently given while moving to roost, and when fledglings were being encouraged to fly.
(6) Kya call (distress call)	Loud, ringing 'kya-kya-kya'	Given when trapped. This call usually summoned the rest of the group at once. Tape recordings of this call were the most effective in attracting jungle babblers.
(7) Gurgle call	Low gurgling noise	Given by males just prior to an attempted copulation, wings waving loosely at the same time.
(8) Scheer call	Low 'scheer'	Given by females while approaching males of another group. Also given by passive birds during 'rough and tumble' (see below).
(9) Begging call (begging call)	Rattling squawk	Given by juveniles while begging. May be used occasionally up to 6 months old.

another lightly on the head or neck the gesture was interpreted as an invitation to allopreen because it was often followed by other soliciting movements (see below). For all interactions observed the identity of the participants was recorded and also the part of the body that was preened. For the latter purpose the body was divided into four areas, as illustrated in Fig. 1.

Birds performing allopreening on others were described as the active participants and those receiving allopreening were the passive participants. Figures given for frequency of involvement include all interactions in which a particular bird took part, whether as the active or passive partner. On many occasions more than two birds were participating simultaneously in allopreening. Any period of time during which two or more birds were continuously involved in allopreening was known as a 'bout' and within each bout each pair allopreening constituted an interaction.

Priority was given to establishing the identity of birds engaged in allopreening and as a result, when more than two birds were taking part in a bout, it was not possible to record the duration of individual interactions. An allopreening interaction was considered complete when the two birds separated or when no allopreening took place for 1 min. If one bird moved to another perch and was followed by the other, which then resumed allopreening, the resumption was treated as a new interaction, even though less than 1 min had elapsed between the cessation and resumption of allopreening.

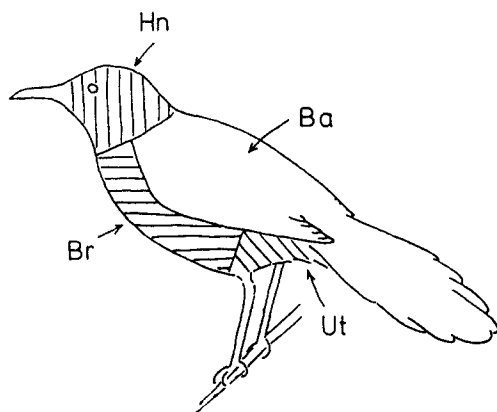


Fig. 1. Parts of a jungle babblers scored separately in recording allopreening behaviour. Hn = head and neck, Br = breast and flanks, Ba = back, mantle, rump and wings, Ut = belly and under-tail coverts.

Each area of the body preened was scored only once in each interaction.

### Description of Allopreening Behaviour

Allopreening took place between birds perched in bushes or trees, and only very rarely on the ground. In most cases the two birds involved perched flank-to-flank on a branch with their heads pointing in the same direction. The passive participant usually crouched low on the branch, with the legs bent, raising its head and stretching its neck, while the active bird stood up on straight legs. Some typical poses, copied from field sketches, are illustrated in Fig. 2. Occasionally the active bird perched below the passive, on a lower branch, and reached upward to preen from below. This happened most frequently when the passive bird was already

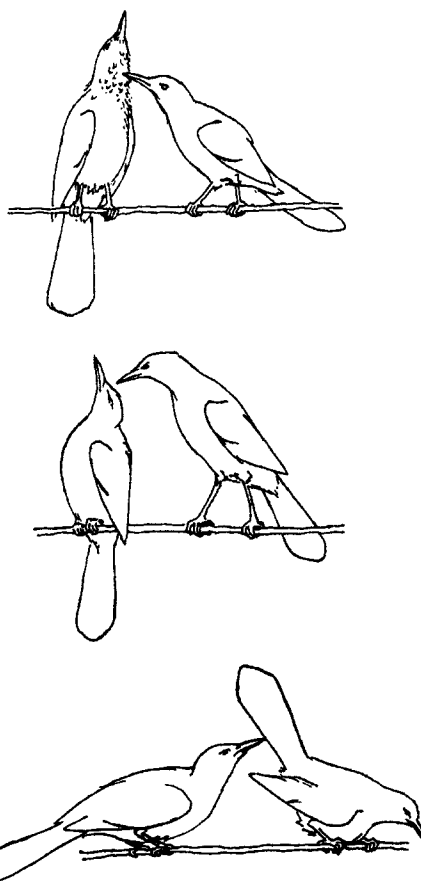


Fig. 2. Poses adopted by jungle babblers during allopreening (redrawn by E. K. Dunn from field sketches).

being allopreened by another bird perched beside it.

Andrews & Naik (1970) briefly describe the typical posture of a bird being allopreened, but a fuller description seems warranted. During allopreening of the head and neck the feathers of this region are erected and the head is tilted away from the preener to expose the chin, while at the same time the eyes are narrowed or closed. The passive bird usually remains completely still, apart from occasional shifts to expose different areas to the preener. During allopreening of the back, breast, or flanks, the feathers of these regions are also erected, particularly those around the preen gland, but the active bird does not move its bill deliberately from the preen gland to other parts of the feathers in the way that might be anticipated if it were oiling the feathers. Active birds give the impression of searching for something among the feathers and short jabs of the bill are often used, presumably to remove particles of dirt, or perhaps ectoparasites. Fletcher & Inglis (1924) mention that a bird soiled with bird lime used in its capture was allopreened particularly on the soiled area, suggesting that allopreening may have a real value in feather hygiene. Running the feathers through the bill, described by Sparks (1964) for the estrildine *Amandava amandava* was not observed among jungle babblers.

Allopreening was actively solicited in some cases, not all of which were followed by preening and the actions involved were similar to those described by Morris (1956) for estrildine finches. The solicitor approached the prospective preener by sidling along the branch on which it was perched until their flanks were in contact. It then adopted the posture used during allopreening of the head and neck regions, with the feathers of these areas erected and the neck stretched away from the bird being solicited. Feathers of other parts of the body were never raised prior to the commencement of allopreening and this may be due to the fact that the body feathers are raised during inter-group agonistic displays.

### Clumping

Clumping, where two or more birds perched side by side in contact with one another, was common during periods of rest. This situation was sometimes followed by the initiation of allopreening and birds would also autopreen while clumped. A bird approaching another in

order to clump would usually approach a bird perched and at rest, or autopreening, but no particular feather posture appeared to invite clumping, unlike the estrildines described by Morris (1956). Occasionally birds attempted to clump with a bird performing sentinel behaviour (see below) and giving a low intensity cackle call.

Babblers approaching an isolated bird did not perch directly beside it but landed 5 to 10 cm away and sidled up to clump as described. Birds joining a pre-existing clump of two or more, however, often flew to perch right beside the clumped birds or even perched on their backs. The vigour with which birds attempted to join a clump seemed to be positively correlated with the number of birds in the clump, and clumped birds appeared to exert a stimulus for others to join them. Groups invariably clumped while roosting.

Practically all instances of clumping or allopreening involved birds belonging to the same group, despite the fact that in winter groups often mixed together for several hours at a time while feeding. The only instance of inter-group allopreening recorded, apart from some associated with attempts to form new groups, involved the breeding male of one group and a juvenile bird from another. Juveniles were allopreened very frequently by all group members.

### Seasonal Variations in Allopreening Frequency

The seasonal distribution of allopreening bouts and the number of birds involved per bout are shown in Fig. 3, which demonstrates that allopreening is more frequent during the winter than during the summer. Breeding takes place from March to October. The observed distribution cannot be related to the amount of time available for allopreening because in winter there is little time for any activities other than feeding. Instead the decline in the frequency of allopreening interactions during the summer appears to reflect a general loss of sociability within babbler groups during the breeding season, perhaps due to a higher level of aggression between adult birds during the period when they are presumably in competition for the chance to breed.

Allopreening was observed at all times of day. In the winter the frequency of bouts rose during the day to a peak in mid-afternoon, but during the rest of the year no definite pattern was apparent (Fig. 4). Many allopreening bouts occurred immediately after the group had suffered some kind of disturbance: an inter-

group confrontation, a predator alarm, or disturbance by the observer, but this could not have accounted for the observed distribution of allopreening bouts because group interactions and disturbance from predators both showed peaks in early morning and late evening throughout the year. The peak of allopreening frequency in mid-afternoon during the winter was probably due to a slackening of feeding efforts at that time of day. During the morning more than 95% of the time was devoted to feeding or sentinel behaviour.

### Allopreening in Relation to Age, Sex and Breeding Status

Four measures of allopreening involvement were used to analyse differences between birds of different age, sex and breeding status classes. (1) The total number of times that a bird took part in allopreening interactions, whether as the active or passive participant. (2) The ratio of the number of times that an individual was the active participant in an allopreening interaction to the number of times it was the passive participant;

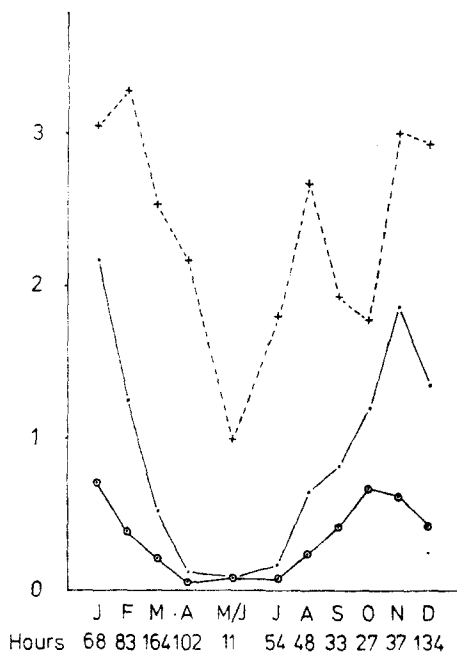


Fig. 3. Changes in the frequency of allopreening interactions with time of year. 'Hours' indicates number of hours of observation in each month. + mean number of birds involved per allopreening bout; • mean number of birds allopreening per hour; ○ mean number of allopreening bouts per hour.

this is called the 'preen ratio'. (3) The relative frequency of allopreening interactions between members of particular classes. (4) The relative frequency with which allopreening was directed at different parts of the plumage.

Data were collected in all 3 years of the study, but the age categories considered (first year, second year and adult) were only identifiable in the 1972 to 1973 and 1973 to 1974 seasons, and only figures for these seasons are used in this analysis, which is confined to the three groups specified above (P, L and M).

Table III shows the total number of involvements recorded for each member of these three groups. Some observations were included in which only one of the two participants in the interaction could be identified, but in most cases both birds were known. During the 1972 to 1973 season L group included two unringed birds, one of which was the breeding male and the other a non-breeding adult male. Scores for unringed birds are divided equally between these two. Only birds that remained with their group throughout the entire winter are included.

Individuals showed little consistency in the relative frequency with which they were involved in allopreening. One non-breeding adult member of P group (PLG) allopreened markedly less

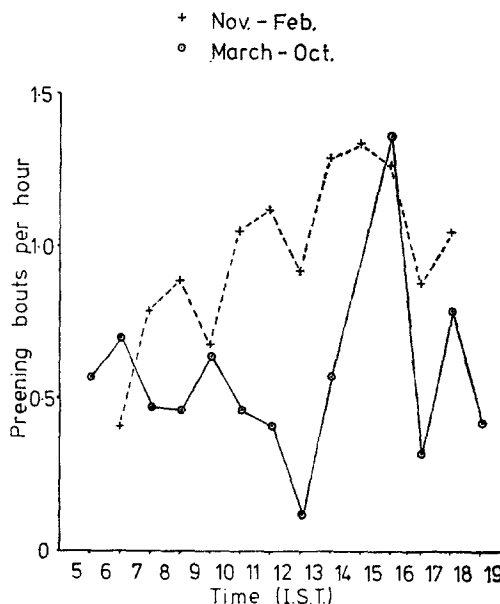


Fig. 4. Changes in the frequency of allopreening interactions with time of day. Winter (November to February) and summer (March to October) are shown separately.

Table III. Frequency of Involvement of Different Individuals in Allopreening Interactions

P group	1972-73	1973-74	L group	1972-73	1973-74	M group	1972-73	1973-74
B ♂ PDB	96	34	UN	101	49	MB	22	13
B ♀ PM	95	39	LBO	124	25	MDB	52	1
NB PW	49	13	LBDB	73	9	UN	15	11
PDG	43	31	LBB	28	14			
PLG	22	33	LBW	77	9			
			UN	100				
2Y PY	33	19	LBY	38	6	MO	20	1
PO	37	18	LBM	75	32	MP	20	11
PB	12	9						
YB	27							
1Y PR	18	23	LGR	16	36	MM	19	5
			LGP	36	20	MLB	43	9
			LGW	11	16			
			DGLG	13	9			
			DGDB	46				
1Y (1973 cohort)			LGY		4	UN (2)		7
			LBLB		5			
			DGM		0			

Ages in the left-hand column refer to 1972-73, add one year for 1973-74.

than the other two non-breeding adults during the 1972 to 1973 season, but in the 1973 to 1974 season the position was reversed. The same applied to LBB, a non-breeding adult in L group. In both years, however, there was a fairly constant tendency for older birds to be involved in more interactions than younger birds. Figure 5 shows the percentage involvement of different classes in all allopreening interactions within the three groups. For classes that contained more than one bird the figures are expressed as mean percentages per bird. In all cases one of the breeding pair was involved in the highest percentage of interactions, and in four cases the breeding pair were first and second. The mean rankings for the five classes shown in Fig. 5 are as follows: (1) breeding male, (2) breeding female, (3) non-breeding adults, (4) second years, (5) first years.

Table IV shows the number of interactions between birds of different classes and their frequency relative to the number of birds of each class available within the group. The data used are the same as for Table III, except that only interactions in which both participants could be identified are included. Interactions between members of the breeding pair were the most frequent combination, followed by interactions between the breeders and birds of any other class. Apart from these, non-breeding adults were involved in more interactions with other non-breeding adults and second years had more interactions with second years, than any other combinations. The least frequent combinations were non-breeding adults with first years,

second years with first years and allopreening between first years.

Table V arranges the data in Table IV to show the active and passive roles of each class and the areas of the body that were preened. The preen ratios for each combination of classes are also given. Breeding adults were more often the active partner in interactions with all other classes. Otherwise birds tended to be more frequently the active partner in interactions with birds younger than themselves and more often passive with birds older than themselves. In all interactions between different age classes the older birds took the active role significantly more often than the younger ( $\chi^2$  values and

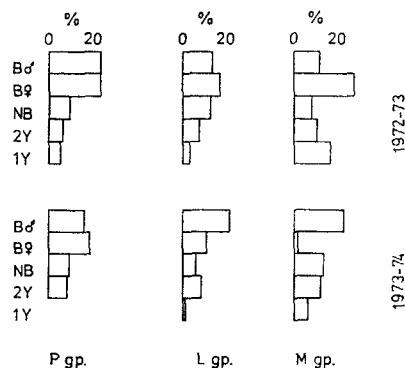


Fig. 5. Mean percentage of all group allopreening interactions in which individuals of five classes were involved. B = breeding adult, NB = non-breeding adult, 2Y = second-year, 1Y = first year. Percentages for each class are expressed 'per bird'.

probabilities given in Table V).

The percentage of allopreening directed at different parts of the body in interactions between all classes is shown in Fig. 6. Breeding adults preened other birds more frequently on parts of the body other than the head and neck than was the case when roles were reversed. Birds taking the active role with those older than themselves directed a larger proportion of their allopreening at the head and neck region than they did when preening those younger than themselves. A significant inverse correlation was found between the preen ratios between different classes and the ratios of the proportion of allopreening directed at the head and neck (C/D in Table V,  $r_s = -0.79$ ,  $N = 7$ ,  $P < 0.05$ ). This indicates that, where two birds of different classes were engaged in allopreening, the bird that was more frequently the passive partner tended to direct a greater proportion of its allopreening to the head and neck region when it was the active partner than did the individual that was more frequently the active partner.

The ratio of the number of times that allopreening was directed at the head and neck regions to the number of times that it was directed at other parts of the plumage was tested by  $2 \times 2 \chi^2$  tests for the combinations of classes listed in Table V. Proportions differed sig-

nificantly in the cases of breeders/non-breeding adults and breeders/second years. Sample sizes were inadequate for testing first years against any other class. A comparison of breeders with non-breeding adults showed that breeders allopreened first and second year birds significantly more often on parts of the body other than the head and neck region. When allopreening interactions within classes were compared for the relative amount of preening directed at the head and neck no significant differences were found except between breeders and second year birds, where the breeding pair were found to allopreen one another less often on the head and neck.

### Soliciting of Allopreening

Although many instances of probable soliciting for allopreening were observed only a few were considered to qualify unequivocally as soliciting. In many cases allopreening appeared to be initiated by the act of clumping, but as this was not always the case, and as clumping might occur for other reasons (e.g. roosting) these were not counted. In other instances where the apparent solicitor raised the feathers of the neck prior to the initiation of allopreening, it was often impossible to see whether this was the result of some intention movement on the part

Table IV. Frequency of Allopreening Interactions Between Birds of Different Classes

	P group			L group			M group		
	Comb.	N	N/C	Comb.	N	N/C	Comb.	N	N/C
<b>1972-3</b>									
BB : BB	1	37	37	1	36	36	1	9	9
BB : NB	6	54	9	8	105	13.1	2	6	3
BB : 2Y	10	60	6	4	20	5	4	25	6.2
BB : 1Y	2	7	3.5	10	73	7.3	4	26	6.5
NB : 2Y	15	27	1.8	8	43	5.4	2	5	2.5
NB : 1Y	3	14	4.7	20	46	2.3	2	6	3
2Y : 1Y	5	2	0.4	10	17	1.7	4	18	4.5
1Y : 1Y	0			10	3	0.3	1	6	6
2Y : 2Y	10	18	1.8	1	7	7	1	0	0
NB : NB	3	20	6.7	6	36	6	0		7.2
<b>1973-4</b>									
BB : BB	1	19	19	1	16	16	1	0	
BB : NB	12	25	2.1	10	16	1.6	6	16	0.7
BB : 2Y	2	10	5	10	26	2.6	4	0	1.8
BB : 1Y	0			6	0		4	3	0.2
NB : 2Y	6	8	1.3	25	38	1.5	6	11	0.5
NB : 1Y	0			15	5	0.3	6	1	
2Y : 1Y	0			15	6	0.4	4	2	2
1Y : 1Y	0			3	2	0.7	1	0	0.7
2Y : 2Y	0			10	12	1.2	1	2	
NB : NB	15	41	2.7	10	6	0.6	3	2	

Comb. = the number of possible pairing combinations between the classes concerned. N = number of interactions observed.



of the bird which was apparently being solicited. Only instances where the solicitor adopted the usual passive allopreening posture without any trace of response from the bird being solicited were included in this analysis. The typical soliciting posture is shown in Fig. 7. Because of the relatively small sample size, figures for all three groups and both years are combined in Table VI which shows the frequency with which different classes were seen to solicit or be solicited and the frequencies in relation to the number of bird-years involved.

First year birds accounted for 50% of all soliciting behaviour although they comprised only 21% of the birds under observation, while 69% of all soliciting was directed at breeding adults which comprised only 19% of the birds. In general, the amount of soliciting behaviour

exhibited was inversely correlated with the number of allopreening interactions in which a class was involved.

### Discussion of Allopreening Behaviour

Harrison (1965), in a review of allopreening behaviour, noted that the active bird in allopreening interactions was usually the dominant, in situations where dominance could be established by other means. Among jungle babblers breeders, which can be assumed to be dominant to other group members on the ground that they have priority of access to a scarce resource (i.e. reproduction), and first year birds, form the opposite ends of a continuum of allopreening involvement. This also suggests that the direction of allopreening reflects dominance relations within the group.

Table V. Preen Ratios and Relative Frequency of Preening Different Parts of the Body During Allopreening Interactions Between Different Age and Breeding Status Classes; Totals for P, L, and M Groups, 1972-73 and 1973-74 Seasons. The Active Participant is on the Left in the First Column

	Areas allopreened				Totals	Preen ratio	$\chi^2$	<i>P</i>	Hn as Percentage of total	C/D	$\chi^2$	<i>P</i>
	Hn	Br	Ba	Ut								
B ♂ : B ♀	23	14	11	4	52	1.73	5.4	<0.02	44(C)	1.1	0.1	0.7
B ♀ : B ♂	12	7	6	5	30				40(D)			
BB : NB	55	29	26	23	133	2.14	13.4	<0.001	41(C)	0.6	14.8	<0.001
NB : BB	44	10	5	3	62				71(D)			
BB : 2Y	35	25	23	20	103	2.78	16.5	<0.001	34(C)	0.5	10.6	<0.01
2Y : BB	24	5	3	5	37				65(D)			
BB : 1Y	25	16	18	12	71	35.50	42.0	<0.001	35(C)	0.3	3.5	<0.1
1Y : BB	2	0	0	0	2				100(D)			
NB : 2Y	40	18	10	9	77	2.40	9.7	<0.01	52(C)	0.8	2.6	<0.2
2Y : NB	22	6	1	3	32				69(D)			
NB : 1Y	23	6	7	3	39	6.50	14.0	<0.001	59(C)	0.7	1.3	<0.3
1Y : NB	5	0	1	0	6				83(D)			
2Y : 1Y	21	9	7	3	40	13.30	19.5	<0.001	52(C)	0.5	2.5	<0.2
1Y : 2Y	3	0	0	0	3				100(D)			
								</				

Comparisons of the proportion of allopreening directed at the head and neck region (Hn) in interactions between different classes.

	$\chi^2$	P		$\chi^2$	P
BB : 2Y / NB : 2Y	5.8	<0.025	BB : BB / 1Y : 1Y	0.03	<0.8-0.9
BB : 1Y / NB : 1Y	5.8	<0.025	NB : NB / 2Y : 2Y	1.7	<0.1-0.2
BB : BB / NB : NB	2.4	<0.1-0.2	NB : NB / 1Y : 1Y	0.3	<0.5-0.7
BB : BB / 2Y : 2Y	6.3	<0.025	2Y : 2Y / 1Y : 1Y	1.8	<0.1-0.2

Feather erection in the head and neck region is described by Hardy (1974) as inviting allopreening and also forming the typical submission display among neotropical jays of the genus

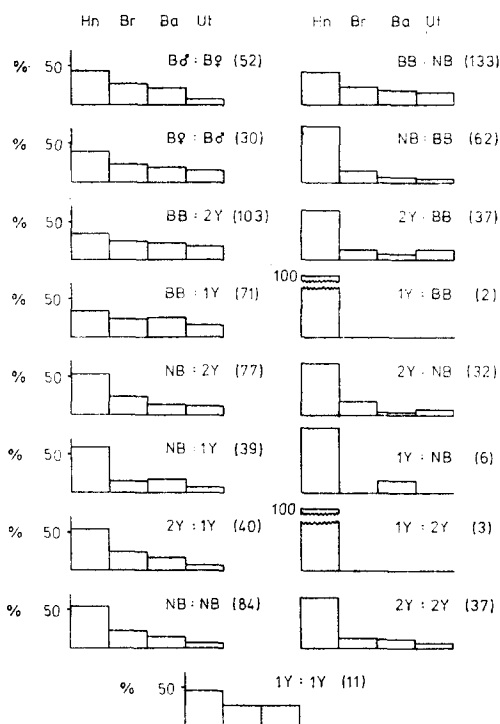


Fig. 6. Percentage of allopreening directed at different parts of the body by birds in different age/status classes. The first-named bird is the active participant. Figures in brackets are sample sizes.

*Cissilopha*. His pictures show that the poses adopted by this genus are similar to those seen in *Turdoides* and his description of their allopreening technique also sounds similar. In the jays however, feather erection is only sometimes followed by allopreening. In the timaline species *Garrulax leucolophus*, which is closely related to *Turdoides*, observations made on captive birds also showed that feather erection in the head and neck region served both to solicit allopreening and to express submission during interactions over food (personal observation). These observations all demonstrate a connection between allopreening and the expression of dominance. Among estrildine finches no consistent direction of allopreening can be observed (Kunkel 1974), but in this case most allopreening is between members of mated pairs.

Allogrooming is a frequent activity among social primates (Marler 1965; Sparks 1967; Jolly 1972) and the frequency of involvement and proportionate participation in active and passive roles have been found to be related to social status in a number of cases (Hall & DeVore 1965; Hall 1967; Kaufmann 1967; Kummer 1968). The tendency seen in birds and some rodents (Armitage 1962; Barnett 1963) for dominant animals to be the active participant more often than subordinates is reversed in the case of primates, with subordinates usually taking the active role. Jolly (1972) gives an example of active participation expressing dominance in the thicktailed bushbaby (*Galago crassicaudatus*) however, and primates may vary in this respect.

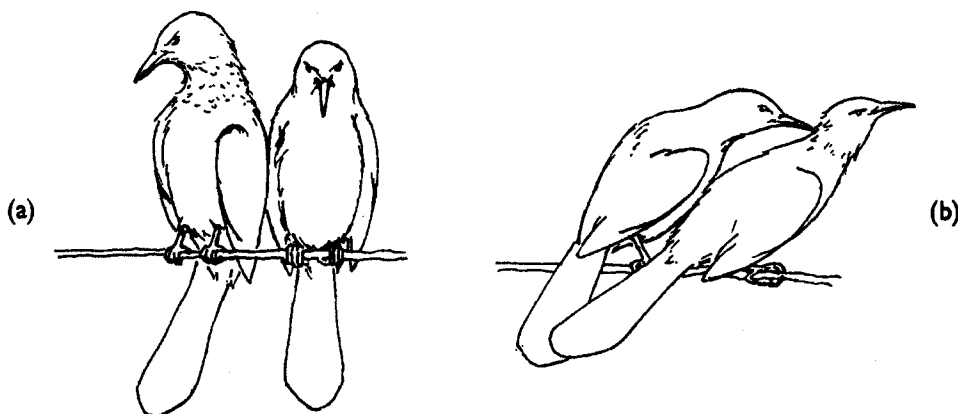


Fig. 7. Soliciting of allopreening in the jungle babbler; (a) the bird on the left solicits; (b) the other bird responds (redrawn by E. K. Dunn from field sketches).

The use of allopreening soliciting postures to express submission in some birds has led Harrison (1965) to suggest that allopreening behaviour evolved originally to reduce aggression by redirecting the behaviour of the potential aggressor. Sparks (1967) also supported this idea. The active soliciting of allopreening by jungle babblers in situations where they approach the potential preener suggests that in this species allopreening behaviour has evolved beyond the point where it serves to reduce aggression in a specific situation, to one where soliciting and receiving allopreening helps to maintain an individual's position within its group. If this is correct, then allopreening can be considered as a factor in promoting group cohesion, as well as a means of expressing social relationships. Similar ideas have been put forward to explain the importance of allogrooming in primates (Sparks 1967; Jolly 1972). The fact that allopreening involvements increase with age and that allopreening between first-year birds is the rarest category of allopreening interaction, suggest that allopreening in jungle babblers is not initially involved in the creation of social hierarchies, but simply expresses relationships already established by other means.

Both allopreening and clumping behaviour have generally been discussed from the point of view of the social relations of the participants. The possibility also exists that allopreening is intended partly as a means of communicating the status of the birds involved to other group members. If the group is viewed as an intensely competitive arena, as suggested by Zahavi (1974), and if coalitions are an important factor in determining individual status, as has been demonstrated for some primates (Hall & DeVore 1965; Jolly 1972; Kaufmann 1967; Southwick & Siddiqi 1967), lions (Schaller 1972) and the turkey (*Meleagris gallopavo*) (Watts & Stokes 1971), then it may be of

advantage for subordinate animals to demonstrate their relationship with other group members, particularly the dominant(s), by allowing themselves to be allopreened/groomed. In the case of the jungle babbler, where most subordinates are probably offspring of the breeding pair, competition among them would damage the interests of the breeders. If the dominant protects low-ranking non-breeders against aggression by higher-ranking birds then it is in the interest of the low ranking birds to demonstrate to other group members the degree to which they are accepted by the dominant(s) and this may be achieved by clumping and allopreening with the dominant. This hypothesis would explain why most soliciting is directed at the dominant and why clumping exerts a stimulus for other birds to clump.

### Sentinel Behaviour

The pattern of behaviour in which one member of a babbler group remains perched several metres above the ground, while the rest of the group feed below, has been described previously by Dharmakumarasinhji (1954) and Andrews & Naik (1970), the latter authors employing the term 'sentinel' to describe the bird remaining perched. This pattern of behaviour was seen commonly among jungle babbler groups, being particularly noticeable in winter.

### Methods

During the winter of 1971 to 1972 the identity of all sentinels that could be recognized was recorded and also the timing of change overs. In the following winters the identity of the sentinel was recorded every 5 min but no attempt was made to time exchanges. Sentinel behaviour was easiest to observe in winter when, particularly in the early morning, there was never more than one member of the group perched at a time. The situation in summer was usually less clear because occasions on which the whole group was feeding simultaneously were less frequent than in winter. For much of the time more than one bird remained perched in trees and although it was sometimes apparent that one bird was keeping more alert than others the selection of a sentinel on this basis appeared open to subjective bias. Accordingly only records of sentinel behaviour collected during the winter were used in the following analysis.

### Results

A sentinel was recorded as present during 82% of the time spent observing jungle babbler

Table VI. Frequency of Soliciting and Being Solicited for Allopreening in Relation to Age and Breeding Status; P, L, and M Groups, 1972-73 and 1973-74 Seasons

	Solicitor (A)	Solicited (B)	Bird years (C)	A/C	B/C
B ♂		19	6		3.2
B ♀		27	6		4.5
NBA	18	16	22	0.8	0.7
2Y	16	4	16	1.0	0.2
1Y	33	1	13	2.5	0.1

groups in December and January, but this represents a minimum figure since sentinels must sometimes have been overlooked. Birds exhibiting sentinel behaviour usually perched in the lower branches of the woodland canopy where they could be easily seen by the rest of the group. Figure 8 shows the distribution of heights at which they perched against a typical vegetation profile.

The mean duration of periods of sentinel activity timed during December 1971 and January 1972, in relation to time of day, are shown in Fig. 9 which demonstrates that mean duration increased from dawn to mid-afternoon, possibly decreasing again before dusk. Changes between sentinels were effected in three different ways: (1) The sentinel flew down to join the group and another bird then moved up to replace it (not necessarily on the same perch). (2) A new bird flew up and perched near the sentinel which then descended. (3) A new bird flew up to perch near the sentinel which then became less alert and often began to autopreen, usually descending after a few minutes.

The lack of a fixed pattern of events at change over suggests a flexible response to different situations. In winter, particularly in the early morning, the sentinel often began to give a low intensity cackle call in the minute before it left its perch and this was sometimes followed by another bird flying up to take its place. In these instances the call appeared to constitute an announcement that the sentinel was about to descend.

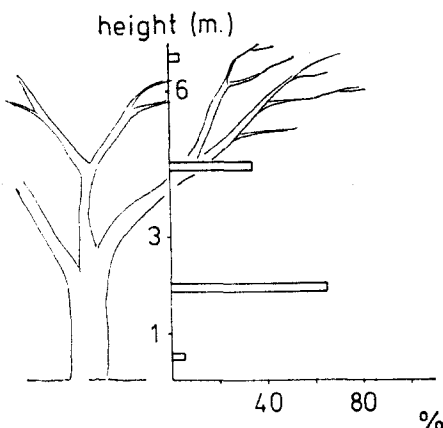


Fig. 8. Height above the ground of birds exhibiting sentinel behaviour in relation to the average vegetation profile.

Table VII shows the frequency with which members of L, P and M groups were recorded as sentinels during the winters of 1971 to 1972 and 1972 to 1973. Figures for L group in 1971 to 1972 include only January and February as one non-breeding adult was not ringed until December. For groups including more than one unringed bird records were apportioned equally between the number of unringed birds known to have been in each age class.

In five out of six cases the bird observed most frequently as sentinel was one of the following season's breeding pair. In M group in both years this was the female and in P group in both years, the male. In L group, where in 1971 to 1972 a non-breeding male (LBB) was apparently the most frequent sentinel, the breeding male was unringed and this bird might actually have performed more sentinel behaviour than LBB. In 1972 to 1973, when there were only two unringed birds in L group, the breeding male was identifiable at close range by plumage characteristics and 66% of records where the unringed sentinel could be identified referred to the breeding male. Table VIII shows the mean amount of sentinel activity performed by

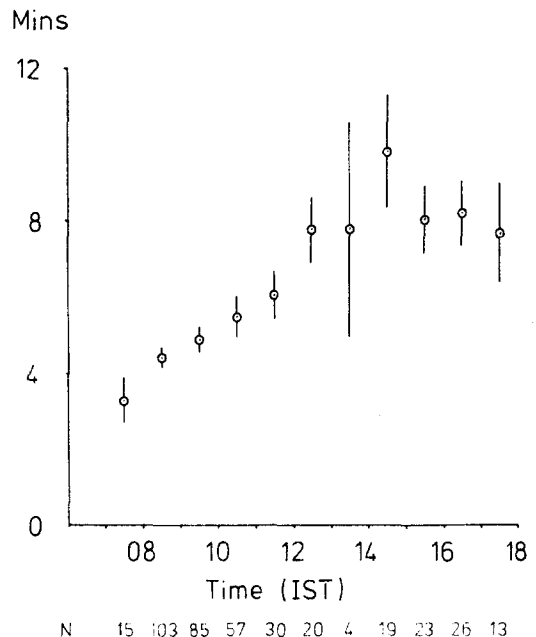


Fig. 9. Changes in the duration of sentinel behaviour with time of day during December 1971 and January 1972. Vertical bars are standard errors. (N = sample size).

different age classes, expressed as percentages. In general the breeding pair performed about 50% of sentinel activity and the rest was shared between non-breeding adults and second-winter birds, first-year birds rarely taking part.

Among non-breeding adults and second-year birds there seemed to be a tendency for males to perform more sentinel behaviour than females. Among second-winter birds in P group in 1972 to 1973 the two males performed more than either of the two females and in M group the male second-year performed more than the female. In L group a non-breeding male performed more than the breeding female in both years, but in P group in both years, among non-breeding adults a female performed most sentinel activity. In 1971 to 1972 this was BR and in 1972 to 1973, PDG and in both cases they performed more sentinel activity than the breeding female (PM). These three females were

apparently rivals for the position of breeder. PDG was breeding female in the spring of 1972, being succeeded by PM in the summer, while BR was driven out of the group by PDG after destroying the eggs in PDG's first nest in 1972. Since these three were all apparently potential breeders in P group, it seems likely that all were immigrants from outside the group. In babblers females do not normally breed in their natal group (Gaston 1976).

Changes in the mean duration of sentinel watches during the course of the day suggest that the amount of time spent in sentinel activity may be determined, at least in part, by the ability of the birds involved to refrain from feeding. If so the amount of sentinel activity performed may reflect the relative food-finding abilities of different group members and this should apply particularly at times of year when food is least abundant and feeding time most limited. Under this hypothesis, if the breeding pair were superior in food-finding to other group members, they might be expected to take a larger share of sentinel activity during December and January, the months of lowest temperatures and shortest days, than during the rest of the winter (November and February).

Table IX compares the amount of time spent in sentinel activity by the breeding pair and by non-breeders in different months. For 1971 to 1972 December and January are compared with February and for 1972 to 1973 December is compared with November and February, because no data were obtained in November 1971 and January 1973. Figures for P group in

Table VII. Frequency of Sentinel Behaviour Among the Members of Three Groups of Jungle Babblers. Records were made at 5-min intervals

	P group		L group		M group	
1971-72						
B ♂	PDB	51	UN	42	MB	64
B ♀	UN	5	LBO	49	MDB	118
NB and 2Y	PLG ♂	9	LBB ♂	60	MLG ♂	42
	BR ♀	38	LBDB ♂	22	MW ♀	49
	UN(2)	9	LBW ♀	22	MR ?	45
			UN(2)	84	UN(2)	32
1Y	PO ♂	1	LBY ♂	1	MO ♂	2
	UN(4)	18	LBM ♂	3	MP ♀	1
					MY ?	2
		131		283		355
1972-73						
B ♂	PDB	61	UN	42	MB	18
B ♀	PM	23	LBO	23	MDB	29
NB	PLG ♂	18	LBB ♂	28	UN	10
	PDG ♀	30	LBDB ♂	17		
	PW ♀	13	LBW ♀	15		
	UN?	21	2UN ♂	41		
2Y	PO ♂	24	LBY ♂	5	MO ♂	16
	PB ♂	18	LBM ♂	13	MP ♀	2
	PY ♀	12				
	YB ♀	4				
	PLB?	17				
1Y	PR ♂	2	LGW	2	two	0
			four	0		
		243		186		75

Table VIII. Mean Amount of Sentinel Behaviour Performed by Individuals of Each Class Expressed as Percentages of the Total Records for the Group. Only Ringed Birds are Included

	P group	L group	M group
<b>1971-72</b>			
	%	%	%
B ♂	39	—	18
B ♀	—	17	33
NB and 2Y	18 (2)	12 (3)	13 (3)
1Y	1 (1)	1 (2)	1 (3)
<b>1972-73</b>			
B ♂	25	—	24
B ♀	9	12	39
NB	8 (4)	11 (3)	13 (1)
2Y	6 (5)	5 (2)	12 (2)
1Y	1 (1)	1 (5)	0 (2)

Numbers in brackets show the numbers of birds involved.

1971 to 1972 are omitted because of the large number of unringed birds in the group that winter. In four out of the five cases the breeders undertook a higher proportion of sentinel activity during December and January than during November and February, but this was not true for M group in 1972 to 1973. When all five sets of data were pooled the difference was found to be significant ( $P < 0.01$ ).

### Discussion of Sentinel Behaviour

Evidence from the change in the duration of sentinel watches during the day and changes in the proportion of sentinel behaviour performed by the breeding pair both suggest that the amount of time devoted to sentinel behaviour may be related to birds' ability to find food. If this ability is also related to social status within the group then sentinel behaviour may provide a clue to status. Since sentinel birds usually perch in clear view of other group members and often give vocalizations at the same time it seems possible that the role of sentinel may be adopted partly to advertise the status of the bird concerned. This hypothesis provides an explanation for the observation that females in their natal group performed less sentinel behaviour than males, since there is no apparent evolutionary reason why they should be concerned to display their social status in a group in which they cannot become a breeder. Among males, however, competition can be anticipated for the privilege of succeeding the breeding male and hence a reason exists to express their social status by performing sentinel behaviour. The same hypothesis might also explain why immigrant females, competing for the position of breeder, should perform sentinel behaviour frequently, as was observed in the case of PM, PDG and BR.

Another hypothesis that might explain differences in the frequency of sentinel behaviour is that breeders have more at stake in the survival of the group than non-breeders, since a high proportion of the group consists of their offspring. The difference in frequency between native male and female non-breeders could then be accounted for by the idea that males have a greater interest in maintaining the strength of the group so that the size and quality of the territory to which they succeed may be preserved. Under this second hypothesis, however, it is hard to explain the high frequency with which females unrelated to the group performed sentinel behaviour and it is necessary to assume

that this was the result of an accident of sampling.

### Leadership

From the beginning of the study an attempt was made to discover whether group movements were initiated or directed by particular birds, but unequivocal evidence was rare. Groups crossing open spaces between trees did so in single file and it was sometimes possible to identify the leading bird. This did not imply that the leader had initiated the movement, or that the other birds were following it, but simply that the group was moving from A to B and that a certain bird was more eager, or less cautious, than the rest. Where some outside stimulus was apparent, such as the challenge of a nearby group, no implication of leadership was required to explain group movements.

In a few instances it was possible to assign the initiation and orientation of a movement to a particular bird. The criteria used to identify such an initiation were: that the initiating bird moved before the rest of the group showed signs of doing so, that it gave the 'cu-cu-cu' call, that the whole group followed, that the movement covered more than 40 m, and that there was no apparent outside stimulus orienting the movement. The last condition was difficult to verify because the birds' ability to detect calls of their own species was probably greater than that of the observer, but in most cases where birds moved in response to audible calls from neighbouring groups subsequent events would have made the cause of the movement clear. Records of the initiation of movements which fulfilled these criteria are given in Table X.

In groups where the breeding male was ringed, this bird initiated 48% of all movements, and in groups where the breeding female was ringed this initiated 33%. Nearly all other records were of non-breeding adults, with a few records of second-year birds. The relative contribution of the breeding pair is probably biased by the large sample of observations for P group, where the breeding male initiated movements significantly more often than the breeding female. In M group in the 1971 to 1972 and 1972 to 1973 seasons the breeding female initiated more often than the male and in the latter season this difference was significant ( $P = < 0.01$ ). Although the breeding male of L group was not identifiable in the 1971 to 1972 and 1972 to 1973 seasons it is likely from the number of initiations made by unringed birds that the contributions

of the breeding pair were approximately equal. This small sample of pairs suggests that on average there is probably little difference between the sexes in the frequency with which members of the breeding pair initiate movements, but that there may be significant differences between members of a particular pair, depending on individual qualities.

### Order of Movement

When a group was moving in single file it was sometimes possible to observe the order of travel. In most cases the birds following immediately behind the leader were adults and those last in line were invariably first-year birds. This pattern was most noticeable when one group was moving to have a territorial confrontation with another. A number of tests were made by replaying tape recordings of group confrontation calls about 60 m away from a group which was feeding. The first birds to arrive in 10 out of 11 tests outside the breeding season were members of the breeding pair, followed by non-breeding adults. The last to arrive, sometimes not appearing at all, were first-year birds. Tests made near nests during the incubation and nestling periods did not produce the same pattern. In two trials a member of the breeding pair was first to arrive but in two others non-breeding adults arrived first, and in the remaining two, second-year birds arrived first, followed by non-breeding adults. These results may reflect the fact that groups are often scattered widely when feeding during the breeding season. Tests along these lines were hampered by the fact that jungle babblers learned to ignore tape recordings after only one or two trials.

Table IX. Comparisons of the Proportion of Sentinel Behaviour Performed by the Breeding Pair in Mid-winter (December to January) and in November and February

	Dec. and Jan.	February	$\chi^2$	P
<b>1971-72</b>	%	%		
L group	35 (N = 205)	26 (N = 74)	2.02	
M group	52 (N = 293)	51 (N = 57)	0.03	
<b>1972-73</b>	December	Nov. and Feb.		
	%	%		
P group	58 (N = 103)	38 (N = 63)	6.35	<0.02
L group	47 (N = 85)	31 (N = 81)	4.57	<0.05
M group	57 (N = 44)	71 (N = 31)	2.53	

Pooled data for all groups in both years,  $\chi^2 = 6.92$ ,  $P < 0.01$ .

### Comparison of Ranking by Allopreening, Sentinel Behaviour and Movement Initiation

Hierarchies constructed on the basis of involvement in allopreening, sentinel behaviour and the initiation of movements are similar to the extent that all three activities increase with age and all are most frequently performed by members of the breeding pair. Apart from this the three hierarchies are not very similar, although some of the difference could be the result of sampling variation. Table XI ranks the second-year and older members of L, M and P groups according to observations made in the winter of 1972 to 1973 and also gives the mean ranks based on all three hierarchies. In mean rankings all but one of the second-winter birds are equal to, or lower in rank than, adult members of their group. This suggests that, at least up until the second winter, social status is closely correlated with age.

In P and M groups second-winter males ranked above second-winter females in the sentinel hierarchy and lower in the allopreening hierarchy. This was also true for four second-winter birds in L group in the 1973 to 1974

Table X. Number of Observations of Birds Initiating Movements of More Than 40 m

	P group	L group	M group
<b>1971-72</b>			
B ♂	PDB 20		MB 8
B ♀		LBO 9	MDB 15
NB or 2Y	BR 2	LBB 7	MR 4
	PLG 1	LBW 1	MW 1
			MLG 1
Unringed	B ♀, 2NB 1	B ♂, 2NB 10	2NB 2
<b>1972-73</b>			
B ♂	PDB 42**		MB 2*
B ♀	PM 14	LBO 11	MDB 11
NB	PLG 1	LBW 2	
	PW 3		
	PDG 11		
	UN 4		
2Y	PB 1		MO 1
	PLB 3		
Unringed		B ♂, NB 12	
<b>1973-74</b>			
B ♂	PDB 5	UN 2	MB 2
B ♀	PM 0	LBO 5	MDB 0
NB	PDG 2	LBDB 1	UN 1

Overall percentage of initiations by each category  
 B ♂ 81/166 = 48%, B ♀ 65/194 = 33%, NB 42/218 = 19%, 2Y 5/136 = 4%  
 \*\* ♂; ♀,  $P < 0.001$ . \* ♂; ♀,  $P < 0.01$ .

seasons, where the male DGLG was the most frequently involved in sentinel behaviour, but the least often involved in allopreening. The other second-winter male, LGW, was also involved in allopreening less than the females, but did not participate in sentinel behaviour either.

The following hypothesis might account for the observed discrepancy between the allopreening and sentinel hierarchies. Non-breeding males are anxious to advertise their social status within the group since their chance of succeeding to the breeding territory, or of pairing with an immigrant female, may depend on this. Consequently they spend as much time as possible

performing the public display of competence which sentinel behaviour represents. Females still in their natal group are less concerned to advertise their status because they will leave before breeding. In the course of allopreening, however, which they perform in order to consolidate their position within the group, many of these females rank higher than males of the same age and hence occupy higher positions in a hierarchy based on allopreening.

### Play

Two patterns of behaviour seen regularly among jungle babblers seemed to come under the heading of play. These were named respectively 'rough and tumble' and 'mad flight'.

Rough and tumble behaviour consisted of two or more birds engaging in a mock fight in which some lay on the ground more or less passively, while others rolled on top of them, or pecked them deliberately but gently. At least four birds usually took part and although it was always difficult to identify the participants, most were first-year birds, while breeding adults were never observed to take part. Ten instances of this behaviour were recorded among the study groups; three in August, two in December, and one each in September, February, March, April and May. Similar behaviour was also observed on several occasions among groups of large grey babblers (*Turdoides malcolmi*), and for this species the behaviour had also been noted previously by Hutson (1954).

Mad flights consisted of one or several birds flying rapidly and apparently aimlessly among the branches of a tree, twisting and turning in aerobatic manoeuvres. This display was never seen in the open and was thought at first to be a leaf-bathing exercise because it was observed after rain. Subsequent observations in dry weather refuted this hypothesis. Like rough and tumble behaviour, most of the birds identified performing mad flights were less than 1 year old and adults were never seen to indulge.

Some mad flights occurred after aggressive interactions between members of the same group. In other cases a mad flight by one bird was followed by other birds performing the same behaviour and in one case a mad flight by two birds together gave the appearance of a mock chase.

The eight instances of mad flights recorded among the study groups all occurred between July and November, with five in August and September. Ten out of the 14 birds involved that

Table XI. Comparisons of Ranking Within Jungle Babbler Groups Based on Sentinel Behaviour, Initiation of Group Movements, and Preen Ratios. Only Birds More Than 1 Year Old are Included. Winter of 1972 to 1973

	Sentinel	Initiation	Preening	Mean
<b>P group</b>				
B ♂ PDB	1	1	1	1
B ♀ PM	4	2	2	2
NB PLG ♂	5.5	6.5	3	4
PDG ♀	2	3	4	3
PW ♀	8	4.5	6	5.5
2Y PO ♂	3	9	8	7
PB ♂	5.5	6.5	9	8
PY ♀	9	9	10	10
YB ♀	10	9	5	9
PLB?	7	4.5	7	5.5
<b>L group</b>				
B ♀ LBO	2	1	1	1
NB LBB ♂	1	4.5	6	3
LBDB ♂	3	4.5	5	4.5
LBW ♀	4	2	2	2
2Y LBY ♂	6	4.5	4	6
LBM ♂	5	4.5	3	4.5
<b>M group</b>				
B ♂ MB	2	2	2	2
B ♀ MDB	1	1	1	1
NB UN ♂	4	4.5	4	4.5
2Y MO ♂	3	3	5	3
MP ♀	5	4.5	3	4.5

Kendall coefficients of concordance (W) for the three rankings:

P group,  $W = 0.73$ ,  $\chi^2 = 19.8$ ,  $df\ 9$ ,  $P < 0.02$ .

L group,  $W = 0.46$ ,  $\chi^2 = 7.0$ ,  $df\ 5$ ,  $P < 0.3$ .

M group,  $W = 0.82$ ,  $\chi^2 = 9.8$ ,  $df\ 4$ ,  $P < 0.05$ .



could be identified were juveniles more than 1 month old and it seems possible that this behaviour is related to the establishment of dominance relations among these young birds. Most instances of overt intra-group aggression involved juveniles between 1 and 3 months old. Some of these were over food being solicited from an older bird, but instances of apparently spontaneous aggression were also observed several times among birds of this age.

### Roosting

Jungle babblers in the study area roosted in trees or bushes from 1 to 5 m above the ground, but usually at least 3 m up. Roosts were often in dense foliage or twigs, usually on a branch 2 to 5 cm in diameter, with the innermost bird close to where it joined a larger branch.

Groups invariably clumped while roosting. Normally the entire roost lined up side by side on the branch, all facing in the same direction, but sometimes large groups occupied two adjacent branches, or a few birds perched on side branches at right angles to the rest.

### Behaviour on Entering the Roost

In some cases all birds entered the roost within a few seconds, flying directly to the roosting branch and settling immediately side by side. In other cases birds moved restlessly from branch to branch, settling briefly, and then moving again before all the group had assembled. Perches on which the group partially assembled and then left to roost elsewhere were named 'false roosts' and sometimes as many as 15 of these were visited, in different parts of the core area, before the group finally settled. Birds entering the roost often clambered over the backs of those already perched and tried to force themselves between birds already clumped. Such struggles sometimes continued until it was too dark for observation, but in many cases they did not occur at all, entry into the roost being quite orderly.

Figure 10 shows the mean time in relation to sunset that groups entered their final roost in each month and also the proportion of nights on which false roosts were visited before finally settling. In general groups went to roost earlier, in relation to sunset, in winter than during the breeding season. The timing did not seem to be influenced by the occurrence of false roosts, which were most frequent in June (small sample) and in November and December.

By the time that birds were entering the roost it was usually too dark to identify colour rings, but in the few cases where this was possible it was one of the breeding pair which entered first and usually non-breeding adults or second-year birds which were last. In some cases adults which arrived near the roost after other birds had entered sat and waited for several minutes before joining onto the end of the roost.

### Order of Perching in the Roost

An attempt was made to investigate the order of perching in roosts by taking colour photographs of the roost by flash. This was only possible at roosts where vegetation did not obscure the birds and where it was possible to approach without disturbing them. Photographs were taken just before dawn, so that if the birds left the roost as a result of the disturbance they had only a short while to wait before commencing feeding. Altogether 30 roosts were photographed, of which 17 provided pictures in which one or more birds could be identified. The results of these identifications are listed in Table XII.

Photographs taken of M group on 4 days during October and November 1972 all showed the same order of roosting with the breeding male on the inside, the breeding female beside

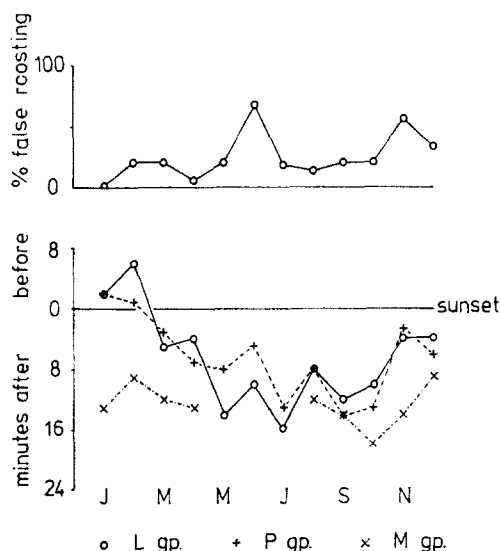


Fig. 10. Time of entering the roost for three jungle babbler groups in relation to the time of sunset (lower graph), and percentage of all roosts preceded by false roosting behaviour (upper graph), in relation to time of year.

Only a few birds were recognizable in the three photographs of P group, but in each case the outermost bird was a non-breeding second-year or adult male and in two cases juveniles were together in the centre of the roost. The position of the juveniles in the middle of the row was also observed in several roosts which were not photographed. In these instances the juveniles, between 2 and 6 weeks old, entered the roost last by squeezing into the centre of the group. The two pictures of L group which included juveniles (11 November 1972 and 3 September 1973) also showed a tendency for them to concentrate in the centre or towards the inside.

The most typical configuration of roosts, with adult birds at either end of the row and juveniles in the centre, seems to confer protection and thermal insulation on those members of the group which should be most in need of it. Unsettled behaviour in the roost seems to be associated with lack of discipline among younger birds and this in turn, like play behaviour, may be connected with the establishment of dominance relations among the year class.

[illegible]

### General Discussion

Intra-group behaviour among wild birds has been studied in a number of species but none in which groups persist for such a long time as those of the jungle babbler. The closest approach to the situation observed in babblers is provided by winter flocks of black-capped chickadees *Parus atricapillus* documented by Glase (1973) and Smith (1976), although these break up during the breeding season. In these flocks unilateral dominance hierarchies based on approach-retreat interactions and aggressive behaviour can be discerned and overt aggression appears to be much more common than within groups of jungle babblers. Dominance hierarchies have also been observed in wild flocks of house finches *Carpodacus mexicanus* (Thompson 1960; Kalinoski 1975) and Harris' sparrow *Zonotrichia querula* (Rohwer 1975), but in some passerines which regularly form flocks no consistent dominance hierarchies can be observed (Ellis 1966; Kalinoski 1975). Some passerines also show a tendency towards site-related dominance, as in Steller's jay *Cyanocitta stelleri* (Brown 1963).

Jungle babblers differ from all the above-mentioned species in the almost total absence of aggressive behaviour within groups, making the presence of a peck-right or approach-retreat hierarchy difficult to determine. Posture displays in intra-group situations were unusual, the only common one being the soliciting posture for allopreening. Although a wide variety of vocalizations could be employed, most of them were rarely used and the only ones heard frequently in intra-group situations were the cackle call (2) and the chuck call (5).

Despite their lack of overt aggressive behaviour jungle babblers showed complete dominance in relation to reproduction, since only one pair in each group bred. Observations on jungle babblers and the related common babbler *Turdoides caudatus* suggested that new breeding males were recruited from within the group, while new breeding females were immigrants. Competition can therefore be anticipated among

non-breeding males for the opportunity to achieve breeding status. In the few cases in which succession was observed the transition was quite orderly and without overt aggression, suggesting that the issue had been decided in advance, and this points to the presence of a cryptic dominance hierarchy, at least among males. The situation among females is more difficult to interpret but since they take part to some extent in all the same social interactions as males the presence of a hierarchy among females is also possible.

The intra-group behaviour of the jungle babbler is perhaps better compared to that of social mammals rather than other birds which have been studied so far. In this context the absence of clear-cut approach-retreat behaviour within groups of jungle babblers is surprising because most groups of primates which have been studied show these to a certain extent, at least among males (Jolly 1972) and so do wolves *Canis lupus*, which resemble babblers particularly in that only one pair within the pack probably breeds (Mech 1970). Dominance interactions are relatively rare among lions (Schaller 1972) and hyaenas (Kruuk 1972), although some hierarchy can be observed, while among hunting dogs *Lycaon pictus* no hierarchy can be discerned at all (Kuhme 1965). Despite their lack of overt dominance interactions hunting dogs resemble babblers in that reproduction is limited to a small proportion of the adult population.

Some of the difference between species which show clear dominance hierarchies based on approach-retreat or peck-right behaviour and those in which this type of dominance cannot be observed, may be the result of differences in the length of time that species have been adapting to a group situation and the degree of flexibility in social structure required by their ecology. Hunting dogs, like jungle babblers, can be considered obligate group-living animals, since they always occur in packs and their system of hunting depends on this (Kruuk 1972). Semi-terrestrial primates on which most studies of primate behaviour in the field have been carried out, tend to be relatively flexible in the type of social configuration that they adopt. Species such as geladas *Theropithecus gelada* may occur in one-male or multi-male groups according to environmental factors (Crook 1966). Hamadryas baboons *Papio hamadryas* maintain one-male groups during the day but join into large groups to sleep (Kummer 1968). Langurs *Presbytis*

Table XIII. Distribution of First-year Birds Within L Group Roost, December and February only

Inner third	Middle third	Outer third	
18	11	9	Adult and 2Y
2	11	13	1Y

$$\chi^2 = 11.7, df 2, P < 0.01.$$

*entellus* occur in heterosexual and all-male groups in the same area (Jay 1965). The price of maintaining this flexibility may be the need to maintain overt dominance interactions as a normal part of the social repertoire.

Wolves belong to a genus which otherwise adopts pair-territorial behaviour (Wilson 1975) and their pack-hunting habits may have evolved relatively recently. The same is true of lions, except that the genus is otherwise largely solitary. By contrast hunting dogs stand relatively isolated, taxonomically, except for the genus *Cuon* which apparently shares their habits (Kleiman & Eisenberg 1973) and they have probably been adapting to group-living for a long time. This almost certainly applies to the genus *Turdoides* in which all of the 20-odd species appear to live in groups of three or more birds except the somewhat aberrant *T. nipalensis* (Ali & Ripley 1971 and personal observation).

The differences in ordering between the rankings based on allopreening, sentinel behaviour and movement initiation suggest that these rankings may be based on independent behavioural mechanisms. A similar conclusion regarding different behavioural hierarchies observed within groups of primates has been reached by Rowell (1966) and Bernstein (1970). In the case of the jungle babbler these differences are likely to be related to differences in the strategies of native and immigrant females and among native birds to differences in strategy between the sexes regarding the maintenance of the group and its common territory.

The development of socialization in the jungle babbler seems to follow a predictable pattern. During the immediate post-fledging period the young birds spend most of their time obtaining food from other group members and avoiding detection by predators. This phase lasts about 1 month, after which they begin to move with their group and do most of their foraging for themselves. At this stage they begin to indulge in play activities and to move outwards from the centre of the roost. The next few months constitute an 'adolescent phase', during which they show signs of social discipline such as chasing adults with food, pecking one another aggressively, and disrupting the roost. Indiscipline declines during the first winter and by their first summer their behaviour is similar to that of older group members, although they occupy the lower end of the rankings of sentinel behaviour, allopreening and movement initiation.

The play activities observed among jungle babblers come under the heading of social play (Loizos 1967) because they usually involve more than one bird, although mad flights were sometimes performed alone. Social play is comparatively rare in birds, but is exhibited by most mammals. Among primates play is most intense during the weaning and sub-adult periods (Loizos 1967; Chance & Jolly 1970) which correspond, in terms of social status, with the immediate post-independence period in the jungle babbler. It seems likely that this 'adolescent phase', during which play activities are most frequent, is the period when social relations are established between peers and young birds are integrated into the social structure of their group. If this is the case then play may be a mechanism through which social status within the group is determined. Carpenter (1964) considered that this was one of the functions of social play in primates, and Mech (1970) also suggested this for wolves.

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