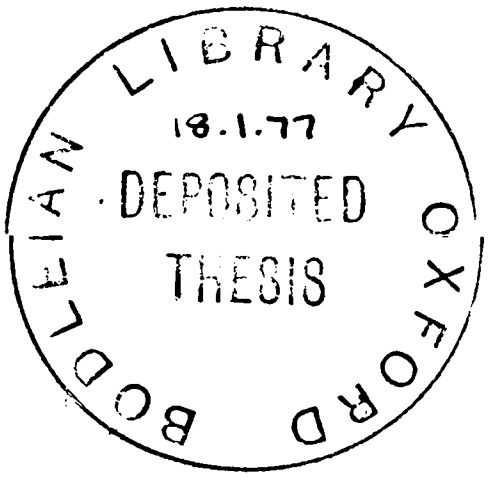
FACTORS AFFECTING THE EVOLUTION OF GROUP TERRITORIES IN BABBLERS (*Turdoides*) AND LONG-TAILED TITS

A. J. Gaston, Oriel College



Note to readers

Many of the hypotheses proposed in this thesis are speculative and analysis of much of the data is only preliminary. Before quoting anything, other than primary observations, you are advised to contact the author (current address with the secretary of the Edward Grey Institute). Parts of chapter 3 have been drastically revised for publication and the relevant paper (Animal Behaviour 1977) should be consulted in preference to this thesis.

FACTORS AFFECTING THE EVOLUTION OF GROUP TERRITORIES IN BABBLERS (*Turdoides*) AND LONG-TAILED TITS

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Thesis submitted for the degree of Doctor of Philosophy

July 1976

ABSTRACT

The thesis is divided into three parts. In part I the ecology and behaviour of the Jungle Babbler Turdoides striatus are described and in part II comparable data on the Common Babbler T. caudatus are given. In part III some observations on other species of Turdoides and on the Long-tailed Tit Aegithalos caudatus are described and a general model for the evolution of group territoriality and co-operative breeding is presented. A description of the habitat in which Turdoides studies were carried out is given in an introduction which includes data on seasonal cycles and a brief outline of the ecology of the resident avifauna. A summary is also given of the biology of Turdoides species, which live in permanent exclusive groups of 2-20 birds, holding common territories throughout the year. In most cases only one pair breeds during the season, but many non-breeding group members take part in nesting activities, particularly feeding the nestlings. The aims of the study are summarised in two questions:

"What circumstances make it advantageous for more than two birds to share a territory?"

"What circumstances make it advantageous for birds to assist in rearing conspecifics which are not their own offspring?"

Part I contains four chapters. The first deals with the population dynamics of the Jungle Babblers within the main study area on the outskirts of Delhi, India. Methods used to estimate recruitment, survival, interchange between groups, group structure and the degree of relatedness between group members are described. Territories are classified into three types on the basis of the vegetation that they contain and differences are found between these categories in the number of young reared and the number of birds per group. Large groups, which occupy territories mainly in woodland, probably produce most of the recruitment into the adult population. Birds from these

groups may move into territories outside woodland to breed, but breeders in woodland territories are probably recruited from territories of a similar type. Although woodland groups are large and have a high breeding success there is no evidence that the number of non-breeders in the group influences the reproductive success of the breeding pair directly.

In Chapter 2 the territorial behaviour of the Jungle Babbler is described. Groups do not cover their home ranges evenly, but tend to concentrate their activities in a small portion, usually comprising closed-canopy woodland with a dense understorey, known as the 'core area'. This was arbitrarily defined as the area within which 50% of the observations of a particular group were made and it comprised about 17% of the total home range recorded. Use of different parts of the home range varies with the time of year and territoriality appears to be most marked at the start of the two peaks of breeding activity. During the winter groups often forage together for periods of several hours.

The size of core areas is correlated with the number of birds in the group. Groups which changed their numbers from one season to the next showed corresponding changes in the extent and quality of their core area. Taken in conjunction with evidence from Chapter 1, this suggests that large groups tend to be stable and persistent, while small groups are vulnerable to encroachment by others and hence tend to be ephermeral.

Chapter 3 describes five aspects of intra-group behaviour in relation to the age, sex and breeding status of the participants. These are allo-preening, sentinel behaviour, leadership, play and roosting. A rough concordance was found between hierarchies based on participation in allo-preening, sentinel and leadership behaviour, but among non-breeding adults differences were found between the sexes. If these three behaviour patterns function partly to express the social status of the participants then

differences between males and females are probably related to their respective breeding strategies; males striving to become breeder in their natal group, while females normally move elsewhere to breed. Play behaviour occurs mainly among first year birds, particularly between 2-4 months after fledging, and may be associated with the establishment of dominance relations among siblings. At the same age they show various signs of social indiscipline which may contribute to the unsettled behaviour shown by some groups while going to roost.

The behaviour of non-breeding birds during nesting is described in Chapter 4. All non-breeders more than one year old contribute to feeding the nestlings and driving off potential predators, but a greater share is taken by males than by females. Like the differences in other aspects of behaviour, this difference between the sexes may be attributable to differences in their strategies for breeding. Non-breeders also take some part in incubation, but do not participate in nest-building.

The introduction to part II explains how limitations on the visibility of Common Babblers in the field led to an emphasis on different aspects of their behaviour. Chapter 5 covers population dynamics and movements, and also deals with seasonal weight changes. These suggest that some birds which were trapped in mid-winter may have been close to the minimum weight guaranteeing survival and it is possible that the availability of food at this season may be a factor controlling the population.

The proportion of unrelated birds found in groups of Common Babblers appears to be higher than estimated for Jungle Babblers. Females leave their natal groups in their first summer and a few males were observed to breed at one year old. The population of Common Babblers in the study area declined throughout the period of the study and this may have affected observed rates of immigration.

In some Common Babbler groups only one pair nests during the season, but in others the same male nests successively with two different females and in a third situation two pairs nest simultaneously. There are significant differences between groups exhibiting these three patterns in the number of birds per group and in the density of birds within the territory. In Chapter 6 the relationship between group size, population density and territorial area is described for the main study area and also for populations in the Salt Range, Pakistan. The results of some inconclusive removal experiments are described.

Behaviour at the nest was studied in greater detail for the Common Babbler than for the Jungle Babbler and the results are described in Chapter 7. Incubation is carried out mainly by the breeding female. Non-breeding females do not usually participate in feeding the nestlings, being driven from the vicinity of the nest by the breeding female. A correlation was found between the number of non-breeders assisting at the nest and the number of nestlings in the nest on day nine, but a causal relationship could not be established.

In part III, Chapter 8, brief observations on five other species of Turdoides are described. A comparison between population densities and group sizes for all the populations of Turdoides studied reveals that there is a close correlation between these parameters. The variance in group size within populations is also similar, suggesting that factors controlling group size operate in a similar way on populations in different habitats and at a wide range of densities.

The behaviour and ecology of the Long-tailed Tit, studied over a period of nine months in Wytham Wood, Oxford, are described in Chapter 9. In winter stable groups of 10-25 birds hold territories. In February these groups break up into pairs during the day although members of the same winter group

continue to roost together. Pairs nest within their winter territory in most cases, although there is some movement between territories, mainly by females. Non-breeding birds contributed to feeding the nestlings at six out of the ten nests where young survived at least seven days. Three single 'helpers' of known sex included two males and a female and these may have been non-breeders, which were estimated to constitute 9% of the population. In one case a pair which had failed in its nesting attempt was apparently involved in helping.

In Chapter 10 the factors considered to play a major part in the evolution of group territories are described. It is assumed that groups form by the retention of offspring within the parental territory and the development of tolerance by the adults is considered crucial in the origin of group territories. It is suggested that high adult survival in a situation where the habitat is fully saturated with territory holders creates the optimal conditions for group territoriality, but other important factors are also described.

Arguments are put forward to suggest that the advantages of group territory are likely to be greater for non-breeding group members than for the breeders, and this inequality is proposed as an important factor in the origin of co-operative breeding. In situations where remaining in the parental territory increases the inclusive fitness of the non-breeder, but does not increase that of the breeders, then non-breeders may be able to make their presence acceptable to the breeders by assisting their reproduction. This hypothesis explains the observation that positive assistance by non-breeders occurs mainly in species where co-operative breeding appears to be of relatively recent origin. In situations where group territoriality is well developed it is proposed that competition created by the addition

of new members to the group is sufficient to offset possible advantages accruing to the non-breeder through kin selection, and hence no positive assistance occurs.

Acknowledgements

For financial support during the field work on babblers I should like to thank the Leverhulme Trustees, the Royal Society and the British Ornithologists' Union. I am grateful to Prof. C. M. Dass of the University of Delhi for providing me with facilities and helping with logistics, to Dr. Salim Ali and other members of the Bombay Natural History Society for advice and access to their collections and to V. S. Vijayan who accompanied me during field work in Kerala. Amotz Zahavi, Glen Woolfenden and Dr. R. M. Naik all discussed general aspects of group territoriality with me and I am grateful to them also for their hospitality and for allowing me the chance to visit their study areas.

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INTRODUCTION

General Introduction

Research into the ecology and behaviour of birds has been concentrated, until recently, in the temperate zone of the northern hemisphere. Observations on temperate birds have been used to form the basis for theories of population regulation and social behaviour (Lack 1954, Wynne-Edwards 1962, Klomp 1972), and patterns of behaviour observed in temperate regions have generally been treated as typical of birds everywhere.

The work of Skutch (1935, 1961) in Central America, and later a number of studies on Australian birds (Harrison 1969) have begun to show that some patterns of behaviour formerly considered, on the basis of temperate zone studies, rare or aberrant, are in fact common in the tropics. One such habit is that of co-operative breeding, as defined by Lack (1968), who referred to most of the studies on this phenomenon carried out up until that time and summarised the evidence for its adaptive significance. Species on which detailed studies of co-operative breeding have been carried out up to the present are listed in Table A which demonstrated that this behaviour is found in many different avian families and among species occupying a wide range of habitats and geographical areas. Almost certainly, many more await discovery.

Skutch (1935) coined the term "helpers" for birds other than the breeding pair attending a nest or feeding the fledged young and he has listed instances of this behaviour in many species of New World birds (Skutch 1961). Harrison (1969) and Rowley (1968, 1976) for Australian birds, Grimes (1976) for African birds, and Zahavi (1976) for Asian birds have compiled similar lists. The main function of these compilations is to emphasize the very widespread nature of the co-operative breeding phenomenon.

Table A. Major studies on co-operative breeding, group territory and related behaviour in birds.

Species	Distribution	Habitat	Reference
Nothoprocta cinerascens	Central America	Scrub & grassland	Lancaster 1964
Crypturellus boucardi (Tinamidae)	"	Semi-evergreen forest	" 1964a
Tribonyx mortierii (Rallidae)	Tasmania	Grass swamps	Ridpath 1972
Crotophaga ani	Central America	Parkland + scattered trees	Davis 1940
C.sulcirostris	"	"	Vehrencamp 1975
Guira guira (Cuculidae)	South America	"	Davis 1940a
Melanerpes formicivorous (Picidae)	California	Warm-temperate oak forest	MacRoberts 1970 MacRoberts & MacRoberts 1974
Dacelo gigas (Alcedinidae)	Australia	Warm-temperate open forest	Parry 1973
Merops bulocki (Meropidae)	Tropical Africa	Savanna grassland	Fry 1972
Todus mexicanus (Todidae)	Central America	Tropical forest & scrub	Kepler 1972
Gymnorhina dorsalis (Corvidae)	Australia	Parkland, open woodland	Carrick 1972

Table A (continued)

Aphelocoma coerulescens	Florida	Oak scrub	Woolfenden 1974, 1975
A.ultramarina (Corvidae)	SW North America	Oak woodland	Brown 1963, 1972
Corcorax melanorhamphus (Grallinidae)	Australia	Open woodland, arable farmland	Rowley 1965a
Malurus cyaneus (Maluridae)	Australia	Scrub	Rowley 1965
Turdoides squamiceps	Arabia	Desert with scattered Acacia	Zahavi 1974
T.striatus (Timaliinae)	South Asia	Dry deciduous and semi-evergreen forest	Andrews & Naik 1965, 1970
Aegithalos caudatus (Paridae)	Temperate palaearctic	Deciduous and coniferous woodland	Riehm 1970 Nakamura 1969, 1972
Phoenostictus mcleannani (Formicariidae)	Central America	Forest, accompanies ant swarms	Willis 1973
Corvinella corvina (Laniidae)	West Africa	Tropical savannah	Grimes 1975

Table B. Classification of types of group territorial and co-operative breeding behaviour.

1) Groups include several full grown birds of both sexes, only one pair nests, territorial.

Turdoides striatus, *Corcorax melanorhamphus*

2) Groups include several full grown birds of both sexes, several females lay in the smae nest, territorial.

Crotophaga ani, *C.sulcirostris*

3) Groups include one male, several females, all lay in the same nest, males territorial, females nomadic.

Nothoprocta cinerascens

4) Groups include several full grown birds of both sexes, more than one pair nest, territorial.

Aegithalos caudatus, *Aphelocoma ultramarina*

5) Colonial or solitary nesters with non-breeding birds regularly visiting nests, but no group territory.

Merops bulocki

Species listed are considered typical of the particular category.

Another behavioural characteristic often associated with co-operative breeding is the communal defence of a common territory by more than two birds and this behaviour occurs in most of the species listed in Table A. It seems possible that the occurrence of "helpers" in species where groups defend a common territory may have a different significance from that in non-territorial species such as the Bee-eater Merops bulocki (Fry 1972) or the Chimney Swift Chaetura pelagica (Dexter 1952). In the present study attention was concentrated on species in which co-operative breeding and communal defence of a group territory (group territoriality) are both found.

Birds exhibiting co-operative breeding behaviour have been classified by Brown (1974), but this classification is based on the supposed origin of observed behaviour patterns, a matter still open to debate, and therefore involves assumptions that it seems improper to make at the outset of this thesis. Instead groups exhibiting aspects of co-operative breeding or group territory have been classified into five types on the basis of apparent behavioural similarities, and these are listed in Table B.

The categories defined in Table B tend to intergrade, and in many species normal pair-territorial behaviour occurs side by side with group territories or co-operative breeding, and this is particularly true of species in categories 4 and 5. There is also an intergradation between species in categories 1 and 4, since some type 1 species have a tendency for more than one pair within a group to nest, either simultaneously or successively. The origin of co-operative breeding and group territory in species of categories 1 and 4 forms the subject matter of the present study.

From the outset it was intended to investigate the relationship between co-operative breeding, group territory, and the ecological factors leading to selection for this type of behaviour. For this purpose babblers of the genus Turdoides, species of which occupy a wide range of habitats in the

Oriental and Ethiopian faunal regions, were selected for study. Because of doubts about the feasibility of the babbler study, however, research was initiated in 1970-71 on the Long-tailed Tit (Aegithalos caudatus) in Wytham Woods, near Oxford. The babbler study was eventually conducted in India, Pakistan, and Nepal from July 1971 to June 1974.

The close assocation between co-operative breeding and group territorial behaviour suggests a causal relationship, but it could also be due to coincident selection for both these behaviour patterns under certain circumstances. The question posed by the difference between pair and group territorial behaviour can be summarised as follows:

"What circumstances make it advantageous for more than two birds to share a territory?"

A similar summary of the problem of co-operative breeding is as follows:

"What circumstances make it advantageous for birds to assist in the rearing of conspecifics which are not their own offspring?"

The answers to these two questions provide the main aim of the thesis. They are deliberately formulated in a comparative manner, assuming that the normal avian pattern of pair territories is adaptive in most circumstances. Because of this assumption no attempt has been made to discuss the general significance of territorial behaviour, which has been dealt with by many authors (Nice 1941, Hinde 1956, Tinbergen 1957, Wynne-Edwards 1962, Brown 1964, Lack 1966, Schoener 1968, Wilson 1975).

Statistical methods

For measurements made in interval or ratio scales parametric statistical tests taken from Bailey (1959) were used, except in instances where data were clearly not normally distributed. This applied in particular to group size among babblers. For measurements in the ordinal scale and those in the

interval scale which were not normally distributed, non-parametric tests from Siegal (1956) were used.

Computing for the following tests was performed on the Nova 1220 computer belonging to the Zoology Department, Oxford University, using library programmes:

Calculation of means, standard deviations and standard errors

Fisher exact probability tests

Student's t test

F test for variance ratios

Correlation coefficients and regression formulae

Spearman rank correlation and coefficients

The mean degree of relatedness among members of a Jungle Babbler group was calculated using a programme written for the Nova computer by the late Michael Webber. The chances of a non-breeding Jungle Babbler surviving to breed in its natal territory were calculated using a programme written by the author. Calculation of the means and standard deviations of small samples, chi^2 values, and Mann-Witney U were performed on a desk-top calculator.

Abbreviations used in the text and in tables and figures

♂, male

♀, female

1Y, first year bird

2Y, second year bird

NB, non-breeding adult

BB, breeding adult of either sex

n, sample size

p, probability

$\bar{x}$, mean

r, correlation coefficient

r^s, Spearman rank correlation coefficient

t, student's t

F, variance ratio

U, Mann-Witney 'U' .

df, degrees of freedom

c., circa (approximately)

Arrangement and numbering of chapters, sections, figures and tables

Chapters and appendices are numbered. Sections of chapters are lettered in small case, hence section 3d means Chapter 3, section d. Figures are lettered in small case and tables in capitals, hence Figure 2f is figure f in Chapter 2, Table 4A is table A in Chapter 4. The thesis is divided into three parts, comprising Chapters 1-4, 5-7 and 8-10.

Introduction to the Turdoides study

a) Aims

Because of lack of prior information regarding the ecology of Turdoides species, much of the field work was pursued along traditional lines in seeking to establish normal ecological parameters; food, habitat, nest sites, timing of breeding, recruitment, mortality and dispersal. Andrews and Naik (1965, 1966 and 1970) have dealt with some aspects of the biology and behaviour of the Jungle Babbler Turdoides striatus, but apart from this no detailed studies of any Turdoides species had been carried out when this project was initiated.

Other basic information which was sought in the course of the babbler study was the age structure of babbler groups, the degree of relatedness of their members, their persistence in time, the pattern of breeding among members

Figure a. Map of the Indian sub-continent, showing the localities visited during the study and mentioned in the text.

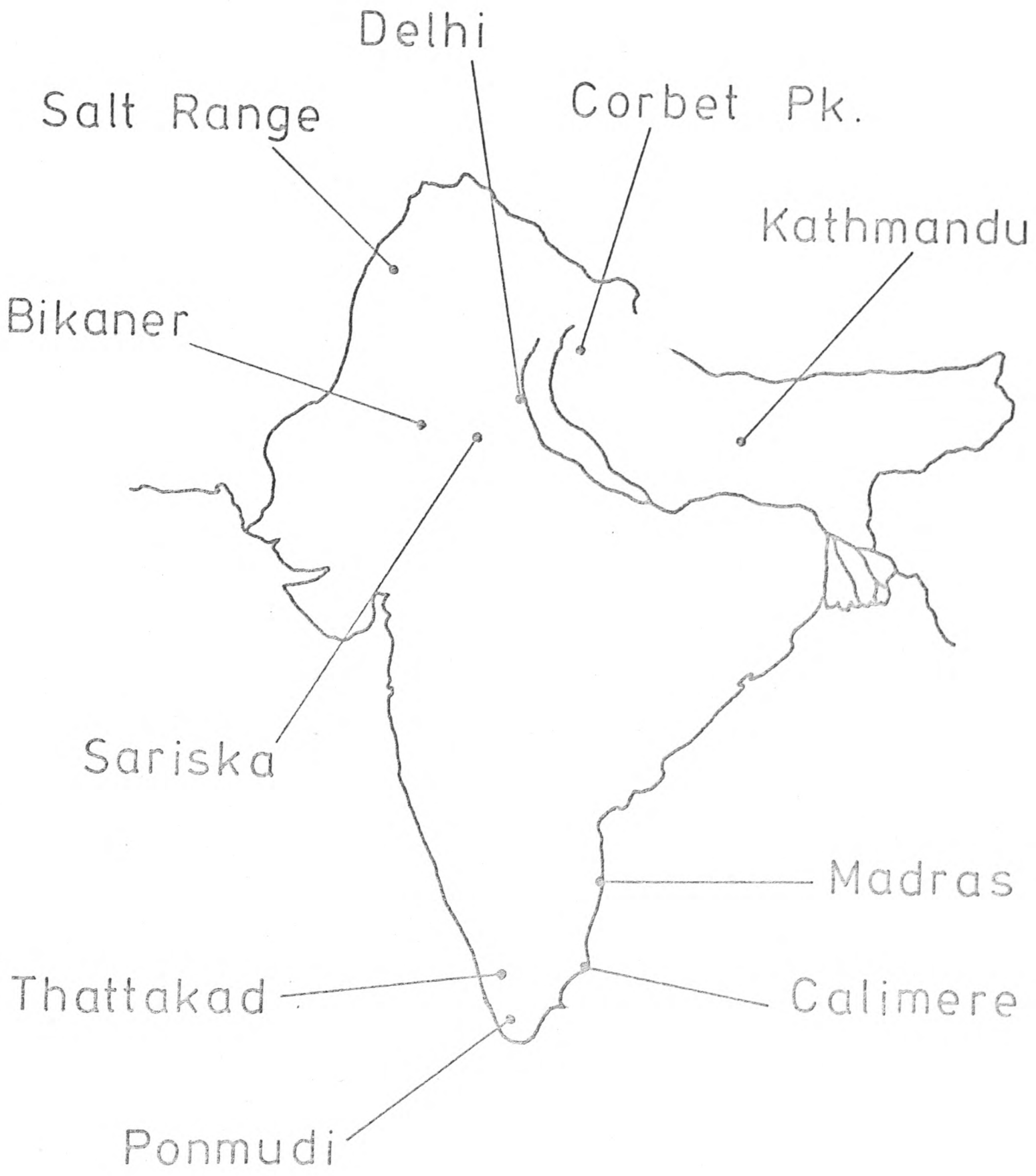


Table C. Areas in which systematic observations of *Turdoides* species were made, and types of habitat occupied. Localities are marked on figure a.

Species	Locality	Habitat
T.striatus	Delhi	Tropical thorn forest (*Prosopis*, *Acacia*) 15m.
	Sariska	Dry deciduous tropical forest 30m
	Thattakad	Tropical semi-evergreen forest 40m, mainly in secondary growth in clearings.
	Corbett Park	Tropical moist deciduous forest (*Shorea robusta*) 30m.
T.caudatus	Delhi	Tropical thorn forest in areas of scrub 3m.
	Bikaner	Semi-desert scrub 2m.
	Salt Range	Arid thorn scrub concentrated in valley bottoms 4m.
T.malcolmi	Delhi	Arable land with scattered trees. Tropical thorn scrub, mainly in areas of open-canopy woodland.
T.affinis	Madras	Coconut plantations Tropical dry evergreen scrub 5m.
T.subrufus	Ponmudi	Overgrown tea estates Clearings in semi-evergreen forest.
T.earlei	Delhi	Marshes (*Typha*) and overgrown water meadows, in winter arable field borders.
T.nipalensis	Kathmandu valley	Sub-montane scrub in areas where forest had been cleared, 1300-1800m above sea level.

of a group, the proportion of non-breeding birds in the population, and the type and degree of assistance that they afforded to breeders. Intra-group behaviour was studied in order to examine the role of different individuals in territorial defence, food-finding, nesting, and other communal activities.

Studies on the Superb Blue Wren Malurus cyaneus (Rowley 1965), the Tasmanian Native Hen Tribonyx mortierii (Maynard-Smith & Ridpath 1972), the Kookaburra Dacelo gigas (Parry 1973) and the Florida Scrub Jay Aphelocoma coerulescens (Woolfenden 1975) have shown that groups including non-breeding birds have a higher breeding success than pairs. Because pairs were rare among the Turdoides species studied in detail, work was concentrated on determining breeding success in relation to group size in order to examine the contribution of non-breeding birds.

b) General biology of Turdoides species

The genus Turdoides includes species distributed throughout the old-world tropics. All are ground-feeding birds with rather weak flight, living typically in scrub, savanna, or open forest, often feeding in the open, but retiring into cover when alarmed, and seldom venturing far away from bushes or trees (Ali & Ripley 1971, Mackworth-Praed & Grant 1957).

Localities and vegetation types in which Turdoides species were observed in the course of the present study are listed in Table C, and the localities mentioned are marked on the map (Fig. a). Habitat segregation was quite marked for the four species found near Delhi, though whether this was due to preference or competitive exclusion was not investigated. The Large Grey Babbler and the Jungle Babbler were observed to hold mutually exclusive territories in some areas, and territorial interactions between the two species were frequent. In areas where their habitats adjoined, Common and Striated Babblers were seen to form mixed feeding flocks in winter,

although associations seldom lasted for more than an hour.

All species of Turdoides studied, apart from the Spiny Babbler T. nipalensis, lived in groups of 3-20 birds which carried out all activities together and held common territories. In all species observed at the nest (Jungle Babbler T. striatus, Large Grey Babbler T. malcolmi, Common Babbler T. caudatus, Striated Babbler T. earlei and White-headed Babbler T. affinis) more than two members of the group contributed at some stage to the rearing of the young.

The overall colour of all asiatic Turdoides species is brown or grey, often streaked, and the sexes are indistinguishable by their plumage. There is very little difference in size between the sexes in most species, according to the measurements given by Ali and Ripley (loc. cit.). Measurements and weights of the three species trapped at Delhi are listed in Table D, which shows that sexual dimorphism is negligible in the Jungle Babbler, but is present in the Common Babbler where the difference in mean weight between adult males and females was found to be 9.25% of their mean combined weights.

Nests. The nests of all species found consisted of a cup of twigs (reeds in the case of the Striated Babbler) lined with grasses and placed in a tree or bush (in the Striated Babbler usually low down in waterside vegetation). Nests of the Common and Striated Babblers were neatly built and quite well concealed, whereas those of the Jungle and Large Grey Babblers were more flimsy and often placed in rather obvious situations, though usually in trees bearing large thorns. Figure b shows the mean height above the ground of nests of four species of babblers found near Delhi.

Nest building was normally carried out by only one pair of birds and subsequent observations showed that it was one of these which laid all the eggs. The other bird concerned in building was assumed to be the male.

Table D. Measurements of Turdoides species trapped at Delhi during the course of the study (± 1 standard deviation).

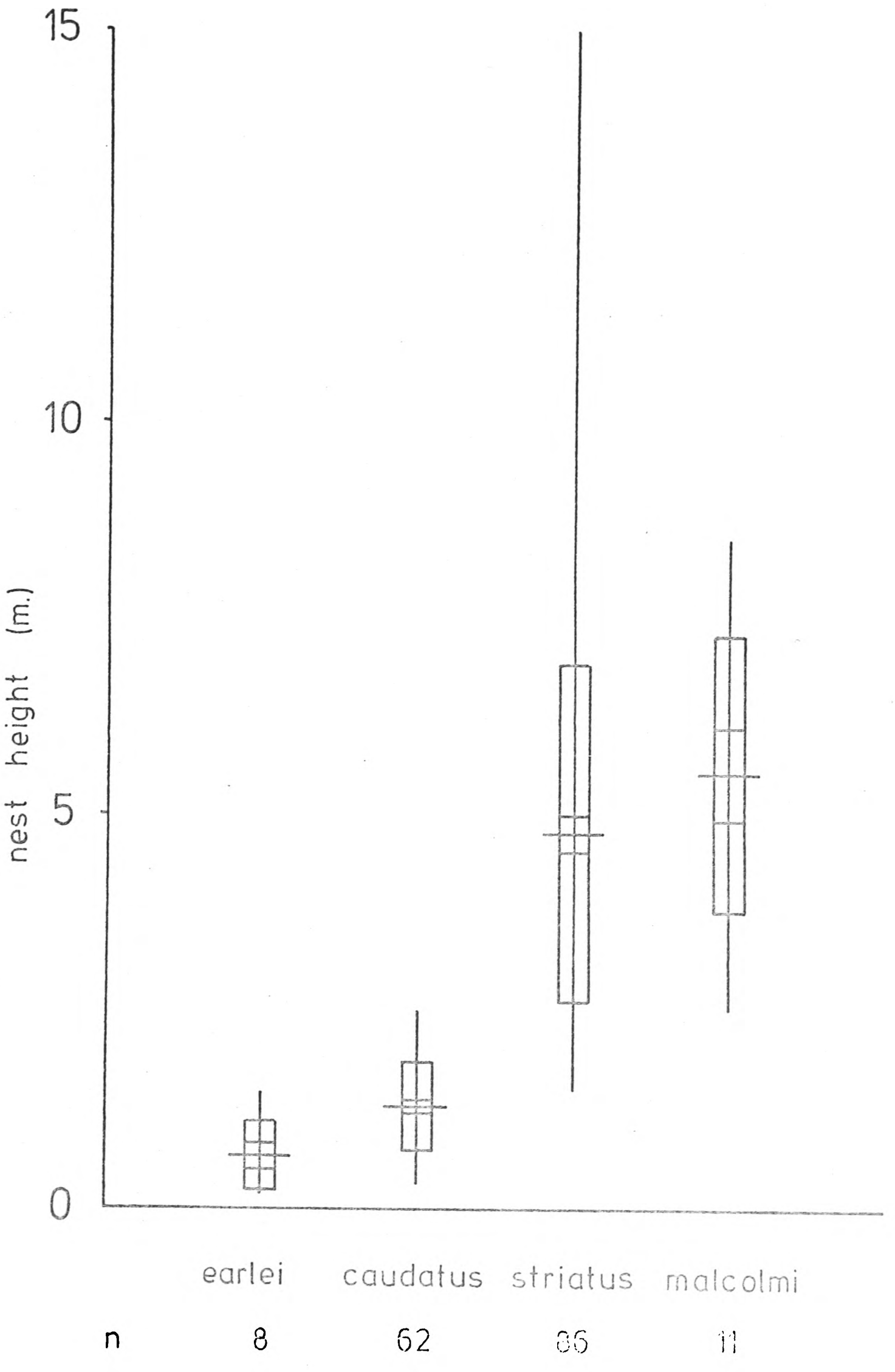
		Wing	Tarsus	Weight	N
T.striatus	♂	105.0±2.4	38.0±1.6	68.5±3.6	22
	♀	104.3±2.4	37.5±0.9	67.5±3.9	22
T.caudatus	♂	77.8±2.1	30.5±0.7	35.2±2.6	31
	♀	74.2±1.5	29.4±0.8	32.1±2.3	37
T.malcolmi	♂♀	117.3±1.9	37.7±1.2	76.5±3.9	12

Only birds trapped in their second year or older are included.

Table E. Clutch sizes observed for species of Turdoides at Delhi

	Number of eggs in full clutches						
	2	3	4	5	6	7	Mean
T.striatus		15	27	1		1	3.75
T.caudatus		24	15				3.38
T.malcolmi	4	4	1				2.67
T.earlei		2					3.0

Figure b. Height above the ground of Turdoides nests found in the Ridge study area and near the River Yamuna. Conventions; horizontal line - mean, vertical line- range, outer box - standard deviation, inner box - standard error.



Nest building by more than two birds was recorded in the Jungle Babbler by Andrews and Naik (1970), and was seen once in the present study in the Common Babbler, when three members of the same group were seen building together. The nest was not successful, and the relationships of the three birds were never established.

Prior to, and during, nest building the pair spent a high proportion of the time together (see section 3c), and when nest building was not observed the identity of the pair could usually be established from their close association. Birds identified as breeding females by observations of egg-laying invariably incubated the eggs and brooded the young during the night, and hence at nests where egg laying was not observed a bird sitting on the nest overnight was assumed to be the female parent.

Eggs were laid at one day intervals, between two and four hours after sunrise. Their colour, in all species, was unmarked turquoise blue, with a strong gloss. Jungle and Large Grey Babblers began incubation from the laying of the first egg, but Common, and probably Striated Babblers incubated only intermittently until the third egg. Clutch sizes are given in Table E. Differences in the timing of the start of incubation may be related to the differential effects of cuckoo parasitism (see Appendix 1).

Incubation, during the day, was shared fairly equally among adult group members in the Jungle Babbler, but in the Common Babbler the share of members other than the breeding pair was smaller, never more than 25% of total observation time. Brood patches were well developed in both parent Common Babblers, and partially developed sometimes in other group members. In Jungle Babblers they were clearly developed in the breeding female, but other group members showed little sign of them.

All adult male Common Babblers collected during the breeding season had fully developed testes, but well developed ovaries were found only in breeding females, all other females having them completely undeveloped. This accords with the findings of Andrews and Naik (1966), that only a small proportion of adult female Jungle Babblers collected during the breeding season had fully developed ovaries, whereas all males had fully developed testes. Few Jungle Babblers were collected during the breeding season at Delhi, but those which were conformed to the same pattern,

Hatching was usually synchronised in Common Babbler broods, but in Jungle Babblers it was spread over two or three days, and there was usually a considerable difference in size between early and late hatched nestlings. The parents ate the egg shells after hatching. The mean incubation period for Jungle Babblers was 14.9 days (n = 10), from the laying of the first egg to the hatching of the first nestling. For the Common Babbler the period was 15.25 days (n = 4), but 13.25 days from the start of incubation.

The feeding of nestlings and nest sanitation were performed by all members of the group except juveniles in the Jungle Babbler. In the Common Babbler the proportion of group members involved varied. The mean fledging period was 14.5 days (n = 18) for the Jungle Babbler and 11.7 days (n = 10) for the Common Babbler. In the latter species nestlings normally left the nest before they were capable of flight.

Immediately after fledging Jungle Babblers led their young into dense spiny bushes, where they usually remained together for the first few days, while being fed by all group members. Common Babbler fledglings also stayed in dense thorn bushes, but in this species individual fledglings usually perched a few metres apart. Juveniles were completely dependent on other group members for food for about 20 days after fledging and were still receiving most of their food at up to 30 days old when some began their post-

juvenile moult. During their first winter birds were often seen to beg from adults and were generally fed, so that intermittent feeding continues until about six months of age.

The number of nesting attempts made in the course of one season varied from nil to six per group for the Jungle Babbler and from one to four per group for the Common Babbler, which began later. Two ~~The~~ groups of Jungle Babblers and one group of Large Grey Babblers were observed to rear three broods in one year, but otherwise most groups of all three species reared one or two broods.

Behaviour. Feeding behaviour was similar in all species, which foraged mainly among dead leaves and other ground litter and among the roots of trees and bushes, scuffing aside the vegetation and digging with their bills in soft earth. The Large Grey Babbler, which appeared to be a stronger flier than the other species, also foraged out in open fields and among standing crops. While foraging a group normally kept within a radius of about 25m, with one bird perched in a nearby tree as sentinel.

Among the species studied, only the Spiny Babbler possessed a normal passerine song, although a call which probably had a territorial function was sometimes given by single Striated Babblers. All the other species had communal territorial vocalisations. Sexual displays of any kind were rare and the most obvious form of intra-group interaction was allopreening, which was observed in all species. Contact calls and territorial calls used in inter-group confrontations were well developed in all species. In the Jungle Babbler confrontations were accompanied by distinctive posture displays. These were also seen in a less exaggerated form in the Striated Babbler but were not observed in other species.

No species of Turdoides is known to be migratory although it seems possible that the Spiny Babbler may undertake some altitude movements in certain parts of its range (Ali & Ripley 1971). The home ranges of all species observed were relatively small and there is no mention in the literature of nomadic or seasonal movements by any species. All apparently defend territories throughout the year.

Definition of a babbler group. For the purpose of this thesis, a babbler group was defined as a collection of birds which foraged together during the day, and roosted together at night. Such groups usually, although not invariably, appeared to hold a common territory, and had a membership which was stable from day to day. In winter two or more groups were sometimes seen to mix together, forming a joint feeding flock, but on separation the original composition of the constituent groups was maintained.

As long as a group held the same territory continuously, and roosted consistently in the same site, or small group of sites, it was considered to be the same group, and called by the same name, even if it contained no marked birds. This assumption was made only in the case of groups observed at least once a month, and by the summer of 1972 practically all of these contained at least one marked bird. In a few cases a group which had been seen regularly holding a particular territory could not be located and was later replaced by another group holding the same area. These were treated as different groups and given different names, although there was no way to be certain ~~whether~~ that some unmarked members ~~could have been~~ were not common to both groups.

Groups which stayed together, and maintained the same territory, for more than three months were described as permanent, those which existed for less than three months were described as ephemeral, and those seen passing through the study area without stopping were described as transient. A few

groups remained for some time in the same general area without trying to defend it, and these were described as non-territorial groups.

c) Methods

Trapping and marking. At the beginning of the Turdoides study an attempt was made to catch as many Jungle Babblers as possible, within the chosen study area, using mist nets. By December 1 1971, 44 birds had been trapped and marked, and four had been marked as nestlings, out of about 100 Jungle Babblers in the study area. Ten groups were selected for concentrated studies of breeding success and territorial behaviour (referred to as the "study groups"), and in these 35 out of the 70 birds were marked by the start of the 1972 breeding season.

Marking was done with coloured plastic leg rings in different combinations, so that each bird could be individually identified. Two rings were placed on each leg, with both legs carrying the same combination, so that the bird could be recognised even if only one leg was visible. Eleven different colours were used, giving 121 possible combinations, which proved sufficient for the entire study. Combinations used on birds which disappeared before the age of six months were used again because it was considered that such birds must have died.

In good light, the coloured rings were visible up to about 80m, using 10 x 50 binoculars, although the direction of the light was very important. In a few cases rings were lost in the course of the study, but never more than one was lost from the same bird, so all remained identifiable. Certain colours became faded, and pink, in particular became hard to distinguish from white, except at close range. Whenever a bird was recaptured, its entire set of rings was replaced, but several birds were still carrying the original set of rings, and still easily recognisable, after almost three years.

Common Babblers were also trapped and marked in the same way, 32 being ringed in 1971, and 83 in 1972, out of a total population in 1971 of about 120 birds. Ring loss was higher in this species, owing to the fact that the rings had a tendency to slip over the feet of the smallest birds, but only one was retrapped with three out of its four rings missing, and only two were impossible to identify on recapture. It seems safe to assume that only a very small number of birds could have lost all their rings during the course of the study. Once the possible combinations of two rings had been exhausted on this species, three-ring combinations were used, but never including more than two colours. Eleven Large Grey Babblers were also marked in the course of the study.

Age determination. Naik and Andrews (1966) discussed methods for ageing Jungle Babblers in the hand. Juveniles, or birds in post-juvenile moult can be easily identified by their soft, rounded primary feathers, and pointed tail feathers. This character is present up to the age of 4-5 months in a bird undergoing a steady post-juvenile moult. In birds reared in September or later, and also in some reared in August, the post-juvenile moult is not completed in the same year, but is arrested, and completed in the following spring. These birds can be aged with certainty in the hand until about April of their first summer and at close range, can also be identified in the field.

After the completion of the post-juvenile moult, it was not found possible to age birds with confidence. Naik and Andrews (loc. cit.) describe differences in shape between first year and later primary feathers, and on this basis it was hoped at the outset that it would be possible to age birds trapped in their first year. The criteria which they describe, however, were

found to vary more or less continuously within the population, and some evidence suggested that feather shape may have been affected by the nutritional condition of the bird while the feather was growing.

The method described by Naik and Andrews was therefore rejected, and an examination of their results suggests that in their own study it may have been quite inaccurate. Birds classified as first years constituted only eight out of 132 birds collected in the course of their study, whereas the collection included 21 'older juveniles', and birds undergoing post-juvenile moult. Since the latter categories span only four months, while the first year category should span eight months, their result suggests a heavy mortality between the end of the post-juvenile moult, and the start of the first annual moult. In the present study, however, mortality was found to be very low during this period (see section 1b). Either the pattern of first year mortality at Baroda was quite different from that observed at Delhi or there had been abnormally poor breeding in the previous season, or the first year age class was underestimated by the collecting or ageing method.

Apart from seven birds trapped as juveniles in 1971, all 79 Jungle Babblers of known age were ringed as nestlings. Figures for nestling survival were calculated from this sample, plus five of the birds ringed as juveniles which had been observed in the same group from fledging and 13 birds fledged in November 1973 which were not ringed, but which retained their juvenile plumage until the following spring and were therefore identifiable until almost the end of the study. Methods of age determination for Common Babblers are given in Appendix 2.

Age classes in the Jungle Babbler. Owing to the length of the breeding season, there could be as much as six month's difference in age between birds

reared in the same year. Because of this the following age classification is employed throughout the thesis:

Juvenile. All birds up to November 1 in the year of fledging.

First winter. Birds in their first winter (November 1 - February 28).

First summer. Birds in their first summer, following the year in which they were fledged (March 1 - October 31).

Second winter and second summer. As above.

First year. Birds less than one year old.

Second year. Birds between one and two years of age.

Adults. Birds in their second summer or older, unless second year birds are specifically excluded.

On March 1 all birds beginning their second summer were in their second year and by November 1 nearly all birds entering their third winter were in their third year. All birds which completed their second winter are referred to as adults unless the separation of an additional age class appears necessary. Although no Jungle Babbler was observed to nest before its third summer some birds exhibited adult behaviour in their second summer, including copulation.

Group members which were known to have been reared in their group are referred to as 'native to that group' and the group as their 'natal group'. Birds observed to shift from one group to another are referred to as 'immigrants' in their new group, irrespective of whether or not the group that they entered was their natal group. This was because it was impossible to distinguish the return of unringed birds to their natal group from the immigration of non-native birds. Birds which were known not to have been reared in the group which they were observed to join are referred to as 'foreign'. Among Common Babblers, where not all nestlings were ringed, birds trapped in autumn in juvenile plumage were considered to be native to the group in which they were trapped because no cases of juveniles changing groups were recorded.

Sex determination. No satisfactory method was discovered for determining the sex of Jungle Babblers in the hand. After dissecting ten adults during the winter of 1971, it was concluded that plumage and external morphology were identical. All sex determinations on birds which were not dissected were therefore done on behavioural criteria, and most of this was retrospective because these criteria only became apparent after prolonged observations.

During the spring breeding of 1972 an effort was made to locate as many nests as possible while they were being built. Once the first egg had been laid the identity of the female was obtained by watching the nest from dawn the next day, and checking the contents each time a sitting bird was relieved. This led to the identification of five females, and established the fact that only one female laid the eggs. Since in each case two birds took part in nest building, the other member of the pair was identified as the male. Subsequent observations showed that the female invariably incubated overnight, and in view of this, at nests where egg-laying could not be observed, the bird incubating the eggs after the rest of the group had gone to roost was identified as the female.

Altogether during the study the identity of the breeding female was established at twelve nests by watching the nest during laying. In most cases the identity of the breeding pair was already apparent before nesting began because they spent a large proportion of their time, while not feeding, perched side by side.

Observations on the behaviour of non-breeding birds proved relatively unhelpful in establishing criteria for sex determination. The only clear behavioural indications came during the infrequent attempts to establish new groups, when attempted copulations were sometimes observed, and from these it was possible to discover the sex of some non-breeders (section 2a).

Once the sex of a few had been determined some other indicators became apparent. Birds leaving their group to attempt to join other permanent groups were invariably female. These birds sometimes called loudly in areas marginal to established territories, and when this occurred they often attracted non-breeding males from neighbouring groups, although never from their own. Alternatively females would sit silently in the territory of a neighbouring group, and attempt to join them as they went to roost. They were generally chased off by the breeding female. Where it was observed repeatedly this type of behaviour was used as evidence of sex, even if mating was not observed, but it tended to provide identification of more females than males, and hence was not valid for calculating sex ratios.

Extra-group matings formed the bulk of evidence for sex determination of non-breeding birds. Most marked adults which remained in the study population for one breeding season, and also several second summer birds, were eventually sexed. Only breeding birds, and those for which the sex was determined by dissections are included in the sample for which measurements are given, but for the purpose of discussing intra-group behaviour, sex determinations made on behavioural criteria had to be used.

Sex determination of Common Babblers proved more difficult than Jungle Babblers because their behaviour was more difficult to observe. Because of the difference in size between the sexes, measurements were used in the case of birds trapped in adult plumage, provided that an individual fell outside the 95% confidence limits of one sex for both tarsus and wing length. The sex of breeding adults was determined by the same methods as those applied to Jungle Babblers, and where the pair could be definitely identified, the larger of the two birds was assumed to be the male even if the measurement criteria given above were not fulfilled. Thirty birds were collected from the study

population in the spring of 1974, and these provided more information about sex in this species. The measurement criterion for sex determination above was found to be 100% correct for this sample.

Methods used in studying breeding success. During 1972, 1973, and the spring of 1974 all nests of the ten study groups of Jungle Babblers were found, and all nestlings ringed, apart from one brood which was inaccessible, and a few fledged in November 1973, already referred to. A number of nests of surrounding groups were also found, and the number of young fledged per year was checked for about ten of these in each year. Adult babblers behave in a very characteristic way when disturbed while feeding newly fledged young, mobbing the observer at distances up to 50m from the fledglings. Because of this it is unlikely that any fledged broods could have gone unnoticed, and only one instance was observed where the nest had not previously been found. As 48% of nests initiated failed to fledge any young, it is possible that one or two other nests went undiscovered, but the proportion of nests located was almost certainly greater than 95%.

No attempt was made to find Common Babblers' nests until the rains of 1972. They proved harder to find than those of the Jungle Babbler, and trapping of birds in post-juvenile moult during October and November suggested that only about 70% of successful nests were found in 1972, and about 80% in 1973. For a few groups it is likely that all nests were found in 1973 when more time was devoted to this species.

Where nests had been located before laying, the eggs were marked as soon as possible after laying, with a felt tipped pen, so that each could be individually recognised. The identity of the layer was established as explained under sex determination. Jungle Babbler nests could usually be

observed without concealment but for Common Babblers it was necessary to erect a hide the evening before the watch was to be made, entering it before dawn the next morning. Owing to the nature of the study area, hides could not be left unattended during the day, and had to be dismantled after each watch.

Nests were normally checked at two day intervals, after the completion of the clutch, and then daily again when hatching was imminent. From 1972 onwards nestlings were marked as soon as they had hatched by clipping the claws of the right foot so that each could be identified until old enough to ring. They were weighed at two day intervals until ten days old, after which they had a tendency to leave the nest prematurely if handled. Common Babbler nestlings were weighed only until day nine.

Nests of the Large Grey Babbler were relatively easy to see, and most successful nests were found, but the majority were quite inaccessible, being built in very thin twigs in the crown of a tree. For this reason few nestlings could be ringed, and the species was not studied intensively, although breeding success was followed using a mirror attached to a long pole.

All three species of babbler in the main study area were parasitised by the Pied Crested Cuckoo Clamator jacobinus, and the effects of this parasitism are dealt with in Appendix 1. Nestlings of the Hawk-cuckoo Cuculus varius were found twice in Jungle Babbler nests.

The following information was sought from nests found in the study area.

1) Nest site.

2) Identity of nest builders.

3) Date of laying, and identity of layer.

4) Clutch size.

5) Presence or absence of cuckoo's eggs, and their subsequent fate.

6) Hatching success.

7) Growth rate, and weight of nestlings at day ten. (later eight)

8) Fledging success, and subsequent survival of fledglings.

9) Age, sex, measurements, and state of moult of parents.

10) Age, sex, measurements, and state of moult of non-breeding group members.

11) Share of non-breeding group members in incubation and feeding of nestlings.

12) Interactions between parents and non-breeders.

Few nests yielded information in all these categories because many were not located until after the clutch had been laid, and in some groups one or both of the parents was unringed. Because of this sample sizes vary considerably for different breeding statistics.

Methods used in studying group territories. In order to study the movements of babbler groups, cyclostyled maps of the study area were prepared on a scale of 25cm to 1km. A separate map was used on each visit to the study area, and the positions of all babbler groups encountered were marked by reference to footpaths and other physical features.

During the winters of 1971-'72, and 1972-'73, and to a lesser extent at other periods, individual groups were followed for periods of up to six hours, their routes marked on the map, and their positions recorded every half an hour; in addition the position of any inter-group interactions, areas of concentrated feeding, and periods of rapid movement were also noted. Groups were identified by the colour-ringed birds which they contained, and named with letters. This technique was similar to that employed in the Long-tailed Tit study (see Chapter 9).

d) Description of main study area.

The main study area was selected in August 1971, on the outskirts of New Delhi in an area designated as reserved forest. Most work was concentrated in one square kilometre which included populations of Jungle, Common and Large Grey Babblers. No previous research had dealt specifically with the ecology and avifauna of this area, although it is referred to frequently by Hutson (1954). A description of the vegetation of the Delhi area is given by Maheshwari (1963), and both he and Donahue (1967) briefly describe the ecology and geology of 'the ridge' which encircles Delhi on the western side, and of which the study area forms a part.

The coarse quartzites, which form the underlying rocks of the ridge, are the northernmost extension of the Aravalli hills, which reach moderate elevations in Rajastan State. The overall form of the ridge is gently rounded, but it is cut by several deeply incised watercourses, which carry water only at the height of the rainy season. In the study area these have been enlarged in several places by quarrying, and in two places run-off is impounded by mediaeval dams which create artificial areas of perennial moisture.

Within the study area, the ridge reaches a height of 260m above sea level in the west, sloping to 230m in the east, where it is still 60m above the level of the River Januna, which flows about three kilometres to the east. A profile taken roughly WNW-ESE across the area (Fig. c) shows it to be stepped, two sloping zones being separated by a more or less level one, which probably results from a structural weakness. The two main watercourses in the study area are incised in the sloping zones, but meander without incision in the level area. Soil accumulates principally in the level area, and at the foot of the lower slope, and consists of a coarse alluvial sand, with a low humus content.

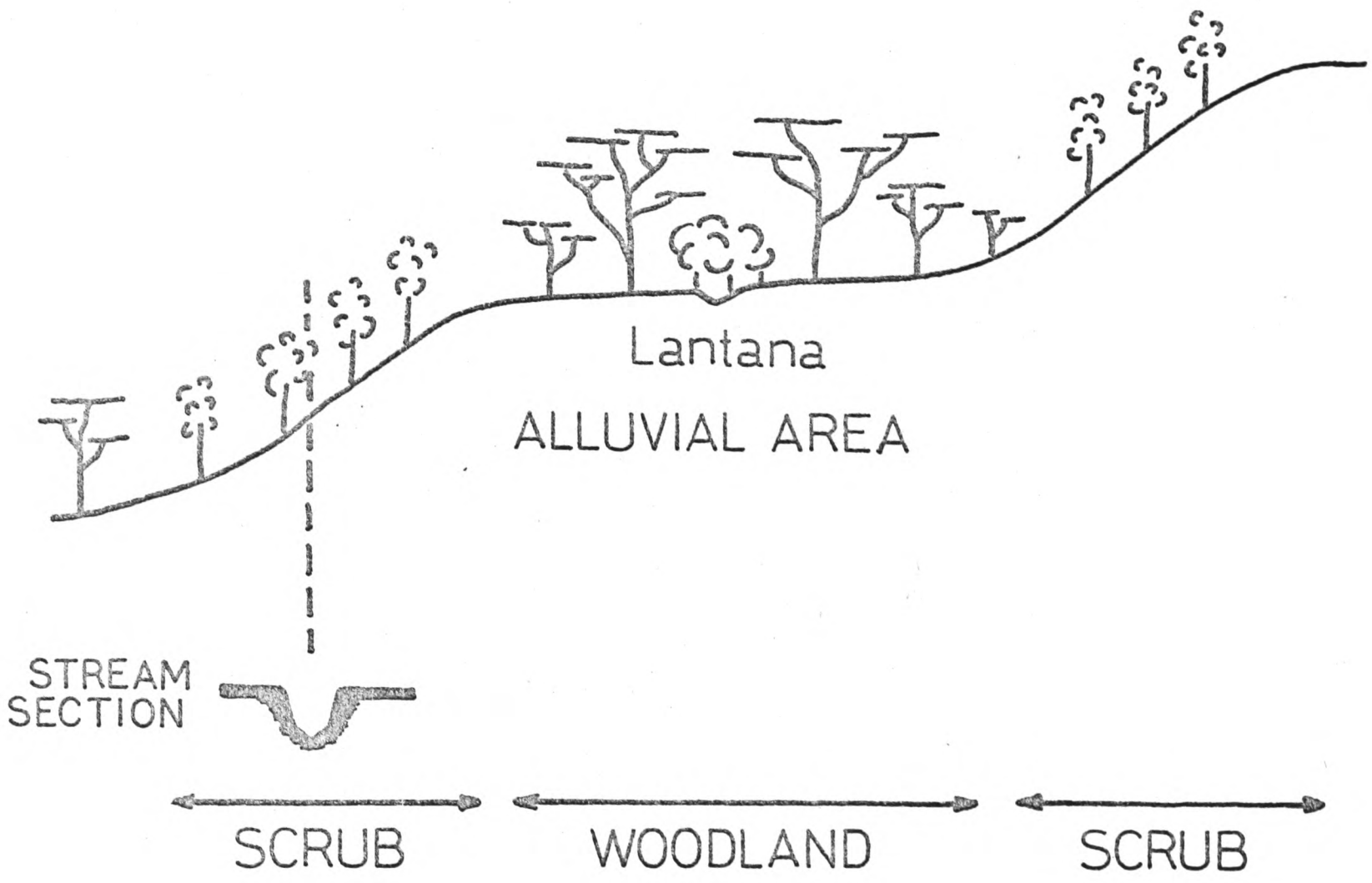
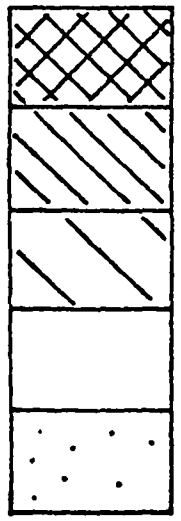


Figure c. Section WNW-ESE across the Ridge study area showing generalised pattern of vegetation in relation to slope. Vertical scale greatly exagerated.

Figure d. Map of the Ridge study area showing the distribution of different vegetation types.



Closed canopy woodland + dense understorey

Closed or open canopy woodland + sparse understorey

Tall scrub, 3m with scattered trees

Low scrub, 1m or bare rocky ground

Parks and gardens not included in the study area



Roads



Pipelines



Seasonal watercourses



Footpaths

X Area where sweep-net samples were taken

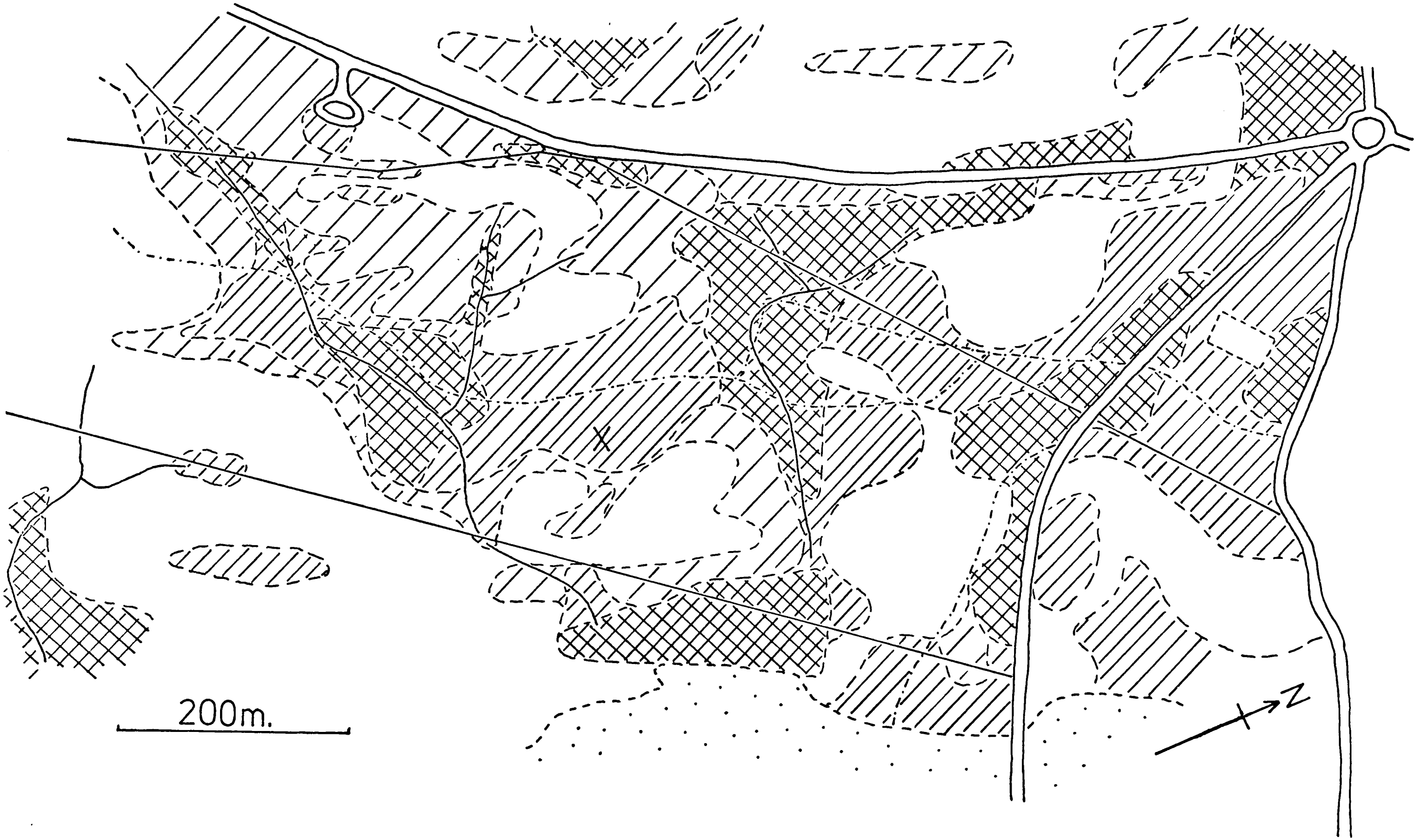

200m.
N



Plate 1 - March



Plate 2 - August

Ridge study area; open grading into tall scrub.



Plate 3 - March



Plate 4 - August

Ridge study area; open scrub grading into woodland with dense understorey.

The development of the vegetation is controlled both by the slope, with its effect on the accumulation of soil, and by biotic influences, particularly grazing and wood-chopping (Dakshini 1968). The effect of the latter factors seems to be greatest in the northern part of the area, adjoining a main road. The least disturbed vegetation occurs in the south-west corner of the area.

Figure d shows the distribution of different vegetation types within the study area. The broad belt of woodland running through the centre coincides roughly with the extent of the level shelf, and its consequent accumulation of soil. All of the woodland has developed during the last fifty years, before which the area was completely clear (Basil-Edwards 1926), and parts of it were planted during the building of New Delhi.

The trees making up the woodland belt increase in species diversity from North to South, presumably along a gradient of decreasing biotic interference. The dominant species throughout is Prosopis juliflora, which was introduced at the time of reafforestation. In the north this is mixed with Albizzia spp. which was also planted, but towards the south there is a progressively greater admixture of Acacia senegal, A. leucophloea, A. modesta, Prosopis apicigera, and Cassia fistula. The woodland ranges in height from 6-18m.

A gradient of species diversity is also noticeable in the composition of the woodland shrub layer. The dominant species throughout is Adhatoda vasica, mixed in the north with Capparis sepiaria. Towards the south there is an increasing amount of Carissa spinarum, Grewia tenax, Flacourtia indica, and Maytenus senegalensis.

The sloping areas are characterised by the outcropping of much bare rock. In the north they support only scattered trees, mainly Prosopis juliflora, and the perennial vegetation is dominated by stunted clumps of prickly Zizyphus nummularia, growing up to 1m in height. Towards the south-west a taller scrub including Carissa spinarum, Capparis decidua, Securinega leucopyrus, Dichrostachys cinerea, Zizyphus mauritiana, and Flacourtia indica develops, with scattered

patches of Anogeissus pendula woodland, up to 5m high. Butea monosperma occurs commonly scattered throughout the area, and growing up to 10m high, but nowhere forms dense stands.

Other shrubs, which occur in localised patches, are Jatropha gossypifolia which grows in steep rocky places, and Balanites roxburghii, which grows in the level zone, on the edge of the woodland. Several dense clumps of Lantana indica occur where the watercourses cross the level zone, and where breaks in the water mains which cross the area provide perennial moisture.

The herbaceous vegetation of the study area flourishes almost exclusively during the rainy season. During this period open areas become clothed in grasses and other herbs, and shrubby perennials such as Hibiscus micranthus, and Tephrosia spp. put on luxuriant new growth. The four vegetation types mapped in Figure d are defined mainly on the basis of their structural characteristics, since these appear to have the greatest influence on the distribution of bird species.

Seasonal events. Figure e shows the ten-day mean maximum and minimum temperatures and rainfall for the Delhi area throughout the study period (figures from the Meteorological Office, New Delhi).

The climate of Delhi falls on the border between the semi-arid and sub-humid tropical types, according to the Koppen system of classification (Trewartha 1954), with a mean annual rainfall of 666mm, and a mean annual temperature of 25.1^{o}C. Rain falls largely as a result of the south-west monsoon moving up the Ganges valley, but some arrives directly from the south-west, in the form of depressions originating over the Arabian Sea. The relative influence of these two rainfall sources varies from year to year, and the total amount and its timing, tend to be rather unpredictable (Meher-Homji 1971). Figure f shows the number of years in which no rain fell in a particular month

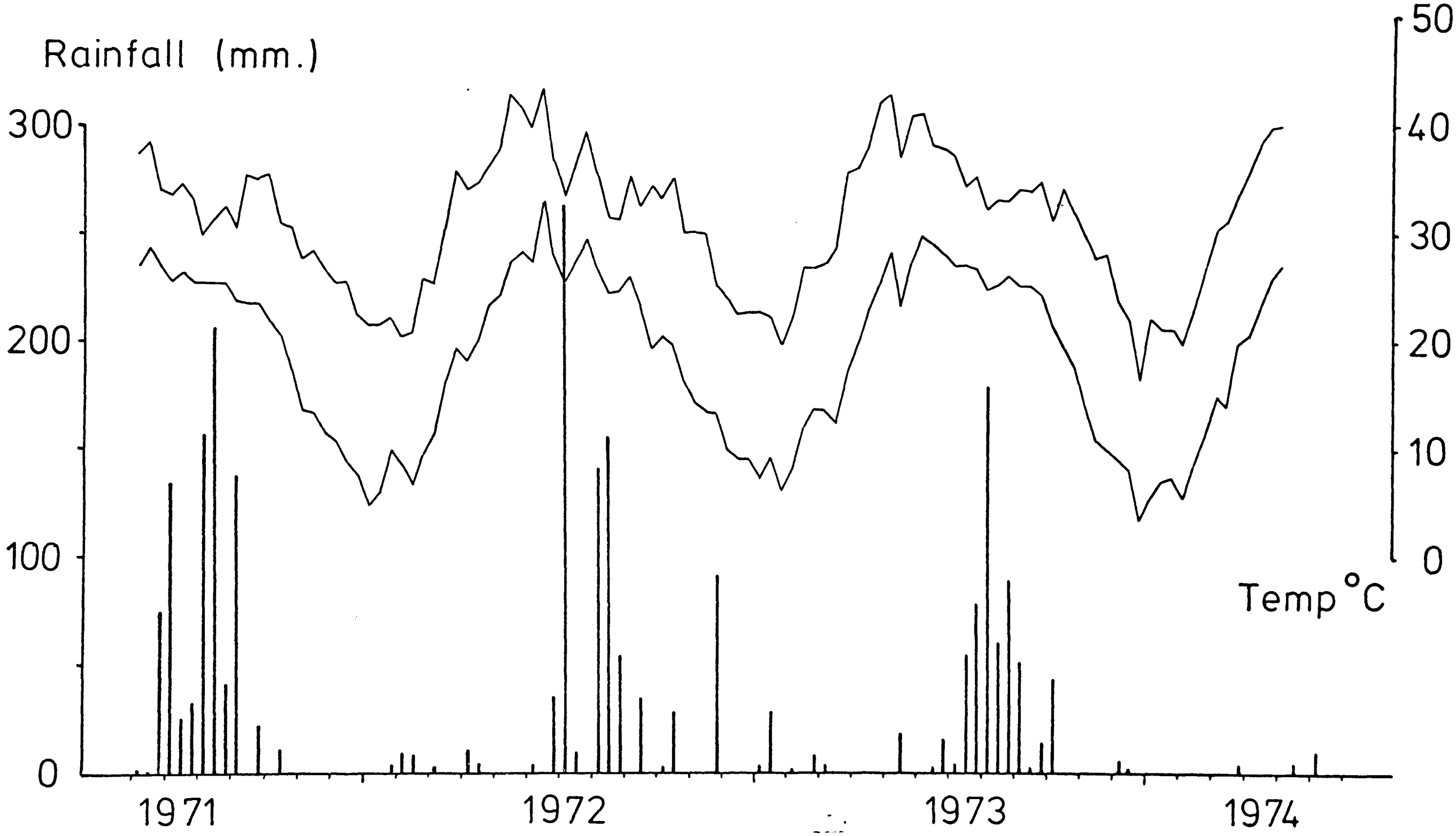
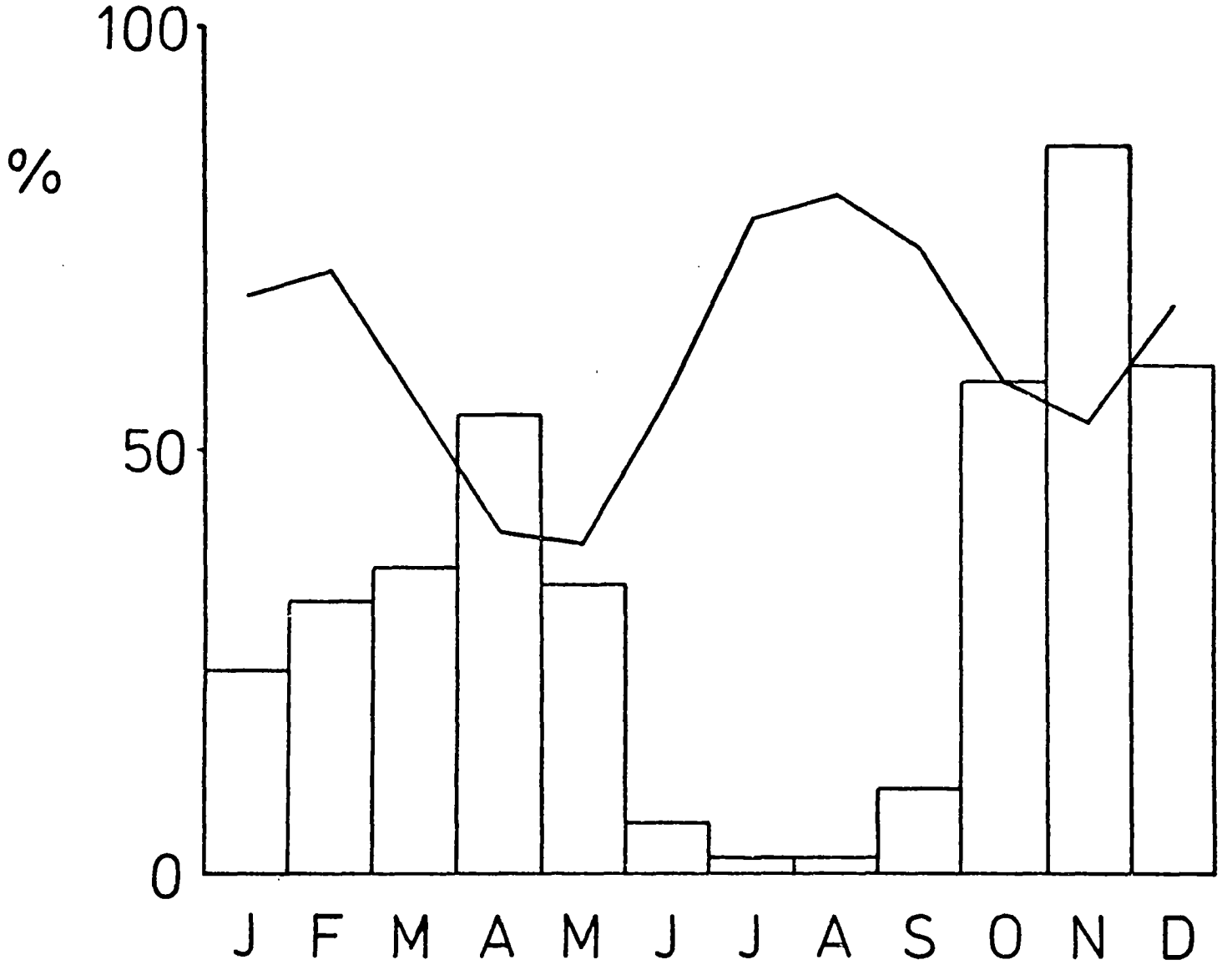


Figure e. Rainfall and temperature at Delhi during the study. Vertical bars, rainfall in 10-day periods; solid lines, maximum and minimum temperatures

Figure f. Reliability of rainfall at Delhi during the years 1901-1950. Histogram shows the percentage of years during which no rain fell at all in each month. The solid line is the mean monthly relative humidity at 0830 Indian Standard Time (IST).



over the 50 years from 1901-1950. For both the two months of highest rainfall, July and August, there was one year out of the fifty in which no rain fell, although the mean annual rainfall for both is in excess of 150mm.

Rainfall is particularly unpredictable in April and May, when it generally falls as thunder showers. In more than half of the years no rain fell at all in April, and in one in three none fell in May. During the study no rain fell in May in one year, and none in April in two years, but some fell in one or other in all three years. The occurrence of rain in this period may be important in influencing the initiation of nesting by babblers in May and June.

The years can be divided into five 'seasons'. Peak rainfall occurs in July-September, which forms the rainy season. This is followed by a brief hot season (October), and then a cool winter (November-February), when temperatures may fall to freezing. Some rain generally falls during the winter, although the amount is small, and the timing unpredictable. The winter rain probably has a disproportionate effect on the growth of spring vegetation, because of the much lower evaporation during the winter. Spring is difficult to define climatically, because daily temperatures increase very rapidly during March, but there is a definite flush of vegetative growth in late February and March, and most of the tree species renew their leaves progressively at this season. Spring is followed by a hot dry summer from the end of March to June, and sometimes into July, depending on the arrival of the monsoon.

The monsoon of 1972 was a poor one over most of North India, causing widespread famine. Rainfall at Delhi during June-September was normal but an unusually large proportion of it fell at the end of June, and this was followed by three weeks of drought, during which evaporation was very high.

The rainfall at Delhi was therefore effectively lower than normal. In the winter of 1973-'74 winter rainfall was early and sparse, again causing crop failure in surrounding regions. This seems to have had some effect on the nesting of Jungle Babblers in the spring of 1974.

The fruiting of trees and shrubs in the study area showed a peak after the onset of the rains, but some were fruiting throughout the year, as shown in Table F. The seeds of grasses and other herbs are most abundant in September and October, just after the end of the rains. Plates 1-4 show two parts of the study area, photographed from the same spot in October and March to illustrate seasonal contrasts.

The abundance of insects in the study area was monitored by taking random sweep-net samples from the vegetation every ten days. Ten samples of twenty sweeps each were taken, while moving steadily on a zig-zag course through Adhatoda understorey ranging from knee to waist high, in the area indicated on Figure d. All samples were made between two and four hours after dawn, but samples taken throughout the day in the summer suggested that there was no significant diurnal variation in the number of insects sampled. Sweeping samples taken in other woodland areas showed that the number of insects taken per sweep in the main sampling area were fairly representative of that type of habitat. During the rainy season samples were also taken in open grassland, but this died back to such an extent in the dry season, that nothing remained to sweep. Figure g shows the pattern of abundance of insects and spiders sampled in this way in woodland during 1971-'73. Only individuals more than 10mm in length were counted.

The dispersion of insects sampled by this means was assessed by comparing the distribution of numbers taken in each sample with the Poisson distribution calculated for the monthly mean. The Poisson distribution is that expected if insects are dispersed entirely at random (Southwood 1966),

Table F. Seasonal occurrence of flowers and fruits taken by birds in the Ridge study area

	J	F	M	A	M	J	J	A	S	O	N	D
Fruits												
Anogeissus pendula											----	
Capparis decidua*				----------								
C. sepiaria					----------							
Carissa spinarum*	-------										----	
Coccinia cordifolia										--------		
Ehretia laevis*			-------									
Flacourtia indica							-------					
Grewia tenax									------			
Jatropha gossypifolia								-------				
Lantana indica*	----------											
Melothria maderaspatana*									----------			
Prosopis juliflora									-------			
Securinega leucopyrus*							----------					
Zizyphus nummularia*									----------			
Z. mauritiana												
Flowers												
Butea monosperma*			------									
Adhatoda vasica	----------											

* ; seen to be eaten by Turdoides species

Table G. Numbers of insects captured in 20-sweep samples made in woodland understorey in the Ridge study area.
s^2 = variance

	Numbers of insects captured													
	0	1	2	3	4	5	6	7	8	9	10+	$\bar{x}$	s^2	$s^2/\bar{x}$
September		1	3	4	1	3	1	1	2	1	3	5.5	9.06	1.65
October	3	3	8	4	4	2	3	2	1			3.25	4.87	1.50
November	6	6	4	4	2	5	2	1				2.6	4.59	1.77
December	3	9	7	7	3	1						2.03	1.71	0.84
Jan.-Feb.	30	6	4									0.35	0.44	1.26
March	6	8	5	1								1.05	0.79	0.75
April	6	13	5	4	2							1.43	1.36	0.95
May	13	7										0.35	0.24	0.69
July	1	3	2	5	1	4	2	1	1			3.65	4.77	1.31
August		1	6	3	3	4	1	2				4.7	3.17	0.67

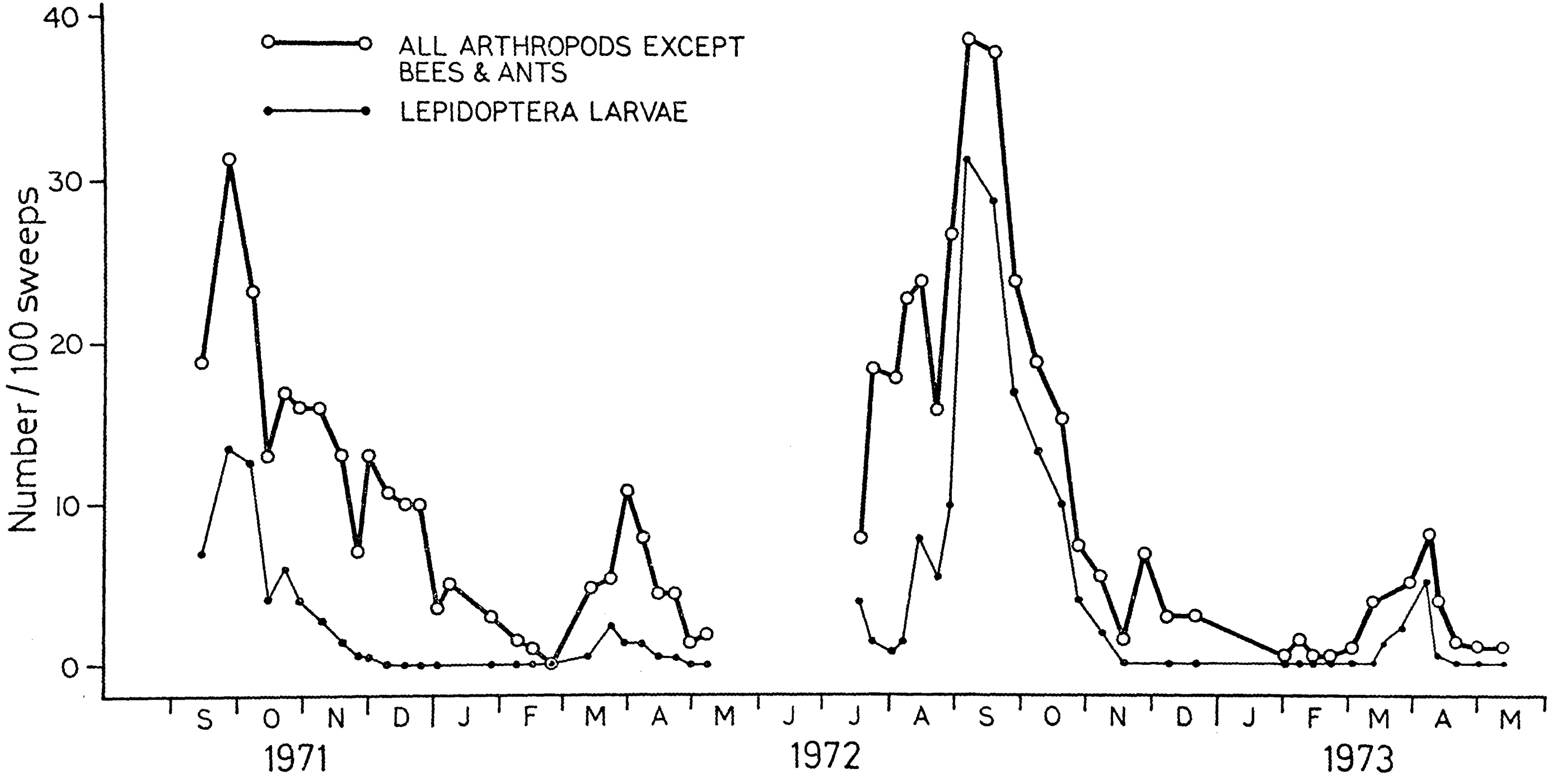


Figure g. Results of sweep-net samples taken in woodland understorey in the Ridge study area. Only arthropods over 10mm in length were counted.

and in this situation the mean is equal to the variance. If the dispersion tends towards clumping the variance is greater than the mean, and if it tends towards over-dispersion the variance is less than the mean.

Table G shows the number of samples in which 0, 1, 2, etc. insects were captured in each month during 1971-72 and the monthly means, variances and variance/mean ratios. The ratios vary from 0.67-1.77 ($\bar{x}$ = 1.14) suggesting that the insects sampled varied in dispersion from moderately clumped to moderately over-dispersed, but that they could, on average, be considered randomly dispersed. Clumping was most marked in September-November, a period when many orthopteran nymphs were hatching.

Figure g shows that insect abundance in the study area, sampled as described, has two annual peaks, a large one corresponding to the rainy season, and a smaller one in spring. The breeding seasons of birds nesting within the study area seem to be considerably influenced by these. Figure h shows the number of species known to have laid eggs in each month, and Figure i the number of nests of Turdoides species known to have been initiated in each month. In both cases only evidence of breeding obtained in the study area is included, and in Figure i only nests found in 1972 and '73 because other years were incomplete.

Some difference was found between the timing of breeding of species nesting in scrub and those nesting in woodland habitat. Figure h includes histograms for these two habitats separately. Although the total number of species-months is similar in each habitat (28, 35) the distribution of nesting attempts throughout the season is more evenly spread in woodland than in scrub, suggesting that more species in scrub are restricted to nesting during the peak of the rains in July and August. Data from sweep netting carried out in scrub also suggested that fluctuations in insect abundance there were more pronounced than in woodland.

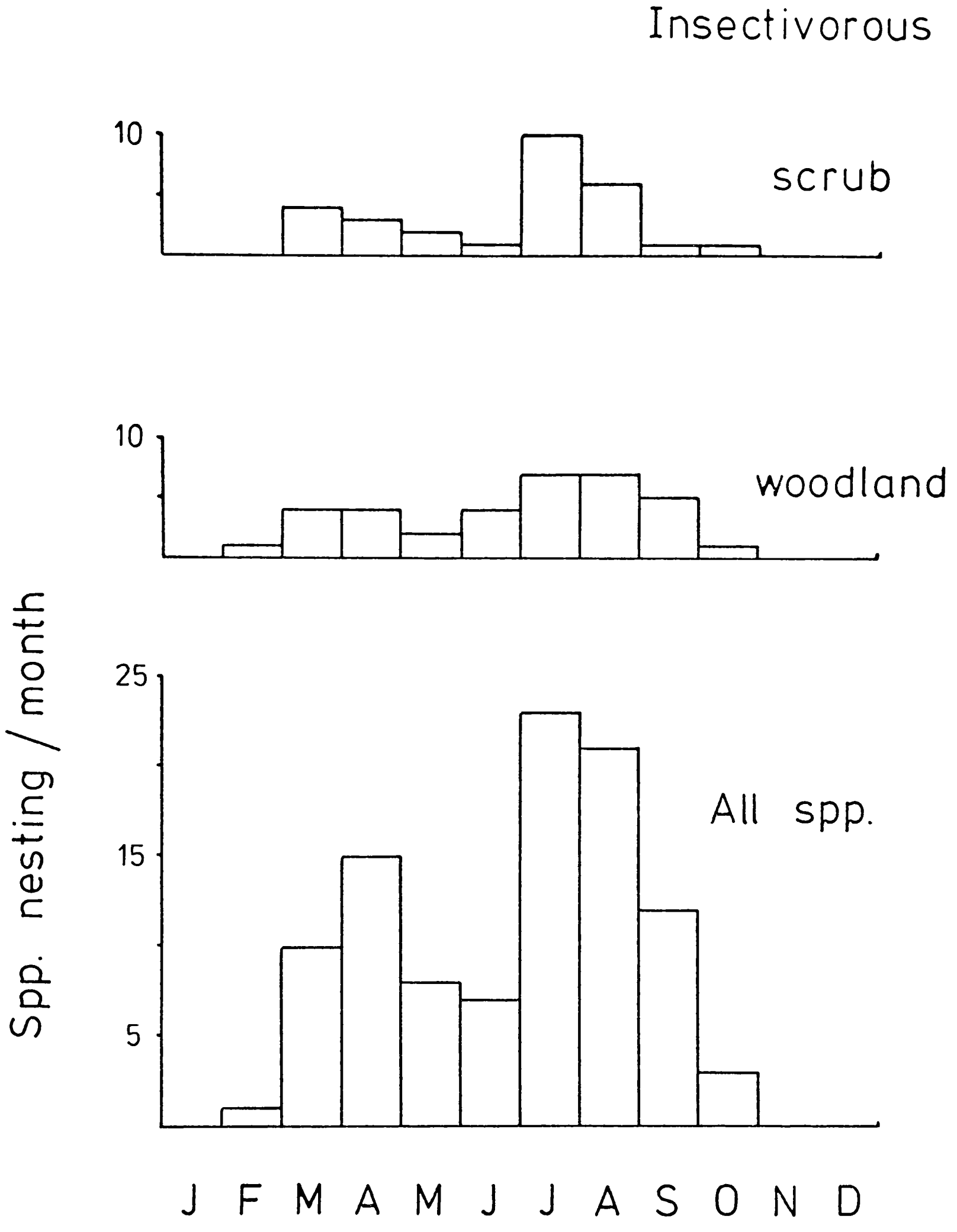


Figure h. Numbers of species of birds initiating nests in each month in the Ridge study area. The lowest histogram includes all species, the upper two include only insectivores, divided into those nesting in woodland and those nesting in scrub.

Table H. Clutch sizes of open nesting passerines recorded breeding in the Ridge study area. Number of clutches in brackets.

	This study	Baker(1932-35)
Mirafra erythroptera		2-4
Lanius vittatus	4.2(4)	4-5
L.schach		4-6
Oriolus oriolus		3
Dicrurus adsimilis		4
Dendrocitta vagabunda	4(1)	4-5
Corvus splendens		4-6
Tephrodornis pondicerianus	3(2)	3-4
Pericrocotus cinnamomeus	2(1)	2-3
Pycnonotus jocosus	3(1)	3-4
P.leucogenys		3
P.cafer	2.9(12)	3-4
Chrysomma sinensis	4.0(6)	3-5
Prinia spp.	5.2(4)	4-5
Orthotomus sutorius		3-4
Saxicoloides fulicata	3.3(3)	3-4
Nectarinia asiatica		2-3
Zosterops palpebrosa		3-4
Petronia xanthocollis		3-4
Lonchura malabarica		5-8

Nomenclature follows Ali and Ripley (1969-74)

Two other studies on birds of the North Indian plains reveal breeding seasons similar to those observed at Delhi for Turdoides species; the House Swift Apus affinis at Baroda (Naik & Razack 1967) and the Collared Dove Streptopelia decaocto at Jodhpur (Rana 1975), and they suggest that a two-peaked breeding season may be typical of many land birds in North India.

The clutch-sizes of all open-nesting passerines known to have bred in the Ridge study area are listed in Table H. Where nests with eggs were not found in the present study the information has been drawn from Baker (1932-35). Clutch sizes at Delhi, and in NW India in general, are large compared to records from elsewhere in India. All clutches of the Red-vented Bulbul Pycnonotus cafer in the study area, for example, were of three eggs, whereas Baker gives two or three as typical of the peninsular race (cafer) and Vijayan (pers. comm.), working in South India, recorded only clutches of two. Compared to clutch sizes recorded in tropical areas elsewhere in the world, also those at Delhi appear relatively large (Marchant 1960, Lack & Moreau 1965, Ricklefs 1973).

The clutch size of nidicolous birds is generally assumed to be related to the amount of food available to the parents, in excess of their own requirements, which can be used to provision the nestlings, and to the amount of time available to harvest it (Lack 1954, 1966). For resident birds this amount is likely to be related to annual fluctuations in the abundance of suitable food. A comparison of clutch sizes suggests that there is no reason to assume that food is less abundant during the breeding season at Delhi than in England (of Lack 1968, Table 9), and what differences there is can be adequately explained by the difference in summer day-length between Delhi (27°N) and England ($50\text{-}55^{\circ}$N).

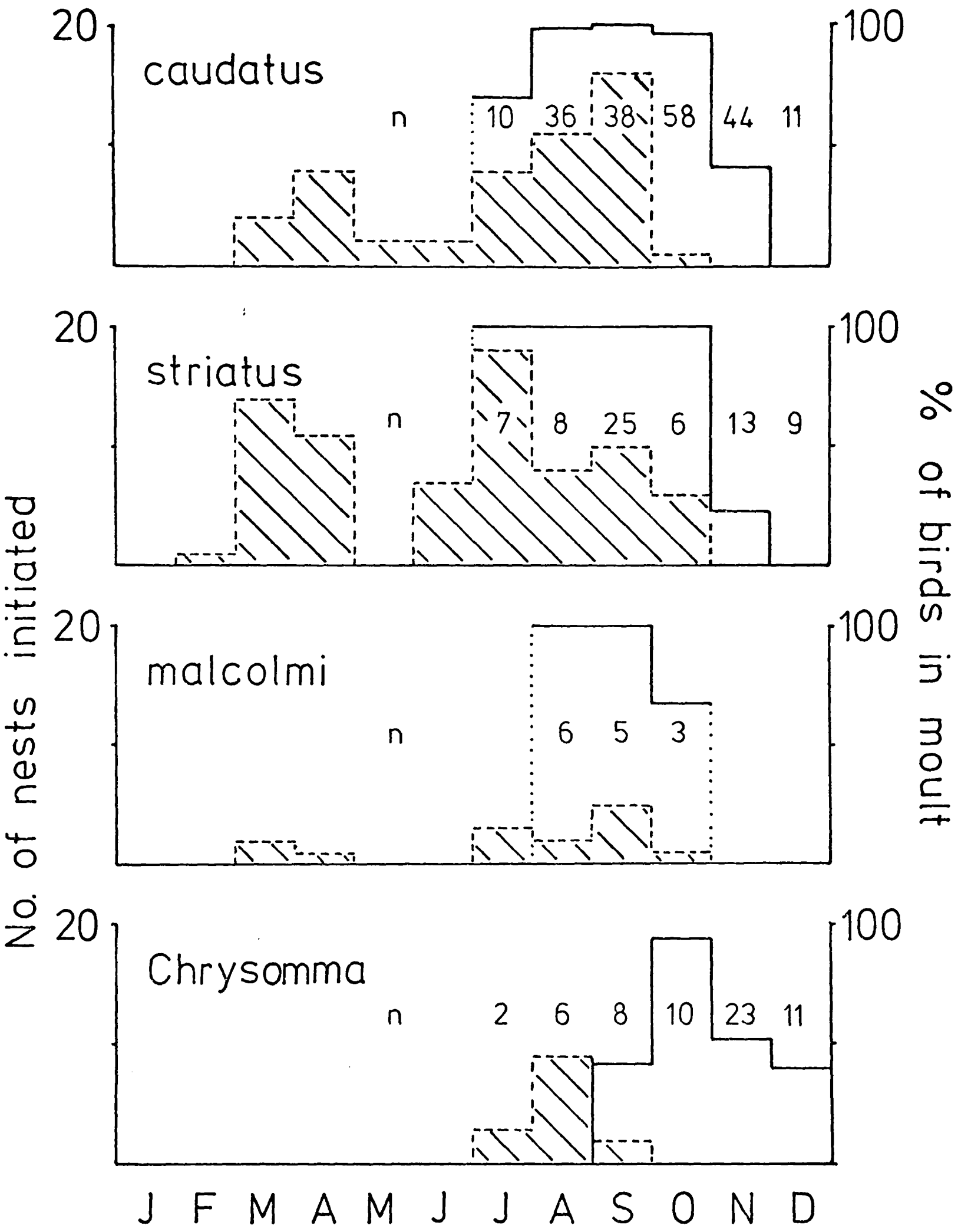
The relatively large clutches laid by open-nesting passerines at Delhi, compared to other tropical areas, may be explained by its strongly seasonal

climate. The fact that the rains occur during the summer makes the effect of temperature and rainfall on the growth of vegetation and on the consequent flush of insects, additive. Winter temperatures are probably lower than those occurring in most tropical climates and added to short day-length this means that conditions in winter are likely to be relatively severe. The combination of low winter temperatures and seasonal summer rainfall combines to produce a more marked fluctuation in the abundance of food for insectivorous birds than is likely in most tropical areas. This probably accounts for the comparatively large clutches of birds nesting around Delhi.

Moult, in most passerine species resident in the study area, was initiated immediately after the end of the breeding season, and was usually completed by the end of November. Figure j shows the number of resident species trapped in each month for which evidence of active primary moult was seen in one or more individuals. Juveniles of all these species usually underwent a complete post-juvenile moult during the same period. The timing and rates of primary moult for the five species of resident passerine for which most data were available are shown in Figure j in relation to their breeding seasons.

The pattern of moult in the three Turdoides species occurring in the Ridge study area differed from that of other passerines in the amount of overlap between moulting and breeding and this is indicated in Figure i. Although none were trapped in June, it seems very likely that most Jungle Babblers began their primary moult in this month, in which case there was complete overlap between the moult period and the rains breeding peak. The abrupt decline in the proportion of moulting birds in November suggested that moult among the population of Jungle Babblers in the study area was relatively synchronised. In the Yellow-eyed Babbler Chrysomma sinensis, the only other

Figure i. Breeding and moulting seasons of Turdoides species and Chrysomma sinensis in the Ridge study area.



Solid line; % of birds trapped which were moulting primaries

n; number of birds trapped for moult sample (adults only)

Hatched histogram; Number of nests initiated, 1972 & '73 only

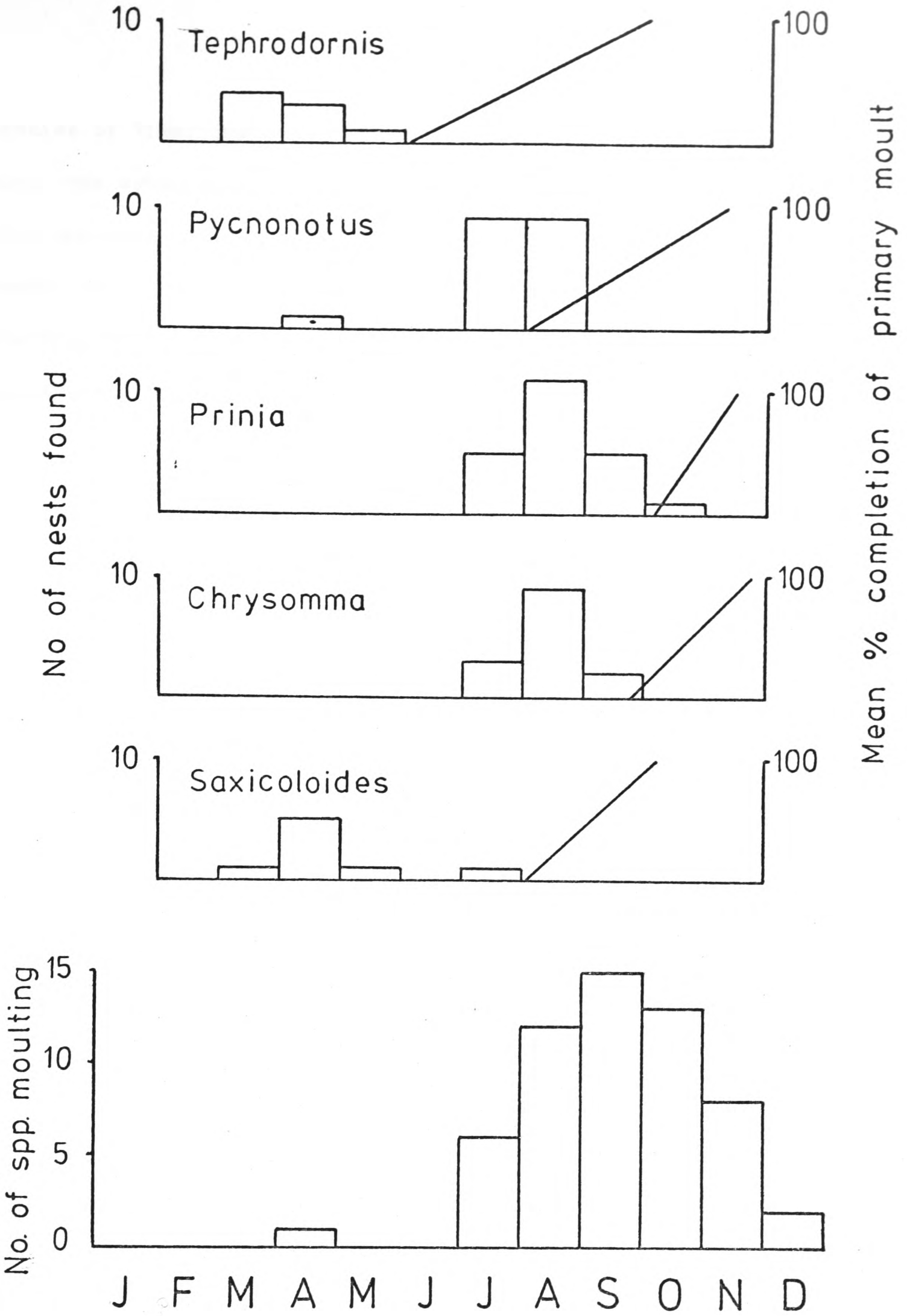


Figure j. Moult seasons of birds in the Ridge study area. Lowest histogram; number of species in each month in which at least one bird showed active primary moult. Upper histograms; approximate progress of the primary moult in relation to the number of nests initiated in each month (note division into "spring" and "rains" breeders).

species of Timaliinae nesting in the study area, the population moult was much less synchronised and although it spread over four months there was only one month in which more than 50% of birds trapped were moulting. It seems likely that the initiation of moult in this species is dependent on the termination of breeding, whereas all three Turdoides species nested and moulted simultaneously.

PART 1

THE JUNGLE BABBLER

Chapter 1. Population dynamics and group structure

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Chapter 1 Population dynamics and group structure

Introduction

Discussions of group territorial and co-operative nesting behaviour in birds have emphasised the presence of a relatively high proportion of non-breeding birds, a biassed sex ratio, and a close degree of relatedness between members of the same group, as factors which may be associated with the evolution of this type of behaviour (Lack 1968, Carrick 1972, Fry 1972, Brown 1974, Ricklefs 1975). An attempt was made to determine these parameters for the study population of Jungle Babblers.

The proportion of non-breeding birds was determined by direct observations of alI breeding attempts, and data on the sex ratio was obtained from a number of sources. The degree of relatedness between members of the same group was assessed by tracing the fate of birds reared within the population, and monitoring the amount of interchange between groups.

In order to study overall population dynamics, fluctuations in numbers were monitored in individual groups and in the population as a whole, both within and between years. Breeding success and factors related to dispersal and mortality were also studied. Different types of habitat were then compared in order to assess the influence of habitat on the population dynamics of individual groups.

Seasonal and annual variations in the total number of birds making up the ten study groups are treated first to illustrate changes in overall numbers. Reproductive success and the survival of the young, the survival of adult birds, the adult sex ratio, and observed movements between groups are then described. This information is utilised to calculate the

typical group structure, and the degree of relatedness of members of the same group. The timing and causes of mortality and dispersal are then described.

The relationship between the type of territory occupied by a group and its size and breeding success is described, leading to a discussion of the importance of the habitat occupied in determining reproductive potential. This is followed by a discussion of the breeding strategies predicted for birds entering the adult population, and the consequences of these strategies in determining group size and structure.

a) Group size and population dynamics

To monitor population dynamics and changes in group membership, ten groups of Jungle Babblers were selected in November 1971 for regular census. These were counted, and the identity of ringed birds recorded, at least every month throughout the study. On the basis of the counts made, Figure 1a shows changes in the combined totals for these ten groups over the period December 1 1971 - June 1 1974. The maximum total recorded during this period was 85, and the minimum 66.

Figure 1b shows the mean totals for the first of each month. Numbers were lowest in March-April and June-July, the beginning of the two breeding peaks (see Figure 1e), and highest in October-November at the end of the breeding season. In 1973, when a number of young were fledged in November, the year's maximum count was on December 1.

The size of the ten groups varied from 2-16 birds, but the variation within a particular group was considerably less. Maximum and minimum counts for each group are given in Table 1A, which shows that the mean range of group size over the period of the study was twofold. Full details of monthly counts are given in Appendix 3. For any particular month variation was much

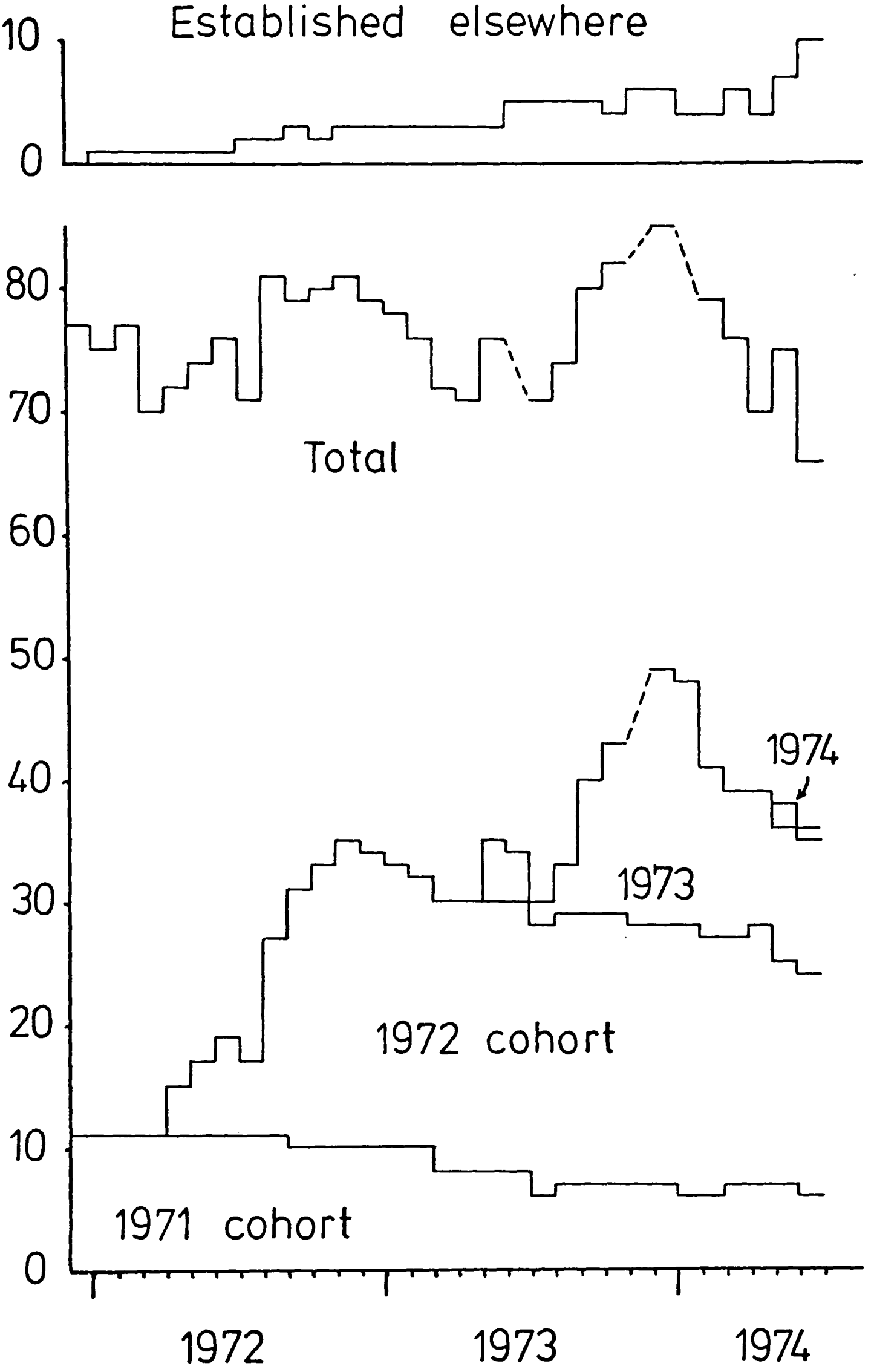


Figure 1a. Fluctuations in the total population of ten groups of Jungle Babblers over 31 months, from Dec. 1 1971. The upper histogram shows the number of ringed birds which established themselves elsewhere.

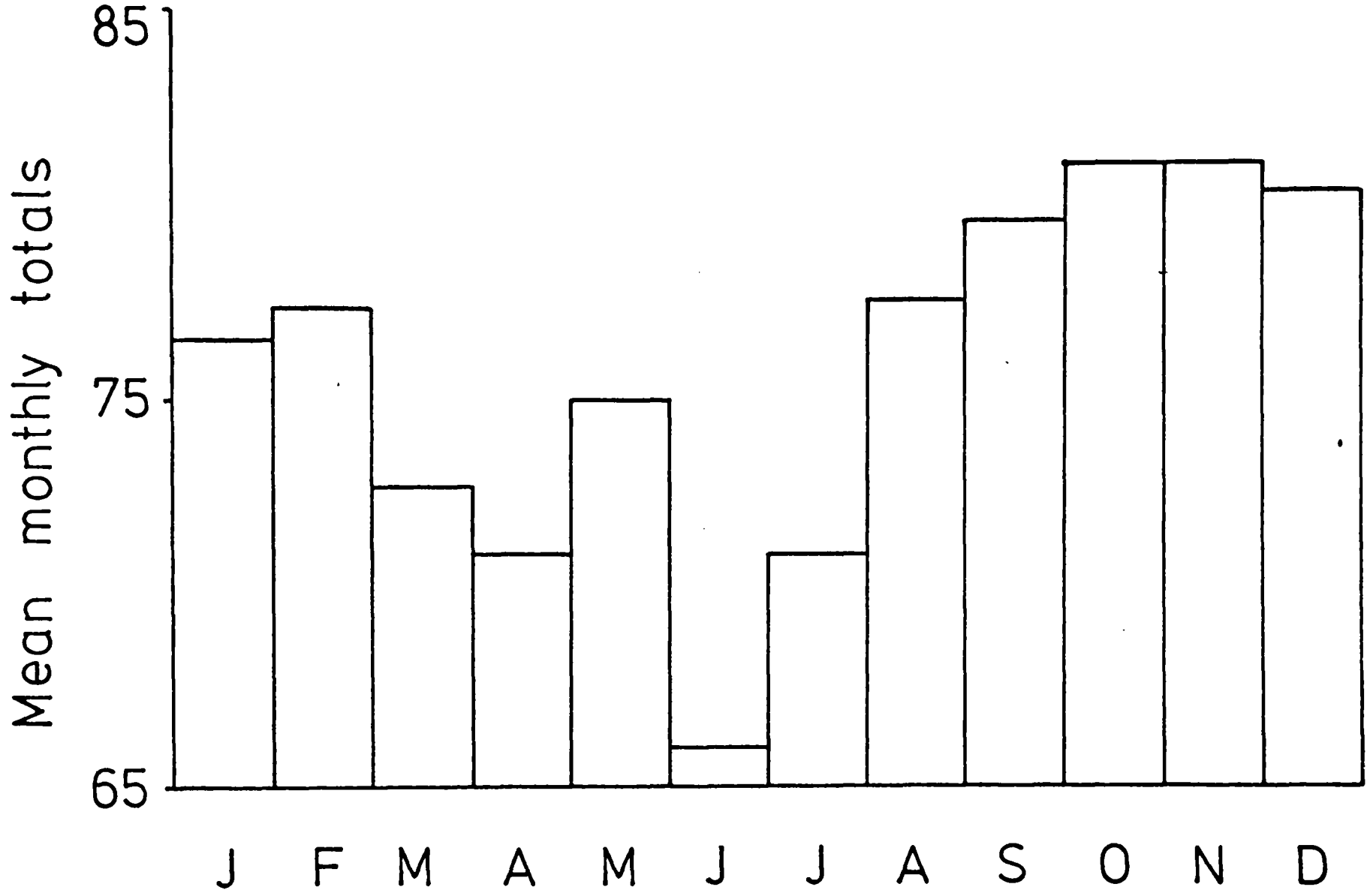


Figure 1b. Mean monthly totals for the ten study groups of Jungle Babblers over 31 months from 1 December 1971.

Table 1A. Annual counts on March 1, and maximum and minimum counts, for ten study groups of Jungle Babblers. Counts were made monthly for 31 months.

	Groups										
	P	L	M	O	D	B	R	G	F	J	Mean
Maximum (x)	14	16	10	10	10	9	9	6	8	7	9.9
Minimum (y)	7	9	7	5	4	5	6	2	5	3	5.3
Ratio (x/y)	2.0	1.9	1.4	2.0	2.5	1.8	1.5	3.0	1.6	2.3	2.0

Counts on March 1

	P	L	M	O	D	B	R	G	F	J	Mean
1972	12	9	10	5	8	6	6	4	5	5	7.0
1973	10	13	7	8	8	5	6	3	7	5	7.2
1974	9	15	9	8	7	6	7	3	7	5	7.6
Max. ratio	1.3	1.7	1.4	1.6	1.1	1.2	1.2	1.3	1.4	1.0	1.23

Table 1B. Clutch size in the Jungle Babbler.

	Clutch size				
No. of clutches	3	4	5	7	Mean
Spring	10	9			3.48
Rains	5	19	1	1	3.96
Totals	15	28	1	1	3.76

Testing the number of clutches with three eggs against the number with more than three, in the spring and the rains, $chi^2 = 5.5$, $p < 0.05$.

less, and Table 1A also gives the counts made on March 1 each year. The mean variation in these counts is only 23% of the minimum. A one way analysis of variance comparing within and between group variance on March 1 showed that within group variation was significantly smaller than between group variation ($F = 3.38$, $p < 0.05$).

The maximum variation in the combined population of the ten groups on March 1 was between 70-76 birds (c. 10% of the minimum). The mean maximum variation in the number of pairs of Great Tits Parus major nesting in Marley Wood, England, over periods of three consecutive years was 86% of the minimum, with only one three-year period out of 16 showing as little variation as that observed for the Jungle Babblers at Delhi (figures from Perrins 1965). This suggests that mechanisms controlling the population of Jungle Babblers are probably more finely adjusted than those operating on the Great Tits in Marley Wood.

b) Reproductive potential and the survival of the young

Only two instances of groups rearing more than two broods in one season were recorded, and the maximum number fledged from one nest was four.[1] The normal maximum reproductive potential of Jungle Babblers in the Delhi area, therefore, appears to be eight young per group per year. The mean size of groups in the Ridge study area at the start of the breeding season was 6.5 birds, and hence groups should have been capable of more than doubling their size in one season. In fact the mean productivity of the ten study groups was 3.1 young fledged per group in 1972 and 3.2 in 1973.

To improve sample sizes for nesting success all Jungle Babbler nests found in the study area from August 1971-June 1974 are included in the following analysis. Figures for the ten study groups were higher than the overall means, probably because all held territories in good quality

[1] In one case four young babblers and one Pied Cuckoo were fledged from the same nest.

habitat (Section 1i). The mean number of young fledged per nest in 1972 and '73 was 1.2, but there was a considerable difference between the fledging success of nests initiated in spring (0.8 young fledged per nest), and those initiated during the rains (1.4 young per nest). Between nests which fledged at least one chick the difference was smaller (2.0 in spring, 2.3 in the rains), and the main difference lay in the proportion of nests which failed completely; 61% in spring (n = 36) compared to 40% (n = 58) in the rains ($chi^2 = 4.16$, $p < 0.05$).

The most likely cause of higher nest failure during the spring breeding peak was predation since at this season nests were most conspicuous due to many of the local trees partially or totally losing their leaves. During the rains 27% of nests were sited in Butea monosperma, a tree with large dense leaves, but this tree was never used in spring when it lost its leaves completely ($p < 0.01$). Acacia and Prosopis, the trees in which 80% of nests were sited in spring, also shed their leaves but did so progressively, putting out bunches of new shoots which provided cover for nests at the same time.

The whole of the difference between the number of young fledged from successful nests in the spring and the rains can be explained by differences in clutch size between the two peaks (Table 1B). The ratio of clutch size in the rains to that in spring is 1.14, while the ratio for the number of young fledged from successful nests is 1.13. Measurements of fledging success during the rains, however, were complicated by the effects of brood parasitism by Pied Crested Cuckoos Clamator jacobinus; these are fully discussed in Appendix 1. Taking only the 1972 and '73 seasons, 71% of nests were parasitised, and the net reduction in fledging success during the period

was 40%. It seems likely that without the presence of cuckoos the number of young fledged per successful nest would have been higher during the rains than during the spring, even after differences in clutch size had been taken into account.

The observed clutch size of Jungle Babblers in the Delhi area ($\bar{x}$ = 3.76, see Table 1B) was similar to that of open nesting temperate passerines of similar size and ecology. Species of the genus Turdus in Britain, for example, lay 3-5 eggs, the modal size being four (Snow 1955). In this respect babblers at Delhi differ from many tropical passerines, which often lay smaller clutches than species occupying similar niches in temperate latitudes (Lack 1966). Lack and Moreau (1965) report a mean clutch of 2.7 for nine species of Timaliinae (all now placed in Turdoides) nesting in tropical Africa outside forests. Among nine passerine families listed by the same authors only the Estrildidae exhibited as large a mean clutch size as that observed for Jungle Babblers.

Several other species of open nesting passerines in the Delhi area were observed to lay similar clutches to those of the Jungle Babbler (see Table G), suggesting that the clutch sizes of passerines nesting around Delhi tend to be larger than those typical of tropical passerines. This is discussed in the Introduction, Section d.

The survival of young after fledging is shown for each breeding period in Table 1C, and overall mortality in relation to age is illustrated in Figure 1c, expressed as a percentage of the birds surviving to the start of each period. The data used include all 77 young reared by the ten study groups, and 20 others reared by adjacent groups occupying similar habitat. Heaviest mortality occurred in the first two months after fledging, and a second smaller peak at four months corresponded to heavy mortality in the late winter of 1973-74, when there was an exceptionally prolonged period of

Table 1C. Survival of Jungle Babblers after fledging.

	No. fledged	No. surviving to age x(months)						
		1	2	3	4	6	12	18
1971 Rains	9	9	9	9	9	9	9	9
1972 Spring	9	6	6	6	6	6	5	5
1972 Rains	30	23	22	21	20	20	20	19
1973 Spring	12	6	3	3	3	3	3	
1973 Rains	33	29	18	18	14	12		
1974 Spring	4	1	1					
Totals for 1972 & '73 only								
Rains	72	61	49	48	44	42		
Spring	21	12	9	9	9	9		

Table 1D. Estimated mean composition of ten study groups of Jungle Babblers on March 1.

	Total number	Per group	Proportion
Breeding adults	20	2.0	27%
First years	16.5	1.65	23%
Second years	15.0	1.5	21%
Native non-breeders	14.2	1.42	19%
Immigrant non-breeders	7.0	0.7	10%
	72.7		

Figure 1c. Percentage mortality per month of fledgling Jungle Babblers. The upper figure shows figures for spring and rains combined.

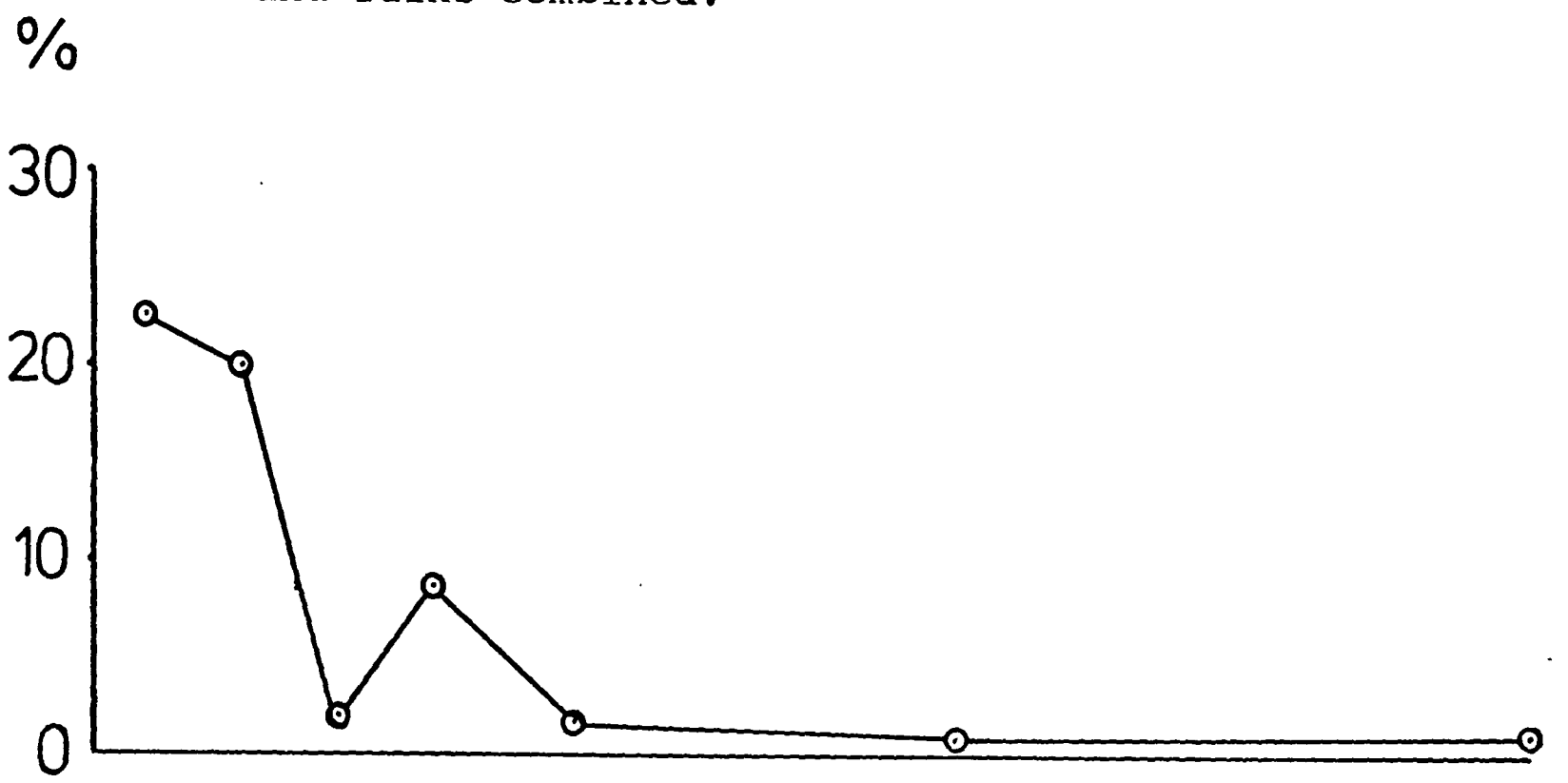
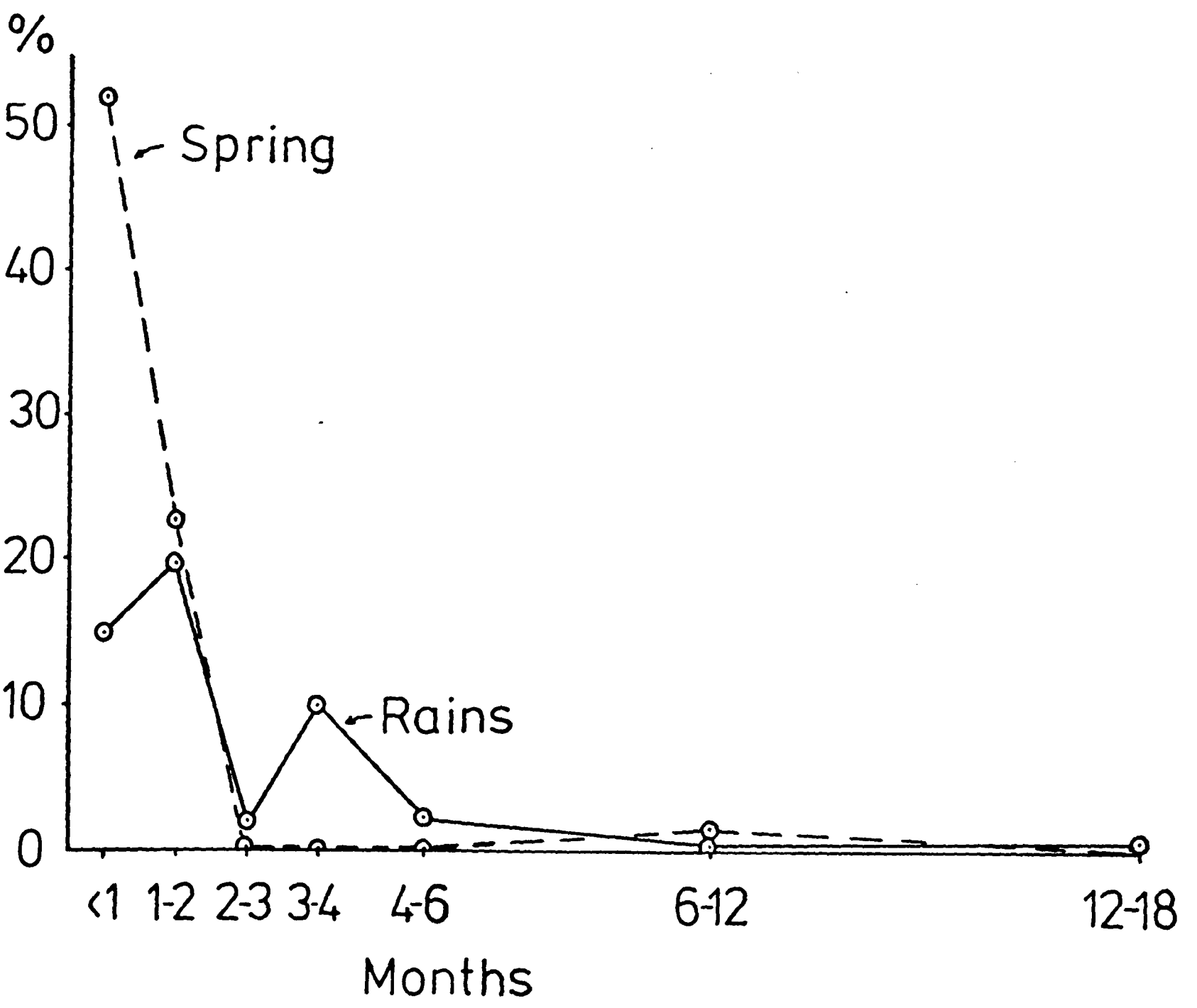


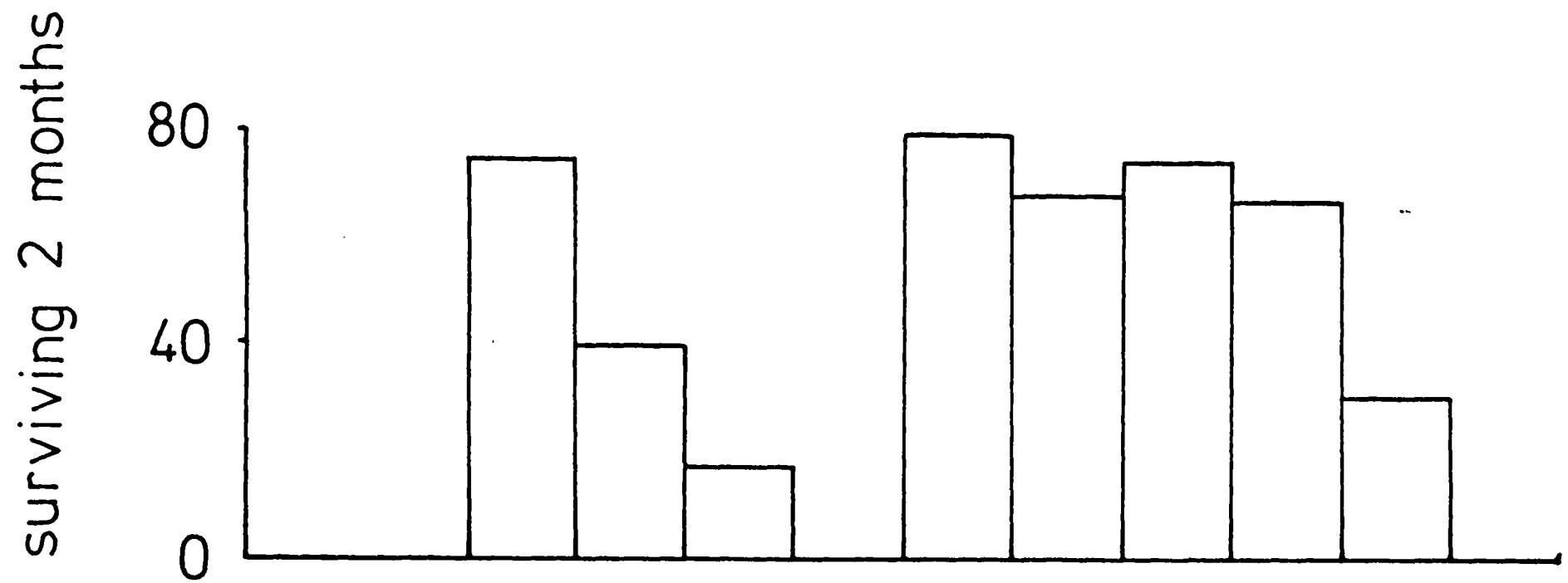
Figure 1d.



hard weather which set records for the century. Birds which disappeared at that time may have died from starvation. One bird which vanished in December 1973 appeared uninjured but only just capable of flight, when seen on the day before its disappearance.

There was a difference in the pattern of survival of the nestlings reared in the two breeding peaks, and these are shown separately in Figure 1d. The difference in the numbers surviving up to one month was significant ($chi^2 = 5.78$, $p < 0.02$), but because of the heavier mortality of rainy season fledglings between two and six months there was no significant difference in the numbers surviving up to one year. Overall survival of birds up to one year was 53% of those which fledged, but the difference between 1972 (64%) and 1973 (33%) was considerable. The difference in the numbers surviving up to one year between the rains of 1972 and 1973 was significant ($chi^2 = 4.62$, $p < 0.05$), and almost certainly due to the very cold winter of 1973-74. An overall survival of 53% over the first year after fledging is high compared to any passerine species previously studied (Ricklefs 1973).

Figure 1e shows the percentage of fledged young surviving to the age of two months, in relation to the month in which they were fledged. The two months of lowest survival, May and November, occur at the end of the two breeding peaks and suggest that poor survival of fledglings may be one reason for the termination of nesting attempts in late April and early October. Survival declines throughout the spring breeding peak, suggesting that there is a selective advantage in early nesting. A situation similar to this was described by Perrins (1965) for the Great Tit, in which the mean date of laying is later than that which would assure maximum fledging success and survival. He postulated that the limiting factor is the ability of the female Great Tit to form an egg, and some similar factor may explain



	M	A	M	J	J	A	S	O	N
No. fledged	4	15	6	1	20	19	19	3	10

Figure 1e. Proportion of fledgling Jungle Babblers surviving at least two months, in relation to the month in which the eggs were laid.

the delay in the initiation of spring nesting by the Jungle Babbler, and perhaps also the fact that some females do not lay at all during the spring.

The observed survival of ringed birds between six and 18 months was 94% (n = 35), significantly higher than the estimated survival of non-breeding second year and adult birds (chi^2 = 11.1, p <0.01), and almost the same as that of breeding adults (see Section 1b). Out of the cohort reared by the ten study groups in 1972, 19 were still present on March 1 1974, at the start of their second summer, and this can be taken as the recruitment into the adult population (ages ranged from 18-23 months). As the mortality between nine and 18 months is low the 1973 cohort present in June 1974, which numbered 11, can be taken as a measure of recruitment in the following year. These two figures give a mean annual adult recruitment of 1.5 birds per group per year.

Losses from the population of birds in their second summer or older amounted to 19 per year, and the difference between observed losses and recruitment was bridged by the observed rate of immigration of 5.5 birds per year. The fact that the figures do not exactly match is the result of a slight increase in the population between March 1972 and March 1974.

All the figures for the survival of different age classes are based on the colour-ringed sample in the population, and it must be borne in mind that most of these belonged to groups occupying good quality territories. Differences in the survival of birds during their first year in relation to the type of territory occupied are discussed in Section 1i, but it is likely that adult survival was also related to territorial quality.

c) Adult survival

Details of the known survival of all birds trapped as post-juveniles are given in Appendix 4. Out of 14 ringed birds which were present on

March 1 1972 and bred in that year, 12 were still present in the same groups on June 1 1974, and two had disappeared. Out of 25 birds known to have been in their second summer or older, and known not to have bred in 1972, only seven remained in the study area in June 1974, and only three were still with the same group. The difference between the two samples in the number remaining within the study area was significant ($chi^2 = 12.04$, $p < 0.01$).

Because emigration was found to be more frequent at certain times of the year, survival rates were calculated only for entire years, and the period March 1 1972 to March 1 1974 was chosen as the most suitable, as March 1 marks the start of the breeding season. For this period the persistence of adults which bred during 1972 was 93% per annum, but this does not strictly represent a survival rate since birds that disappeared may have established themselves elsewhere. Survival rates of breeding adults were high compared to most temperate passerines (Ricklefs 1973), but not when compared to tropical passerines (Willis 1961, Snow 1962, Fogden 1970, Snow & Lill 1974).

The same problem of distinguishing emigration from mortality also presents itself when dealing with the non-breeding birds. During the same period 37 birds more than 18 months old which had not been known to breed left the ten study groups. These included 18 of the 25 non-breeders which were ringed at the start of the period, giving a persistence of 52% per annum for this class. This was significantly different from that of the breeding birds ($chi^2 = 14.08$, $p < 0.01$). These figures can be used to calculate a survival rate using the assumption that the number of emigrants which succeeded in establishing themselves in other groups was equal to the number of immigrants which entered the study groups during the same period. The observed ratio of immigrants to emigrants was 11 to 37 (30%), and using the above assumption this indicates that five of the 18 marked birds which left should have succeeded in establishing themselves elsewhere. Three of them were actually observed to do this.

Using the above method to estimate the number of non-breeding birds which established elsewhere, the survival of this class can be estimated as 69% per annum over the two years. Figures for immigration and emigration included one bird which moved from one of the study groups to another, but later returned to its former group. Such movements on the part of unringed birds would have gone undetected, and hence the actual rate of immigration may be lower than that used in the foregoing estimate, and the survival of non-breeders correspondingly lower.

d) Sex ratio

The true adult sex ratio of the population could not be determined accurately because not all birds could be sexed, even among those ringed, and because the sexing criteria (see methods) may have led to the identification of a higher proportion of females. Among 20 birds reared in L, M, P and O groups during the study and surviving more than 18 months, nine were male, eight female, and three could not be sexed. This suggests that the sex ratio prior to dispersal from the natal group does not depart significantly from unity.

Among birds in their third year or older which remained with the group in which they had been trapped, 17 were male and eight female ($p = 0.05$, binomial test) on March 1 1974. Three out of four birds which succeeded in joining established groups were females, the other being of unknown sex, and altogether 13 out of 18 marked birds observed to leave their group to join new or established groups for periods of one month or more were females ($p = 0.05$, binomial test). The movements of all these birds are plotted on Figure 1f. Since the two tests given above involve the same population of birds they cannot be considered independent, but there is still a strong indication that adult birds in established groups are likely to

include a higher proportion of males, due to emigration and associated mortality being more frequent among females.

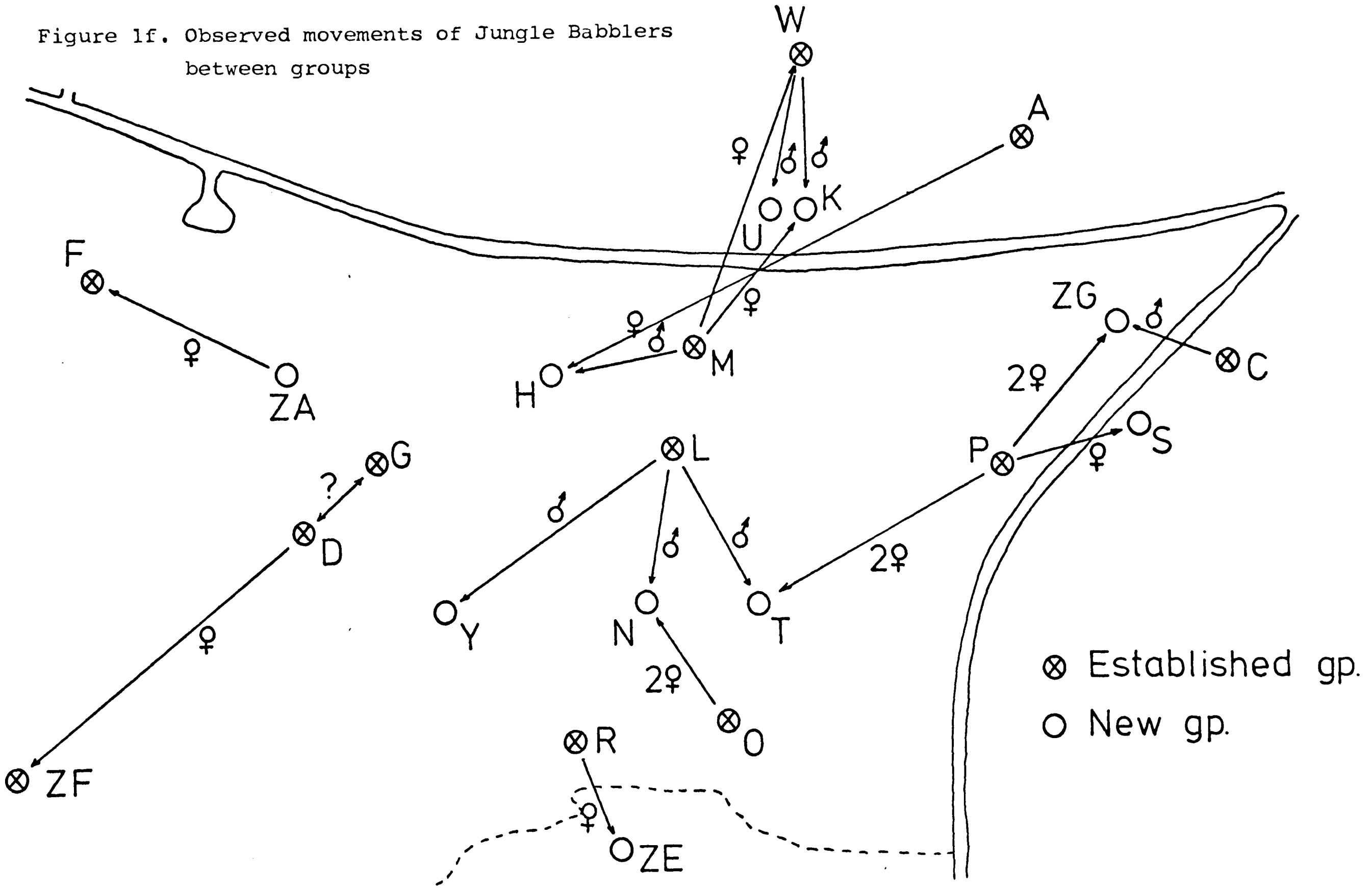
e) Changes in group membership

Only three examples of the replacement of breeding adults were observed during the study; one male and two females. In one case the female which was replaced (DBLG) disappeared; the fate of the breeding male, which was unringed, could not be followed, but it ceased to breed in that group because the new pair included a ringed male (DBR) which had previously been a non-breeder in the same group. In the other instance one ringed female (PDG) was replaced by another (PM) from the same group, while the male breeder remained unchanged. The female which was replaced stayed with the group for a further two years, while making numerous attempts to establish itself elsewhere (see Section 2f).

Only one bird reared during the study was observed to breed. This was a female (YB) which left its natal group at 20 months to join a group in the process of formation, and laid its first clutch in the first nest of that group ten months later.

Many females in their second summer or older wandered away from the vicinity of their group and into adjacent territories at the start of the two breeding peaks. The age at which this tendency was first noticed in 13 birds reared during the study was 12-23 months ($\bar{x}$ = 19.5), at which age most birds were in their second summer. No bird known to be less than three years old was observed trying to join an established group, but eleven which joined in the formation of new groups did so at 12-24 months ($\bar{x}$ = 19.5). Of these groups, containing birds making their first attempt to leave their natal group, only the one containing YB, mentioned above,

Figure 1f. Observed movements of Jungle Babblers between groups



eventually nested. This suggests that most birds participate in several 'trial runs' before finally leaving their natal group.

The furthest movement observed between groups was 500m. All movements between groups recorded in the course of the study are marked on Figure 1f. Out of 18 movements made by ringed birds only one was between groups which did not have adjacent home ranges, although any one group had a home range contiguous with 2-7 others ($\bar{x} = 4.5$). If dispersal had been random within the study area, which usually contained 18 groups, only c. 25% of changes should have been between adjacent groups ($p < 0.01$). Most of the movements observed were to newly formed groups, as indicated in Figure 1f; hence the membership of these was normally drawn from the groups immediately adjacent to the area in which they were established. On three occasions birds were seen alone more than 500m from the centre of distribution of their natal group. One of these birds returned later to its natal group but the other two disappeared.

f) Group structure and degree of relatedness

The mean population of the ten study groups on March 1 was 72.7 birds, comprising 16.5 first years, 15 second years, 20 breeding adults, and 21.2 non-breeding adults. An unknown proportion of the non-breeding adults were not native to the group to which they belonged. To calculate this proportion the following assumptions were made:

1) That immigrants disappeared from the groups which they joined at the same rate that was observed for all non-breeding adults (31% per year, Section 1b). This seemed reasonable because known immigrants did leave the groups which they had joined on several occasions, either to establish new groups, to rejoin their natal group, or to disappear. Their rate of mortality should have been similar to that of native group members.

2) That the rate of immigration was not dependent on group size but was determined by the reactions and abilities of the resident breeding female. Although other group members sometimes joined the breeding female in driving off isolated females from the group's territory the breeding female was always the most active participant and no instances of single females being driven off in the absence of the breeding female were observed.

3) That the number of birds living in groups to which they were not native remained stable.

Using these assumptions the number of birds in the ten study groups not living in their natal group (x) was calculated. If the rate at which immigrants enter established groups is "a" birds per year and the proportion leaving is "b", then in a steady state $x = a/b$ (1)

The proportion of birds leaving, using assumption 1, is already known, and the number of immigrants is also known. The crude number of immigrants has to be corrected for the fact that some are actually returning to their natal groups. Out of the eleven observed immigrants five ringed birds were known to have been returning to their natal groups. The number of unringed immigrants actually returning to a natal group (y) can then be estimated from the total unringed immigrants (z), and the proportion of unringed birds among all emigrants (p).

Hence, $y = zp$ (2)

Substituting observed figures in equation (2) the number of unringed immigrants actually returning to a natal group is calculated below.

$$y = 6 \times 9/37 = 1.5$$

The number of immigrants unrelated to the group which they joined can then be calculated by subtracting the above figure, plus the number of marked birds known to have been returning to their natal groups, from the observed

number of immigrants:

a = 11 - (5 + 1.5) = 4.5 in two years = 0.225 per group per year

The number of birds living in groups to which they were not related can then be estimated by substituting the rate of immigration calculated above, and the observed proportion leaving, in equation (1).

Hence, x = 0.225/0.31 = 0.70 birds per group

Even if all unringed immigrants were unrelated to the groups that they joined the rate of immigration would still have been only 0.3 birds per group per year. Using this figure in equation (1) gives a total of 1.0 unrelated birds per group.

These calculations result in an estimated composition for the ten study groups which is shown in Table 1D.

Three emigrants from the study groups succeeded in joining other established groups over the two years, a figure of a similar order to that calculated for the number of unrelated immigrants entering the study groups (4.5 birds). Extensive searches for marked birds outside the study population were carried on throughout the study, and particularly during the spring, when the largest number of birds disappeared, and it seems unlikely that more than one or two birds could have joined other groups, or established new ones, within 500m of the study area, without detection. Since nearly all observed movements were between groups with adjacent home ranges, it seems likely that most of the emigrants that survived outside their native groups were accounted for.

The degree of relatedness among members of the same group depends not only on the proportion of immigrants, but also on the frequency of changes in the breeding pair. This frequency was observed as two out of 14 marked birds over two years, a survival rate as breeders of 92% per annum. This rate, assuming that the replacement of one member of the breeding pair is

independent of replacement of the other, suggests that each group has a new breeding bird approximately every six years.

Because females apparently change groups more frequently than males, a new breeding female is likely to be less closely related to the other members of the group than a new breeding male. Data on the Common Babbler suggest (Chapter 5) that breeding females are usually unrelated to the group in which they breed, but that new males are drawn from within the group. Evidence from Jungle Babblers suggests that this is probably true of them also, and hence to calculate the relatedness among members of the same group new females were assumed to be unrelated to other group members, while new males were assumed to be siblings of other native members of the group, although they might sometimes be siblings of the former breeding male. Using these assumptions the mean degree of relatedness among non-breeding members of the same group was calculated according to the formula below.

$$R = \frac{\sum_{i=1}^{a-} \left[\sum_{j=i+1}^{a-1} \left\{ n_i . n_j . \; (0.125 + 0.375 . s^m) \right\} + {}_{n_i}C_2 \times 0.5 \right]}{{}_{n}C_2}$$

where $n = \sum_{i=1}^{a} n_1 + I$

a = number of cohorts

I = number of unrelated immigrant non-breeders

s = mean annual survival rate of breeding adults

m = number of years between cohorts (j-i)

${}_{n}C_2$ = number of combinations of two in n = (n(n-1))/2

To calculate the mean degree of relatedness of non-breeders in the ten study groups the formula above was applied to the figures given in Table 1D, the non-breeders of three years and older being arbitrarily assigned to three cohorts, containing 0.8, 0.4, and 0.2 birds respectively. These figures give a mean degree of relatedness of 0.46 among native non-breeders, and 0.33 among all non-breeders. The annual survival rate of the breeding adults was derived from a small sample but the same calculation performed assuming a survival rate of 0.8 gives a mean relatedness of 0.4 among native non-breeders, and 0.29 among all of them, both closer than the relatedness of first cousins (0.25). These figures also represent the mean relatedness of non-breeders to the breeding pair.

One problem with the foregoing calculation is that changes of breeding males and females are unlikely to be independent. For the Common Babbler there was evidence that changes of female were more frequent than changes of male, and that changes of breeding male were normally accompanied by a change of breeding female (Chapter 5). Data for Jungle Babblers were insufficient for conclusions to be drawn.

g) Causes of mortality and dispersal

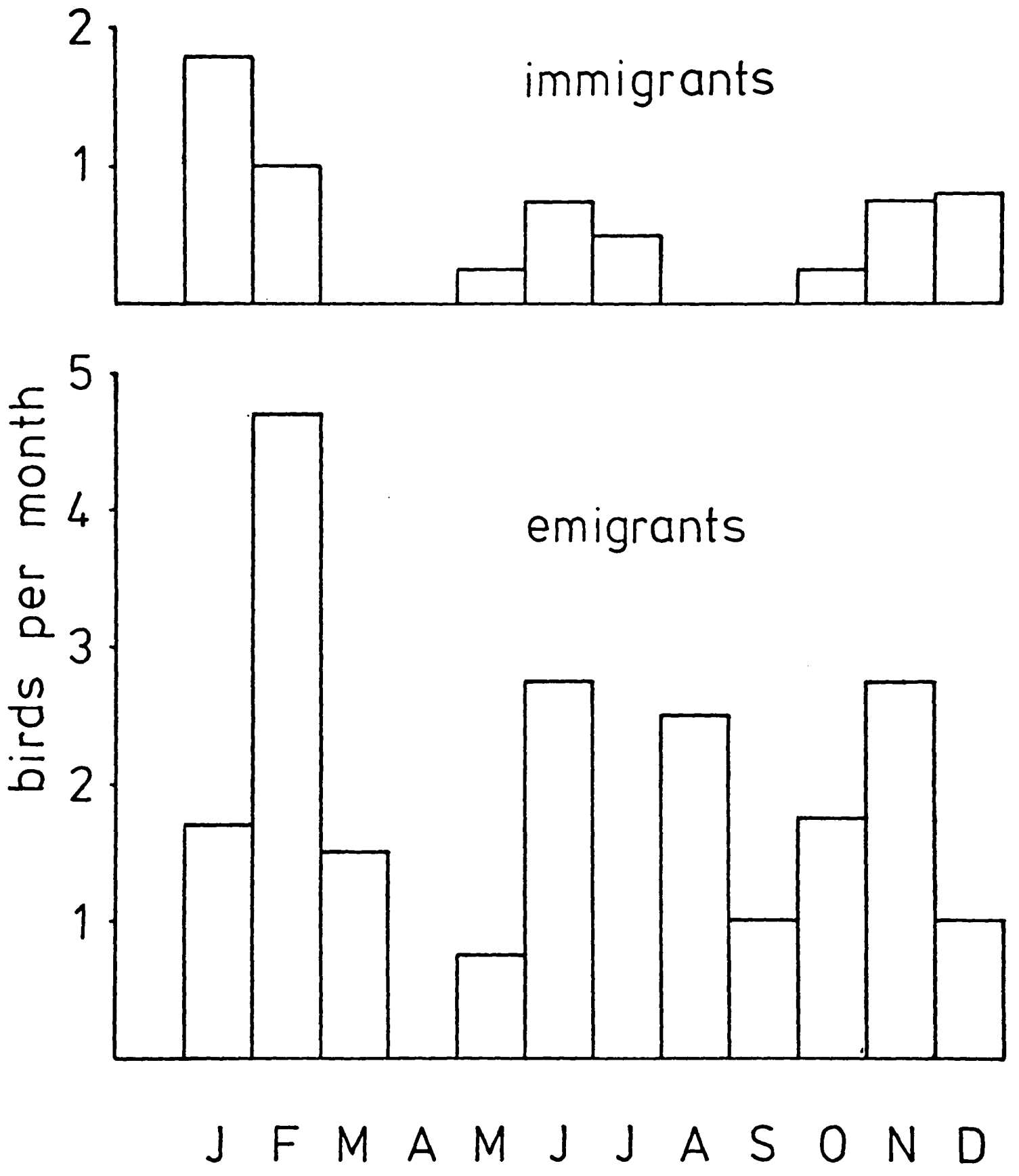
Little evidence was obtained on causes of mortality among Jungle Babblers. The mortality of fledglings soon after leaving the nest was probably due, in some cases, to starvation. Three juveniles caught by hand in May, a few days after leaving the nest, weighed 41%, 45% and 54% of mean adult weight (normal fledging weight is 66%), and none of these birds were seen again. At this stage also, while barely able to fly, they were probably liable to predation by a wide variety of predators, including snakes, mongooses, crows, and raptors.

Juvenile Jungle Babblers continued to be noticeably worse at flying than the adults until they had completed their post-juvenile moult. This may have been partly due to the fact that the juveniles' flight feathers are shorter than those of the adults (Naik & Andrews 1966) and appear to be weaker, and this may make them more vulnerable to predation by hawks. The Shikra (Accipiter badius) occurred in the study area throughout the year, and the Sparrow Hawk (Accipiter nisus), in winter, and both species have been recorded taking babblers (Ali & Ripley 1968).

The heavier mortality of emigrant birds, which is implied by their rate of disappearance, may also be due to predation. Outside their native territory all adult birds are liable to attack from groups which defend the area on which they encroach. Because of this they are forced to feed outside the main foraging areas of territorial groups, in places with less vegetation cover (see chapter on territory), and this may expose them to predation. The danger is likely to be enhanced by the absence of conspecifics to perform sentinel behaviour (see Chapter 3), and by the fact that emigrants make themselves conspicuous by calling and perching in the tops of trees.

The timing of departures of birds in their second summer or older from the ten study groups are shown in Figure 1g. This includes birds known to have dispersed to other groups or to have established new ones. The seasonal pattern suggests that most disappearances were preceded by dispersal, rather than occurring due to mortality within the natal group. Maximum rates of departure occurred in February and June, the two months immediately preceding the two breeding peaks. January, the month in which low temperatures, short day-length, and scarcity of insects made food shortage most likely, was the month in which immigration was highest. One of these birds was returning to its natal group, however, and the same may

Figure 1g. Mean numbers of birds observed to leave and join the ten study groups in each month.



have been true of others because ephemeral groups had a tendency to break up in winter. Another period of high emigration occurred in October-November.

New groups were generally formed at the beginning of the two breeding peaks and their formation is described in Chapter 2. The timing of the formation of eleven new groups which included ringed birds was similar to the timing of emigrations; three were formed in March, six in May-June and two in October-November. The groups established in October-November may have been as a result of an autumn territoriality phase, a phenomenon documented for other species of passerines (Morley 1943, Gibb 1956, Kalela 1958).

Six of the new groups were still defending territories at the end of the study, although one had lost several of the original members and another had been in existence for only one month. Out of the other five, two initiated in March broke up in April, and the other three dissolved in August, November and December respectively. Only seven of the groups succeeded in producing eggs, and only four in fledging any young.

Zahavi (1974, and in litt.) has suggested that, in the case of the Arabian Babbler (Turdoides squamiceps), particular territories impose a certain population level on the group which occupies them. He derived this hypothesis from the observation that group size within a particular territory varied much less than the variation between territories, and this was also true in the present study (Section 1a).

In order to test the applicability of Zahavi's hypothesis in the present instance, the number of birds disappearing from each group in the year beginning October 1 was compared with the number of young reared during the preceding breeding season. Under Zahavi's hypothesis a positive correlation should be detectable between these two parameters. The comparisons for

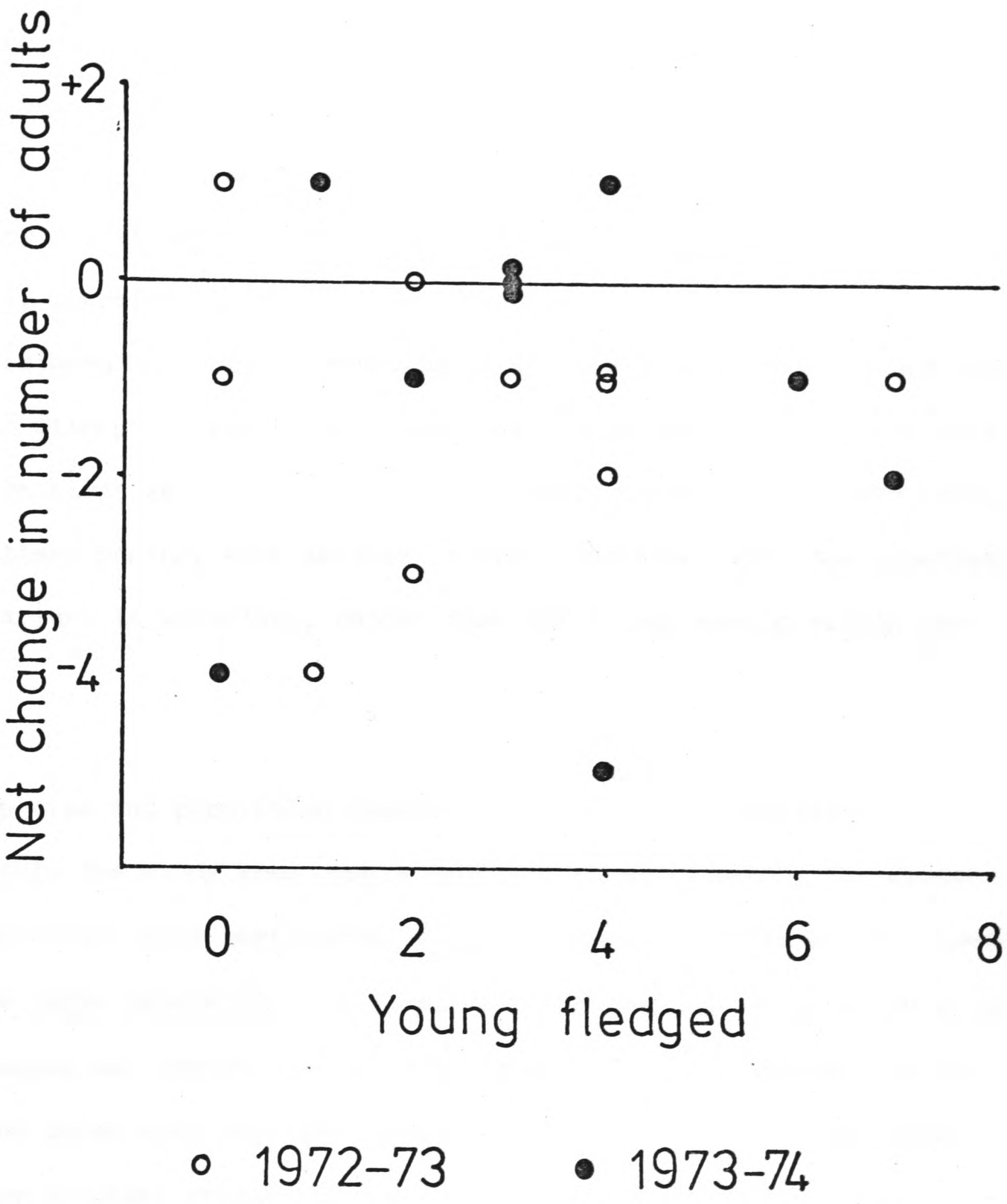


Figure 1h. Net change in the number of adult Jungle Babblers per group during the year beginning October 1, in relation to the number of young fledged in the previous breeding season; study groups only.

1972-73 and 1973-74 are shown in Figure 1h. Since emigration figures were only available until June 1974 the two years are shown separately. In neither year is there any suggestion of a correlation between the number of birds recruited into the group and the number which left during the following year.

There may, ultimately, be a connection between the number of birds reared in a group and the number which emigrate from it, but it seems unlikely that within the study population this was as a direct result of population pressure within the group territory. Evidence is presented in Chapter 2 that territories expand with increases in group size. It is suggested, therefore, that observed group sizes were the result of a balance between the rate of recruitment and the tendency of non-breeding adults to attempt to establish themselves elsewhere. The relative ease with which birds were accepted back into their natal groups after weeks, and sometimes months, with another is also consistent with the hypothesis that departure is voluntary, rather than due to aggression within the group.

h) Group size and population dynamics in relation to habitat

Within the study area Jungle Babblers occupied mainly the closed canopy woodland, most territories being centred on patches of tall trees with some dense understory. Although most feeding was done on the ground, some foraging was carried out on the trunks and larger branches of the trees, and these also provided nesting and roosting sites. The dense understory provided shelter for juvenile babblers during the first weeks after fledging, and was used by the whole group for resting in the middle of the day, when it provided shade and possibly some protection from predators.

Territories occupied by Jungle Babblers varied considerably in the amount of closed canopy woodland which they contained, and they were classified into three types on this basis. The area within which 50% of encounters with a particular group were made was described as the core area, and the whole area within which they were recorded as the home range. The core area usually constituted less than 30% of the home range. This is discussed further in Chapter 2.

Territory types:

1) Home ranges falling largely within closed canopy woodland, and containing some area with dense understory.

2) Core area in, or on the edge of, closed canopy woodland, but most or all of the home range in scrub.

3) Home range devoid of any closed canopy woodland, containing only scrub with isolated trees.

Nests and roosts in the first two territory types were located within areas of closed canopy woodland, but in type 3 territories they were in isolated trees away from the woodland edge, or occasionally in bushes.

Groups occupying different types of territory were compared for a number of parameters, the figures being drawn from Appendix 5, which gives the size and reproductive success of all groups observed. It was preferable to use three discrete categories of territory, despite the fact that variation in the habitat was more or less continuous, because most territories were readily assignable to one of the above categories, and because no measurable parameter was found that adequately expressed the difference between apparently 'good' and 'bad' territories. The mean size of groups in each type of territory on March 1 are given in Table 1E.

Most new groups were established in type 3 territories, although the classification was made difficult because they usually moved about a

Table 1E . Group size in relation to the type of territory occupied.

	1972	1973	1974
Type 1	7.75(8)	8.12(8)	8.27(11)
Type 2	5.5(4)	4.8(5)	5.0(5)
Type 3	5.0(2)	4.2(4)	4.5(4)

Differences between type 1 and type 2 territories;

1972, Mann-Witney "U" = 9, p = 0.14

1973 U = 5, p = 0.01

1974 U = 7, p = 0.02

great deal immediately after their formation. Out of groups which had been holding territories for more than three months, all the eight groups which had been occupying type 1 territories during the breeding season of 1972 were still present, and holding similar territories, in 1974 (one had altered its home range to such an extent that it was reclassified from type 1 to type 2). Out of ten groups holding type 2 and 3 territories in 1972 only seven were still holding territories in 1973, and out of four more established in that season, only two survived to 1974. Fisher exact probabilities calculated for the two years separately were 0.15, and 0.32. The two samples are not independent, since the same groups are involved, but evidence from both years suggests that groups holding type 1 territories are more persistent than those holding type 2 or type 3 territories.

The tendency of individual birds to move between groups did not seem to differ much between territory types. Out of 28 adult birds marked in type 1 territories in the course of the study, 20 were observed to leave their groups in 605 bird-months of observation, giving a mean duration for the period that they remained in the group in which they had been marked of 30 months. The corresponding figures for 25 adults trapped from groups in type 2 and 3 territories were 11 departures in 483 bird-months, giving a mean of 44 months per bird, not significantly different from the birds in type 1 territories ($chi^2 = 1.0$, $p = 0.3$).

The age at which adult birds left their group was unknown in many cases, because most of them were more than one year old when trapped. Among birds of known age, the mean age of disappearance from type 1 territories was 20.7 ± 2.2 months ($n = 9$), and from type 2 and 3 territories 16.7 ± 4.4 months ($n = 4$); this comparison includes only birds which disappeared at more than one year old (Mann-Whitney 'U' = 4, $p < 0.05$, two tailed test). This difference could be due either to earlier dispersal from type 2 and 3 territories, or to higher mortality, but the former seems more likely as three

of the birds were seen away from their groups shortly before they disappeared.

During February 1974 a census was made of Jungle Babbler groups in an area adjacent to the campus of Delhi University. The vegetation here consisted of closed-canopy woodland about six metres in height, with some larger trees, and dense understory throughout. The structure of the vegetation was similar to that found in type 1 territories in the Ridge study area, and it was fairly uniform over 0.58km^2. The area was surrounded by urban development on three sides, and hence there was little opportunity for the groups living within it to forage outside.

Surveys were made on three mornings by transects backwards and forwards across the area, and these were conducted as rapidly as possible to minimise duplication. Groups were counted when seen and their positions mapped. The mean group size for the area was calculated from eight groups counted accurately and known to be different. The total population of the area was then estimated from the mean group size (10.25) and the estimated number of groups (15) to be 154 birds, giving a density of 266 birds/km^2 and 26 groups/km^2.

The corresponding figures for the Ridge area were calculated using the mean group sizes in February for thirteen groups occupying an area of 0.8km^2, the entire range covered by the ten study groups. The three other groups included were H, I, and Z (later V in same territory). The mean total for these groups on March 1 was 85 birds, giving a density of 105 birds/km^2 and 16 groups/km^2 (see further discussion in Section 2g). A comparison of the densities and group sizes observed in the Ridge and the University areas supports the observation made within the Ridge area, that as the quality of the habitat, as measured in this case by the density of birds, improves, so group size increases despite a decrease in the size of territories.

Table 1F. Reproductive success of Jungle Babbler groups in relation to the type of territory occupied, whole season, 1972 & '73 only.

	Type 1(A)	Type 2	Type 3	Type 2&3(B)	A/B	Z
Nesting attempts / group	2.94(16)	1.5(10)	1.0(8)	1.28(18)**	2.30	65%
Young fledged / nest	1.25	1.13	1.38	1.22	1.02	4%
Young fledged / group	3.69	1.7	1.38	1.56*	2.36	6%
Young surviving 1 month	2.75	1.3	0.87	1.11	2.48	-5%
Young surviving 3 months	2.25	1.2	0.62	0.94	2.39	30%
Young surviving following March 1	2.0	0.8	0.5	0.67*	3.0	

The last column (Z) shows the percentage contribution of each stage to the final difference between columns A and B.

**; difference between type 1, and type 2 & 3 territories significant at $p < 0.01$

* ; difference between type 1, and type 2 & 3 territories significant at $p < 0.05$

Table 1G. Reproductive success of Jungle Babbler groups in relation to the type of territory occupied, 1972 and '73, nests initiated during the rains (June-October) only.

	Type 1(A)	Type 2	Type 3	Type 2&3(B)	A/B	Z
Nesting attempts / group	1.69	1.2	0.87	1.06*	1.59	51%
Young fledged / nest	1.48	1.25	1.57	1.37	1.08	13%
Young fledged / group	2.5	1.5	1.37	1.44	1.74	4%
Young surviving 1 month	2.19	1.5	0.87	1.22	1.79	6%
Young surviving 3 months	1.75	1.2	0.62	0.94	1.86	26%
Young surviving following March 1	1.44	0.8	0.5	0.67*	2.16	

The last column (Z) shows the percentage contribution of each stage to the final difference between columns A and B.

* ; difference between type 1, and type 2 & 3 territories significant at $p < 0.05$

i) Breeding success in relation to territory type

Table 1F gives the numbers of nests in which eggs were laid, the numbers of young fledged per group per year, and the number of fledglings surviving up to the beginning of the next breeding season, for groups in each of the three territory types. The figures in the penultimate column show the ratio of the figures for type 1 territories to those for types 2 and 3 combined. A comparison of these ratios shows that a major portion of the observed difference between the numbers surviving at the start of the next breeding season (65%) is contributed by the difference in the number of nesting attempts. The differences contributed by the number of young fledging per nest (4%) and the number surviving up to three months (6%) are small. The largest difference, apart from the number of nesting attempts, is contributed by the survival beyond three months (30%) which includes the period of maximum food scarcity in January.

The overall figures given in Table 1F conceal some details. Twenty out of the 47 nests in type 1 territories were initiated during the spring breeding peak when, as discussed in Section 1b, the rate of nest failure is higher than during the rains peak. Table 1G sets out the same data as Table 1F but includes only nests initiated during the rains (June-October). It shows a similar pattern although the importance of the number of nesting attempts is reduced.

From the data presented in Tables 1F and 1G it is clear than pairs nesting in type 1 territories are at a considerable advantage compared to those in type 3 territories, with type 2 territories providing intermediate results. Groups in type 1 territories include an average of six non-breeding birds per group, twice the number present in type 2 and 3 territories, and this raises the possibility that the assistance of non-breeding group members contributes substantially to the success of the breeding pair. This suggestion

has been put forward to account for the increased breeding success of pairs assisted by non-breeding birds in the case of the Superb Blue Wren (Rowley 1965), the Kookaburra (Parry 1973), the Puerto Rican Tody (Kepler 1973), and the White-winged Chough (Rowley 1965a). Other authors also make this assumption on the basis of the proportion of food fed to the nestlings by non-breeders (Brown 1972, Skutch 1961), although Skutch notes that species with regular assistance from non-breeders do not normally lay larger clutches than similar species without them.

The most obvious form of assistance which might be rendered to the breeding pair by other members of the group is the feeding of nestlings and fledglings, and observations showed that at some nests a considerable proportion of the food fed to nestlings was brought by non-breeders (see Chapter 4). There was little evidence to suggest that the number of helpers had any effect on fledging success or survival in the immediate post-fledging period, however, since there was little difference between groups occupying different territory types, despite large differences in the numbers of non-breeding birds per group. Table 1H shows the distribution of the number of young reared per nest in relation to the type of territory occupied, and gives probabilities. Full details for individual groups are given in Appendix 5.

It is apparent from Tables 1F and 1G that differences between groups occupying type 1 territories and those in type 2 and 3 territories are most marked at the stages in the reproductive cycle when assistance from non-breeders appears least likely; the initiation of nests and the survival of young birds beyond three months old, by which time they are largely independent. The number of nests initiated, however, depends partly on the number of nests which fail, since re-nesting is delayed by the presence of dependent young, and hence the frequency of nesting attempts cannot be treated as a measure of breeding success.

Scattergrams of the number of young fledged per year, and the number

surviving on March 1 following against group size for groups occupying type 1 territories are shown in Figure 1i. No significant correlations were found. Figures for 1972 and '73 were used together since the number fledging in each year was similar. When all groups observed in these years were included there was a small but significant correlation between group size and the number of young fledged per year in 1973 ($r^s = 0.54$, $p < 0.05$) and a smaller, though still positive, correlation in 1972 ($r^s = 0.28$, $p > 0.1$). These correlations seem more likely to be related to differences in habitat than to group size alone.

To further investigate the influence of group size on breeding success Spearman rank correlation coefficients were calculated to compare the correlation of group size with various parameters of breeding performance. To minimise the effect of territorial quality only groups occupying type 1 territories were included in this analysis. Table 1I summarises the results of these correlations.

The only parameter found to be significantly positively correlated with group size was the number of nesting attempts per group, but this, as pointed out above, cannot be treated wholly as a measure of breeding performance. In both years there was an insignificant negative correlation between group size and the number of young fledged per nest. Testing the number of young fledged per nest in spring this negative correlation was significant at $p < 0.05$ but during the rains there was an insignificant positive correlation. In the absence of other evidence these probabilities seem too large to draw any conclusions regarding the possibility that the number of young fledged per nest decreases with increasing group size. They do suggest strongly, however, that there is no positive correlation between the two parameters.

Table 1H. The number of young reared per group of Jungle Babblers in relation to the type of territory occupied, 1972 and 1973 only.

Whole year

	Numbers of young fledged					
	0	1	2	3	4	Mean
Type 1 (A)	22	5	9	8	3	1.25
Type 2	7	3	2	2	1	1.13
Type 3	3	1	2	2		1.38
Type 2 & 3 (B)	10	4	4	4	1	1.22

A : B (lumping broods of 3 and 4), chi^2 = 0.63, df 3, p = 0.8-0.9

Rains only

	Numbers of young fledged					
	0	1	2	3	4	Mean
Type 1 (A)	11	3	5	5	3	1.48
Type 2	5	3	1	2	1	1.25
Type 3	2	1	2	2		1.57
Type 2 & 3 (B)	7	4	3	4	1	1.37

A : B (lumping broods of 3 & 4), chi^2 = 0.86, df 3, p = 0.8-0.9

Table 1I. Spearman rank correlation coefficients for analyses of different breeding parameters in relation to group size. Only groups occupying territories classified as type 1 on March 1 1972 are included.

Independent variable	Dependent variable	r^s
Group size, March 1 '72	Nesting attempts, 1972	0.71*
" " '73	" 1973	0.55
Mean gp. size, 1972 & '73	" 1972 & '73	0.73*
Group size, March 1 '72	Total young fledged, 1972	-0.23
" " '73	" 1973	0.40
Group size, March 1 '72	Young fledged/nest, 1972	-0.39
" " '73	" 1973	-0.11
Mean gp. size, 1972 & '73	Young fledged/nest, spring	-0.70*
" "	" rains	0.35
" "	" whole year	-0.12

The same eight groups (P,L,M,O,D,B,R,G) were used for all correlations.

* ; correlation significant at $p < 0.05$

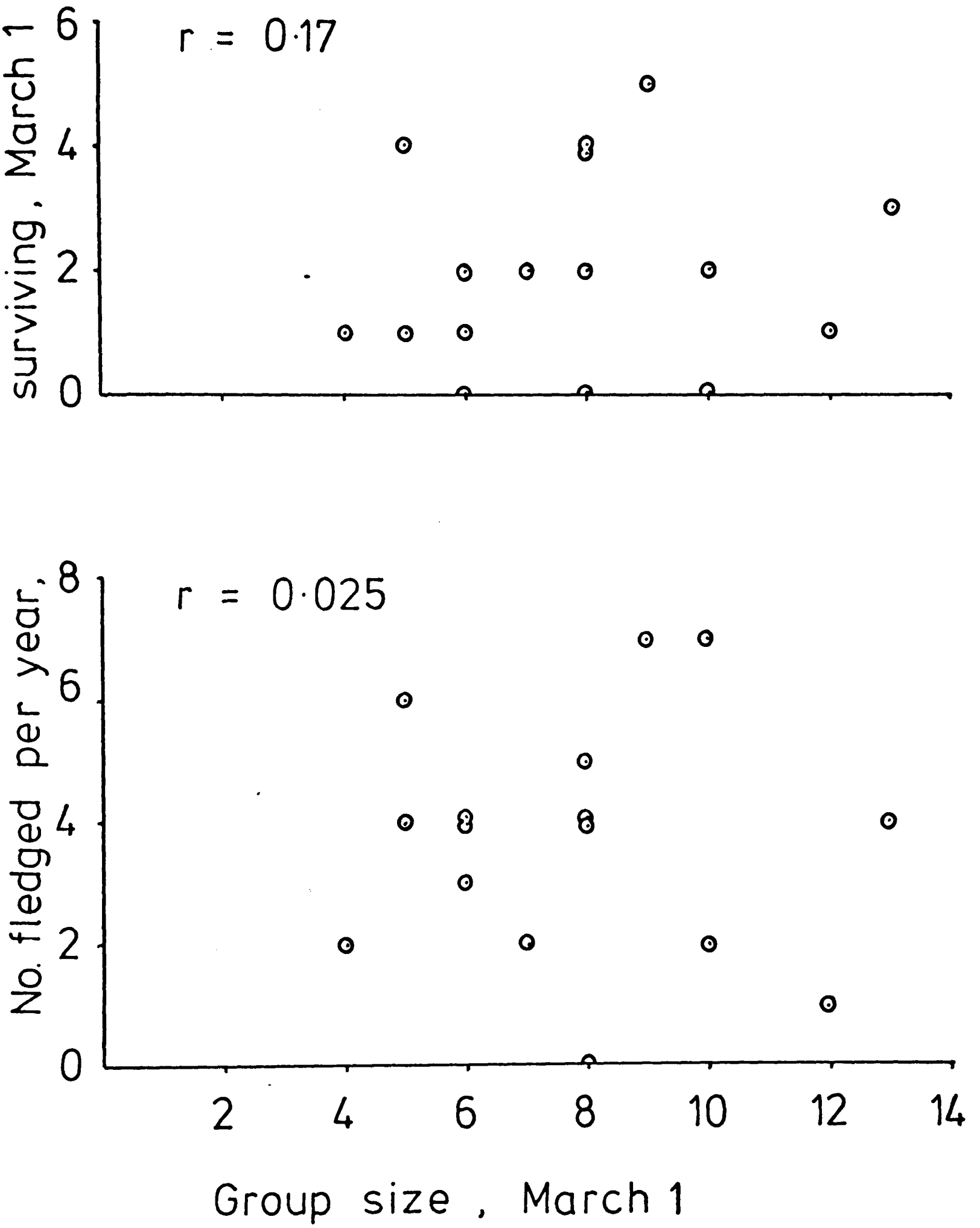


Figure 1i. Number of Jungle Babblers fledged (lower) and number surviving on March 1 following (upper), in relation to group size on March 1 preceding; type 1 territories only.

j) Concentration of reproductive potential within the population

In July 1972 the population of the entire study area was estimated as 108 Jungle Babblers in 19 groups (one or two small ephemeral groups may have been missed, but this should be the only possible error; for counts see Appendix 5). Out of these groups 17 pairs attempted to breed, 13 did so successfully at least once, but only 11 had young surviving the following March 1, on which date the eight pairs breeding in type 1 territories accounted for 19 out of the 26 young surviving (73%, $chi^2 = 5.77$, $p < 0.05$). In 1973 19 pairs attempted to breed out of 112 birds in 19 groups, but the eight groups in type 1 territories accounted for 13 out of the 18 young surviving the following March 1 (72%, $chi^2 = 4.4$, $p < 0.05$). Hence over the two years the eight pairs breeding in type 1 territories were responsible for 73% of the recruitment into a mean population of 110 birds ($chi^2 = 8.36$, $p < 0.01$).

Since breeding adults have a significantly higher rate of survival than non-breeders, and since groups occupying type 1 territories tend to be more persistent than other groups, breeders in type 1 territories probably beget an even higher proportion of the recruitment into the population during their lifetime than the above figures would suggest. In addition there was some evidence to suggest that new territories were most easily established by 2 or 3 sibling females in combination with 2 or 3 sibling males from another group (see Section 2f). Only the large groups in type 1 territories contained sufficient non-breeding birds of the same sex to fulfil this condition, and hence the establishment of new groups was possibly easier for birds reared in type 1 territories. The value, in terms of natural selection, of holding and breeding in a type 1 territory is therefore very great.

Assuming that the observed rate of replacement of breeding adults is representative, it is possible to calculate the chances of any bird reaching

its second year eventually becoming a breeder in an established group. One vacancy is available per group every six years, and since the recruitment of birds entering their second summer is 1.5 birds per group per year, this suggests that only one in nine birds can actually become breeders, i.e. about 11% . These figures apply to the ten study groups only. The chances of male birds reared in type 3 territories becoming breeders in their natal territory are higher because there are fewer siblings to compete, but the value of doing so is correspondingly lower.

Three marked birds became breeders in newly formed groups during the study, and since ~~12~~ 9/37 birds which left their groups in the same period were unmarked it seems likely that one unmarked bird also managed to become a breeder in this way. The overall rate of establishment is 0.2 birds per group per year; 13% of the annual recruitment. From these figures it seems unlikely that more than 25% of the birds which survive to their second summer ever succeed in attempting to breed, and less than half of these do so in the type 1 territories which produce the bulk of the recruitment into the population.

If, as appears likely, only birds reared in type 1 territories succeed in breeding in them, then since the breeders represent 10% of those reared in type 1 territories, and since these territories provide 70% of the recruitment into the population, then 7% of all birds recruited are the parents of 70% of the next generation. Under these conditions any adaptation which increases competitiveness is likely to be strongly selected.

k) Breeding strategies

Assuming that interchange between established groups is confined to females, there are two options open to males; either remaining with their native group until they can take over as breeder, or leaving to join one

or more females in establishing a new group. The decision on which option to take must be determined by a number of factors:

1) the competitive ability of the bird concerned relative to its male siblings.
2) the number and actions of its siblings.
3) the breeding success of its own and neighbouring groups, which determine the population pressure on the habitat.
4) seasonal changes in the suitability of the habitat for independent nesting attempts.

The first two factors alter the chances of inheriting the native territory. The second two affect the suitability of adjacent areas for establishing a new territory. All of the factors can be continuously monitored throughout the bird's life, and hence the decision to opt for trying to establish a new territory need not necessarily occur at the same age or season for each bird. This accords with the observed variation in the age of birds involved in establishing new groups, and the timing of their formation.

For a bird with a low social status, even the small chance of successful breeding presented by a marginal territory may be a better option than remaining in a group where it can never hope to become the breeder. For a bird of higher status, however, the breeding success attendant on succeeding to an established territory may outweigh the short term gain of forming a new territory, even though it might be able to obtain a better one than a bird of lower status.

The observed rate of change of breeding adults, one per group every six years, is very low compared to temperate passerines (Cody 1971), and may be exaggerated by the small sample size. The survival of the breeders, however, does little to affect the options of the non-breeders. As their

survival increases, the chances of a particular non-breeder succeeding to the territory become smaller owing to sibling competition. At the same time, however, the increase in potential fitness accruing through succession to a good quality territory increases since the number of potential offspring is likely to be proportional to the length of the breeding period. A general discussion of strategies for male non-breeders in a group territorial situation is given in Chapter 10.

For females two options are also open; either joining an established group, or forming a new one. Observed attempts at joining established groups were frustrated by the aggressive reactions of the resident breeding females, which chased off any females from outside the group if they attempted to mingle with the group while feeding or going to roost. Several females seen attempting to join established groups later took part in the formation of new ones.

No birds known to be in their second summer were seen trying to join established groups, and all those which successfully did so were at least two years old. Second summer birds took part in the formation of new groups on several occasions, however, and it therefore seems likely that only older, more experienced non-breeding females had any chance of joining established groups.

Conclusions

Compared to the temperate passerines on which most studies of population dynamics have so far been conducted, Jungle Babblers showed little seasonal or annual changes in population size. The proximate mechanism by which this stability was achieved was the emigration of birds in their second summer or older. The survival of post-juvenile birds remaining with their natal group was high, about 90% per annum, but this also applied to breeding birds, and hence the opportunity to attempt

breeding was so limited that only a quarter of the birds reaching maturity ever managed to do so.

Despite the rate of interchange observed between groups, the mean degree of relatedness of all group members to the breeding pair was probably about 0.3, higher than that between half-siblings. Under theories of kin selection (Hamilton 1964, Eberhard 1975) the selection pressure for altruistic behaviour is proportional to the degree of relatedness of the donor and the recipient, and hence babbler groups apparently present an excellent situation for the evolution of altruistic behaviour.

The quality of habitat occupied varied on a larger scale than is typical of most temperate situations, and this resulted in wide differences in the reproductive success of different groups[1]. Once the influence of territorial quality was taken into account there was no significant correlation between group size and breeding success, and there was some indication that larger size may have been correlated with lower fledging success in the spring. This appears to contradict the prediction of kin selection than non-breeding members of the group should make a positive contribution to the reproduction of the closely related breeding pair.

Dispersal is more important to females, which probably do not breed in their native groups, than it is to males. Both sexes have the option of joining in the estalishment of a new group, but remaining in the native group may constitute a more attractive strategy for males which can eventually inherit the parental breeding territory. The differences in reproductive success between different territory types must influence the strategies of males, and may account in part for differences in the size of groups.

1 Dawson (1972) found similar large differences in breeding success between pairs of House Sparrows Passer domesticus in relation to nesting areas.

Summary of population dynamics

1) The number of Jungle Babblers in established groups within the study area was relatively stable.

2) Stability was maintained by a balance between recruitment and emigration.

3) Differential emigration of females probably led to an unbalanced adult sex ratio.

4) The mean degree of relatedness of birds in the same group was about 0.3.

5) Group size, reproductive success, and emigration varied in relation to the type of territory occupied.

6) Increased reproductive success in good quality territories was more likely to be a cause of larger groups than a result.

7) The great selective value of holding a good quality territory was a major factor limiting the number and quality of birds emigrating to establish new groups.

Chapter 2. Territory

Chapter 2. Territory

Introduction

Group territoriality can be defined as the defence of a common territory by more than two birds. Most species which live in stable groups throughout the year exhibit this kind of territorial behaviour (see references to Table A). To examine the factors leading to group territoriality in the Jungle Babbler observations were made to determine the way in which territories were utilised, seasonal changes in the intensity of territorial defence, the manner in which new territories become established, and the relationship of group size to the area of the group territory.

Nearly all groups of Jungle Babblers observed in the study showed intolerance towards other groups, resulting in mutually reduced access to certain areas. Broad overlap was found between the areas in which different groups were encountered, however, and because of this the idea of rigidly bounded territories was not employed. The whole area within which a group was recorded was defined as its home range, following Burt (1940), while territoriality was considered to be the mechanism by which the home ranges were spaced out. The term territory is used to describe that area over which the group was observed to show territorial behaviour; largely but not wholly coincident with the home range.

Methods

To analyse the pattern of range utilisation by Jungle Babblers a grid of 40m squares was superimposed on each daily range map, and the position of each group recorded by numbered co-ordinates. Where groups were followed for more than 30 minutes the position of the group at the end of each 30 minute period was recorded. Squares of 40m were selected because Jungle Babbler groups usually spread over 20-30m while feeding, and hence the

squares approximate to the maximum area over which a group was likely to be spread. The time scale of 30 minutes was chosen because then feeding groups nearly always registered a change of location during that period.

a) Territorial defence .

Territorial defence was maintained by vocal and feather posture displays, and occasionally by fighting, and all post-juvenile members of the group regularly took part in these. The threat posture used by Jungle Babblers in inter-group confrontations has been described by Andrews and Naik (1970). At high intensity the contour feathers of the entire body are raised, the wings and tail dropped, and the head held fairly low with the beak open. The wings are vigorously shivered, and a continuous harsh cackling call is delivered. Flight in this condition of feather erection is so laboured that two groups taking part in a confrontation soon end up facing one another on the ground. Members of the same group bunch together while confronting so that the entire group concentrates within 2-3m, compared to the usual spread of 20-30m while feeding.

The reaction of a group to the presence of another nearby depended on a number of factors; the time of year, time of day, locality of the meeting, and the degree of familiarity between the two groups. Reactions varied from apparently non-existent, to fighting in which all members of both groups took part. A few groups which existed for short periods of time made no attempt to defend territories. A territorial group encountering one of these would fly towards them and the non-territorial group would move off at once. In these instances no vocalisations or feather posture displays occurred.

High intensity confrontations, defined as those in which all adult members of both groups took part, adopting full feather-fluffing postures, were seen in the study area on 371 occasions, but only 18 of these were

violent confrontations, involving fighting. Postures and vocalisations used in inter-group displays were never seen in intra-group situations, or when individual intruders were being driven off. A very similar display was used to mob predators, although in this situation it was never expressed at the highest intensity.

The relative contribution of different group members to territorial defence was difficult to assess. Adult group members were involved more frequently than younger birds, and were usually first to arrive when a confrontation was developing. Tests were carried out in February 1972 to observe responses to recorded calls. Contact and confrontation calls were used (see Chapter 3 for a description of Jungle Babbler vocalisations) and elicited similar responses. The first bird to arrive in ten out of 11 tests was a member of the breeding pair (six times the male, four times the female). In all tests the first three birds to arrive were adults, and the last were first year birds. These results suggest that the older members of the group play a more active part in territorial defence than the younger ones.

b) Structure of the home range

Figure 2a shows the approximate home ranges of the ten study groups, constructed by joining the furthest point at which each was recorded. The amount of overlap is considerable, and would be greater if other adjacent groups were included. Not all of the areas enclosed were actually used, and it seems likely that all areas used regularly were visited by more than one group during the course of the study.

Analysis of the distribution of records within each group's home range suggests that two entities are present; an inner, heavily used zone, and an outer zone which is much less frequently visited. The distribution

Figure 2a. Home ranges of ten groups of Jungle Babblers in the Ridge study area.

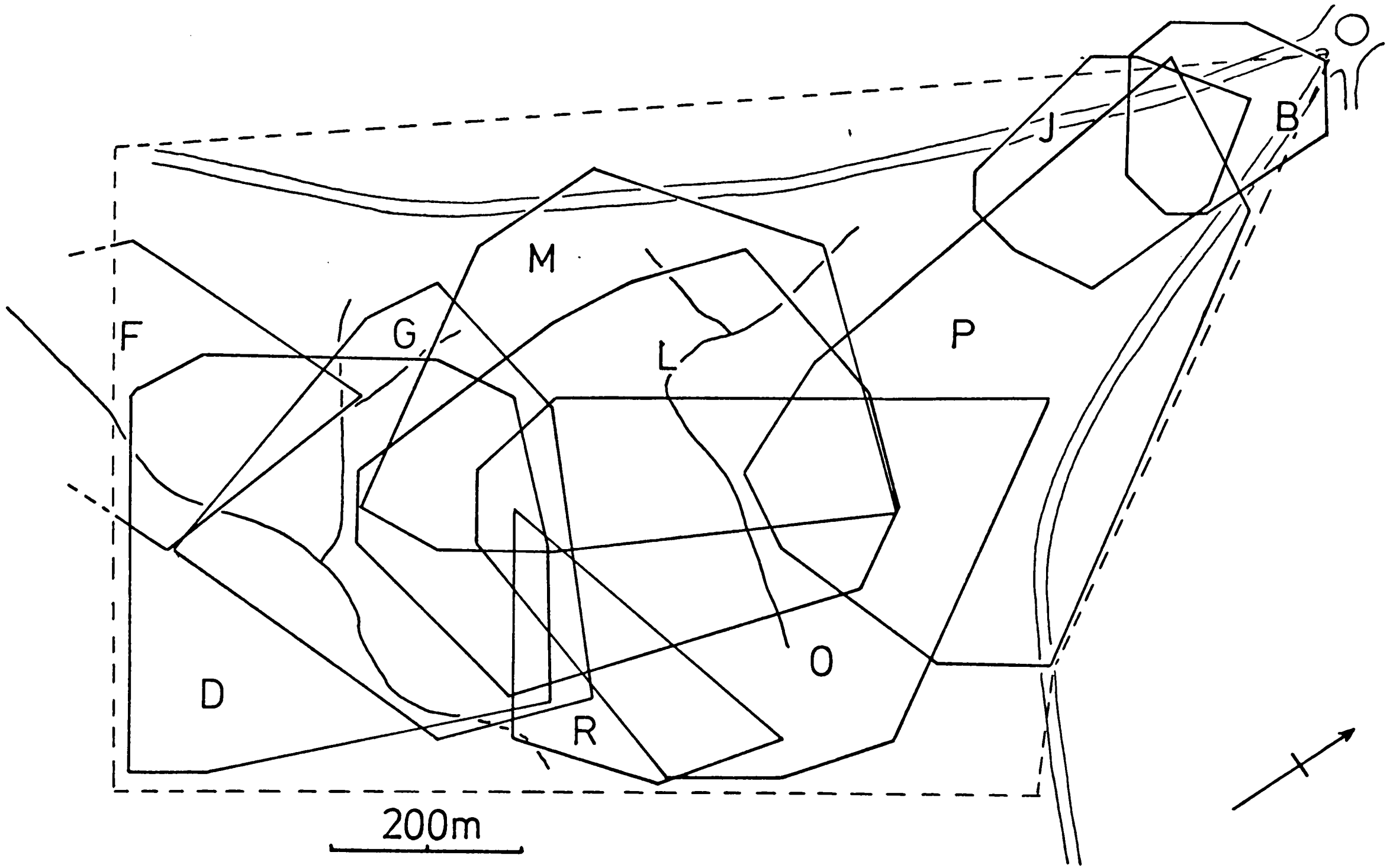


Figure 2b. Contour map showing the intensity of utilisation by L group of different parts of the home range. Contour interval; five records.



Figure 2c. Contour map showing the intensity of utilisation by M group of different parts of their home range. Contour interval; five records.

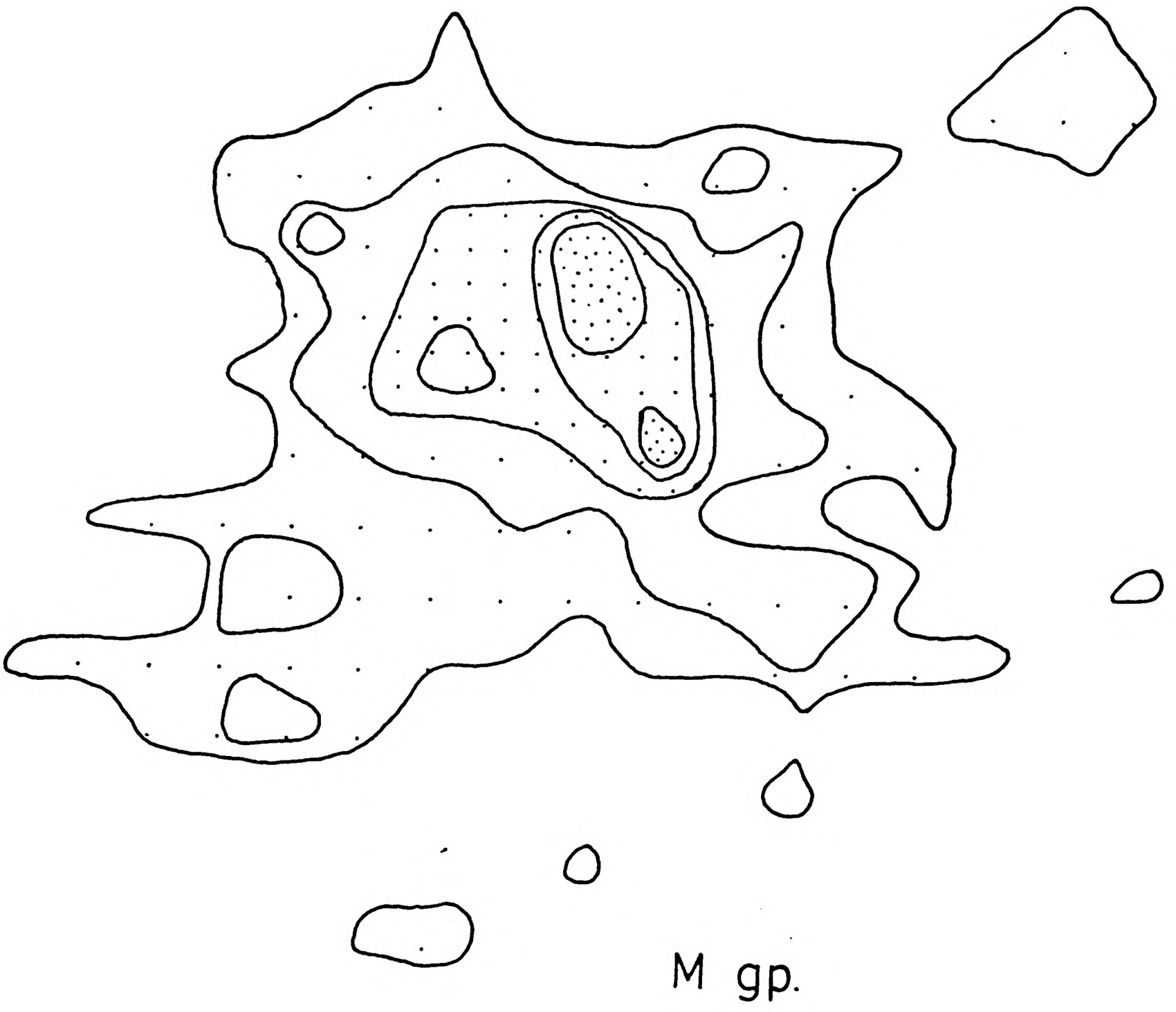


Figure 2d. Ridge study area showing positions of core areas (shaded).

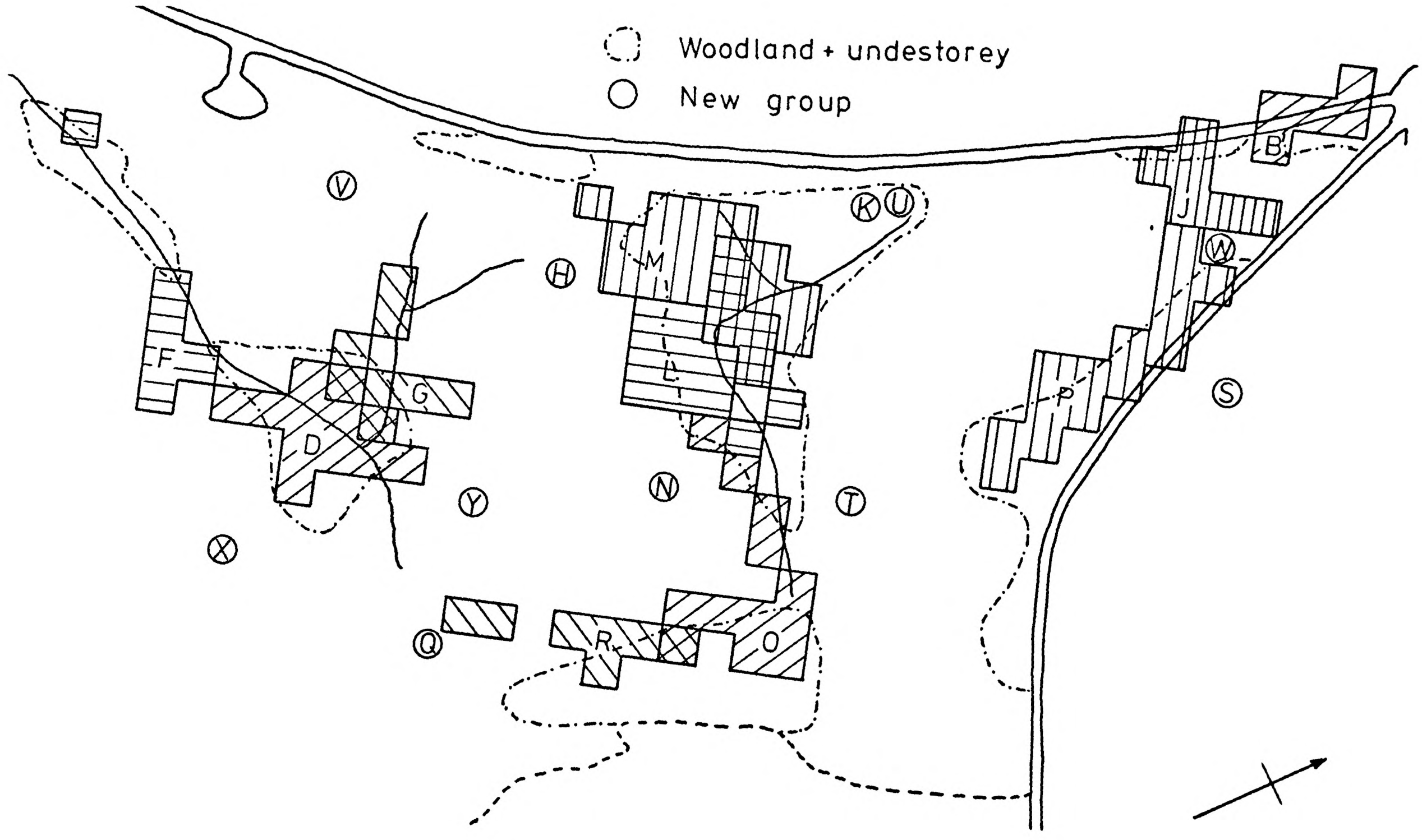
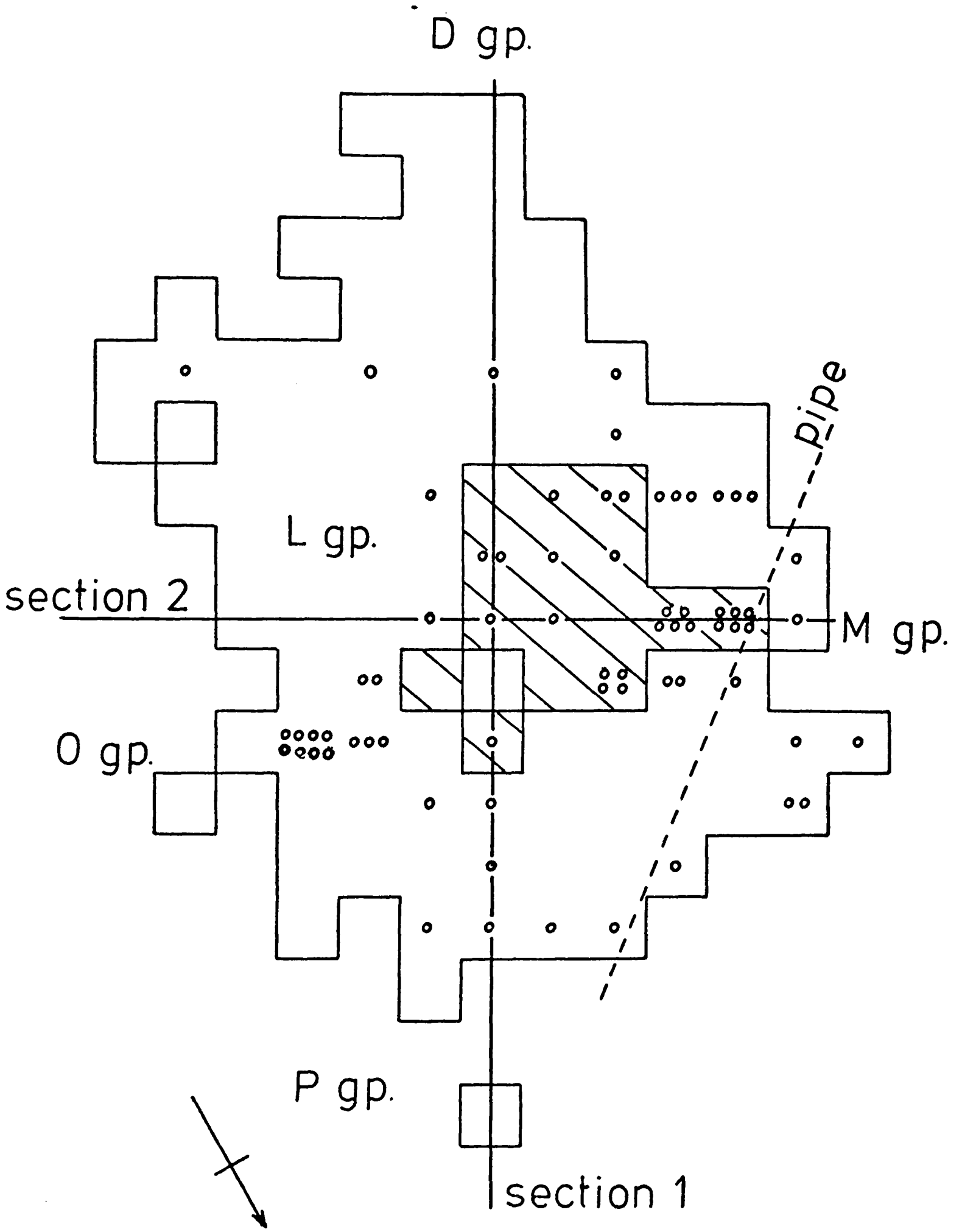


Figure 2e. Map of L group home range showing the position of the core area and of interactions with other groups of Jungle Babblers. Circles mark ~~numbers of~~ interactions in each grid square.



of records for L and M groups over the whole study is shown in Figures 2b and 2c, and illustrates this point. The two zones will be referred to as the core and peripheral areas, following the terminology used to describe similar entities in the home ranges of certain mammals (Kaufmann 1962, DeVore & Hall 1965). No rigid distinction could be made between the two areas, and for the present study the core area was arbitrarily defined as those squares of the 40m grid which enclosed 50% of all records for a particular group.

The positions of the core areas of the ten study groups is shown in Figure 2d which demonstrates that there is relatively little overlap between core areas compared with the wide overlap of home ranges. For the three groups observed most intensively the core areas comprised a mean of 17% of the whole range (L 15%, M 20%, P 15%).

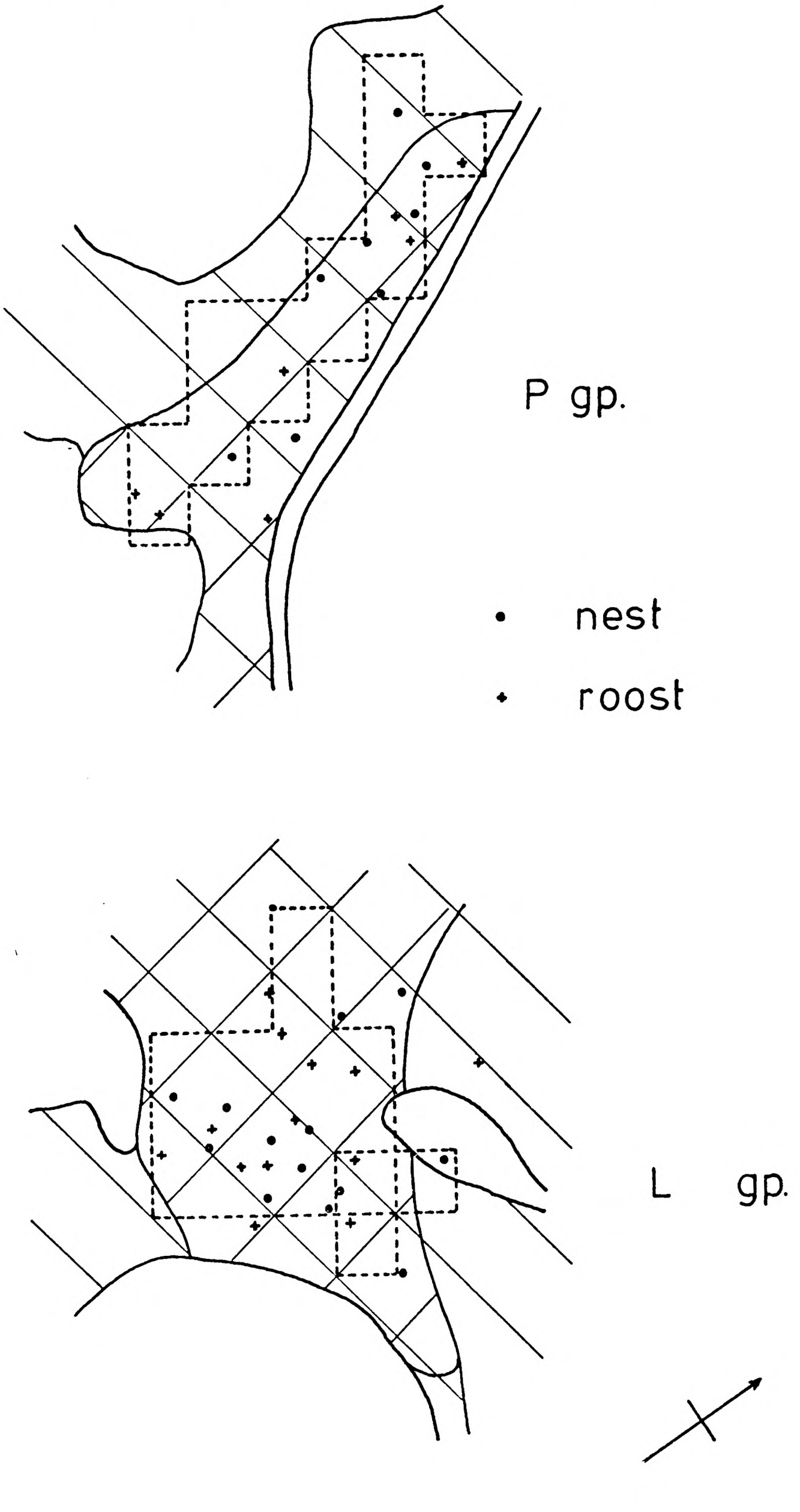
Territorial behaviour was most frequent around the core area, rather than at the limits of the home range. Figure 2e shows the position of high intensity confrontations involving L group, in relation to the position of the group's core area. Low intensity confrontations between L and M groups were very frequent, often consisting of brief vocal displays, and most were localised along the pipeline (dotted line in Fig. 2e). Fighting was never observed between these two groups. In contrast L group encountered D and P groups relatively seldom, but when it did so fights occurred on several occasions, suggesting that fights are more likely to happen when the groups encountering one another do so only infrequently.

Most nests and roosts were located within the group's core area, which usually coincided with a patch of tall closed-canopy woodland with dense understorey. Table 2A shows the relative proportion of nests and roosts situated inside core areas. The distribution of nests, roosts, and core areas, in relation to the vegetation types within their home ranges, is

Table 2A. Proportions of Jungle Babbler nests and roosts located inside core areas, in relation to the total area covered by home ranges.

	Area (ha.)	Nests	Roosts
Core area	18.5	39	34
Peripheral area	50.2	16	9
chi^2 =		52	56
p =		<0.001	<0.001

Figure 2f. Maps of P and L group core areas showing the position of nests and roosts. Diagonally hatched area indicates closed-canopy woodland, double hatching signifies presence of understorey.



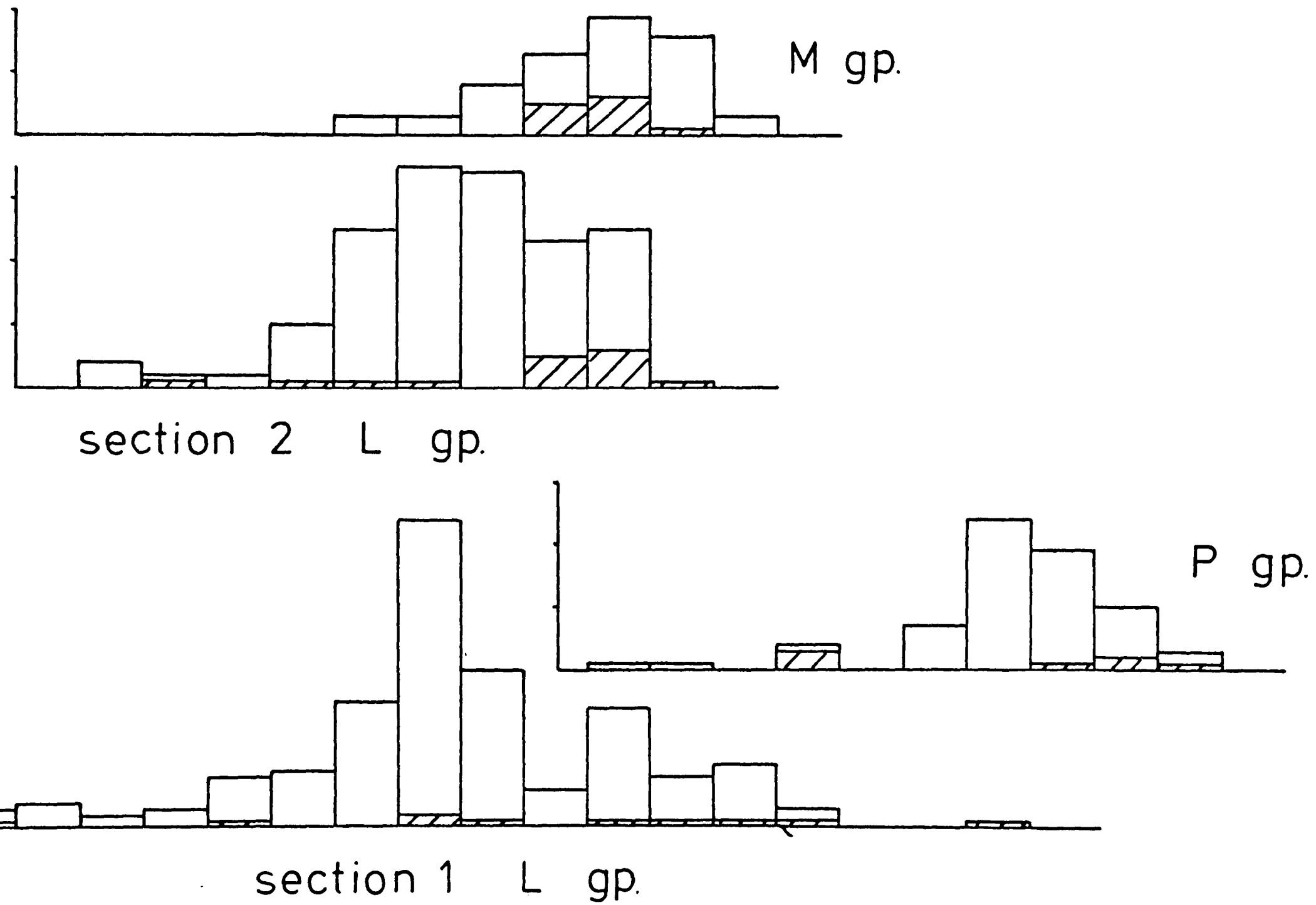


Figure 2g. Numbers of records in each 40m square along the two sections across L group range marked on figure 2e. Shaded portions indicate the number of high-intensity confrontations.

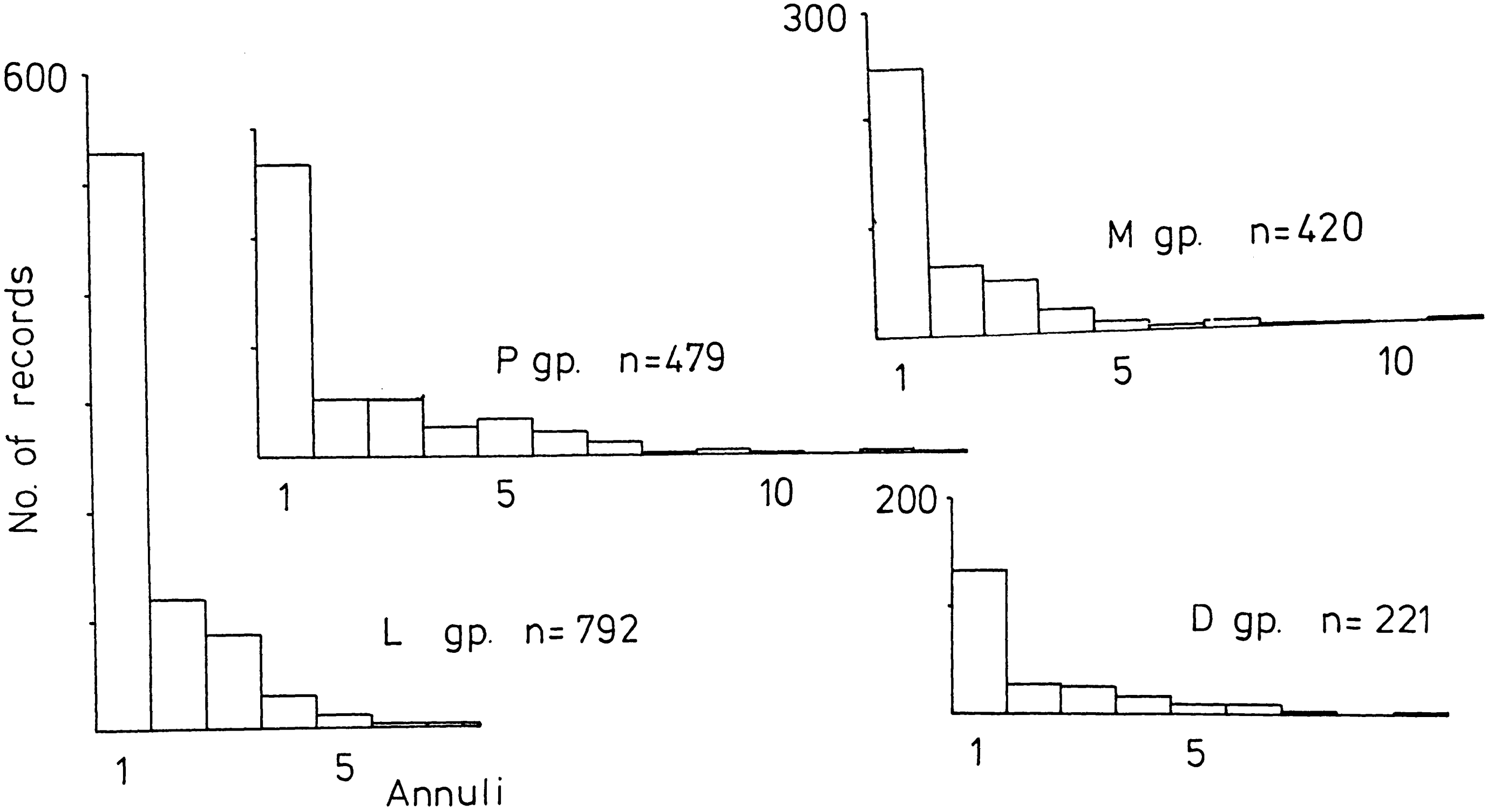


Figure 2h. Frequency distribution of sightings of four groups of Jungle Babblers in concentric annuli of equal area centred on their centres of distribution.

shown for L and P groups in Figure 2f. Because of the patchy distribution of vegetation types in the study area, the position of core areas was often asymmetrical in relation to the rest of the home range, and in several cases the core areas of adjacent groups were contiguous (four cases are illustrated in Figure 2d). Boundaries between contiguous core areas were the site of very frequent displays, as in the case of M and L groups, but where home ranges bordered open scrub confrontations were very infrequent, and boundaries consequently difficult to define.

The sections shown in Figure 2g, taken through L, M, and P group ranges, illustrate the difference between the frequently disputed boundary which separates L and M groups (sect. 2), and the poorly defined contact between L and P groups (sect. 1). Despite the wide area of overlap, there is a rather steep decline in the number of records of L and M groups across their mutual boundary. The area in which confrontations were most numerous separated the nesting/roosting areas of the two groups. When L group was feeding elsewhere this line was regularly transgressed by M group, which apparently managed to detect the arrival of L group in time to shift back to the area of confrontation before they arrived.

Figure 2h plots the distribution of records for four groups in concentric annuli of equal area, to show the way in which use of the home range varied with distance from the core area. The centre used for plotting the annuli was the geometric centre calculated from all records for each group, and this fell inside the core area in all cases. The same scale was used for each group, and the innermost annulus in all cases enclosed the entire core area. The area of each annulus was 4.5 hectares. The observed distributions suggest that no attempt was made to systematically exploit the home range, but that the frequency with which a particular group was encountered was inversely correlated with the distance from their core area. A similar pattern

Figure 2i. Tracks of L group followed between 0800-1200 hrs during January 1972. The dotted line encloses the squares in which 50% of all sightings of the group were made.

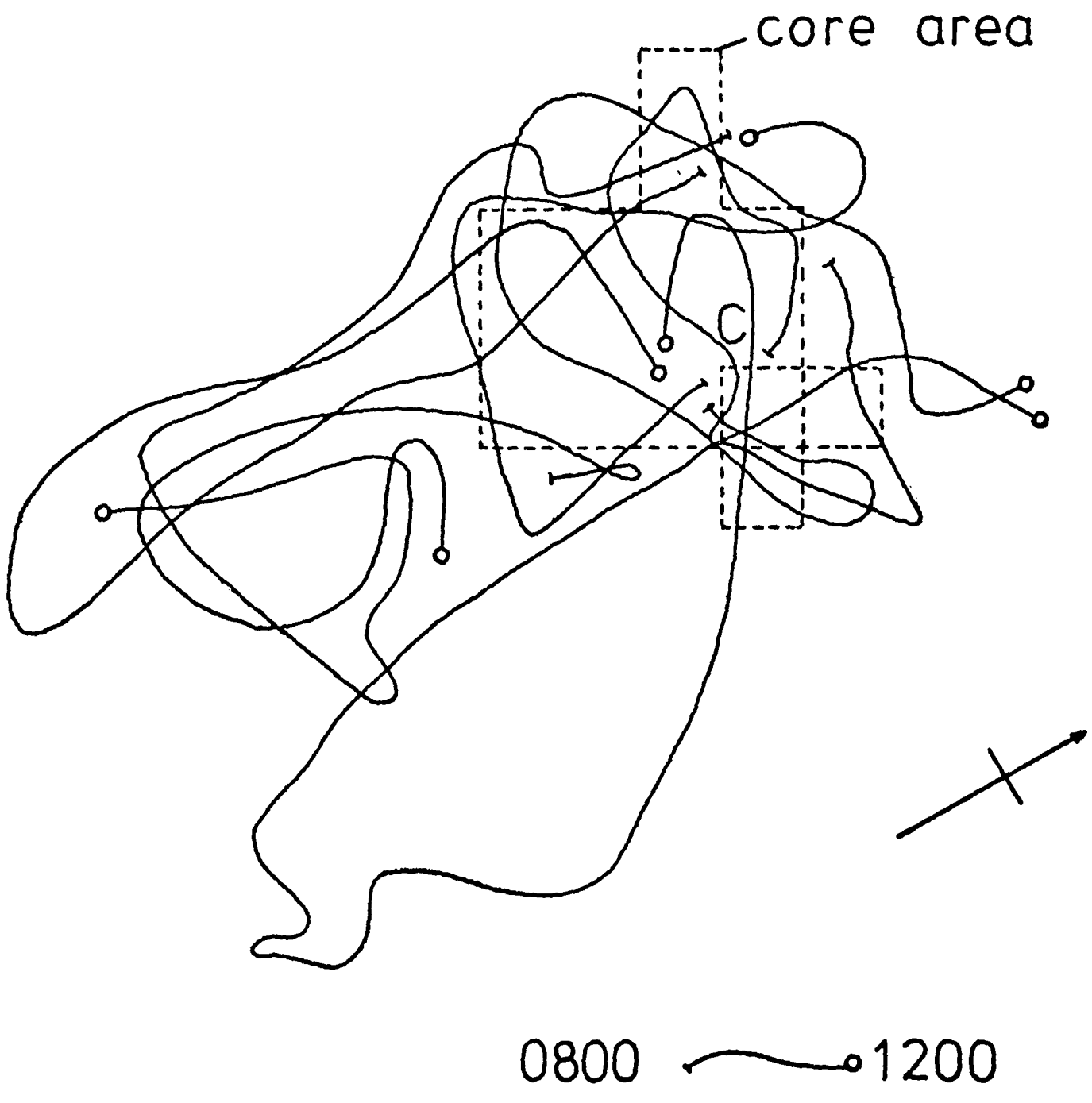
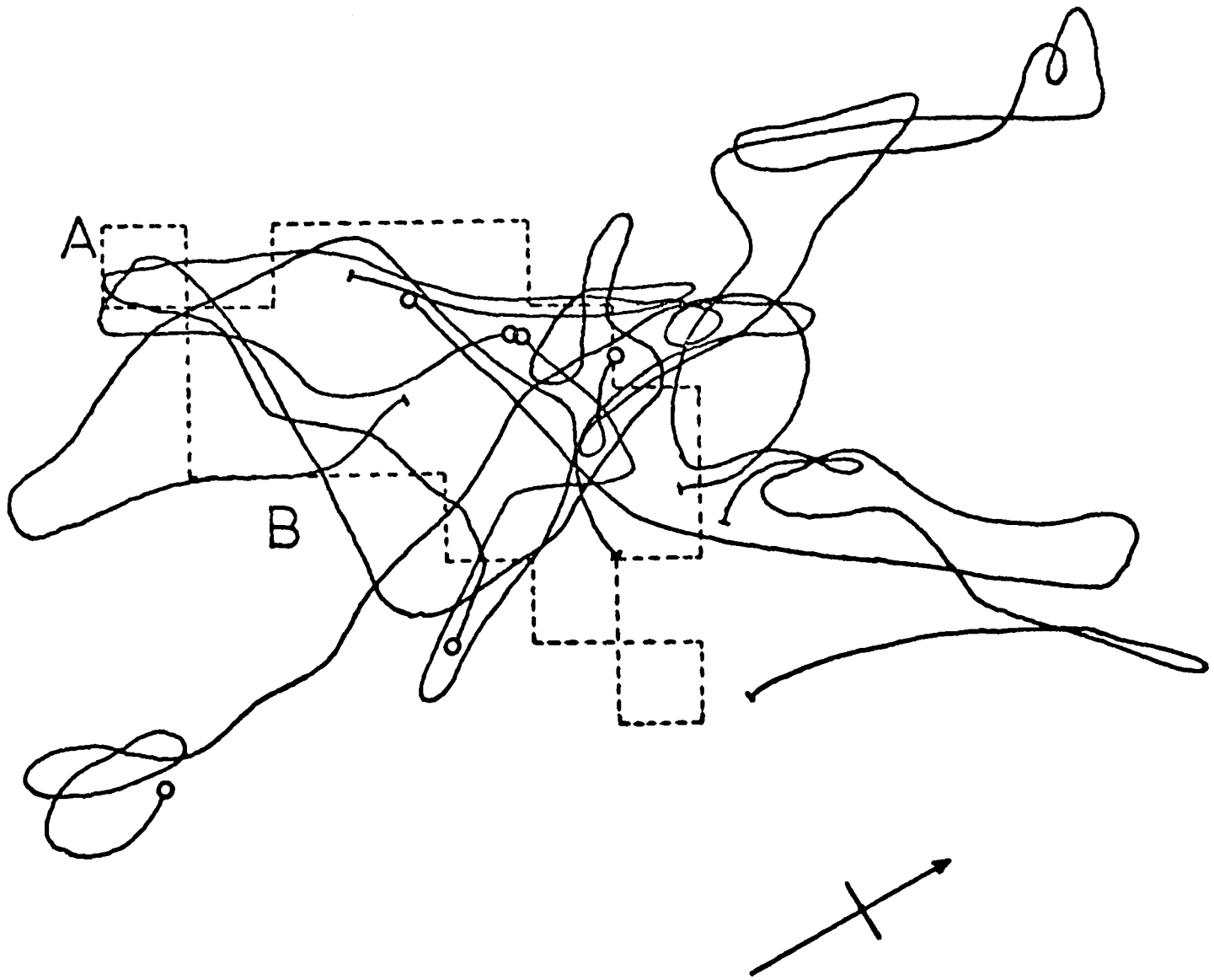


Figure 2j. Tracks of M group followed between 0800-1200 hrs during January 1972. The dotted line encloses the core area.



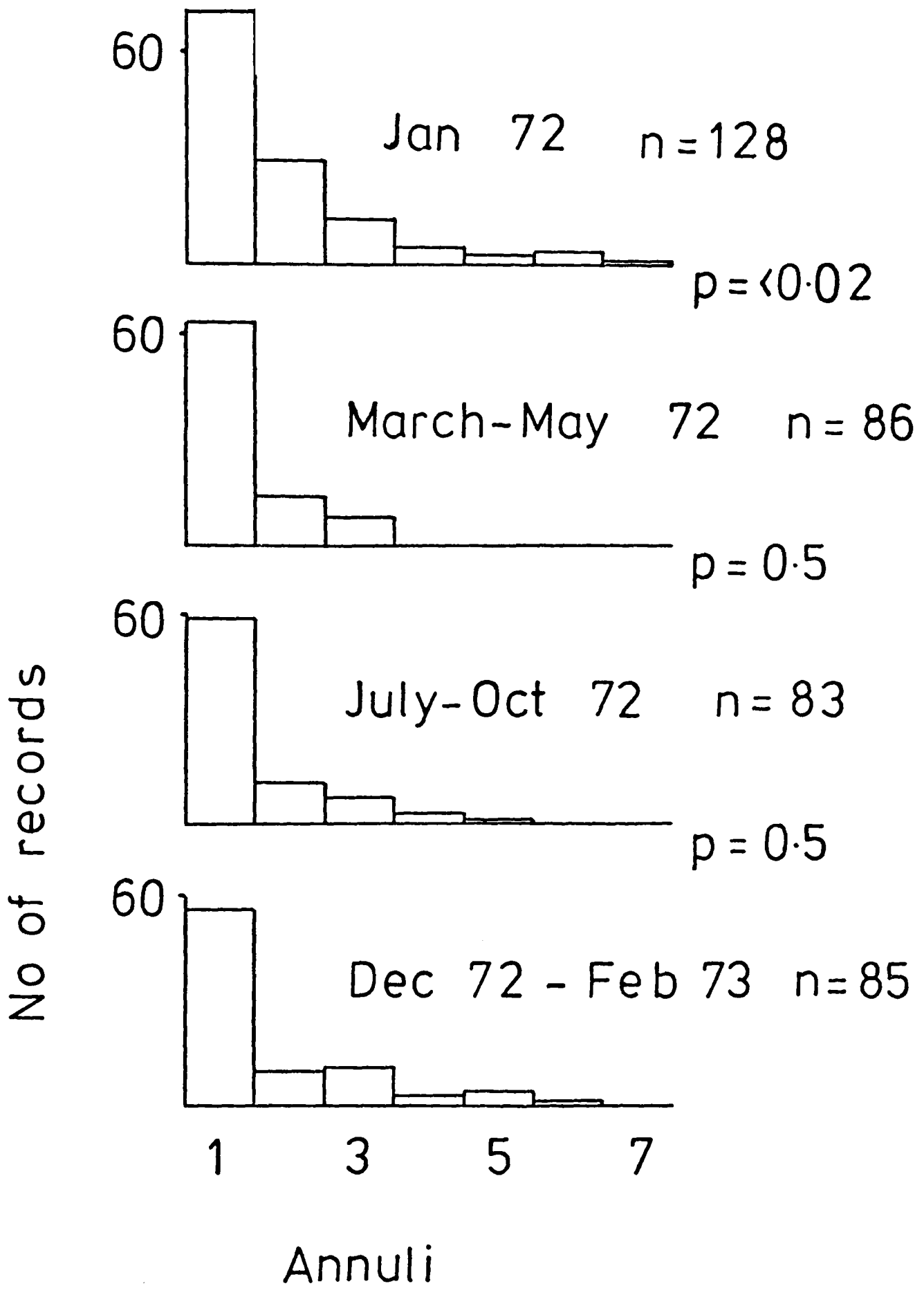
of decreasing use of the home range with increased distance from the centre was found by Willis (1967) for Bicoloured Antbirds Gymnopithys bicolor among which adjacent pairs also maintained broad overlap in their home ranges.

Analysis of daily movement maps suggests that foraging in winter consisted of a series of sorties from the core area into peripheral areas, returning to the core area within two or three hours, and making two or three such sorties per day. Figures 2i and 2j show the tracks of L and M groups recorded between 0800-1200 hrs during January 1972, illustrating this pattern of periodic sorties. This type of movement, terminating at a random distance from the core area, can be predicted to produce the type of distributions found in Figure 2h (Pielou 1969).

The daily movements of seven groups of Jungle Babblers on the campus of M.S. University of Baroda in January was described by Andrews and Naik (1965). The pattern of home ranges in this instance appeared slightly different from that observed at Delhi. Six of the groups spent part of their time foraging in a common foraging area, and the rest of their time in discrete territories, and the seventh remained wholly within its territory. A substantial part of their feeding time was spent by the six groups within the common foraging area (Naik, pers. comm.), but groups returned to their territories several times each day, giving a similar pattern of recurrent sorties to that observed at Delhi.

The pattern of range use observed for Jungle Babblers at Delhi resembles that described for Baboons Papio cynocephalus (DeVore & Hall 1965, Rowell 1972), Rhesus Macaques Macaca mulatta (Southwick, Beg, & Siddiqui 1965), and other species of semi-terrestrial primates (see review in Jolly 1972). This type of behaviour, in which groups have exclusive use of a core area, and forage over a larger home range, was termed 'radial pack' by Hamilton and Watt (1970). They suggested that such an organisation occurs in situations

Figure 2k. Frequency distribution of L group in annuli of equal area around its centre of distribution.



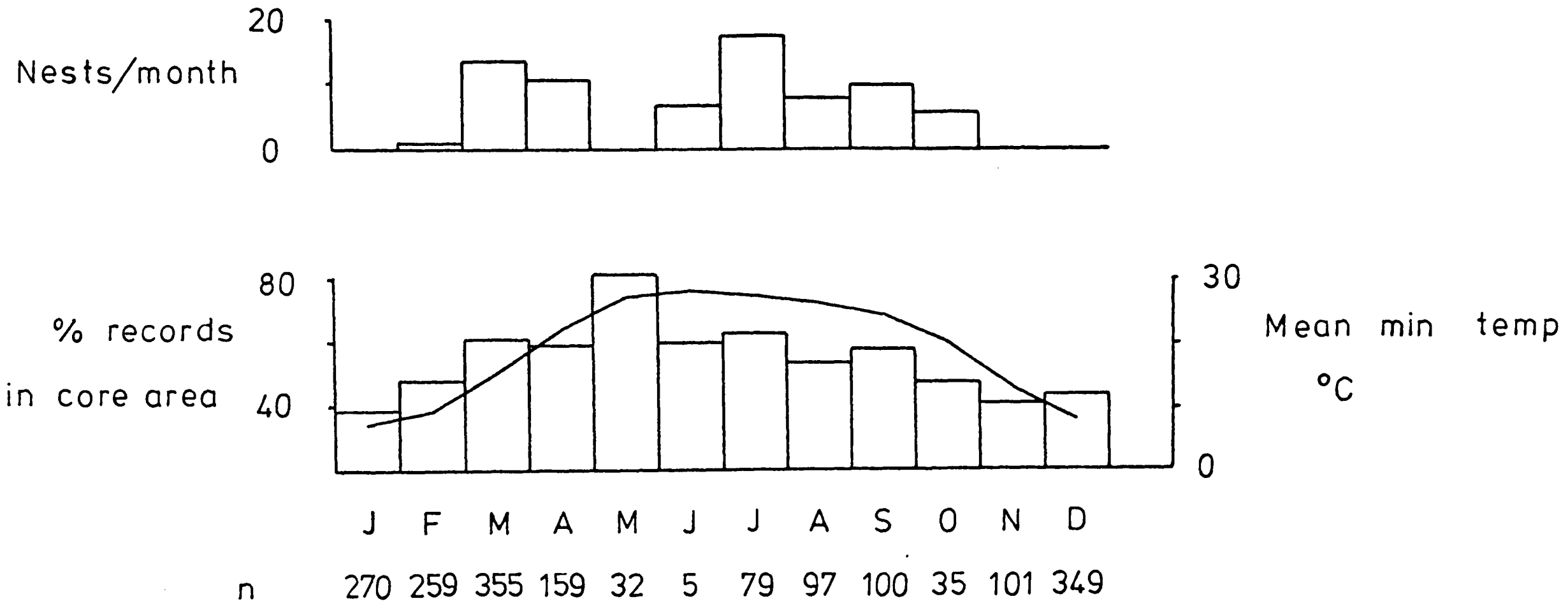


Figure 21. Monthly changes in the percentage of sightings of L, M, and P groups in their respective core areas. The solid line shows mean minimum temperature, and the upper histogram, the number of nests initiated in each month.

where, as group size increases, the area necessary for foraging becomes too large for adequate boundary defence without fragmentation of the group.

The mean home range diameter of about 500m for groups of Jungle Babblers at Delhi was sufficient, given the nature of the habitat, to make it impossible for groups to detect intruders near the periphery of their home range. Observed rates of movement were such that it is unlikely that groups visited all parts of their home range daily (see Figures 2i & 2j). A similar explanation was given by Brown (1963a) to account for overlapping territories in Steller's Jay Cyanocitta stelleri. These observations appear to support the conclusions of Hamilton and Watt regarding the origin of radial pack organisation.

2c) Seasonal changes in the use of the home range

Some seasonal changes in the way in which home ranges were used were detected. Figure 2k shows the number of records of L group falling in each annulus in four consecutive periods for which similar numbers of observations were made. A comparison of the winter records (January 1972, December 1972-February 1973 combined) with summer records (March-October 1972) demonstrates a tendency for the group to forage further afield in winter than in summer ($chi^2 = 11.98$, 5 df, $p < 0.05$). The same pattern is apparent in Figure 2l which shows the proportion of records for L, P and M groups combined which were made in their core areas in each month. This is compared with the distribution of dates of first eggs, and of mean monthly minimum temperatures. The proportion of records falling within the core areas (calculated on the basis of all records for the groups concerned) correlates closely with temperatures ($r^s = 0.78$, $p < 0.01$), but less well with the number of first eggs laid per month ($r^s = 0.61$, $p < 0.05$).

The observed correlation between time spent in the core area, and monthly temperature is probably related to the amount of time spent feeding. During the winter, when temperatures are low, groups spent most of the day feeding, and sorties outside the core area tended to last longer and carry the group further than in-summer. The proportion of time spent feeding in summer and winter is compared in Table 2B which is compiled from observations of the activities of all flock members recorded every five minutes.

Table 2B. Proportion of time devoted to feeding. Figures derived from records of the activities of all visible group members made at five minute intervals. Only observations before 1100 hours in summer, and before 1300 hours in winter, are included.

	August-September 1971		December 1971-January 1972
	Groups without fledglings	Groups with fledglings	All groups
N	528	960	2108
Proportion feeding	39%	63%	92%

Group home ranges overlapped extensively outside the breeding season, and the occurrence and intensity of interactions between groups meeting in areas of overlap was unpredictable. In some cases groups showed no sign of a change in behaviour on encountering one another, while in other instances high intensity confrontations, followed by retreat towards their respective core-areas, were observed. During the breeding season areas of overlap were smaller, and encounters between neighbours consequently less frequent.

Figures 2m and 2n show the home ranges of L and M groups during the winter of 1971-72, and the breeding season of 1972. All four diagrams show

Figure 2m. L and M group ranges in winter 1971-'72. Solid line encloses all squares used, diagonal hatching encloses 50% of records, dotted area covers overlap of groups, double diagonal hatching covers overlap of 50% areas.

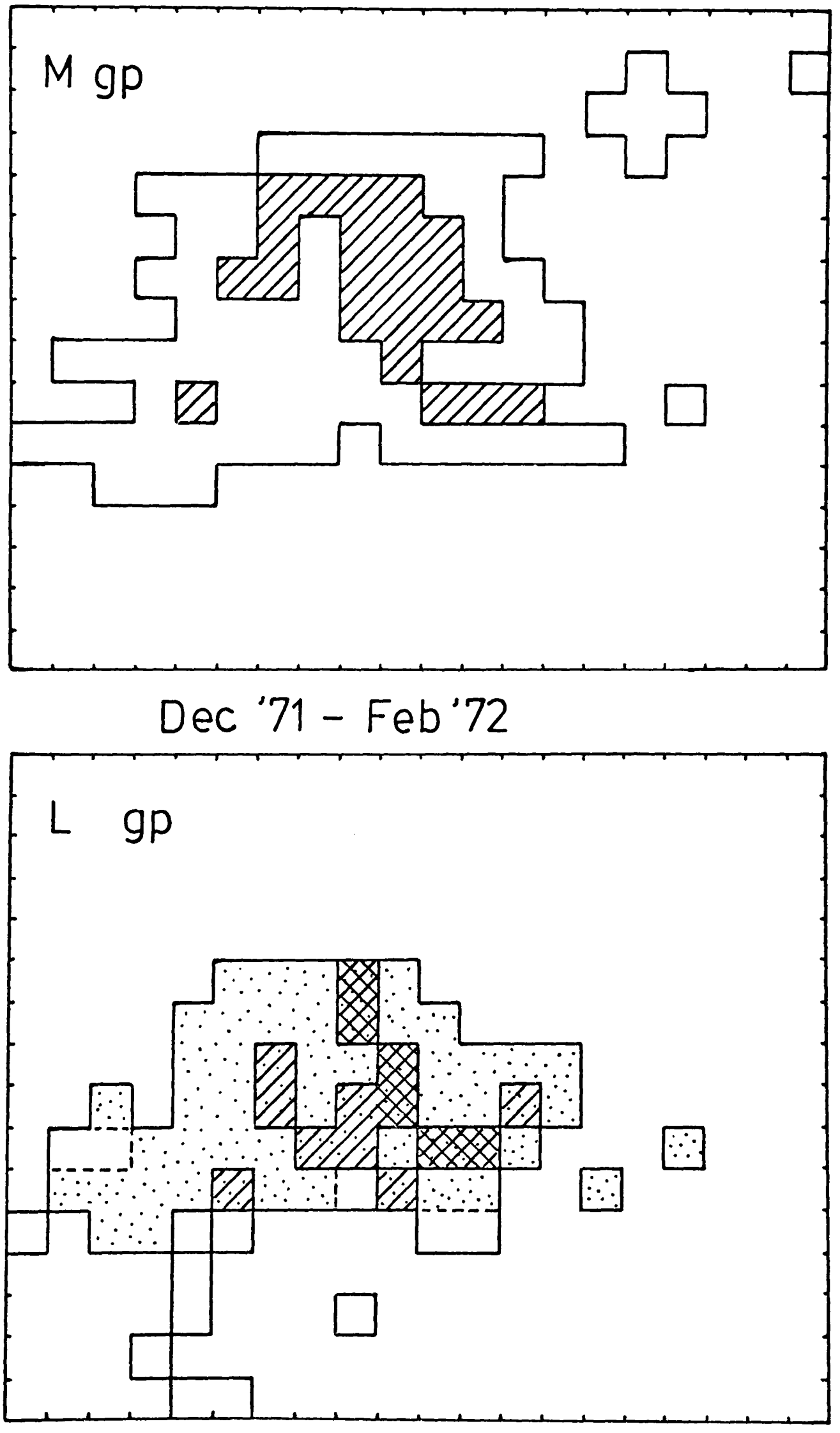
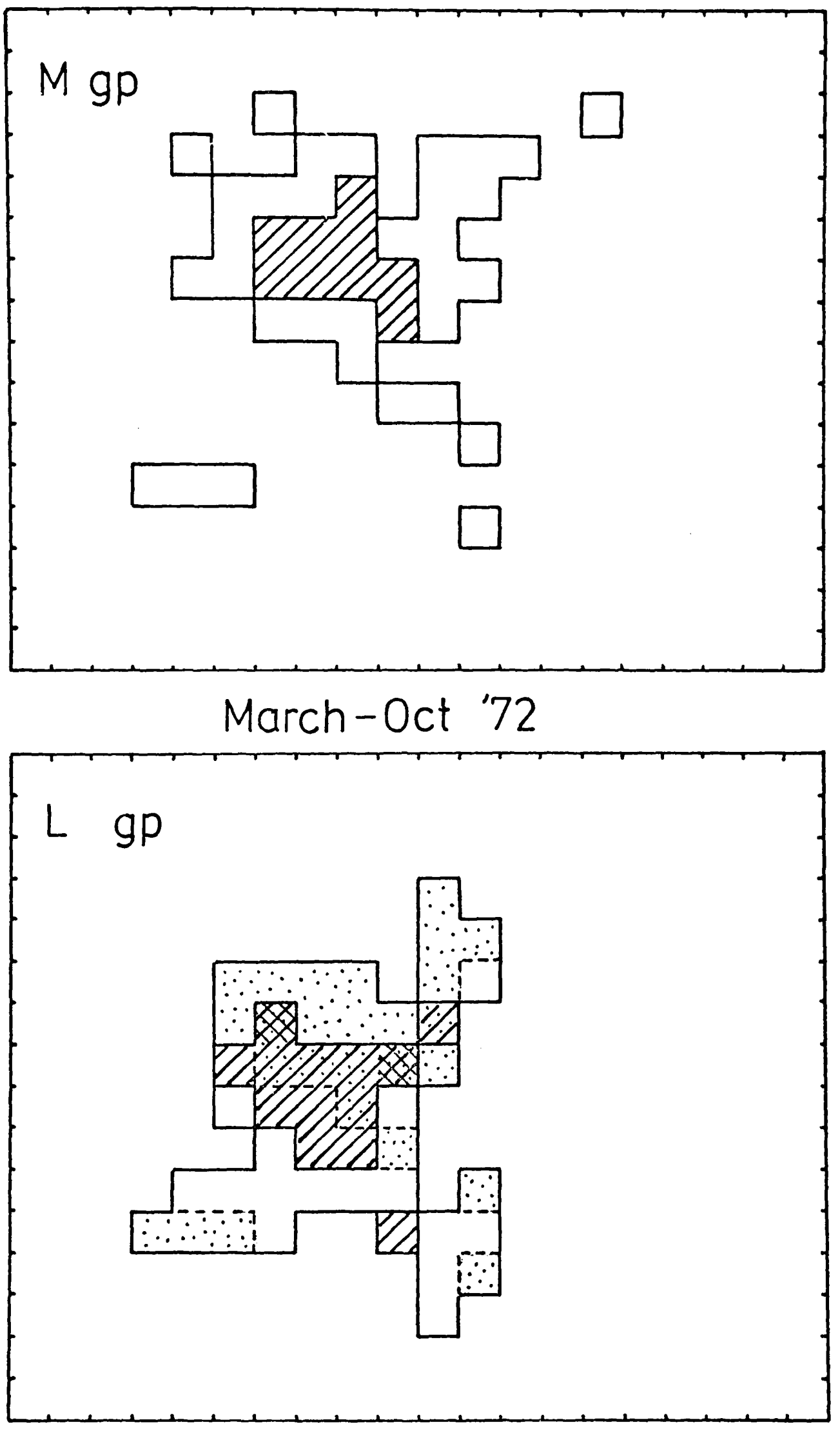


Figure 2n. L and M group ranges in the summer of 1972.
Conventions as for figure 2m.



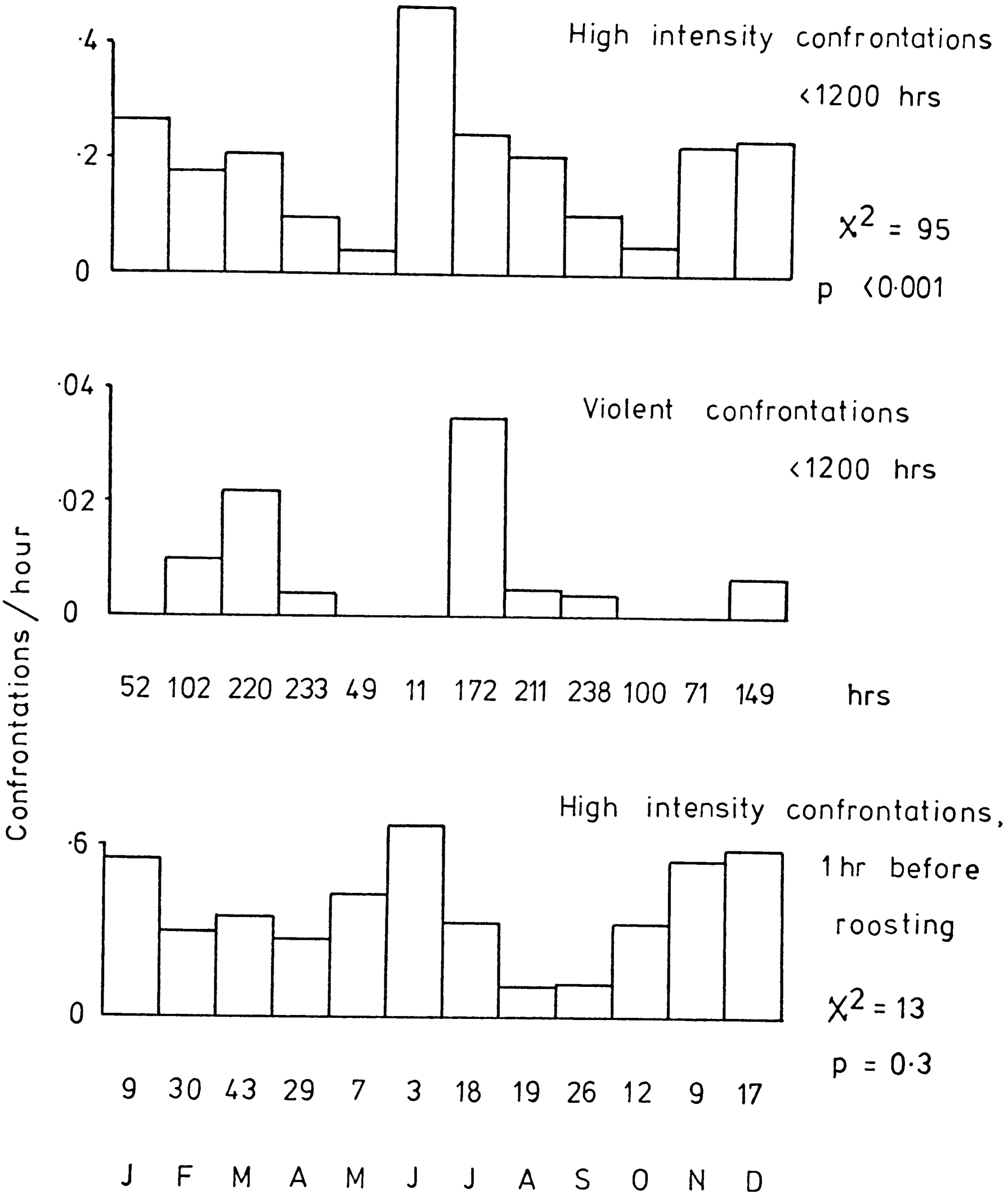


Figure 2o. Seasonal changes in the frequency of confrontations between groups of Jungle Babblers; vertical scale, confrontations per hour.

the same section of the study area, and demonstrate not only that home ranges are larger in winter, but that the areas enclosing 50% of the observations for each group (diagonally hatched) overlap considerably more in winter (six squares, cross-hatched) than during the breeding season (two squares). These two groups were exceptional in the degree of overlap of their core-areas, as shown in Figure 2d. In other cases, where core areas were relatively isolated (B, F, and P groups), they were never trespassed by other groups during the breeding season.

2d) Frequency of inter-group confrontation

Figure 2o shows the distribution throughout the year of high intensity confrontations observed before 1200 hours, and in the last hour before roosting, and also of violent confrontations observed before 1200 hours. Two periods of apparently low territorial activity are discernable; one in April-May, and another, more marked, in August-October. These two periods coincide with the latter halves of the two breeding peaks. Violent confrontations showed marked peaks in March and July, the two months in which the largest number of nests were begun.

Large Grey Babblers showed a similar seasonal pattern of territorial behaviour to that observed for Jungle Babblers. This species has a loud, far-carrying, territorial call, often given by several members of the group simultaneously, and this call was recorded whenever it was heard in the course of the study. The call was apparently given spontaneously sometimes, but the call of one group was often followed by calls from neighbouring groups. No visual contact was necessary, although the call was invariably given during inter-group confrontations with other groups of large Grey Babblers, and also following interactions with groups of Jungle Babblers. Because this call was given independently of inter-groups contacts, its

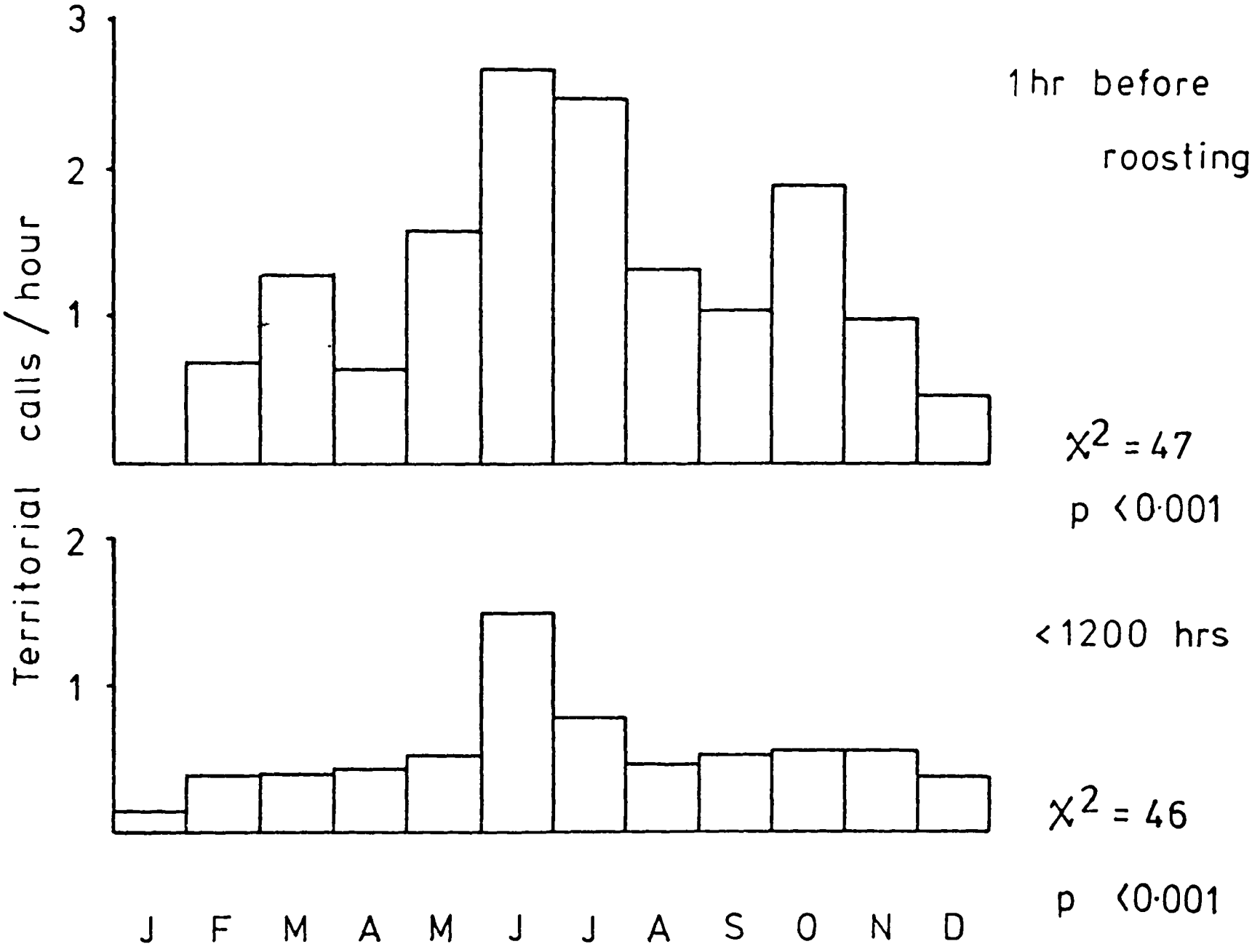


Figure 2p. Seasonal variation in the frequency of territorial calling by Large Grey Babblers. Vertical scale; calls per hour.

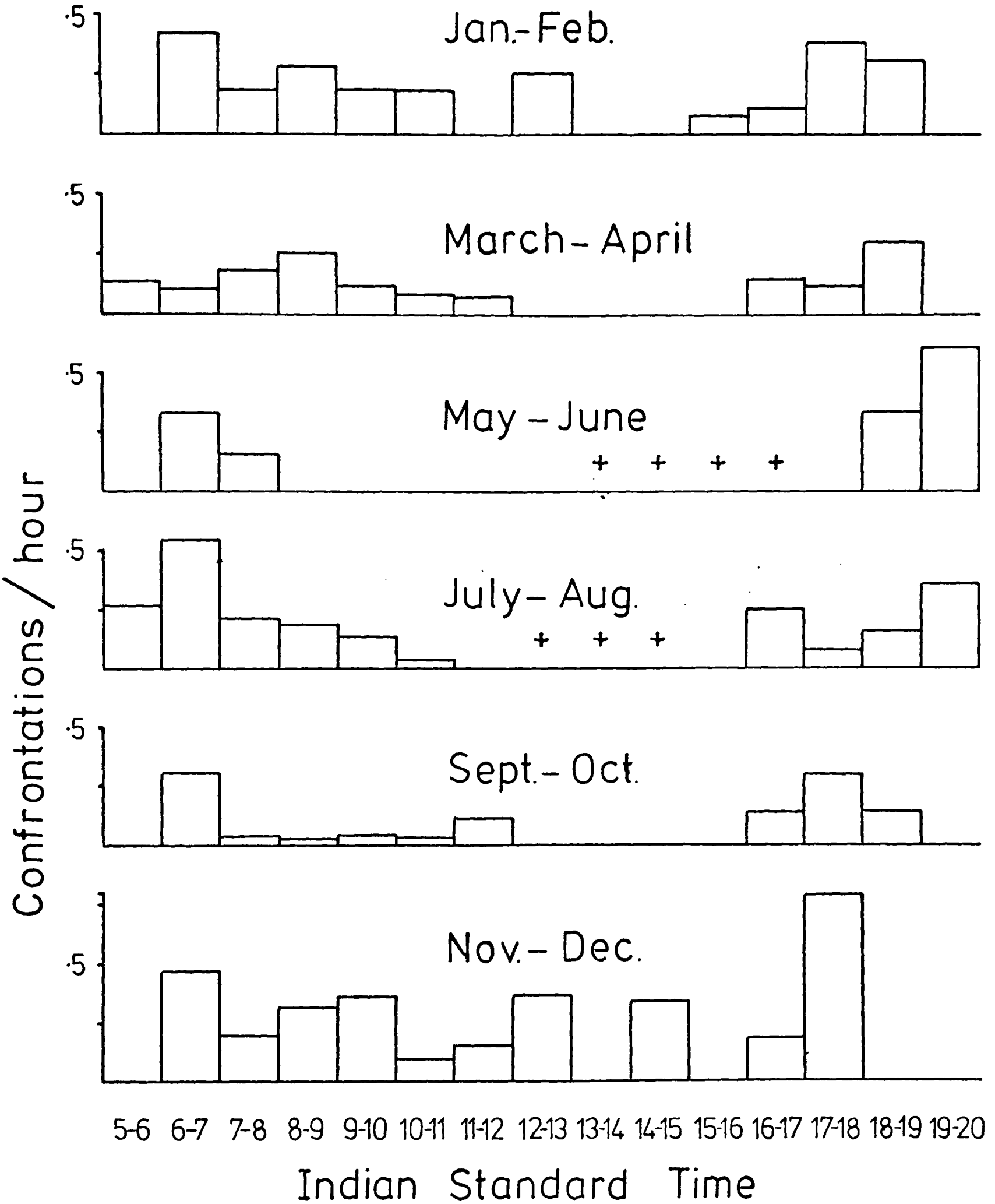


Figure 2q. Diurnal variation in the frequency of confrontations between groups of Jungle Babblers. Vertical scale, confrontations per hour.

frequency was less likely to be biassed by seasonal changes in foraging patterns.

Figure 2p shows the frequency with which territorial calls of the Large Grey Babbler were recorded in each month. Peak rates of calling occurred in June and July, at the beginning of the main peak of breeding activity (see Figure i for the breeding season of the Large Grey Babbler), and calling was particularly frequent during periods when nesting was actually taking place.

Figure 2q shows the same figures used to compile Figure 2o, broken down to illustrate diurnal variation in the territorial activity of Jungle Babblers at different times of the year. The periods during which confrontations were most frequent were in the first two hours after leaving the roost, and the last hour before entering. During the winter months confrontations continued throughout the day. The low frequency of confrontations in the middle of the day during the summer is probably because most groups were relatively inactive at that time.

The frequency of involvement in inter-group confrontations varied from group to group. It was lowest for F group, which occupied a territory almost entirely surrounded by scrub, and hence comparatively isolated from other groups, and highest for R, O, and J groups, all of which had core-areas contiguous with those of other groups. The mean rate of confrontations for four newly established groups was 0.22 per hour, significantly higher than the 0.12 confrontations per hour recorded for eleven older groups ($U = 4$, $p = 0.02$).

Rank correlations between the amount of time spent in the core area (as shown in Fig. 21) by Jungle Babbler groups L, M, and P, and the rate of confrontations in each month, show only slight correlation, either with confrontations before 1200 hours ($r^s = 0.224$, $p > 0.1$), or with confrontations in the last hour ($r^s = 0.175$, $p > 0.1$). This suggests that the frequency

of confrontations is not wholly dependent on the extent to which groups are moving about. It may be determined by other seasonal factors, of which the most important appears to be the timing of the breeding season.

2e) Provisioning experiments

During February 1973 provisioning experiments were carried out to test whether Jungle Babbler groups would defend localised food sources in winter, and how the location, and the relative sizes of competing groups, would influence the outcome of competition over such food sources. Provisioning was with millet, which babblers eat readily in winter.

A major difficulty encountered in this experiment was the large size of Jungle Babbler home ranges, and the consequently low chances of a particular group finding a provisioning site placed outside its core area before the grain was eaten by Peacocks Pavo cristatus, Parrakeets Psittacula spp., or other animals. Satisfactory observations were made at only two sites, marked A and B on Figure 2j, both on the edge of M group core area.

At site A grain was placed regularly at 0800 hrs every morning. Observations after five days of provisioning showed that three groups, M, Y, and H were using the site regularly, soon after the food arrived. The sizes of these groups were 7, 6, and 4 birds respectively.

In 10 minutes of observation on Feb. 5th, and 25 minutes on the 7th, members of all three groups were seen feeding side by side in an area of less than one square metre. Nine supplanting attacks, consisting of lunges with the bill, or short chases, were seen, all involving birds from different groups. On February 5th members of Y group supplanted members of M group six times. On the 7th members of M group supplanted members of Y group twice, and a member of H group once, suggesting that M group might have been improving its status at this site. In no case was any bird excluded from the

food source by this behaviour. On the 5th all three groups moved off together from the food source, and on the 7th Y group moved off in one direction, while the other two groups moved off together in another.

At site B food was placed regularly at 0815 hrs, but there was no evidence that any groups visited the site on a regular basis. On February 14th L and M groups fed at the site, which was close to their regular area of confrontation, for ten minutes before going to roost, and the same was observed for five minutes on February 16th, in the morning. In neither case was there any sign of inter-group aggression or of territorial display. Grain placed at 'C' within the core area of L group (Fig. 2i) was taken regularly by members of that group. No other birds were seen doing so and there was little opportunity for other groups to locate this food source in the normal course of their foraging. It was concluded that Jungle Babblers do not attempt to defend localised concentrations of food in winter, at least where these lie outside their core areas.

2f) Function of territorial behaviour in the Jungle Babbler

Assuming that territorial behaviour, leading to the exclusion of other groups from certain areas, is intended to conserve some resource, then it appears that the food supply at the most critical period is unlikely to be the factor selecting this behaviour. Measurements of insect abundance (see Introduction, Section d), and observations on the intensity of feeding, both suggest that food is least abundant in December-February. Although territorial confrontations are quite frequent at that season, violent ones are not, and the territorial vocalisations of Large Grey Babblers are also infrequent. Jungle Babbler groups frequently join together to feed during the winter, sometimes for periods of up to three hours, and they make no apparent attempt to defend localised food sources.

Figure 2r. Distribution of nests of Jungle Babblers in relation to the type of vegetation.

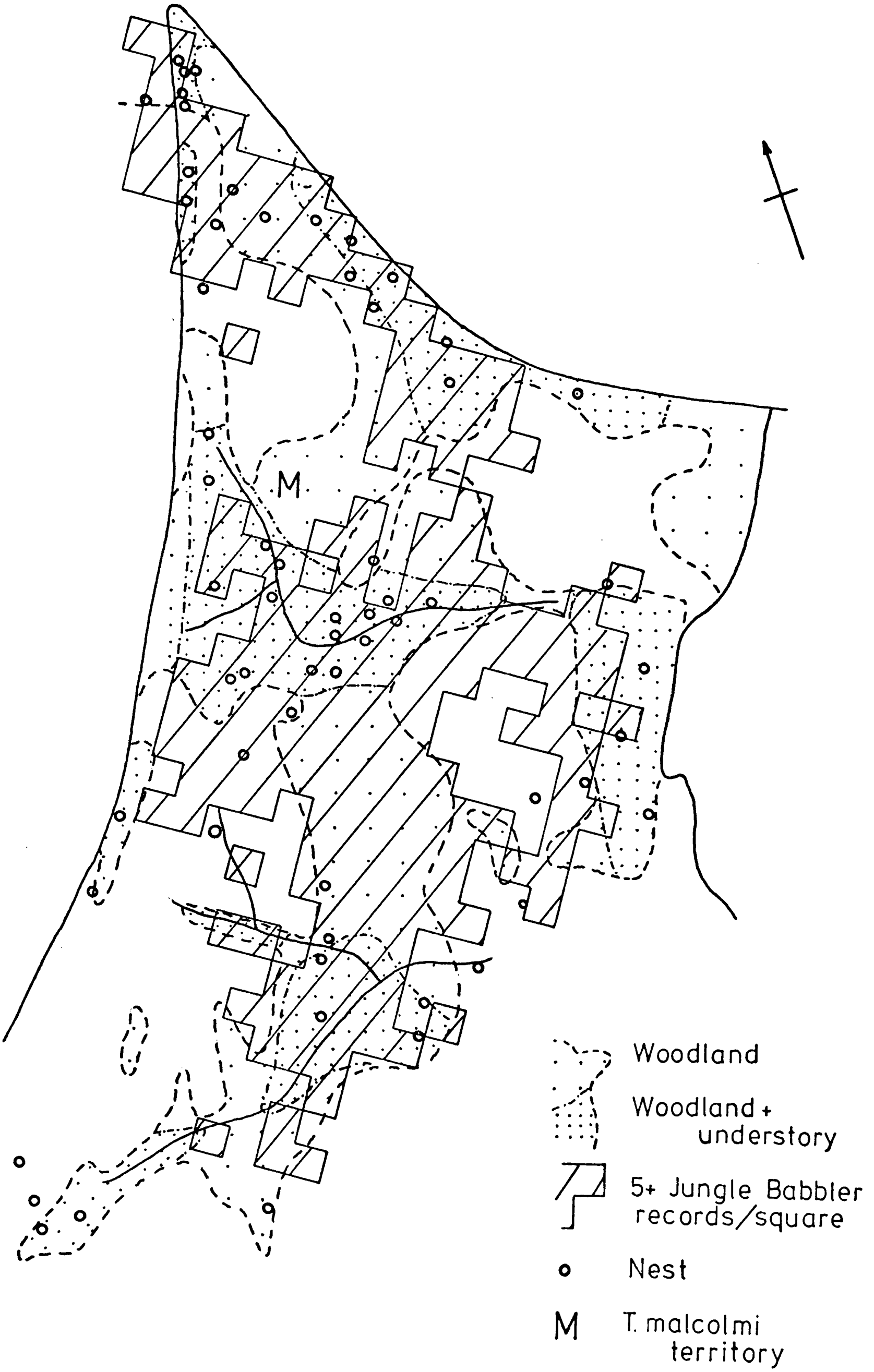


Table 2C. The proportion of different vegetation types within the home ranges of ten groups of Jungle Babblers, and the distribution of core areas and nests in relation to these vegetation types.

	Total area(ha.)	Core areas(ha.)	Nests
Closed-canopy woodland			
with understorey	17.1(25%)	9.3(50%)	40(66%)
without understorey	21.9(32%)	6.6(35%)	11(18%)
Scrub	29.8(43%)	2.7(15%)	10(16%)

Testing the observed distribution of nests against the nul hypothesis that they are distributed randomly in relation to the vegetation types, $chi^2 = 8.9$, df 2, $p < 0.02$

An alternative explanation, that territorial behaviour is adapted to defending a resource which is of greatest value during the breeding season, fits the observed occurrence of confrontations more closely. This also fits with the evidence that most confrontations occur on the edge of core areas, within which most nests are situated. Periods of low territorial activity in April-May and September-October correspond with the periods during which nestlings and fledglings are being fed.

An analysis of the distribution of Jungle Babbler nest sites, illustrated in Figure 2r, suggests that the most favourable nesting habitat consists of closed-canopy woodland with a dense understorey. Table 2C shows the proportion of nests in closed-canopy woodland in relation to the overall availability of this habitat, which confers the following advantages for nesting Jungle Babblers:

1) An abundance of suitable nesting sites which can be approached without leaving cover.

2) A food supply which is more consistently available than in other areas (see Introduction), allowing a longer breeding season.

3) A dense understorey which provides suitable protection from predators for newly fledged young.

Summary of territorial behaviour in Jungle Babblers

1) Home ranges of Jungle Babbler groups comprise an inner core area, within which most nests and roosts are located, and an outer peripheral area.

2) The proportion of time spent in the core area is greater in summer than in winter. Foraging patterns in winter can best be described as a series of forays from the core area into surrounding areas.

3) Territorial behaviour is maintained throughout the year, but is most intense at the beginnings of the two peaks of breeding activity. Territorial confrontations occur more frequently at the edge of core areas

than in peripheral areas.

4) All members of a group take part in territorial defence, but older birds play a more active part than younger ones.

2g) Establishment of new groups

Although eleven new groups became established in the study area during the course of the study, only four contained sufficient ringed birds for their formation to be accurately traced. The events observed in each instance are described in detail, using extracts from field notes, in Appendix 6, and the positions of the centres of activity of the new groups are marked in Figure 2d.

The formation of K group, in June 1973, apparently followed the successful infiltration of an established group (W) by a foreign female (MW). The new group was then formed as a breakaway and included a breeding male drawn from W group and three unringed non-breeders which may also have come from W group. None of them had come from MW's former group, and their sex could not be determined.

In the other three cases the nucleus of the new group consisted of several non-breeding females which roamed about in peripheral areas and attracted a succession of males. Only one of these groups became firmly established and went on to nest (S group) and in this group the coalition of females broke up soon after establishment, leaving only one (YB) which went on to lay.

The case of T group provided the most complete series of observations, although the group failed to become established. Two females, PDG and PW, sometimes accompanied by YB (at that time in its second year), tried to attract males to form a new group by hanging about on the edge of the neighbouring group L. After partial success, including attempted copulations,

they lost the attention of the two males involved to another coalition of three females from a nearby group, all of which were known to be siblings. In the case of both female coalitions they began to spend a lot of time away from their groups while the breeding pairs were incubating, and in both cases they returned after hatching and assisted in feeding the nestlings. The first nest of L group failed during the initial attempts at establishment of the new group and a new one was not started for ten days. During the interim the breeding female of L group spent a great deal of time chasing PDG and PW. If the first nest had been successful it is doubtful if the breeding female could have devoted so much time to driving the other females off, and the group might have stood a better chance of becoming established.

During the spring of 1972, PDG was a member of the breeding pair in P group, but in the rains of 1972 it was succeeded by PM, which continued to breed with the same male (PDB) until the end of the study. PDG stayed with P group until the end of the study as a non-breeder, apart from several attempts to establish new groups. If PDG had been the regular breeding female in P group until succeeded by PM, then YB certainly, and PW probably, were its daughters. Of the three females involved in the establishment of S group, YB and PY were known to be siblings, and PW was probably also a sibling.

The relationships among males involved in the establishment of new groups is less clear, but in the case of N group the two males involved, DGLG and LBDB, both came from the same group, and were therefore almost certainly related. The same was true of LBDB and the unringed male which took part in the formation of T group.

The close degree of relatedness between birds of the same sex involved in the formation of new groups gives an opportunity for kin selection to operate. At the same time it is reasonable to assume that groups comprising

individuals that are familiar with one another are likely to be more stable than ones made up of birds which have no previous knowledge of one another. In some cases the behaviour of one bird starting to move away from its group may have stimulated others. In 1973 YB showed no sign of restlessness until PDG and PW had begun to leave the group, and OR, then still in its first year, took part in the initial moves which led to the establishment of N group. In both these instances the breeding pairs of the groups concerned were involved in nesting, and at this time group cohesion seems to be low (Chapter 3).

When a new group is first formed there is probably severe tension within it, as social relations are resolved in the new context. When S group was being established PW was more prominent in territorial confrontations than either of the other two, younger, females, but it was eventually YB which went on to breed, after PY and then PW had left. Pressure from outside the group does not become strong until they begin to undertake concerted group displays, which generally did not start until several days had elapsed. It appeared that, at least initially, confrontations with groups from which members had been derived were of low intensity, as though former members were still recognised, and the easy re-integration of birds which abandoned an attempt to establish a new group also suggested this.

No evidence of isolated pairs attempting to establish new territories was found. All new groups included 3-6 birds (mean 4.45), with up to three males, and up to four females recorded. This suggests that isolated pairs stand little chance of defending a territory suitable for breeding.

Areas in which new territories were established are marked on Figure 2d, which shows how they were distributed in relation to the core areas of established groups. In three areas new groups, made up of different individuals, were formed on two different occasions, suggesting that the distribution of habitat, and the spacing of existing groups, made these areas

particularly attractive. Group Q was established in an area which previously formed an outlying fragment of D group's core area. This was one of only two cases where not all parts of a core area were contiguous, and the defence of such an outlying area is presumably more difficult. In addition D group had expanded its core area in the opposite direction and was perhaps less interested in maintaining control of the outlier for this reason.

The area defended initially by new groups was small, although N group ranged over a large area during the first few days, perhaps testing possible sites. In the case of three successful establishments the area was enlarged during the first year to about normal size. As discussed in Chapter 1, most new territories were classified as type 3. Of the two established as type 1 territories one was not initiated until right at the end of the study and its persistence was not known. The other had survived one year by the end of the study.

Summary of information on the formation of territories

1) New territories are mainly formed at the beginning of the main breeding peaks, and tend to be located in areas peripheral to established group ranges.

2) New groups consist of two to four birds of each sex, in their second year or older.

3) Formation may be direct, following the joining of males and females from different groups, or indirect, by a breakaway from a single group following its infiltration by a foreign female.

4) The initiation of new groups appears to be performed by females which roam in groups in peripheral areas, calling to attract males.

5) Birds from the same original group are usually of the same sex, but some of these are sometimes lost after the group has become established,

perhaps due to social pressures within the group.

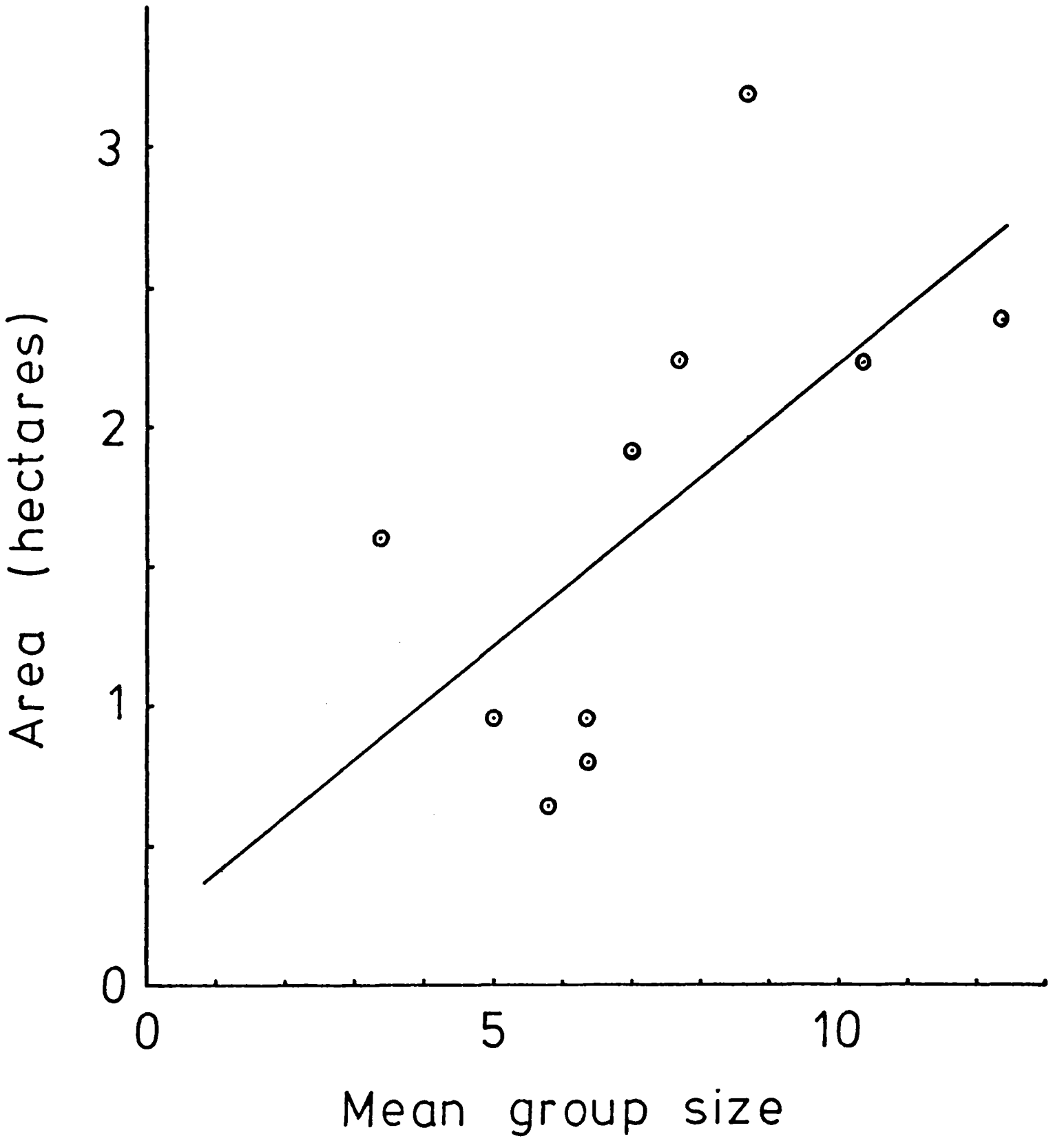
2h) Territory in relation to group size

The size of Jungle Babbler territories was difficult to assess. Boundaries adjoining areas little used by other groups were indistinct, while those clearly demarcated by group displays were nevertheless regularly transgressed. Despite the length of the study, the total size of known home ranges was probably dependent partly on the length of time spent in observing different groups. The three groups most frequently observed, P, M, and L, were recorded in 96, 100, and 104 40m squares respectively, giving total home ranges of 15.3, 16.0, and 16.7 hectares, but this only includes positions recorded every half-hour. By including every square in which the three groups were observed, the size of P and LB group ranges remain almost the same, but that of M group is increased by nearly 30% because of one very long and rapid sortie made in January 1972.

Although nearly 400 hours of watching were devoted to L group alone, this was still only a small sample of the total time that they spent foraging during the study. Time/area curves, suggested for measuring the size of territories by Odum and Kuenzler (1955), when plotted for individual months, suggested home ranges much smaller than those given above, but the curves were rather shallow, with little change of slope, and hence difficult to extrapolate accurately to an asymptote.

Because of the problems involved in measuring total home range size, the size of the area enclosing 50% of all records (core area) was chosen to make comparisons between groups. For L group seven monthly samples of 80-130 records gave core areas of 8-15 squares (mean 10.84), compared to the figure of 14 squares based on all records. More records were made in the winter than in summer, and this probably biassed the overall figure upwards.

Figure 2s. Relationship between the mean size of Jungle Babbler groups on March 1 and the extent of their core areas.



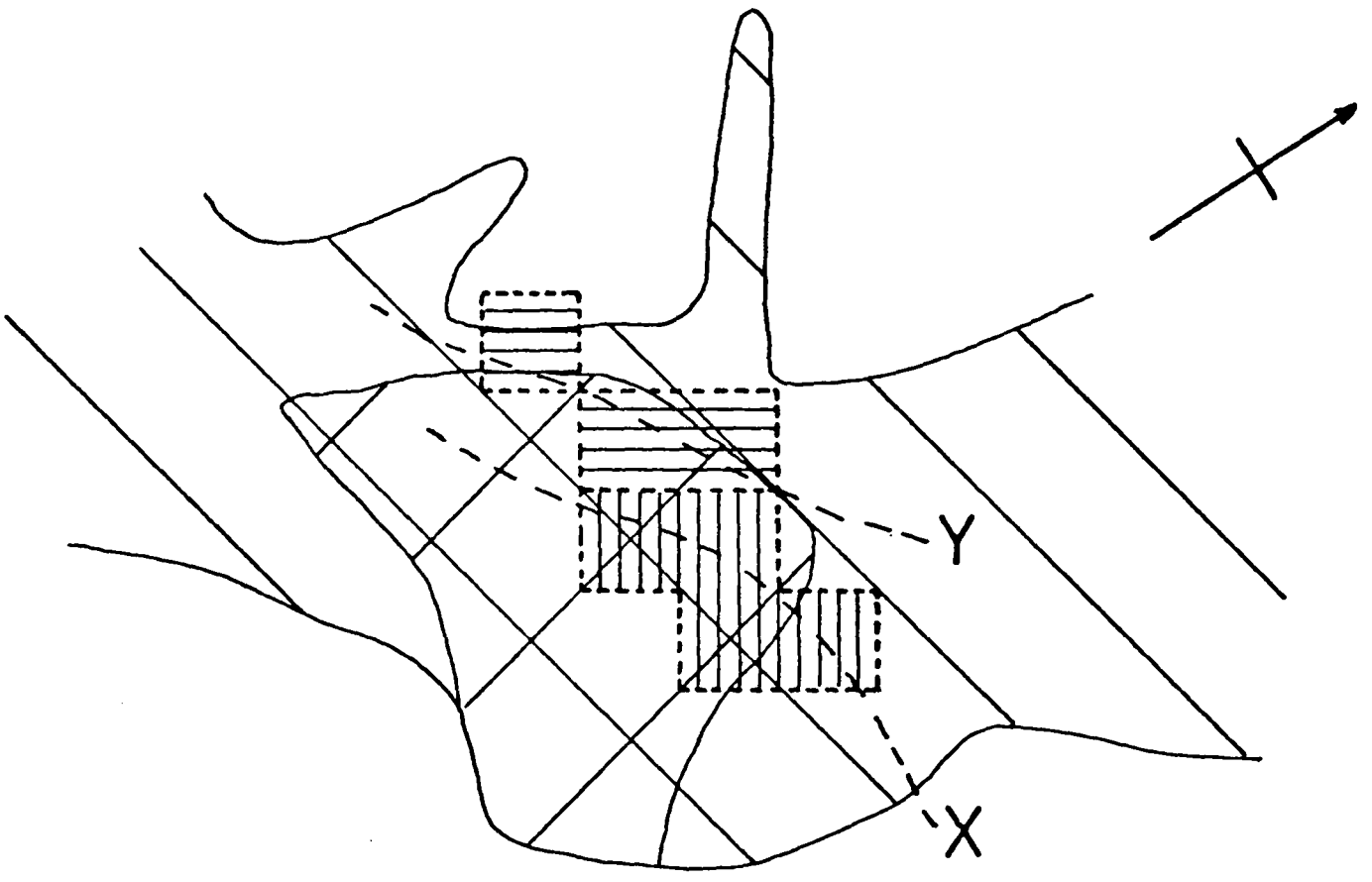
For three winter months only the core area estimates were 11, 14, and 15 squares, a fairly good fit with the overall figure, and one which suggests that the size of the core area is not unduly biassed by sample size. Seasonal biasses in the frequency of observations were similar for all ten study groups.

As illustrated in Figure 2d, core areas varied from 4-20 squares (0.6-3.2ha) among the study groups ($\bar{x}$ = 10.6 squares, 1.7ha). Figure 2s shows the relationship of core area size to mean group size on March 1. The correlation is significant ($r_s = 0.73$, $p < 0.01$) and the regression line for area dependent on group size passes close to the origin, with a slope which gives an 82% increase in the size of the core area for a doubling of group size from five to ten birds. Hence over the most common range of group size there is an almost one to one relationship between the size of the core area and the number of birds in the group.

A similar relationship between the number of birds in a group and the size of the territory is suggested by an examination of the sizes of core areas before and after alterations in the size of particular groups. During the winter of 1971-72, M group contained ten birds, and L group, with which it shared a common core area boundary, contained nine. In this winter M group core area covered 22 squares (257 records), and L group 14 squares (271 records). In the following winter the size of M group had fallen to seven birds, and that of L group had risen to 13, with core areas of eight squares (83 records) and 15 squares (85 records) respectively. The total range over which M group was recorded also fell sharply, but this was not comparable because of the difference in the numbers of observations.

A similar case involved D and G groups, which in the winter of 1971-72 both consisted of six birds, occupying adjacent core areas in a relatively isolated patch of woodland. The area over which their core areas overlapped

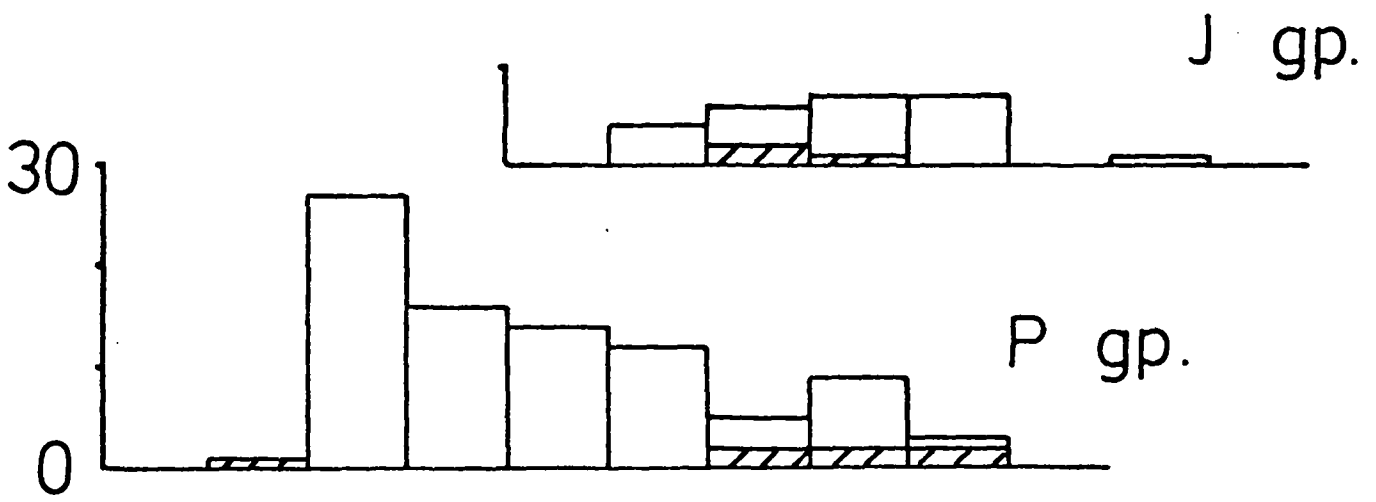
Figure 2t. Boundaries of D and G group core areas in the winters of 1971-'72 and 1972-'73. Diagonal hatching, closed-canopy woodland; double hatching, with dense understorey. X, approximate line of confrontations in 1971-'72; Y same in 1972-'73.



Core area overlap, 1972-'73

Core area overlap, 1971-'72

Figure 2u. Numbers of sightings of P and J groups along a line drawn through their home ranges. Hatched parts denote numbers of confrontations.



is vertically hatched in Figure 2t, and the approximate line of confrontations is marked. In the following winter D group had increased to ten birds, while ~~DBL~~G group contained four. The area of overlap (horizontally hatched) shifted towards the edge of the woodland with dense understorey, along with the line of confrontation. For the following breeding season ~~DBL~~G group territory was reclassified as type 2, instead of type 1.

Both of the above examples suggest that groups expand their territories to accommodate recruitment. The second case also suggests that maintaining a certain group size may be important for retaining control of a core area including suitable nesting habitat, and this is supported by the fact that new territories could only be established by coalitions of several birds. Group G made three nesting attempts in 1972, but only one in 1973, and uncertain tenure of the core area may have contributed to the relative failure in the latter season. Changes in the size and position of core areas in response to changes in group size were less clear cut in situations where several core areas met, but several other instances seemed to show the same pattern, and none contradicted it.

Some small groups appeared to have difficulty in maintaining the exclusive use of an area, in the face of competition from a larger group. An example of this is shown in Figure 2u, which illustrates the overlap between P and J groups. P group, which ranged from 7-14 birds in the course of the study, had a home range which covered 66% of that of J group (3-7 birds), and included J group's entire core area. In contrast J group never penetrated more than a short distance into P group's home range, and were only recorded in one square of the core area. On another boundary J group bordered the territory of B group (range 5-9 birds), and with this group the degree of overlap was more or less equal, with both being recorded several times in parts of the other group's core area.

Ignoring the overlap between adjacent home ranges, the mean size of group territories can be calculated by dividing the total area occupied by the number of groups within it. Considering only those 13 groups with the majority of their core area situated within the area of 80 hectares outlined in Figure 2a, the mean size of territories calculated by the above method was 6.1ha per group. The mean number of birds occupying this area on March 1 was 85, and the density is therefore equivalent to 42 pairs, giving a mean area for hypothetical pair territories of 1.9ha.

The mean size of non-overlapping nesting territories in which the pair carry out most of their feeding is detailed for 59 species of passerines by Schoener (1968). The crude comparison provided by these figures, unfortunately mainly for temperate species, suggests that the density of Jungle Babblers is no higher than would be expected for species occupying a similar niche. Six species of ground-feeding insectivores, similar in size to Jungle Babblers, which are listed (Aphelocoma coerulescens, Mimus polyglottos, 2 Turdus spp, and 2 Sturnella spp.) have pair territories of 2.2, 0.4, 0.7, 0.1, 3.0, 3.0 ha. The regression of territory size on body weight given by the same author predicts a territory of 2.8ha for Jungle Babblers. These figures suggest that the mean size of Jungle Babbler group territories is greater than would be expected for a similar pair territorial species. This is consistent with the hypothesis that territories are larger because of the presence of non-breeding birds, rather than non-breeders being accommodated within a territorial system of similar dimensions to that which would exist under a pair territorial regime.

Summary of territory in relation to group size

1) The core area of the ten study groups varied in size from 0.6-3.2ha, and their size was found to be significantly correlated with mean group sizes on March 1.

2) Over the most common range of group size the area of the core area was found to have an almost one to one correspondence to the number of birds in the group.

3) Groups which changed in numbers between one year and the next showed similar changes in the size of their core areas.

4) Changes in group size were sometimes followed by changes in the position of the core area which affected the quality of the territory.

5) The group territories of Jungle Babblers within the study area were found to be larger than might be predicted for similar pair territorial species.

Conclusions

The distribution of territorial interactions between groups of Jungle Babblers in space and time suggest that territoriality in the species is principally directed at maintaining control of suitable habitat for breeding. This is supported by the coincidence of peaks of territorial behaviour with the onset of the two breeding peaks, and the concentration of territorial behaviour in and around the core area, rather than at the edges of the home range.

Evidence from the relationship of group size to the dimensions of the core area suggests that the size and quality of territories maintained by groups of Jungle Babblers is determined partly by the number of birds making up each group. Taken in conjunction with the evidence presented in Chapter 1, that large groups result from the tenure of good quality territories, this leads to the following picture of territorial stability.

Pairs breeding in good quality territories have a high reproductive rate. Because of this there is a low incentive for males to leave their group, since any new territory is likely to be inferior. These two factors cause

groups in good quality habitats to remain large, and because of this they are able to defend their territory easily. Hence large groups persist.

Pairs breeding in low quality habitat, conversely, have a low reproductive rate, and hence there is plenty of incentive for males to leave, since there are many territories available which are of almost the same quality (i.e. marginal). These two factors combine to make group size remain low in poor quality habitat, and this makes these groups vulnerable to expansion by neighbouring groups in better quality habitat, or encroachment by newly established groups. Hence small groups tend to be ephemeral. That this was in fact the case was shown in Chapter 1.

Chapter 3. Social behaviour within the group

Chapter 3. Social behaviour within the group

Introduction

The permanence and exclusiveness of Jungle Babbler groups is comparable, among birds, only with that of other group territorial species. So far no detailed analyses of social relations within such groups have been published. Among birds the only mechanism of socialisation widely recognised is dominance (Wood-Gush 1955), the recognition of which is dependent on differential success in competition for a scarce resource (Rowell 1972), or on the recognition of consistent aggressive-submissive relations between individuals (Wilson 1975).

The concept of dominance has often been used in the interpretation of social behaviour within primate groups, which are similar in their size and permanence to those of the Jungle Babbler (Hall 1968, Rowell 1972, Richards 1974). More recently several authors have criticized the concept, when applied to criteria other than approach/retreat situations (Howell 1966, Bernstein & Sharp 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 and Sharp suggest that analysis in terms of sex, 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.

Hall (1968) notes that among primates there appears to be a correlation between territoriality, and the occurrence of clear cut dominance hierarchies based on agonistic behaviour, but this was not true of the Jungle Babblers, where, although territorial interactions were frequent, intra-group aggression was very rarely seen. Because of this it did not prove possible, as had been anticipated, to describe dominance hierarchies within groups. Even at artificial feeding sites, where food was very concentrated, and in aviary

situations, no evidence of conflict over food was observed, except between birds from different groups.

In the absence of typical dominant/subordinate interactions, the following behaviour patterns were analysed in relation to age, sex, and breeding status, in order to determine the relations of different individuals with other members of their group.

1) Allopreening behaviour

2) Sentinel behaviour

3) Leadership behaviour

4) Play

5) Roosting behaviour

Before these are discussed, the vocalisations of the Jungle Babbler need to be described, so that reference can be made to them, where appropriate.

a) Vocalisations

Andrews and Naik (1970) list eight vocalisations of the Jungle Babbler, and describe the situations in which they are used. A list made independently in the present study includes eleven calls, but two of those described by Andrews and Naik are included under one heading, while two of those defined here they clearly included under one heading. Descriptions made in the present study are listed in Table 3A, with notes on differences between this scheme and that of Andrews and Naik.

Table 3A. Vocalisations of the Jungle Babbler

1) Alarm call	Short, high-pitched shriek	Given by any bird on the unexpected appearance of predator. Group seeks cover immediately, and may freeze.

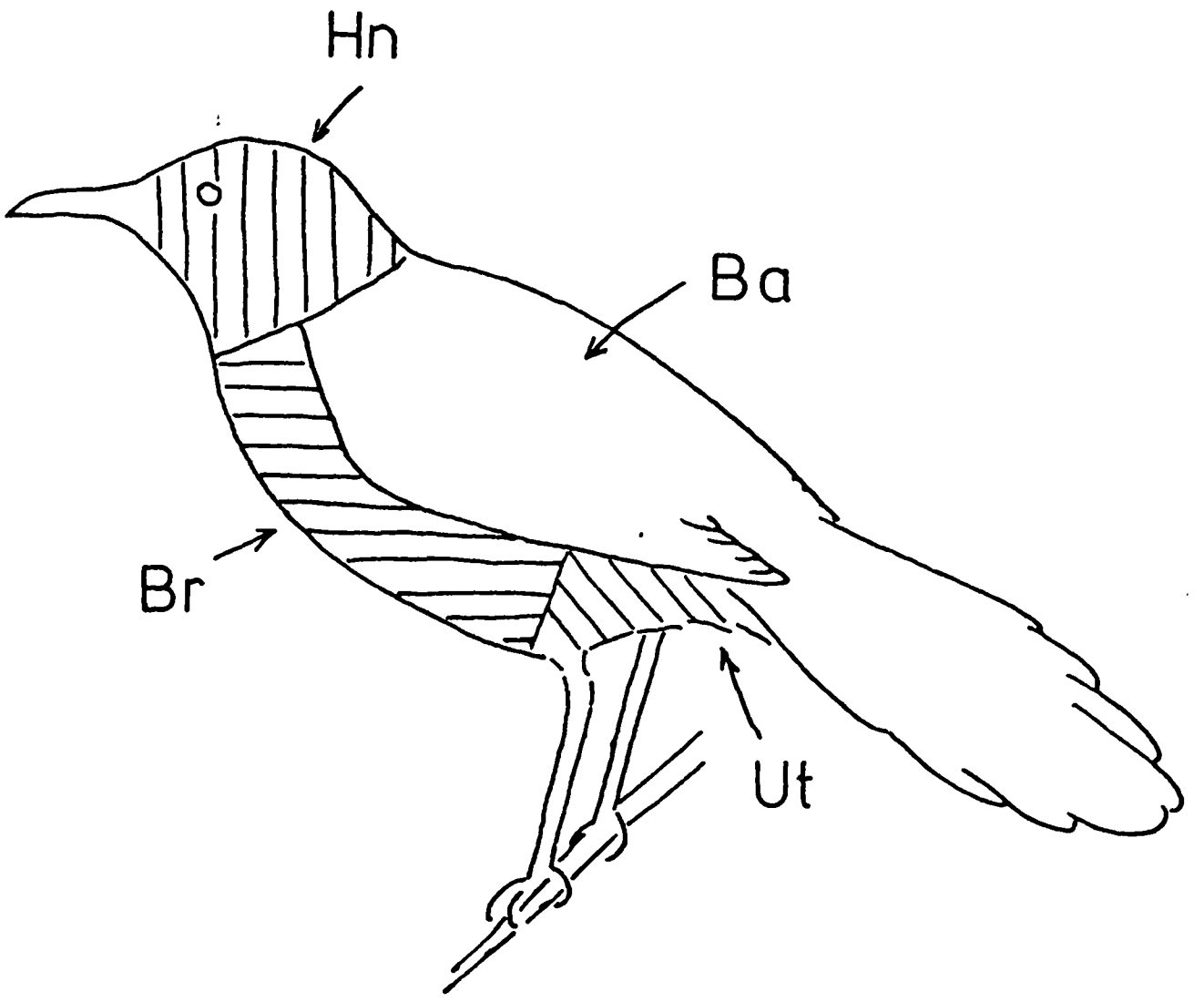
2)	Alert call = "exciting call" of A & N	Intermittent wheezing	Given by sentinel birds in the presence of potential danger, as yet remote, often given at approach of observer. Usually no visible reaction by group.
3)	Mobbing call 3 and 4 included under mobbing by A & N	Loud wheezy cackle	Given by part or all of the group in response to a ground predator, or a perched raptor.
4)	Confrontation call	Similar to 3), but including a rattling guttural noise, rising and falling slightly in pitch.	Given by the entire group during inter-group confrontations.
5)	Contact call	Short "chack" given at irregular intervals	Given by birds detached from their group, or in reply to other contact calls. Sometimes given by birds sitting on the nest.
6)	Feeding call	Short, low "cuk" given intermittently	Given by any bird while feeding, but not often used.
7)	Follow call (not inlcuded by A & N)	Low, guttural "cu-cu-cu", usually repeated several times.	Given by adult birds just prior to initiating a movement to a new feeding site. It was frequently given while the group was moving to roost, and also when fledglings were being encouraged to fly.

8) Distress call	Loud ringing "kya-kya-kya"	Given when trapped. This usually summoned the rest of the group at once. Tape recordings of this call were the most effective in summoning Jungle Babblers.
9) Pre-copulatory call (not included by A & N)	Low gurgling noise	Given by adult males just prior to attempted copulation, wings waved loosely at the same time.
10) "Scheer" call (not included by A & N)	Low "scheer"	Given by females while approaching males of another group. Also given by passive birds during rough and tumble behaviour.
11) Begging call	Rattling squawk	Given by juveniles when begging.. May be used occasionally up to 6 months old.

The alarm call was similar to that of the Common Babbler and the bulbuls (Pycnonotus spp.) which occupied the same habitat. The alert, mobbing, and confrontation calls, although distinct from other vocalisations described, formed a continuum of increasing intensity. The contact call was similar in form to the feeding call, but these did not intergrade in volume, the contact call always being audible up to about 50m, the feeding call not usually being audible beyond 10m. The latter call may have been used more frequently than was apparent since only a few groups permitted me to approach within 10m. All the other vocalisations appeared to constitute relatively discrete signals, with little variation in volume or intensity, although numbers 9 and 10 were heard only a few times.

Vocalisations 2-5 were the most frequently heard. The intergradation

Figure 3a. Parts of a babbler for which allopreening was recorded separately.



of three of these most commonly used calls probably allows greater flexibility of communication (Struhsaker 1966). This is a characteristic of the calls of primates compared with those of birds (Mulligan & Olsen 1969) and it is also true of the vocalisations of Hyaenas Crocuta crocuta (Kruuk 1972) and Lions Felis leo (Schaller 1972), both highly social animals.

Social relations within the group

b) Allopreening and clumping

Allopreening occurs when one bird preens another (Cullen 1963). It is seen in a variety of bird species, and is most common in social species, where it is generally associated with clumping (Sparks 1964). Many co-operative breeders exhibit allopreening behaviour (Crook 1965), and while it must have a value in feather hygeine, it has also been regarded as having a social function (Morris 1956, Sparks 1965, Harrison 1965, Kunkel 1974).

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 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 which was preened. For the latter purpose the body was divided into four areas, as illustrated in Figure 3a.

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 in allopreening simultaneously.

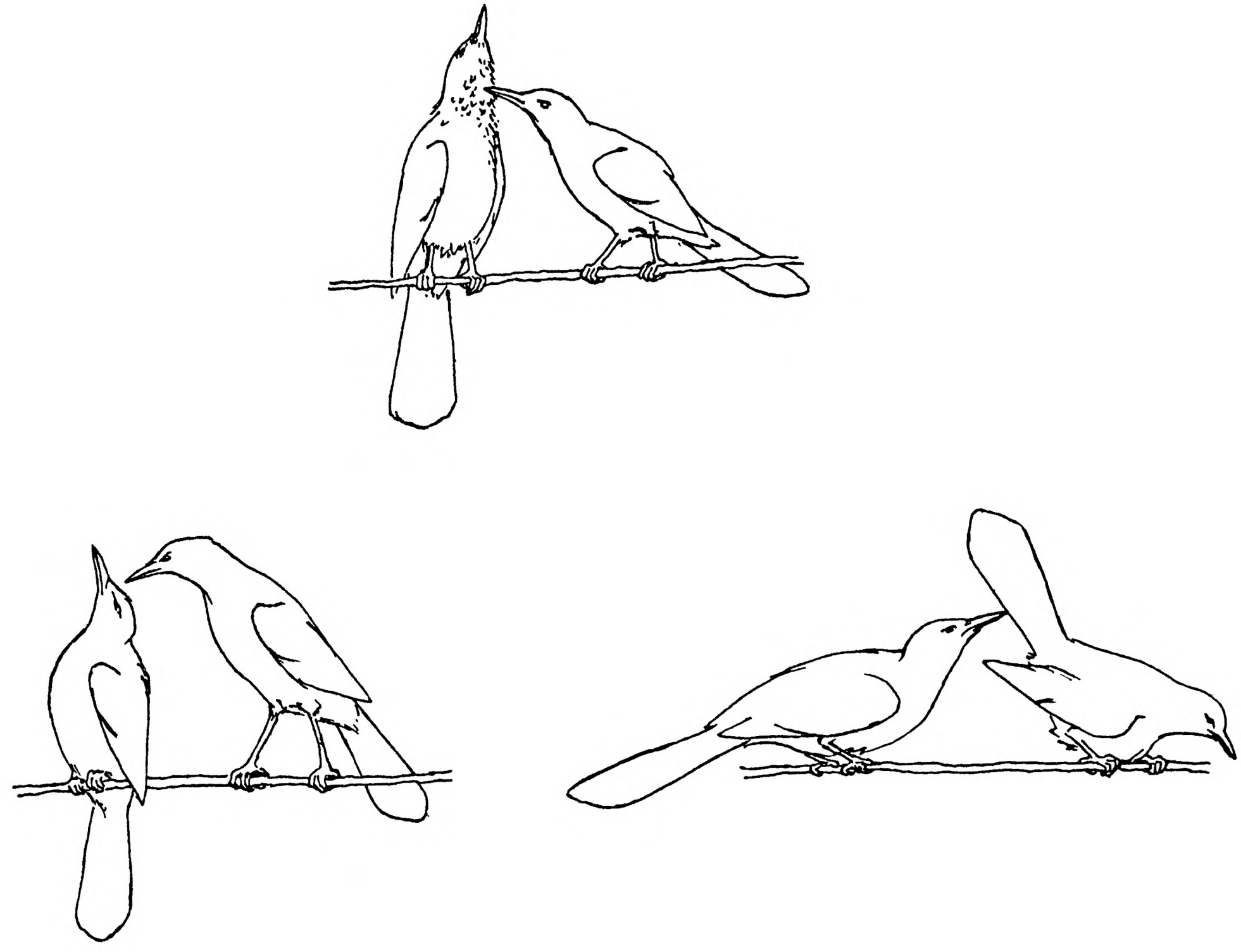


Figure 3b. Some positions adopted by Jungle Babblers during allopreening (from field sketches).

Any period of time during which two or more birds were involved continuously 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 completed when the two birds separated or when no allopreening took place for one minute. 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 a minute had elapsed between the cessation and resumption of allopreening. 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 Figure 3b. 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 being allopreened by another bird perched beside it.

Andrews and 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 and 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~~ related 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 allopreening, 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 alarm call.

Babblers approaching an isolated bird did not perch directly beside it but landed 5-10m 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 variation in allopreening frequency

The seasonal distribution of allopreening bouts, and the number of individuals involved per bout, are shown in Figure 3c, which demonstrates that allopreening is more frequent during the non-breeding season than during the breeding season. This distribution cannot be related to the amount of time available because in winter there is little time for any activities

Figure 3c. Seasonal variation in the frequency of allopreening interactions between Jungle Babblers.

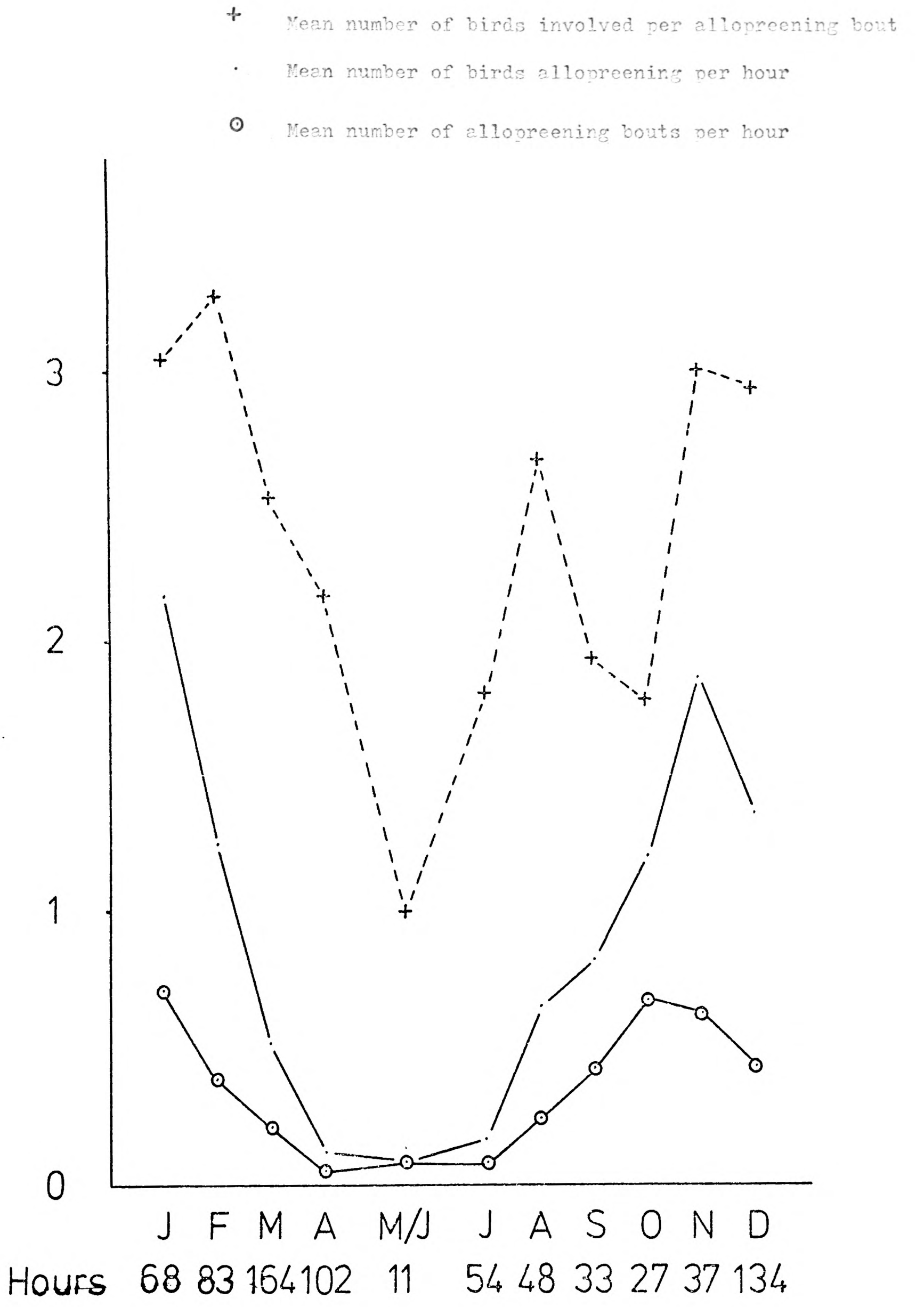
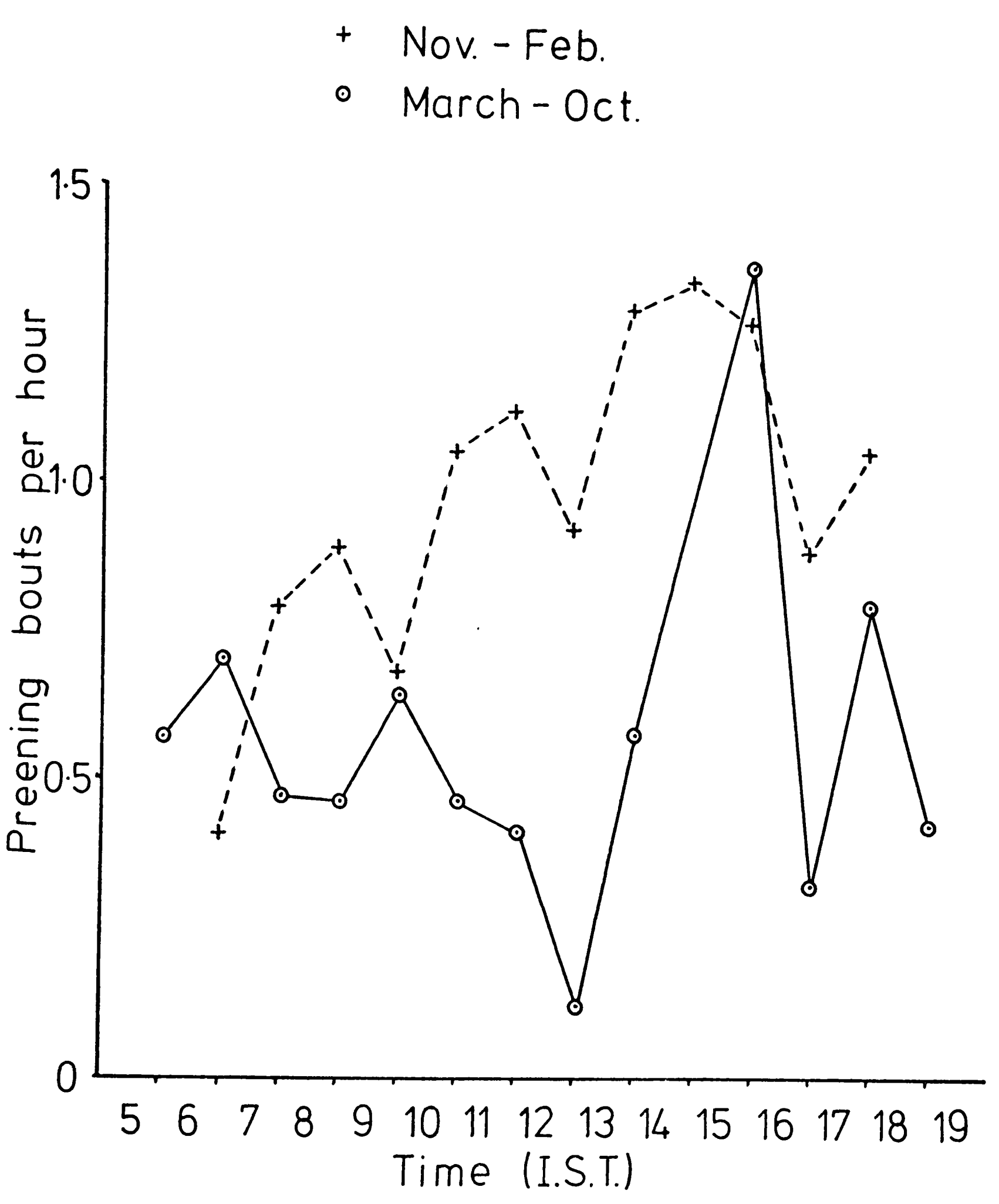


Figure 3d. Variation in the frequency of allopreening interactions between Jungle Babblers with time of day.



other than feeding. Instead it would appear to reflect a general loss of sociability in the babbler groups during the breeding season, perhaps due to a higher level of aggression among adult members of the group.

Allopreening was observed at all times of the day. In winter (Nov-Feb) the frequency of bouts rose from early morning to a peak in mid-afternoon, but during the rest of the year no particular pattern was apparent (Fig. 3d). Many allopreening bouts occurred immediately after a group had suffered some kind of disturbance; an inter-group confrontation, a predator alarm, or disturbance by the observer, but this could not account for the observed distribution of allopreening interactions because disturbance by predators and group confrontations both showed peaks in early morning and evening throughout the year (see territory). The peak of allopreening in mid-afternoon during the winter is probably due to a slackening of feeding effort at this time of day. During the morning more than 95% of the time is devoted to feeding or sentinel duty.

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) Total number of involvements of each bird, whether as an active or a passive participant.

2) Relative frequency of allopreening interactions between individuals of particular classes.

3) 'Preen ratio'; the ratio of the number of times that an individual was the active participant in an allopreening interaction to the number of times that it was the passive participant.

4) The relative frequency with which allopreening was directed at different parts of the plumage.

Table 3B. 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			

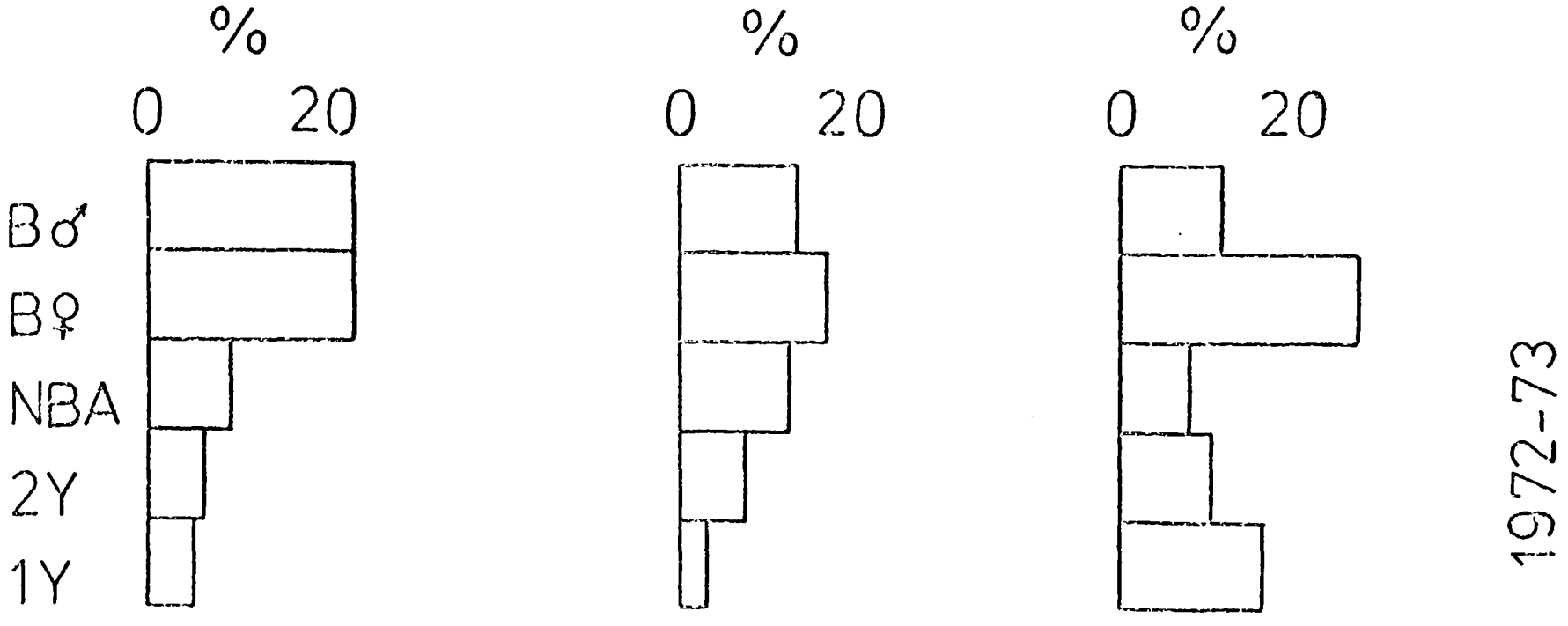
Ages in the left hand column refer to 1972-'73, add one year for 1973-'74

Data were collected in all three field seasons but the age categories considered (first year, second year, and adult) were only identifiable in 1972-'73 and 1973-'74, and only figures for these seasons were used in this analysis, which was confined to the three groups most frequently observed, P, L, and M.

Table 3B shows the frequency of involvements by individual members of these three groups including all birds participating either in active or passive roles. Some observations were included where only one of the two participants in the encounter could be identified, but in most cases both birds were identified. During 1972-'73 L group included two unringed birds; one of them the breeding male, and the other a non-breeding adult male. Scores for unringed birds are divided equally between these two birds. Only birds which remained the whole year with their group are included.

Individuals showed little consistency in their degree of involvement between different years. One non-breeding adult in P group (PLG), which allopreened markedly less than the other two birds in the same class in 1972-'73, showed the greatest amount of involvement in the following year, and the same was true of a non-breeding adult in L group (LBB). In both years, however, there was a fairly consistent tendency for older birds to be involved in more interactions than younger birds. Figure 3e shows the percentage involvement of different classes in all group allopreening interactions. These are expressed as mean percentages per bird where the classes contained more than one individual. 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 placings for the five classes shown in Figure 3e were ranked as follows:

Figure 3e. Percentage involvement of different age/status classes of Jungle Babblers in allopreening interactions.



1) Breeding male

2) Breeding female

3) Non-breeding adults

4) Second years

5) First years

Table 3C shows the number of interactions between birds of different classes, and their frequency relative to the number of birds of each class available in the group. The data used are the same as those in Table 3B, except that only interactions where both the participants could be identified were included. Interactions between the breeding pair, and between the breeders and birds of any other class were the most frequent type of allopreening combination. Apart from these, adult birds were involved in more interactions with other adults, and second years more interactions with second years, than any other combinations. The least frequent allopreening combinations were non-breeding adults or second years with first years, and allopreening among first years.

Table 3D arranges the data in Table 3C to show the active and passive roles of each class, and the areas of the body which 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 participant in interactions with birds younger than themselves, and more often passive when allopreening with older birds. In all interactions between different age classes the older bird took the active role significantly more often than the younger (chi^2 values given in Table 3D).

Figure 3f shows the percentage of allopreening directed at different areas of the body in interactions between all classes. Breeding adults allopreened other birds more frequently on parts of the body other than the head and neck

Table 3C. Frequency of allopreening interactions between birds of different classes.

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

1972-'73	P group			L group			M group		
	Comb.	N	N/C	Comb.	N	N/C	Comb.	N	N/C
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		

Table 3C (continued)

1973-'74	P group			L group			M group		
	Comb.	N	N/C	Comb.	N	N/C	Comb.	N	N/C
BB : BB	1	19	19	1	16	16	1	0	
BB : NB	12	25	2.1	10	16	1.6	6	16	2.7
BB : 2Y	2	10	5	10	26	2.6	4	0	
BB : 1Y	0			6	0		4	3	0.7
NB : 2Y	6	8	1.3	25	38	1.5	6	11	1.2
NB : 1Y	0			15	5	0.3	6	1	0.2
2Y : 1Y	0			15	6	0.4	4	2	0.5
1Y : 1Y	0			3	2	0.7	1	0	
2Y : 2Y	0			10	12	1.2	1	2	2
NB : NB	15	41	2.7	10	6	0.6	3	2	0.7

Table 3D. 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								Hn as %age			
	Hn	Br	Ba	Ut	Totals	Preen ratio	chi^2	p	of total	C/D	chi^2	p
Bσ♂ : B♀	23	14	11	4	52	1.73	5.4	<0.02	44(C)	1.1	0.1	0.7
B♀ : Bσ♂	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)			

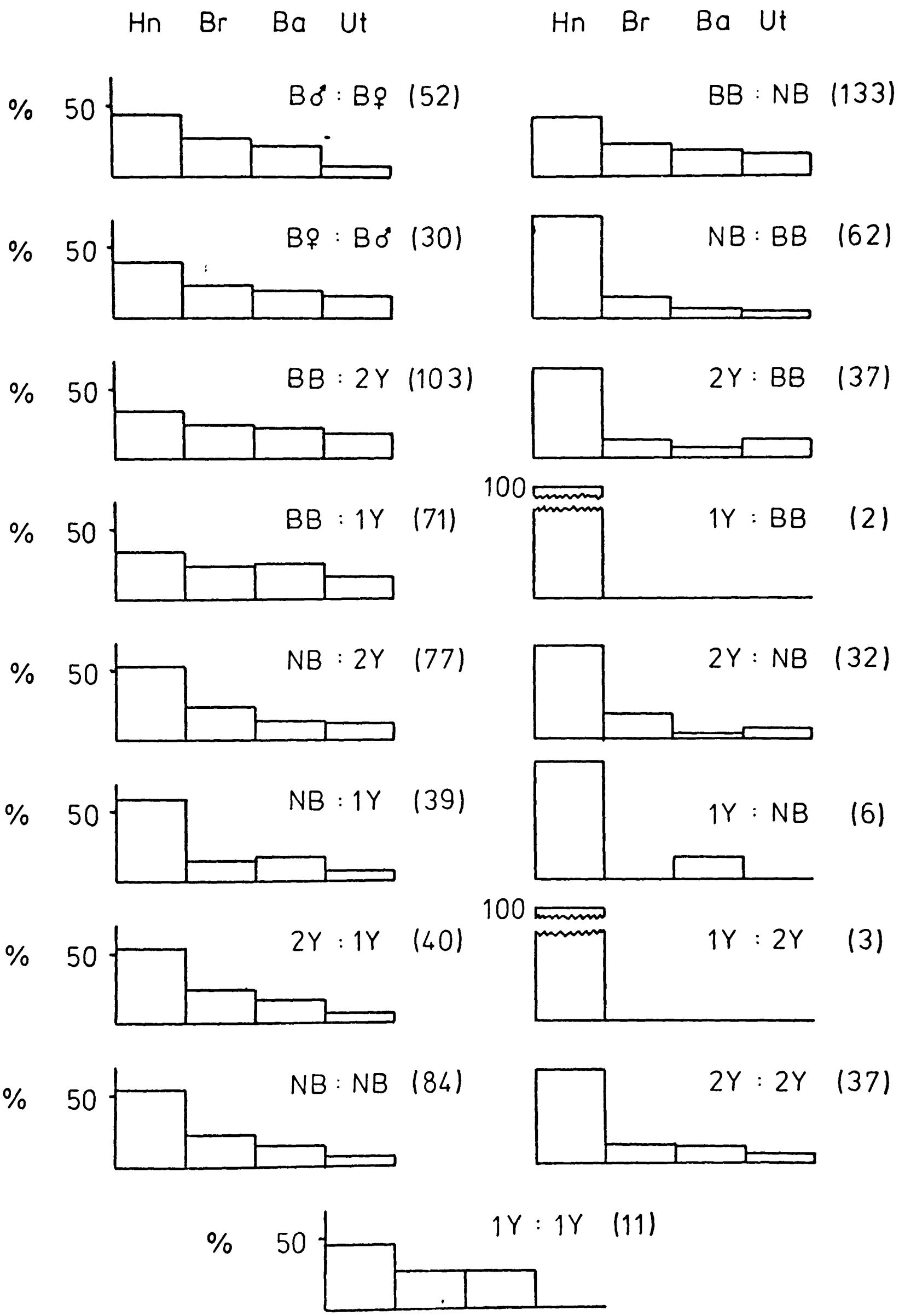
Table 3D (continued)

	Areas allopreened					
	Hn	Br	Ba	Ut	Totals	Hn as % of total
NB : NB	46	18	13	7	84	54
2Y : 2Y	25	5	4	3	37	68
1Y : 1Y	5	3	3	0	11	46
	410	171	138	100	819	

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

Figure 3f. Percentage of allopreening directed at different parts of the body during interactions between birds of different age/status classes. Results from P, L and M groups are combined. The active preener is the first named in each case.



than was the case when roles were reversed. Birds allopreening those older than themselves directed a larger proportion of their efforts to the head and neck region than they did when allopreening those younger than themselves. A significant inverse correlation was found between the preen ratios and the indices C/D in Table 3D (r^s = -0.793, n = 7, $p < 0.05$). This indicates that where two birds of different classes were engaged in allopreening the individual which was more frequently the passive partner tended to direct a higher proportion of its preening at the head and neck region than did the individual which 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 directed at the rest of the body was tested by 2 x 2 chi^2 tests for the combinations of classes listed in Table 3D. Proportions differed significantly in the case of breeders/non-breeding adults, and breeders/second years. Also a comparison of breeders with non-breeding adults showed that breeders allopreened first and second year birds significantly more on parts of the body other than the head and neck. (Chi^2 values are given at the foot of Table 3D.) When birds of different classes were compared for the relative amount of preening directed at the head and neck region while allopreening members of their own class no significant differences were found except between breeders and second year birds, where the breeding pair was found to allopreen one another less often on the head and neck than did second year birds.

Soliciting of allopreening

Although many instances of probably soliciting for allopreening were seen only a few were considered to qualify as unequivocal 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.

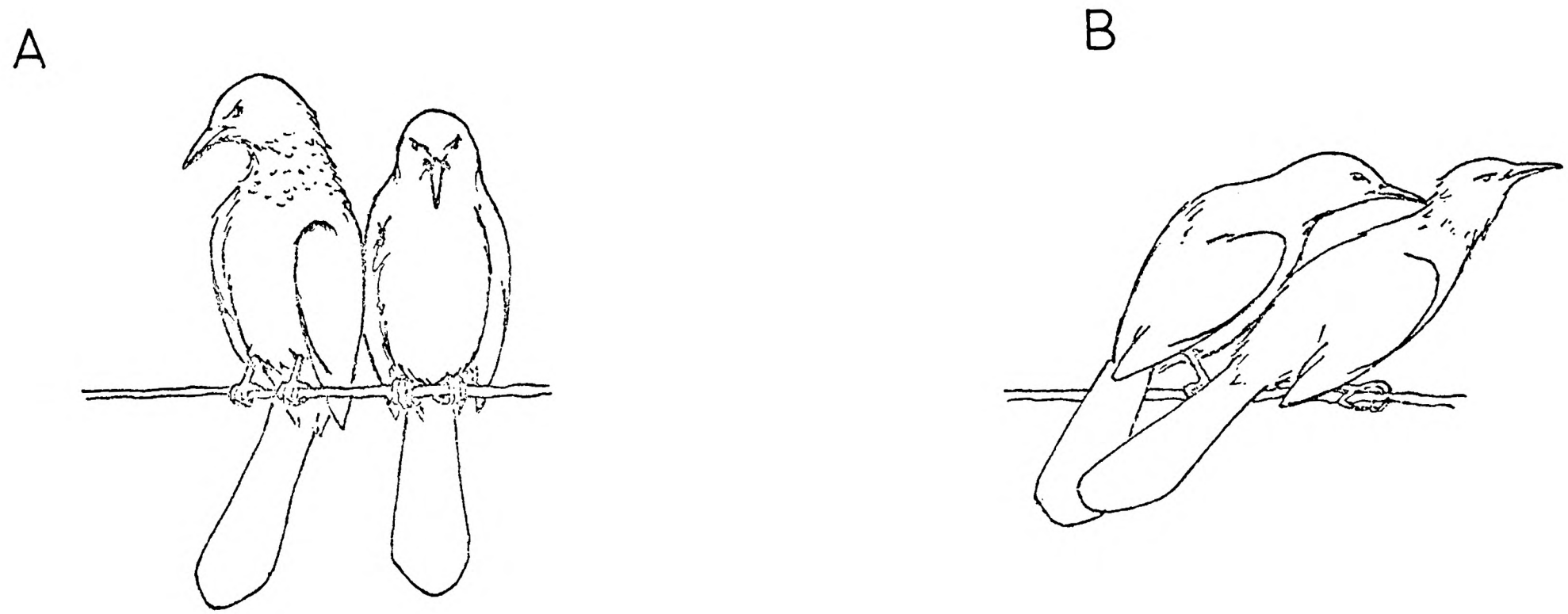


Figure 3g. Posture adopted during the soliciting of allopreening. A; the bird on the left solicits the bird on the right. B; the invitation is accepted.

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 of the bird which was apparently being solicited. As a result only instances where the solicitor adopted the usual passive allopreening posture without any trace of response from the bird being solicited were counted (Fig. 3g). Because the sample was rather small the figures for all three groups and both years were combined in Table 3E, which shows the number of times that different classes were seen to solicit or be solicited, and the frequency 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.

Table 3E. 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

Allopreening in Garrulax leucolophus

Some observations were made during the summer of 1973 on four captive Garrulax leucolophus of unknown age and sex. This species has behaviour similar in many respects to that of Turdoides, and allopreening behaviour resembled that of T. striatus very closely, although more preening was directed to the base of the bill, possibly because the type of sticky food that they received tended to adhere to the feathers of this region. At close range it was clear that the intention of the preener, in most instances, was to remove particles trapped in the plumage or adhering to the skin.

In several instances where disputes over food were observed the unsuccessful bird raised the feathers of the crown and neck, as if being preened in that region. The timing of the posture suggested that it was intended as a display of submission. The same type of feather erection was seen frequently when one bird turned to point its bill directly at the head of another, perched beside it, whereupon the second bird would give the display.

Overt aggression between the four captive birds was never observed. The disputes over food referred to above consisted of a tug-of-war, followed by the winner turning away from its competitor to eat the morsel. Hence it was not determined whether the raising of the neck and crown feathers was generally intended to solicit allopreening or to appease. As in the case of T. striatus, soliciting (or appeasement) was performed most often by the birds which were least often involved in allopreening.

The possibility that in Garrulax leucolophus the posture for soliciting allopreening has developed into a submissive display strengthens the hypothesis that allopreening behaviour has a social significance in group territorial birds.

It also suggests that it may be related to dominance hierarchy within the group.

Discussion of allopreening behaviour

Harrison (1965), in a review of allopreening behaviour, noted that the active bird in allopreening interactions was usually dominant to the passive in situations where dominance could be established by other criteria. 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 spectrum of allopreening involvement. This also suggests that the direction of allopreening reflects dominance relations within the group.

Feather erection in the head and neck region is described by Hardy (1974) as the typical submission display among neotropical jays of the genus Cissilopha. His pictures show that the poses adopted by this genus are similar to those seen in Garrulax and his description of their allopreening technique also sounds similar. In the jays, however, feather erection is only sometimes followed by allopreening. These observations also demonstrate a connection between allopreening and the expression of dominance. Among estrildine finches no consistent direction of preening 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.

The use of allopreening soliciting postures to express submission in some birds has led Harrison (loc. cit.) 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 interactions, suggests 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 analysed 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 individuals 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 primates (Hall & DeVore 1965, Jolly 1972, Kaufmann 1967, Southwick & Siddiqui 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 offspring of the breeding pair, competition among the group would damage the interests of the breeders. If the dominant protects low ranking non-breeders against potential 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 clumping with the dominant and allowing themselves to be allopreened. This hypothesis might explain why most soliciting is directed at the most dominant birds and why clumping by some group members exerts a stimulus for others to clump.

Summary of allopreening

1) Allopreening interactions between members of the same group show a gradient of involvement from breeding adults, through non-breeding adults and second years, to first years.

2) Birds tend to be passive in interactions with those higher in this hierarchy and active in interactions with those lower than themselves.

3) When preening a bird higher in the hierarchy they concentrate more attention on the head and neck region than they do when preening a bird lower in the hierarchy.

4) The fact that a particular bird is consistently preened on different parts of the body by different members of its group, depending on their relative age and breeding status, suggests that allopreening not only serves a hygienic function but also has some significance in expressing social relations.

c) 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 previously described by Dharmakumarsinhji (1954) and Andrews and Naik (1970), the latter authors using the term "sentinel" to describe the bird remaining perched. This pattern of behaviour was noted in the present study for all species of Turdoides ~~and~~ except T. nipalensis.

Methods

During the winter of 1971-'72 the identity of all sentinels that could be recognised was recorded and also the timing of change overs. In the following winters the identity of the sentinel was recorded every five minutes 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 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

Figure 3h. The height distribution of perches adopted by birds exhibiting sentinel behaviour, in relation to the normal size of trees in the Ridge area.

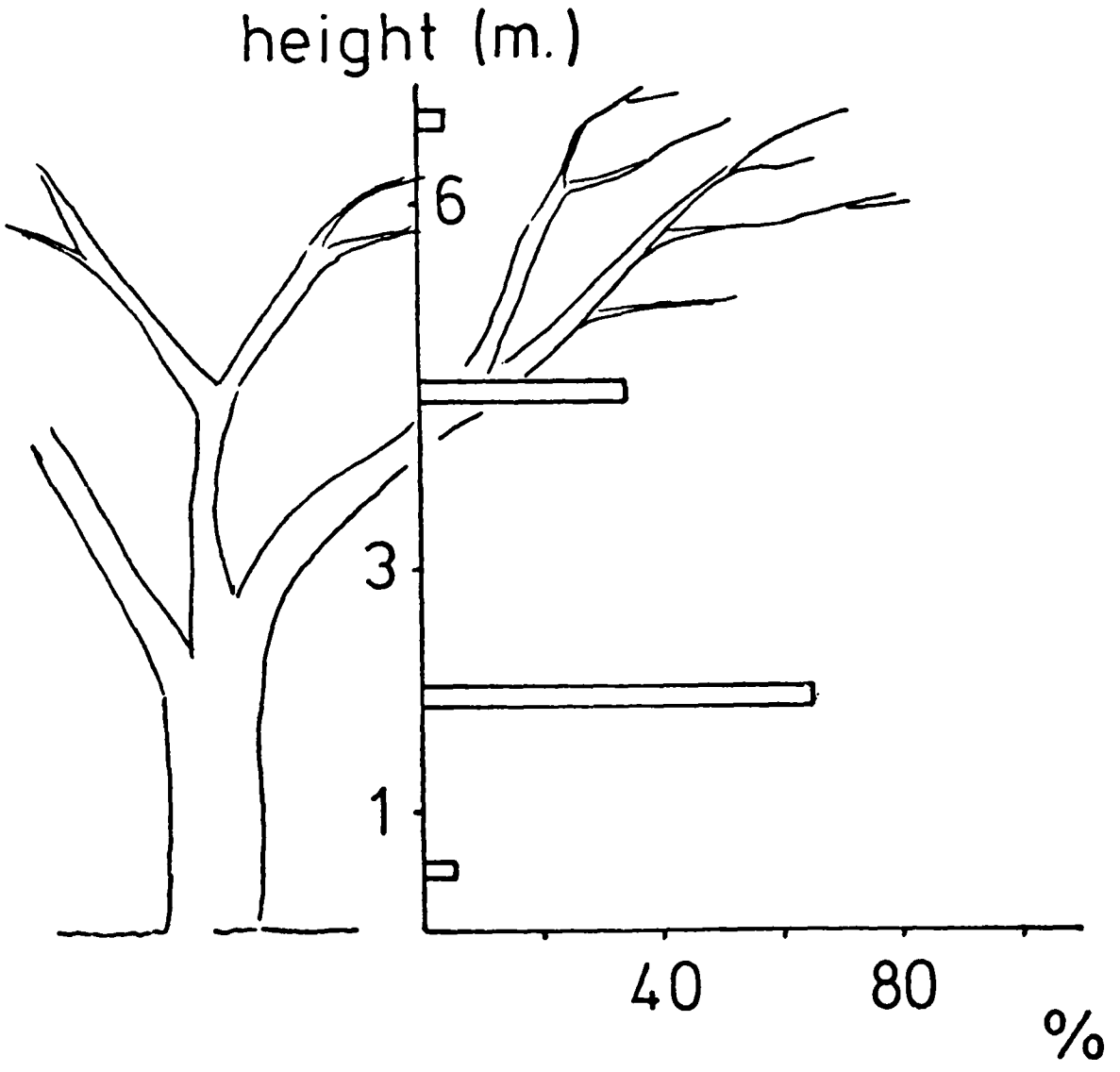
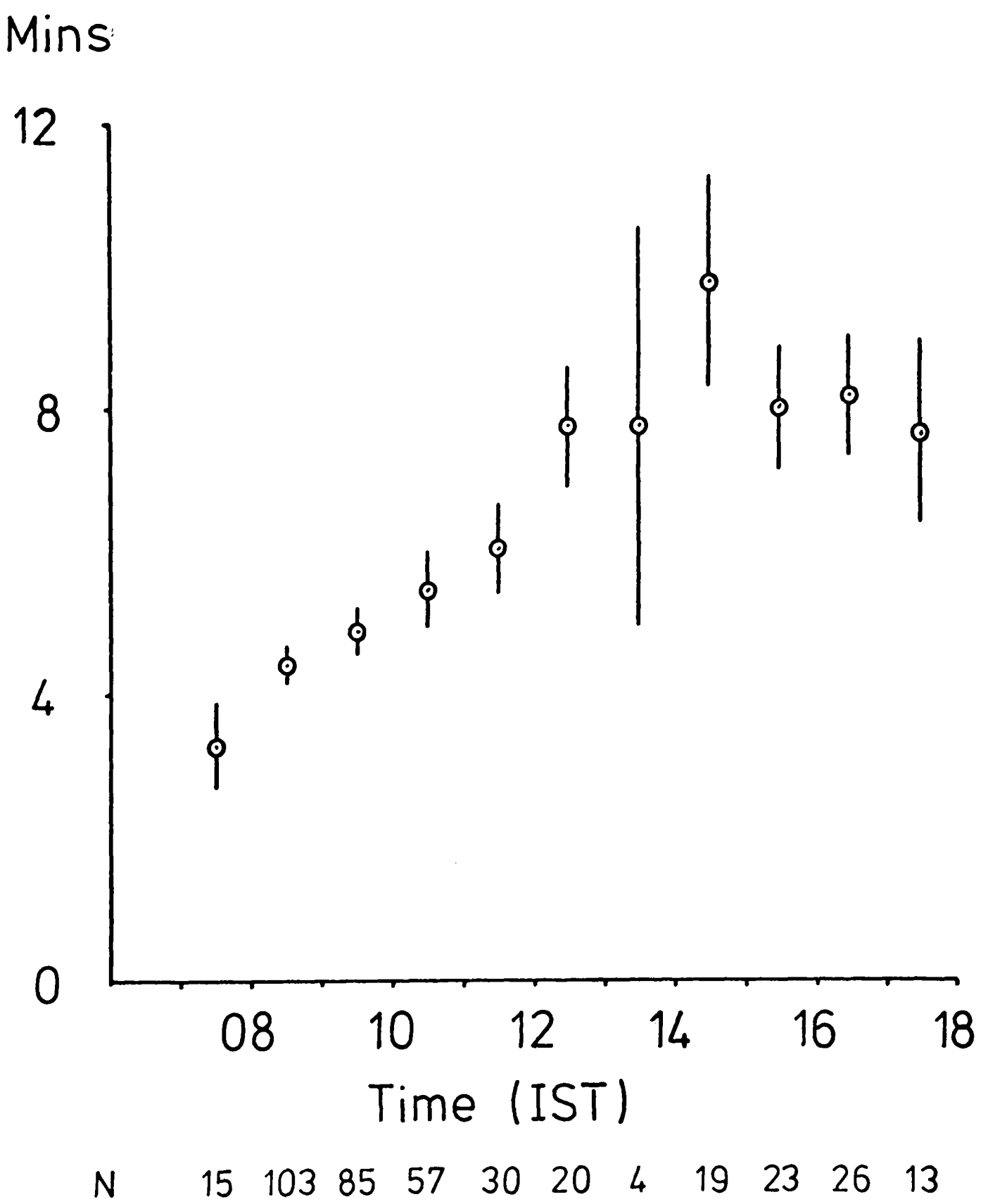


Figure 3i. The duration of time spent at sentinel behaviour in one stretch in relation to time of day. December 1971 and January 1972 only.



canopy and Figure 3h shows the distribution of the heights at which they perched in relation to the average canopy 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 Figure 3i, which demonstrates that mean duration increases from dawn to mid-afternoon, possibly decreasing again before dusk. Changeovers between sentinels were affected 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 changeover suggests a flexible response to different situations. In winter, particularly in the early morning, the sentinel often began to give a low intensity alarm 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.

During observations of groups made in winter the identity of the sentinel was recorded every five minutes. Table 3F shows the frequency with which members of L, M, and P groups were recorded as sentinels, during the winters of 1971-'72 and 1972-'73. Figures for L group in 1971-'72 include only January and February as one non-breeding adult was ringed during December. For groups which included more than one unringed bird sentinel records were apportioned equally between the number of unringed birds known to be 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

Table 3F. Frequency of sentinel behaviour among the members of three groups of Jungle Babblers. Records were made at five minute intervals.

1971-'72	P group		L group		M group	
B♂	PDB	51	UN	42	MB	64
B♀	UN	5	LBO	49	MDB	118
NB & 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	PRo	2	LGW	2	two	0
			four	0		
		243		186		75

was the female, and in P group in both years, the male. In L group, where in 1971-'72 a non-breeding male (LBB) was apparently the most frequent sentinel, the breeding male was unringed, and this bird may actually have performed more sentinel behaviour than LBB. In 1972-'73, when there were only two unringed birds in L group, the breeding male was identifiable at close range on plumage characters, and 66% of records where the unringed sentinel could be recognised referred to the breeding male.

Table 3G shows the mean amount of sentinel activity performed by different age classes, expressed as percentages. In general the breeding pair carried out about 50% of all sentinel activity, and the rest was shared between non-breeding adults and second winter birds, with first year birds rarely taking part.

Among non-breeding adults and second winter birds there appeared to be a tendency for males to perform more sentinel activity than females, although this was not very clear cut. Among second winter birds in P group in 1972-'73, the two males performed more sentinel behaviour 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 sentinel activity than the breeding female in both years, but in P group in both years, a female performed most sentinel activity, among non-breeding adults. In 1971-'72 this was BR, and in 1972-'73 PDG, and in both cases they performed more sentinel activity than the breeding female (PM). It seems worth noting that BR, PDG, and PM were apparently rivals. PDG was the breeding female in the spring of 1972, being succeeded by PM in the rains, while BR was driven out of the group by PDG after destroying the eggs at PDG's first nest in 1972. Since these three were apparently in contention for the position of breeding female in P group, it seems likely that all were immigrants from outside the group. Females may undertake less sentinel activity than males only while they remain in their natal group.

Table 3G. 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.

1971-'72	P group	L group	M group
B♂	39%	-	18%
B♀	-	17%	33%
NB & 2Y	18%(2)	12%(3)	13%(3)
1Y	1%(1)	1%(2)	1%(3)
1972-'73			
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 number of birds involved.

Table 3H. Comparisons of the proportion of sentinel behaviour performed by the breeding pair in mid-winter (Dec.-Jan.), and in November and February.

1971-'72	Dec. & Jan.	February	chi^2	p
L group	35%(n = 205)	26%(n = 74)	2.02	
M group	52%(n = 293)	51%(n = 57)	0.03	
1972-'73	December	Nov. & 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, $chi^2 = 6.92$, $p < 0.01$

The 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 by a bird's ability to refrain from feeding. If so the amount of sentinel activity performed may reflect the relative food-finding abilities of different birds, and this should apply particularly at times of year when food is least abundant and feeding time most limited.

Table 3H compares the amount of time devoted to sentinel activity by the breeding pair, and by non-breeding adults and second winter birds, in different months. For 1971-'72 December and January are compared with February, and for 1972-'73 November and February are compared with December, because of the absence of data for November 1971 and January 1973. If the breeding pair were superior to other members of their group in food-finding ability they should have performed a larger share of sentinel behaviour during December and January, since these were the months of lowest temperatures and shortest days. This pattern was observed in L group in both years, in M group in 1971-'72, and in P group in 1972-'73. It was not true of M group in 1972-'73 but when all five sets of data were pooled the relationship was found to be significant. Figures for P group in 1971-'72 were omitted because of the large number of unringed birds in the group during that winter.

Some evidence that the ability to find food differed between birds in the same group was provided by observations on specialised feeding habits. Most feeding by Jungle Babblers was carried out on the ground, amongst leaf litter, where it was difficult to observe either the food items obtained, or the rate of success in finding them. In winter, however, members of LB and M groups often fed on the fruits of Carissa spinarum and Lantana indica. The identity of individuals seen taking these fruits was recorded, and the number of observations of first winter birds, and of those more than

one year old, are tabulated in Table 3I, together with the proportions expected if fruit-eating behaviour was independent of age. In all cases a larger number of first winter birds was recorded than would be expected if fruit eating was unrelated to age.

Records were also kept of another feeding strategy, recorded occasionally, which consisted of searching rough bark and termite tunnels on tree trunks. This behaviour was observed more frequently among adult birds, as shown in Table 3J.

Although both these measures of feeding behaviour show differences only between first winter and older birds, they support the general hypothesis that the ability to find food alters with age. Fruits of Carissa spinarum are available from November to March, but despite this the frequency with which they were taken rose from 0.24 feeding birds per hour in November to 0.79/hr in December, and to 1.13/hr in early February, falling sharply in mid-February, and rarely being seen at all in March. Lantana fruits were available throughout the year, with a peak in September-December, but these were taken regularly only in November and December. This evidence suggests that fruit was not a preferred part of their diet for Jungle Babblers, and that it was consumed only when other food sources were scarce. The fruits of Ehretia spp, and Securinega leucopyrus, both of which occurred during the summer, were taken sometimes, but far less often than the winter fruits, and apparently irrespective of age. The nectar and flowers of Butea monosperma were taken very frequently by Jungle Babblers of all ages, as they were by practically every other species of bird in the study area.

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

Table 3I. Number of observations of birds taking fruit, October-February inclusive.

1971-'72	No. of observations		Expected		chi^2	p
	2Y & older	1Y	2Y+	1Y		
L group	38	12	38.9	11.1	0.09	
M group	23	33	39.2	16.8	9.3	<0.01
1972-'73						
L group	54	39	59.8	33.2	1.57	
M group	8	12	14.3	5.7	3.7	0.05-0.1

Table 3J. Number of observations of birds probing rough bark or termite tunnels on tree trunks.

	No. of observations		Expected		chi^2	p
1971-'72	2Y & older	1Y	2Y+	1Y		
P group	15	0	8.7	6.3	7.9	<0.01
L group	14	0	10.9	3.1	3.2	0.1-0.05
M group	70	13	58.1	24.9	4.9	<0.05
1972-'73						
P group	87	8	86.3	8.7	0.1	
L group	21	13	21.8	12.2	0.1	
M group	11	6	12.1	4.9	0.1	

Proportions of 1Y to older birds

	P gp.	L gp.	M gp.
1971-'72	5 : 7	2 : 7	3 : 7
1972-'73	1 : 11	5 : 8	2 : 5

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.

d) Leadership

From the beginning of the study an attempt was made to discover whether group movements and activities 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, however, that the leader had initiated the movement, or that the others 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 group 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 "follow call", that the whole group followed, that the movement carried the group more than 40m, and that there was no apparent outside stimulus orienting the response. 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. Records of movement initiation fulfilling these criteria are given for L, M, and P groups in Table 3K.

In groups where the breeding male was ringed this bird initiated 48% of all movements in which the leader was identified, and in groups where the breeding female was ringed this initiated 33% of movements. Nearly all other records were of non-breeding adults, with a few records of second year birds. The relative contributions of the breeders are biassed by the large sample of observations on P group, where the breeding male initiated movements significantly more often than the breeding female. In M group in 1971-'72 and 1972-'73 the breeding female initiated more often than the male, and in 1972-'73 this difference was significant. Although the breeding male of L group was not identifiable in 1971-'72 and 1972-'73 it is clear from the number of initiations by unringed birds that the contributions of

Table 3K. Number of observations of birds initiating movements of more than 40m.

1971-'72	P group		L group		M group	
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
1972-'73						
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		
1973-'74						
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

the breeding pair were probably about equal. This small sample of pairs suggests that overall there is probably little difference 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.

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 confront another. A number of tests were made by replaying tape recordings of group confrontation calls about 60m away from a group which was feeding. The first birds to arrive in ten 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 always produce the same pattern, and in two out of six trials second summer birds were the first to arrive, followed by non-breeding adults. This may have reflected the fact that groups are often scattered while foraging at this period. Tests along these lines were hampered by the fact that Jungle Babblers learned to ignore tape recordings after only one or two trials.

Comparison of allopreening, sentinel, and leadership hierarchies

A comparison of the hierarchies constructed from observations of allopreening, sentinel and leadership behaviour shows that these are similar to the extent that all three activities increase with age, and that all are most frequently performed by the breeding pair. Apart from this the hierarchies constructed on these three criteria are not very closely comparable, although some of the difference could be the result of sampling variation.

Table 3L. Comparisons of ranking within Jungle Babbler groups based on sentinel behaviour, initiation of group movements, and preen ratios. Only birds more than one year old are included. Winter of 1972-'73.

P group		Sentinel	Initiation	Preening	Mean
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
L group					
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

Table 3L (continued)

M group		Sentinel	Initiation	Preening	Mean
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, $p < 0.05$

Table 3L ranks the second year and older members of L, M, and P groups according to observations made during the winter of 1972-'73, and also gives mean ranks based on all three hierarchies. In the mean rankings all but one of the second winter birds are equal to, or lower in rank than, adult members of their group, suggesting that social status is closely correlated with age, at least up to the end of the second year.

In P and M groups second winter males rank higher than second winter females in the sentinel hierarchy, and lower in the allopreening hierarchy. This was also true for the four second winter birds in Lgroup in 1973-'74, 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 take part in sentinel behaviour either.

The following hypothesis might account for the observed discrepancy between the frequencies of sentinel and allopreening behaviour. Young male birds are anxious to advertise their social status within the group, since their chances of succeeding to the breeding territory, or of pairing with any immigrant females,depends on this. Consequently they spend as much time as possible performing the public display of competence which is represented by sentinel behaviour. Females still in their native group are not so concerned to perform sentinel behaviour, as they must establish themselves elsewhere before breeding. In the course of allopreening, however, which they perform to cement their position within the group, many of these females are dominant to males of the same age, and hence occupy higher positions in a hierarchy based on allopreening.

e) Play

Two patterns of behaviour seen regularly seemed to come under the general 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. The same behaviour was also observed on several occasions among groups of Large Grey Babblers, and in this species such behaviour had been previously noted by Hutson (1954).

Mad flights consisted of one, or sometimes 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 at first thought 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 the mad flight were less than one year old, and adults were never seen to indulge.

In some cases 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 flight behaviour recorded among the study groups all occurred between July and November, with five in August and September. Ten out of the fourteen birds involved which could be identified were juveniles more than one 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 one and three months old. Some of these involved fights over food being solicited from an older bird but instances of apparently spontaneous aggression were also observed several times among birds of this age.

f) Roosting behaviour

Jungle Babblers in the study area roosted in trees or bushes from 1-15m above the ground, but usually at least 3m up. Roosts were often in dense foliage or twigs, usually on a branch from 2-5cm in diameter, with the innermost bird close to where it joined a larger branch.

Jungle Babbler 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 fifteen 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 3j. Mean time of roosting of three groups of Jungle Babblers in each month, in relation to the time of sunset. The upper graph shows the percentage of all roosts at which false roosting behaviour was observed.

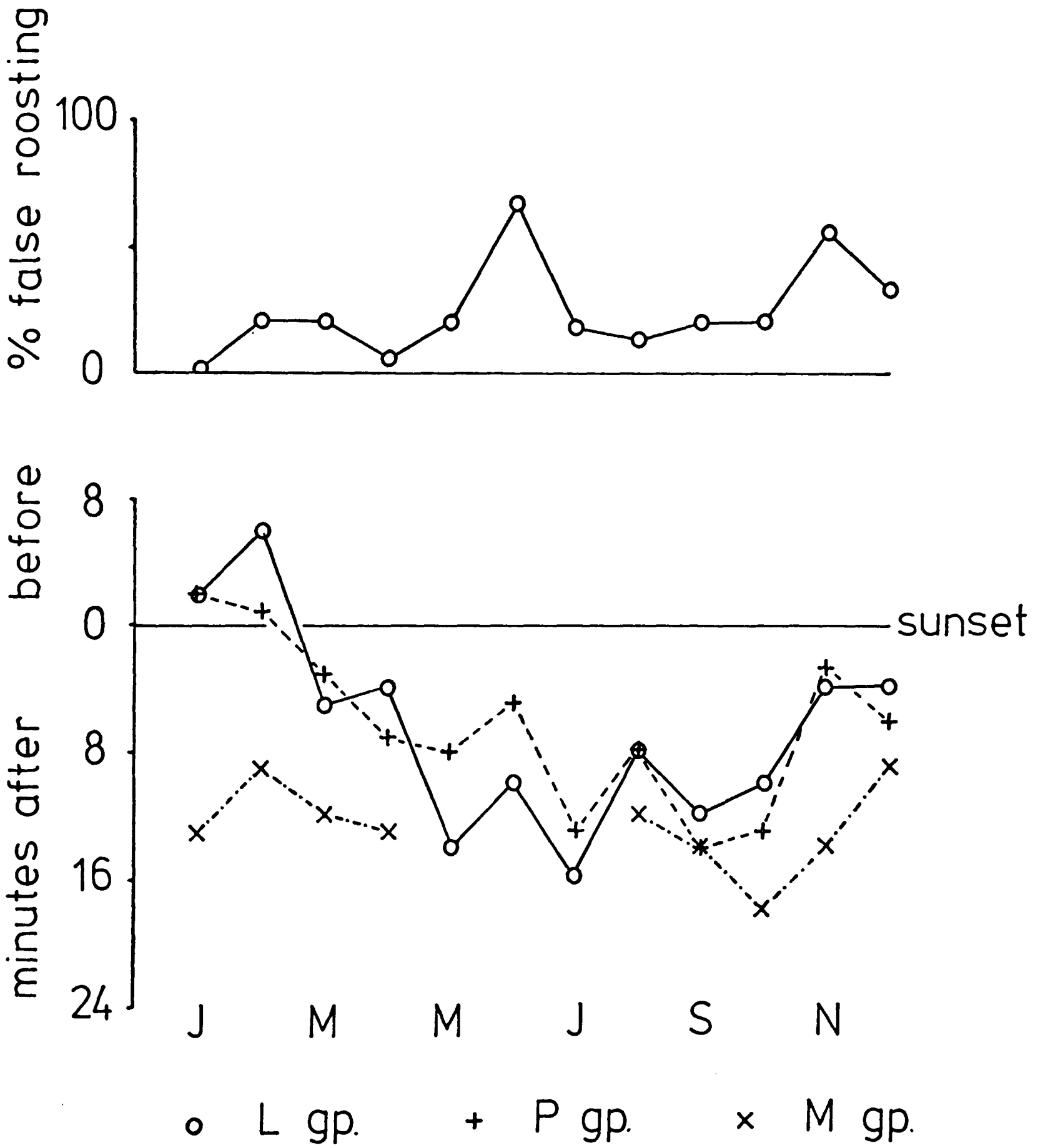


Figure 3j shows the mean time in relation to sunset that groups entered their final roost in each month and also the proportion of nights on which false roosts were visited before finally settling. In general groups went to roost earlier, in relation to sunset, in winter than during the breeding season. 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 thirty roosts were photographed, of which seventeen provided pictures in which one or more birds could be identified. The results of these identifications are listed in Table 3M.

Photographs taken of M group on four days during October and November 1972 all showed the same order of roosting with the breeding male on the inside, the breeding female beside it, then a second year male, two first year birds, a second year female, and on the outside a non-breeding adult male. The pattern in the series of photographs of L group taken between

Table 3M. Positions of birds identified in photographs of Jungle Babbler roosts. Numbers 1 - x refer to the order of roosting, the first being closest to the trunk of the tree. Abbreviations; J, juvenile; 1S, first summer; 2S, second summer; 2/A, second year or adult; A, adult; others, usual conventions.

L group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1972 Nov 11	?	?	?	?	1Y	1Y	2/A	1Y	A	?	1Y	?	NB♂	B♀	NB♂	
Dec 12	?	?	?	?	?	?	?	?	1Y	A	?	?	2/A	?	NB♂	
Dec 27	A	1Y	2Y♂	A	1Y	A	B♀	1Y	1Y	NB♂	1Y	NB♂	NB♀			
1973 Feb 3	?	?	?	2Y♂	?	1Y	?	?	1Y	?	?	?	?	?		
Feb 5	A	A	NB♀	2Y♂	NB♂	A	A	1Y	1Y	1Y	1Y	A	1Y	NB♂		
Feb 7	A	A	2/A	2Y♂	B♀	1Y	2/A	A	A	1Y	1Y	1Y	1Y	NB♂		
Feb 9	A♂	NB♂	A♂	2Y♂	1Y	1Y	A♂	2Y♂	B♀	1Y	1Y	1Y	NB♀	NB♂		
Aug 17	?	?	?	?	?	?	?	?	NB♂	1S	A♂	?	1S	?	1S	?
Sep 3	B♀	1S	J	J	J	?	2S♂	A♂	NB♂	?	?	?	?	?	?	

Table 3M. (continued)

M group		1	2	3	4	5	6	7
1972	Oct 3	B♂	B♀	2Y♂	1Y	1Y	2Y♀	NB♂
	Oct 26	B♂	?	2Y♂	1Y	?	?	?
	Nov 9	B♂	B♀	2Y♂	1Y	1Y	2Y♀	NB♂
	Nov 11	B♂	B♀	?	1Y	1Y	2Y♀	?

P group		1	2	3	4	5	6	7	8	9	10	11	12
1973	Apr 12	?	?	?	?	J	J	?	?	?	?	?	2Y♂
	Jul 17	?	?	?	?	1S	2S♂	NB♂					
	Sep 14	?	?	J	J	?	2S♂						

Table 3N. Distribution of first year birds within L group roost, December and February only.

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

$chi^2 = 11.7$, df 2, $p < 0.01$

November 1972 and February 1973 was less rigid, perhaps because more birds were involved, but certain features were fairly constant. A non-breeding adult male was the outermost bird in five out of six cases. The innermost was an adult in all four cases where it could be identified and there was a significant tendency for first year birds to be concentrated in the outer third of the roost. Table 3N shows the distribution of first year birds in the roost during December 1972 and February 1973.

Only a few birds were recognisable 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 two and six weeks old, entered the roost last by squeezing into the centre of the group. The two pictures of L group which included juveniles (11-11-72 & 3-9-73) also showed a tendency for them to concentrate in the centre or towards the inside.

From the evidence of the photographs it seems reasonable to conclude that the position of birds in a roost is determined, at least in part, by their age. Juveniles first perch in the centre of the roost, moving to the outer third, though not the extreme edge, at between two and three months of age, and then moving to the edge or the inner third as the next generation of juveniles arrives. The outermost position is nearly always occupied by a non-breeding second year or adult male. The breeding pair are usually on or near the inside. The change in the position of the first year birds at two or three months of age may be connected with the generally unsettled behaviour, including false roosting, which was observed at roosts in November and to some extent in December, corresponding to broods fledged in August and September.

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.

Discussion

The intra-group behaviour of Jungle Babblers resembles that of social mammals rather than that of most passerine birds that have been studied. In contrast with most birds, no clear dominance hierarchy could be discerned by observing aggressive interactions between individuals. Posture displays in intra-group situations were unusual, the only common one being the soliciting posture for allopreening. Although a wide range of vocalisations might be employed, most of them were rarely used and the only ones heard frequently in intra-group communication were the contact call and the alert call.

The absence of clear approach-retreat behaviour or peck-right hierarchies within groups of Jungle Babblers is perhaps surprising because most groups of social primates which have been studied show these to a certain extent, at least among males (Jolly 1972). Although this may be partly an artifact of the situations in which many primates have been studied (Rowell 1967), there does appear to be a real difference between primates and babblers. Situations similar to that observed for the Jungle Babbler have been found in studies of social mammals other than primates. Lions Felis leo (Schaller 1972) and Spotted Hyaenas Crocuta crocuta (Kruuk 1972) have relatively few dominance interactions, although some hierarchy can be observed, while among Hunting Dogs Lycaon pictus no hierarchy can be

discerned at all (Kühme 1965).

The difference between species showing clear dominance hierarchies based on approach-retreat or peck-right behaviour, and those in which this type of dominance hierarchy cannot be observed may be concerned with the stability of their respective social structures. 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 such as baboons Papio spp. and Theropithecus gelada, Langurs Presbytis, Macaques Macaca and Chimpanzees Pan troglodytes, on which most studies of primate social behaviour have been made (see Jolly 1972 for a review), tend to have rather flexible social organisations so that the same species may adopt one-male or multi-male configurations in different areas, at different seasons, or even from day to day in the case of the Chimpanzee. The price of this flexibility seems to be the necessity for more overt dominance behaviour and more rigid hierarchies when multi-male groupings are adopted.

Another parallel between Hunting Dogs and Jungle Babblers emerges when intra-group communications are compared. Both species have relatively few intra-group displays compared with social primates or lions, possibly for the same reason, that among more stable groups there is less need for communication.

The differences in ordering between the hierarchies within Jungle Babbler groups based on sentinel behaviour, allopreening, and movement initiation behaviour suggest that these hierarchies are 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 strategy between the sexes regarding

the maintenance of the group and its territory. Among females there may also be differences in the strategies of native and immigrant birds.

The development of socialisation in the Jungle Babbler seems to follow a fixed 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 one month, after which they begin to move with the group and do most of their foraging for themselves. At this stage they begin to indulge in play activities and to move away from the centre of the roost. The next few months constitute an 'adolescent phase' during which they show signs of social indiscipline such as chasing adults with food, pecking one another aggressively, and disrupting the roost. For birds reared during the rains indiscipline declines during the winter and by their first summer their behaviour is similar to that of older group members, although they occupy the lower end of the hierarchies of movement initiation, allopreening, and sentinel behaviour.

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 weening and sub-adult periods (Chance & Jolly 1970, Loizos loc. cit.) 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 frequently performed, is the period during which dominance 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.

Summary of social behaviour within the group

Observations on social behaviour within the group led to the following conclusions.

1) The degree of participation of individuals in the various group activities is related to their age and sex.

2) In general the frequency of participation in allopreening and sentinel behaviour increases with age, while participation in play decreases.

3) Hierarchies based on the performances of allopreening and sentinel behaviour differ in a way that suggests a difference in the relative importance of these activities between the sexes.

4) Group activities are initiated most frequently by the breeding pair.

5) Observations of play, and of behaviour and ordering at roost, suggest that young birds become integrated into the social structure of their group at about 2-4 months old, and that dominance relations among siblings may be defined at this period.

6) Allopreening and sentinel behaviour not only reflect the social structure of the group, but may also be mechansisms for maintaining it. If the continual participation of individuals in such behaviour helps to maintain their social status, then this explains the value of the apparent sacrifice made in performing sentinel behaviour, and the eagerness with which allopreening is solicited.

Chapter 4. Co-operative breeding

Chapter 4. Co-operative breeding

Introduction

An interesting feature of the breeding biology of Turdoides spp. is the frequent participation of non-breeding birds in various aspects of the nesting cycle. Casual mention of this habit among species of the genus has been made by several authors (Hutson 1947 & 1954, Macdonald 1959, Ganguli 1964) and Andrews and Naik (1970) describe it in some detail for the Jungle Babblers which they studied at Baroda. Little was known about the age and sex of non-breeding birds participating, or about their relationship to the breeding pair.

In the course of the present study, non-breeding birds were known to have participated in nesting activities at all 55 Jungle Babbler's nests which were observed sufficiently to have had a reasonable chance of detecting them. Systematic watches on nests were inhibited by a number of factors; the density of foliage around many nests, the fact that several groups refused to tolerate a hide, and the height of nests above the ground. Satisfactory records of birds participating at nests where all members of the group could be individually identified were achieved in only five cases, involving two groups and two seasons. Records of feeding rates and general behaviour were made at many other nests, but these were unsatisfactory for analysis, either because many visitors to the nests could not be identified, or because the groups concerned contained an insufficient variety of age and sex classes to make comparisons possible.

a) Nest-building

In all eighteen cases where nest building was observed only two birds were involved. Birds engaged in nest building often collected nest material within a few metres of other group members which were feeding. Occasionally non-breeding birds visited a nest during the building stage, but none were

Table 4A. Time spent incubating by members of L group in 1972 and 1973.

1972			1973		
Bird	Time(mins)	%	Bird	Time(mins)	%
LBO(B♀)	234	28	LBO(B♀)	98	33
LBB(NB♂)	221	27	UN(B♂)	71	24
LBDB(NB♂)	57	7	LBB(NB♂)	30	10
LBW(NB♀)	28	3	LBY(2Y♂)	1	0.3
UN(inc. B♂, 2 NB)	281	34	LGW(1Y♂)	48	16
LBY,LBM(1Y)	0	0	DGLG(1Y♂)	41	14
			LGR(1Y♀)	10	3
			LBW(NB♀)	0	0
			LBDB(NB♂)	0	0
			LBM(2Y♂)	0	0
			LGP(1Y♀)	0	0

ever seen to carry building material. This contrasts with the observation of Andrews and Naik (1970) at Baroda, where they found non-breeding birds participating in nest building at most nests.

b) Incubation

At all eight nests subjected to prolonged observation during incubation most of the adult members of the group sat on the nest for some time. The periods of time spent on the nest by different members of L group during the 1972 and 1973 seasons are shown in Table 4A. Non-breeding males contributed 34% of the time in 1972, and 40% in 1973, while the corresponding contributions by non-breeding females was 3% in both years. Records of non-breeding birds incubating at nests of M group included eight of males, and only two of females. These observations suggest that non-breeding males play a greater role in incubation than females.

At two nests of L group in 1973 males in their first summer performed some incubation, and in one instance a first summer female also incubated. Apart from these, all records of incubation were of birds in their second summer or older.

Birds trapped during incubation were examined for brood-patches. These were present and well-developed on breeding females (3/3), and also present, though less prominent, on breeding males (2/2), and on non-breeding males (3/3) trapped during the period when they were taking part in incubation. One first summer male, known to have been incubating the previous day, showed no sign of a brood patch when trapped

c) Participation of non-breeders in feeding nestlings

Feeding of the nestlings was performed by most, and in some cases all, post-juvenile members of the group. Table 4B shows the total number of feeding visits by members of L group at three nests and P group at two nests, derived from watches made every four days during the nestling period.

Table 4B. Numbers of feeding visits made by all group members at five nests.

	P1972/3	P1973/1	L1972/5	L1972/6	L1973/4
B♂	PDB 23	PDB 26	UN 11	UN c20**	UN 15
B♀	PM 12	PM 15	LBO 7	LBO 17	LBO 7
NB♂	PLG 16	PLG 9	LBB 2	LBB 22	LBB 9
	UN 16		LBDB 2	LBDB 24	LBDB 5
NB♀	PDG 30	PDG 8	LBW 2	LBW 20	LBW 1
	PW 8	PW 10			
2Y♂	*	PO 10	*	*	LBM 3
		PB 7			LBY 5
2Y♀		PY 5			
		YB 6			
1Y♂	PO 8	PR 5	LBM 0	LBM 12	LGW 7
	PB 5		LBY 0	LBY 2	DGLG 4
	PLB(?)15				
1Y♀	PY 7				LGP 3
	YB 0				LGR 3

* In 1972 second year birds could not be distinguished from adults.

**The male of L group could not always be identified at this nest.

Feeding visits by birds less than two years old increased markedly with the age of the nestlings, while the feeding rates of older group members remained the same. This is illustrated for nest P1973(1) in Figure 4a, which includes only counts made between 0630 and 1000 hrs. Because of this change in the proportion of feeding visits made by different age classes, the contribution of non-breeding birds could only be assessed for nests where watches had been evenly distributed over the nestling period.

The frequency of feeding visits varied with the time of day, and with the age of the nestlings. The contribution of different individuals was calculated on the assumption that for any given age of the nestlings the proportion of visits by birds of different age classes was constant with respect to time of day. This may not have been true, as there was some indication that parent birds fed more frequently at times when the overall feeding rate was low, but the error introduced by this factor was probably small. Using this assumption the contribution of the parents at the nest shown in Figure 4a was calculated as 39% of all feeding visits (n = 101). The contributions of all age classes are given in Table 4C, which gives similar figures for two other nests L1972(6), L1973(4).

There was some evidence that the number of feeding visits by non-breeding birds was related to their sex. Table 4D shows the total number of feeding visits recorded for members of L and P groups in 1972 and 1973, broken down into age and sex classes. These figures include all observations, on the assumption that the relative frequency of visits by birds of either sex was not influenced by the time of day or the age of the chicks. The ordering of birds within each age/sex class is also shown, and this illustrates the tendency, within a given age class, for males to maintain a higher rate of feeding than females. To test the significance of this observation each class was split into equal halves on the basis of whether they did more or less feeding. The numbers of males and females in each half were then summed

Figure 4a. Proportion of feeding visits by different age classes at nest P1973(1) in relation to the age of the nestlings.

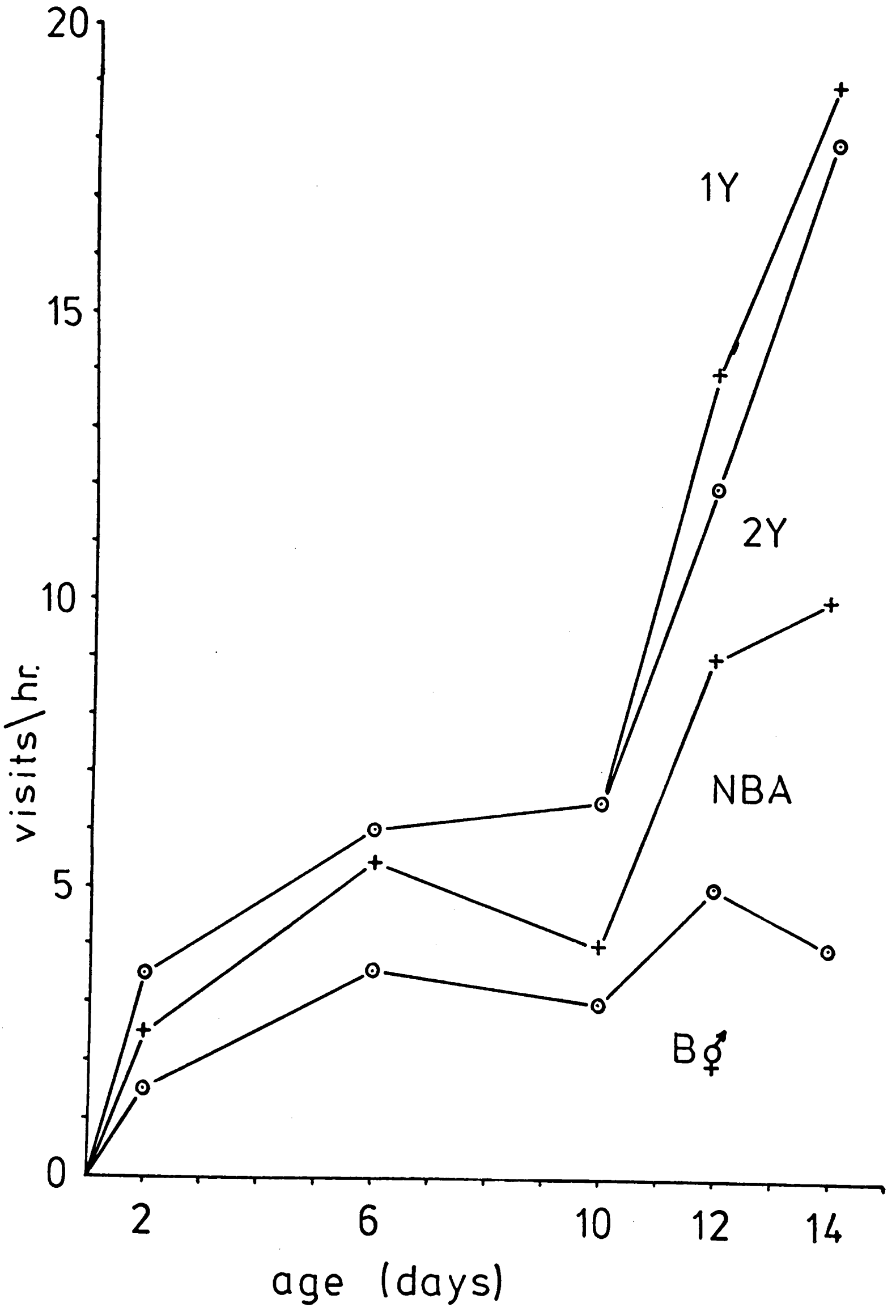


Table 4C. Proportion of visits made by birds in different age classes at three nests.

P1973/1	No. of visits		Proportion from figure	Proportion per bird
BB	41	40%	39%	19.5%
NB	27	27%	28%	9.5%
2Y	28	28%	28%	7.1%
1Y	5	5%	4%	4.2%

Excluding the breeders, heterogeneity $chi^2 = 7.9$, $p < 0.02$

L1972/6				
BB	37	32%	34%	17%
NB + 2Y	66	56%	55%	18.4%
1Y	14	12%	11%	5.5%

Excluding the breeders, heterogeneity $chi^2 = 5.5$, $p < 0.02$

L1973/4				
BB	22	33%	35%	17.4%
NB	15	23%	22%	7.3%
2Y	8	12%	11%	5.3%
1Y	21	32%	33%	6.5%

Excluding the breeders, heterogeneity $chi^2 = 2.4$, $p > 0.1$

Table 4D. Numbers of feeding visits made by birds in different age/sex classes at all nests combined.

	L group		P group	
	1972	1973	1972	1973
B♂	27	15	31	26
B♀	24	7	16	15
NB♂	26, 24	9, 5	19, 18	9
NB♀	22	1	36,9	8,10
2Y♂		5,3		10, 7
2Y♀				5,6
1Y♂	12, 2	7,4	15,8,8	5
1Y♀		3,3	8,0	
Totals	137	62	168	101

Order of feeding frequency among classes containing both sexes

L group	1972	NB	♂	♂	♀	
	1973	NB	♂	♂	♀	
		1Y	♂	♂	♀	♀
P group	1972	NB	♀	♂	♂	♀
		1Y	♂	♂	♀	♂ ♀
	1973	NB	♀	♂	♀	
		2Y	♂	♂	♀	♀

for all classes, and the proportions in each half tested. These were found to be significantly different ($chi^2 = 5.57$, $p < 0.02$).

At all the nests listed in Table 4C non-breeding birds contributed 60% or more of the feeding visits over the entire nestling period. In all cases the groups involved were large and permanent, with five or more non-breeders. Feeding behaviour was observed in detail at the nest of only one newly formed group (K) which was established in May-June 1973, and reared a single chick and one Pied Crested Cuckoo in July of that year. During two watches the breeding pair made 40/109 (37%) of the feeding visits. The other four birds in the group, which were presumed, though not known, to be second year or adults, made approximately equal contributions. At least two birds apart from the breeding pair were observed to incubate the eggs.

One nest of a permanent group containing five birds and occupying a type 3 territory was observed in detail. Here the breeding pair made 27/42 (64%) of all feeding visits, and 31% were made by one of the non-breeders. The nest fledged three babblers and one Pied Crested Cuckoo, and hence produced as many young as any of the nests of larger groups. The weights of the chicks on the eighth day after hatching was normal.

There was no evidence from any group to suggest that the assistance of non-breeders improved the rate of growth of the nestlings. No significant correlations were found between the number of non-breeders and the mean or total weights of nestlings on the eighth day. However, no nestlings were weighed at nests with fewer than three non-breeding members assisting.

d) Behaviour of non-breeders in the vicinity of the nest

Some non-breeding birds approaching a nest with food exhibited less confidence than the breeding pair. This applied particularly to first and

second year birds, which often waited near the nest for periods of up to ten minutes before feeding the young. In many cases they eventually fed the chicks only after one of the breeders or non-breeding adults had done so. As far as could be determined the type and size of food items delivered was similar.

Not all birds which visited nests containing chicks brought food, and among those that did, not all gave the food to the nestlings. Of the five nests most intensively observed all but one received visits from birds which did not feed the chicks. In one case (P1972/2) 27% of visits (n = 192) were from birds which did not feed, and at the other three the proportions were 5% (n = 42), 11% (n = 160), and 11% (n = 101) of all visits. Out of 84 visits which did not result in feeding, 33% were by birds which brought food but then ate it themselves, or took it away with them. The rest involved birds which brought nothing.

Cases of bringing food and then eating it without feeding any to the nestlings all involved non-breeding birds, of which 54% were in their first summer. Visits without food involved the breeding pair in 43% of cases, and other age classes approximately in proportion to their representation in the group.

One instance was observed where a non-breeding bird smashed the eggs of the group's nest. A condensed summary of the field notes is given below.

Nest: P group 1972/1

March 23 First egg laid by unringed but identifiable female (from shape of tail)

March 25 1100 Unringed non-breeder relieves breeding female on nest; rest of group in same tree

1120 Breeding male (PDB) leaves perch behind nest

1135 Non-breeding female (BR) approaches the nest from below.

Unringed female leaves. BR perches on the rim and gives several firm pecks into the cup, wiping a sticky substance from its bill between pecks. Also makes swallowing motions.

1137 BR leaves

1140 Breeding female returns, sits rather restlessly

1230 Still sitting, I leave

1450 I return with climbing shoes. One bird flies off from the nest as I approach. Nest cup is empty

1605-1615 Whole flock feeding together

March 26 No bird sitting

March 27 1100 Bird sitting

1550 One egg in the nest, but no bird sitting

March 28 Egg broken in the nest. Same pair begin to build another nest

March 29 BR not seen with the group in 30 minutes observations. Roost contains one less bird than formerly

April 3 First egg laid in second nest

April 7 1858 Much confused struggling as birds enter the roost, as though an intruder is present. Too dark to identify rings

April 10 Roost split into two groups, one including BR, PB (first year male), and an unringed non-breeding adult male

April 12 1750 Whole group except BR feeding together

1831 BR arrives and gives contact call nearby. Breeding female chases it off

1851 BR attempts to join the group as they go to roost, but the result is not seen. Roost, in a new site, is not located.

April 13 0840, 1230 Group seen without BR

1750 BR seen feeding alone within the group's core area, and I shoot it.

Wgt 68g, fairly heavy. Oviduct prominent, quite thick, but no oocytes developed.

BR was shot in order to determine its sex with certainty. It had clearly been driven out of the group by this stage, and there was a danger that it might disappear before its sex could be confirmed. The possibility of the group fragmenting appeared to have passed.

It seems clear that although there was no immediate reaction to BR's destruction of the first clutch, friction developed soon afterwards between BR and the breeding female, resulting at one stage in the group splitting up to roost, but eventually resulting in the expulsion of BR from the reunited group. The cause of the friction appears to have been rivalry over the position of breeding female, since BR was apparently coming into breeding condition. In the Common Babbler non-breeding females collected while attending nests showed no development of oviduct or oocytes (see Chapter 7), and the same was true for most female Jungle Babblers collected during the breeding season by Naik and Andrews (1966).

There was some evidence that tensions within P group continued after the removal of BR. In the second nest one of the chicks showed signs of injury to wings and legs which could have been caused by pecks. It was unable to fly and disappeared at fledging. The female of this nest (PDG, ringed in April) was replaced before the next nesting attempt by PM, which bred with the same male (PDB). The subsequent history of PDG is described in Section 2f.

Only one case of a large clutch (7 eggs), to which two females probably contributed, was recorded, out of 45 clutches observed at completion. In one case two eggs were laid on the same day, but the final clutch was only four, and this raises the possibility that double laying may have been more common than the observed clutch sizes suggested. At twelve nests where egg-laying was observed daily, however, all eggs were laid by a single female.

e) Contribution of non-breeding birds to the defence of the nest from predators

Non-breeding birds were observed driving potential predators and parasites away from the vicinity of the nest on a number of occasions. In many cases the interactions involved the participation of most members of the group, but in some only one or a few birds were involved. Table 4E shows the age and sex of all birds identified driving potential predators or parasites away from the nests of L, P, and M groups, when three or less birds were involved. The proportion of male to female non-breeding second year and adult birds attending these nests was 13 to eight. The proportion among those taking part in driving off potential predators or parasites was 11 to two, and the proportion doing so in the absence of either of the breeding pair was nine to nil ($p = 0.035$, Fisher exact probability test).

Among the species driven off, only the Tree Pie Dendrocitta vagabunda was actually observed predating a babbler's nest, and the Pied Crested Cuckoo was a frequent parasite. All the other species, with the possible exception of the Koel Eudynamys scolopacea, might have done so. Other potential predators driven off by concerted group action were Crow Pheasants Centropus sinensis, and the Kite Milvus migrans. The latter was observed to take nestling babblers on one occasion. The concerted mobbing of a babbler group was generally sufficient to drive away any potential predator, and Crows Corvus splendens were seen watching nests on several occasions from which young were subsequently fledged.

Summary of co-operative breeding in the Jungle Babbler

Non-breeding group members took no part in nest-building, but performed some incubation, and contributed 60% of the feeding visits at all nests of L and P groups. These were both large groups with at least five non-breeders attending at all nests.

Table 4E. Involvement of different age/sex classes in driving off potential predators and brood parasites from the vicinity of nests.

	Crow	Tree Pie	Koel	W-e Buzzard*	P-c Cuckoo	Squirrel**	Lizard	Totals
B♂	2	2		1	2	4		11
B♀		1			1	2	1	5
NB + 2Y♂		5	1		3	2		11
NB + 2Y♀					1	1		2
1Y♂		1				1		2
Totals	2	9	1	1	7	10	1	31

* Butastur teesa **Funambulus pennanti

No evidence was found that nestlings grew faster at nests where non-breeding birds contributed a large proportion of the feeding visits.

Male non-breeders were more prominent than females in incubation, feeding the nestlings, and in driving off potential predators from the vicinity of the nest.

Conclusions

Because non-breeders took part in feeding the nestlings at all Jungle Babbler nests observed it was not possible to determine their effect on the reproductive success of the breeding pair. Such evidence as could be obtained did not suggest that non-breeders made any significant positive contribution. The significant differences between male and female non-breeders suggested that the optimum strategy for non-breeders differs between the sexes, and that male non-breeders may have more reason than females to assist the reproduction of the breeding pair.

PART II

THE COMMON BABBLER *Turdoides caudatus*

Introduction

The Common Babbler occurred in the Ridge study area in numbers similar to those of the Jungle Babbler. It could be trapped more easily than the latter, but because of its preference for feeding in dense bushes it proved difficult to observe. Seventy-three were marked in August-November 1971, 78 in the same period in 1972, and 27 in 1973. Many of these birds were recaptured subsequently, often several times.

Because of difficulties experienced in trying to observe these birds, studies on Common Babblers were concentrated on seasonal weight changes, moult, movements, and behaviour at the nest, where observations were made from a hide. The population declined during the period of the study, and it is possible that habitat suitable for Common Babblers was being significantly reduced by human activity. This may have affected the overall patterns which were observed.

Observations at nests were carried out only from July 1972 onwards. Trapping was carried out intensively in September-November of 1971, '72, and '73 and also in Feburary 1973, and February- April 1974. During February 1974 a number of birds were removed from the population in order to observe the effects of the manipulation of group size. No attempt was made to census groups monthly, but an assessment based on the number of ringed birds observed, and the proportion of unringed birds observed was made in October-November each year, and again in February.

In addition to the Delhi study area Common Babblers were also observed inPakistan in November 1973, and in January-February 1975 and '76. Here they were encountered in semi-desert conditions in western Sind, where they inhabited bushes and low Zizyphus and Acacia trees in wadis surrounded by barren stoney flats. In the Salt Range, Punjab,they were seen in thorn scrub on hillsides and around cultivation. Their behaviour in all habitats was

similar to that recorded at Delhi. Two nests with chicks were found in November 1973, both attended by more than two birds. Group sizes encountered were similar to those seen at Delhi.

Methods

Despite concentrated searching, not all Common Babblers' nests within the study area were found. During incubation the birds were very inconspicuous, but after hatching they had a tendency to give alarm calls at the approach of the observer, and this provided a clue to the whereabouts of the nest. Once the young had fledged high intensity alarm calls, given by several members of the group, betrayed their presence, but at this stage it was usually impossible to determine how many young had fledged. Because of these problems only a few nests were located during building and laying, and the most complete data obtained referred to the number of broods fledged.

Observations at nests were made from a hide placed about 10 metres away. Part of the nest bush had to be trimmed or pulled aside in most cases to make it possible to observe the visiting adults. Nests were kept under observation for four hours from dawn, on one day during incubation and one day during the nestling period, if possible when the nestlings were between nine and eleven days old. The hide was erected in the evening and I entered it before dawn the next morning, dismantling it after completion of the watch.

Nests were visited and nestlings weighed at two day intervals. Common Babblers had a tendency to leave the nest prematurely if handled after the tenth day from hatching, so the last weighing was usually made on day nine.

Territorial mapping was carried out by entering daily observations on the same maps used for Jungle Babblers. It was not found practicable to

follow Common Babbler groups, because at the range necessary to maintain observations their progress was clearly influenced by my presence. Territorial boundaries were defined on the basis of spot sightings and deliberately driving birds, but these methods were not used to construct contours of range use because of the bias introduced by my presence.

All trapping in 1971 and '72 was done by siting nets in suitable areas and driving birds towards them. This method seldom resulted in more than half of the group being trapped at once, and the catch may have been biassed towards a higher proportion of less experienced first year birds. In 1973 some, and in 1974 nearly all trapping was carried out at roosts, where a larger proportion of the group could be trapped together, and there was probably less bias in the sample.

The identification of colour ring combinations in the field was more difficult for Common Babblers than for Jungle Babblers. For this reason it was not possible to record the timing of disappearances and movements between groups. Survival was estimated from December (1) to December (2), assuming that all birds trapped in the preceding September-November were present in the population in December (1), and that all those not recorded in the population in the following September-November had disappeared by December (2). A few cases were noted where a bird was not recorded in September-November (2) but was seen subsequently, so the method can only yield a minimum estimate of survival.

General behaviour

The behaviour of the Common Babbler was similar to that of the Jungle Babbler but the range of variation in vocal and feather posture displays appeared smaller. Groups/members foraged together, remaining within a radius of about 30m of the centre of the group, and moved together between different

parts of their home range. At night they roosted side by side in a dense thorn bush, usually between 1-3m off the ground. In some cases individuals roosted alone close to the main clump, but the identity of these birds was not established.

Allopreening, usually involving adult birds, was seen quite frequently, but was almost invariably directed at the head, neck or breast. Soliciting allopreening was performed in a manner similar to that described for Jungle Babblers. Rough and tumble behaviour and chasing among first year birds was seen in autumn.

Vocalisations were all variations on a whistling trill of 15-25 notes. At high intensity this call was given when potential danger was detected (alert call), such as on the appearance of the observer. It was given with a low husky tone by birds moving from one part of their range to another, or by adults leading juveniles (follow call), and at intermediate intensity it attracted other members of the group towards the caller (assembly call). An alarm call, consisting of a single high-pitched squeak, similar to that given by the Jungle Babbler, was uttered at the close approach of a bird of prey. During inter-group interactions both groups uttered loud assembly/ alert calls.

Chapter 5. Population dynamics

Chapter 5. Population dynamics of the Common Babbler

a) Seasonal weight changes

The large number of Common Babblers trapped, many of them on several occasions, made it possible to monitor seasonal weight changes in this species. Body weight in tropical passerines does not follow the pattern established for temperate passerines, in which highest weights occur during the winter due to the deposition of fat reserves as an "insurance" against temperature fluctuations (Baldwin & Kendeigh 1938, Helms & Drury 1968, Evans 1969, Schifferli 1976). Instead weights tend to reflect the general abundance of food and the body protein level (Ward 1969, Fogden 1972). Since the climate of Delhi includes a marked cold period in mid-winter, a situation intermediate between that observed in temperate passerines, and that of the non-seasonal tropics might be anticipated.

Most trapping of full-grown Common Babblers was carried out either in the early morning, or late in the evening, just before the birds entered their roost. In order to compare weighings made at different times of day a correction factor was applied based on the observed overnight weight losses of captive birds. Eight birds, trapped and weighed in the evening, were kept overnight in cages, at least three in each, where they were able to roost side-by-side in the normal fashion. They were weighed again in the morning. This was carried out in February and August, and the mean overnight loss in weight was subtracted from evening weighings to make them directly comparable with early morning measurements. The February correction factor was applied to weights in November-February, and the August factor to all other weightings. The correction was applied to evening weighings because those done in the morning were more numerous, and hence the maximum number of uncorrected data could be used.

The mean overnight loss of weight recorded in February was 8% of evening weight (range 6.7-8.7), and in August 5% (range 4.1-7.1). To reduce variation due to size an index of weight/tarsus length was calculated. Weights and measurements of all Common Babblers used in this analysis are given in Appendix 7.

Figure 5a shows the mean corrected weight index for four periods of the year. Adult and juvenile/first year birds are shown separately. Differences between adults and juveniles/first year birds are significant in July-October and in November-December, and approach significance at the 5% level in January-February. The magnitude of the difference is smaller in November-December than in July-October, reflecting an increase in the weight of first year birds following the completion of the post-juvenile moult. For both age classes weights are significantly lower in January-February than in November-December, which probably reflects decreased availability of food and lower temperatures, leading to a general loss of condition in the latter half of the winter.

To investigate the relationship between temperature and body-weight the corrected weights of birds captured were compared with the minimum temperature recorded during the preceding 24 hours. In order to eliminate size variation only differences between weighings of the same individual were considered. Minimum temperatures were divided into seven, four-degree categories, ranging from 5-33 degrees C. A total of 63 birds were trapped at temperatures falling into two or more of these categories, and these weights are listed in Appendix 10.

Figure 5b shows the mean differences between weights of the same birds at different temperatures. Differences positively correlated with temperatures were treated as positive and successive categories summed to give a cumulative difference starting from the highest temperature category. Where trappings were not made in adjacent temperature ranges the difference was divided equally between the intervening categories. Hence a bird trapped

Figure 5a. Mean weights of first year and adult Common Babblers trapped in the Ridge study area at four periods during the year.

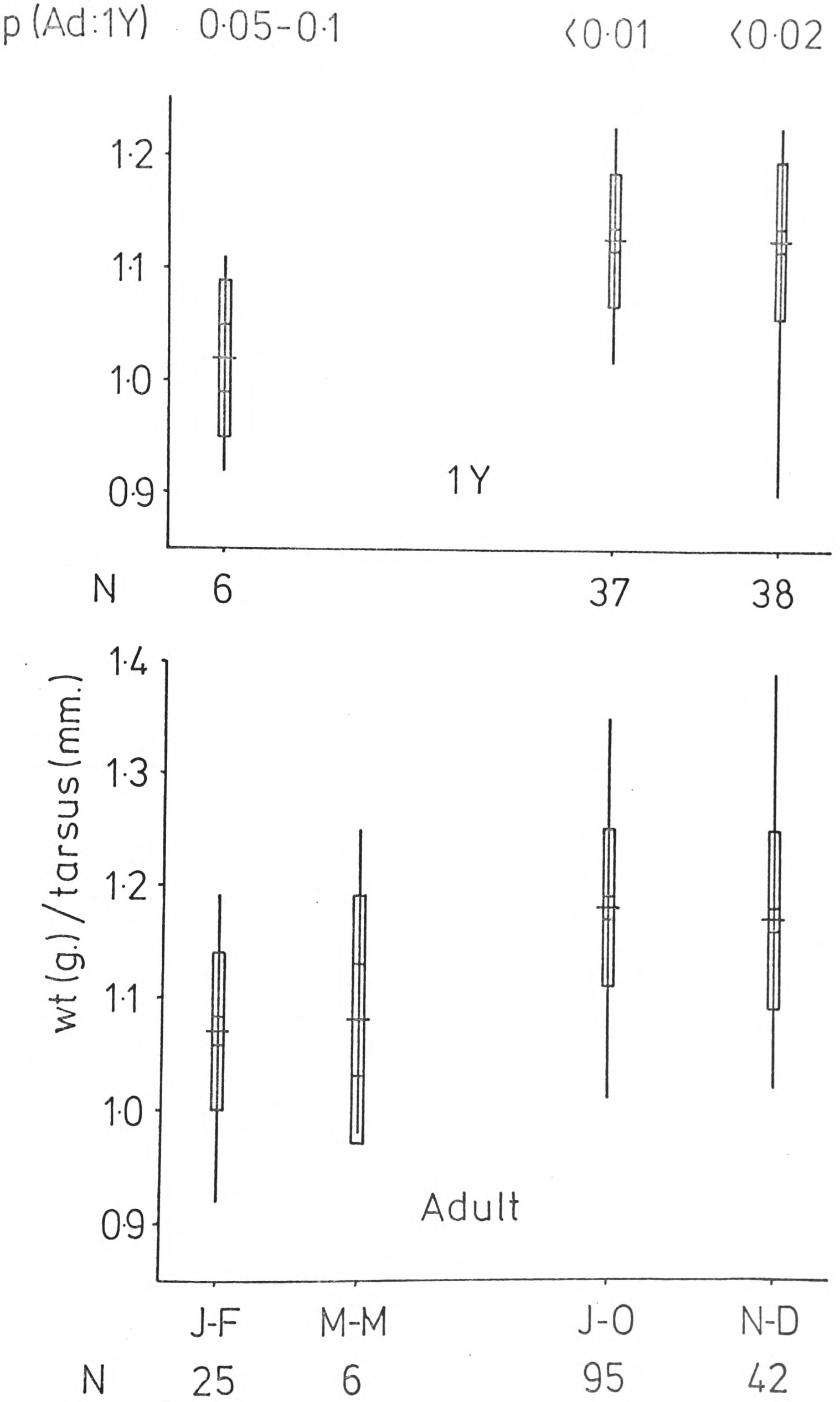


Figure 5b. Differences in weight between trappings of the same bird at different temperatures. Temperature categories; A 5.1-9.0, B 9.1-13.0, C 13.1-17.0, D 17.1-21.0, E 21.1-25.0, F 25.1-29.0, G 29.1-33.0 (^{o}C.). For further explanations see text.

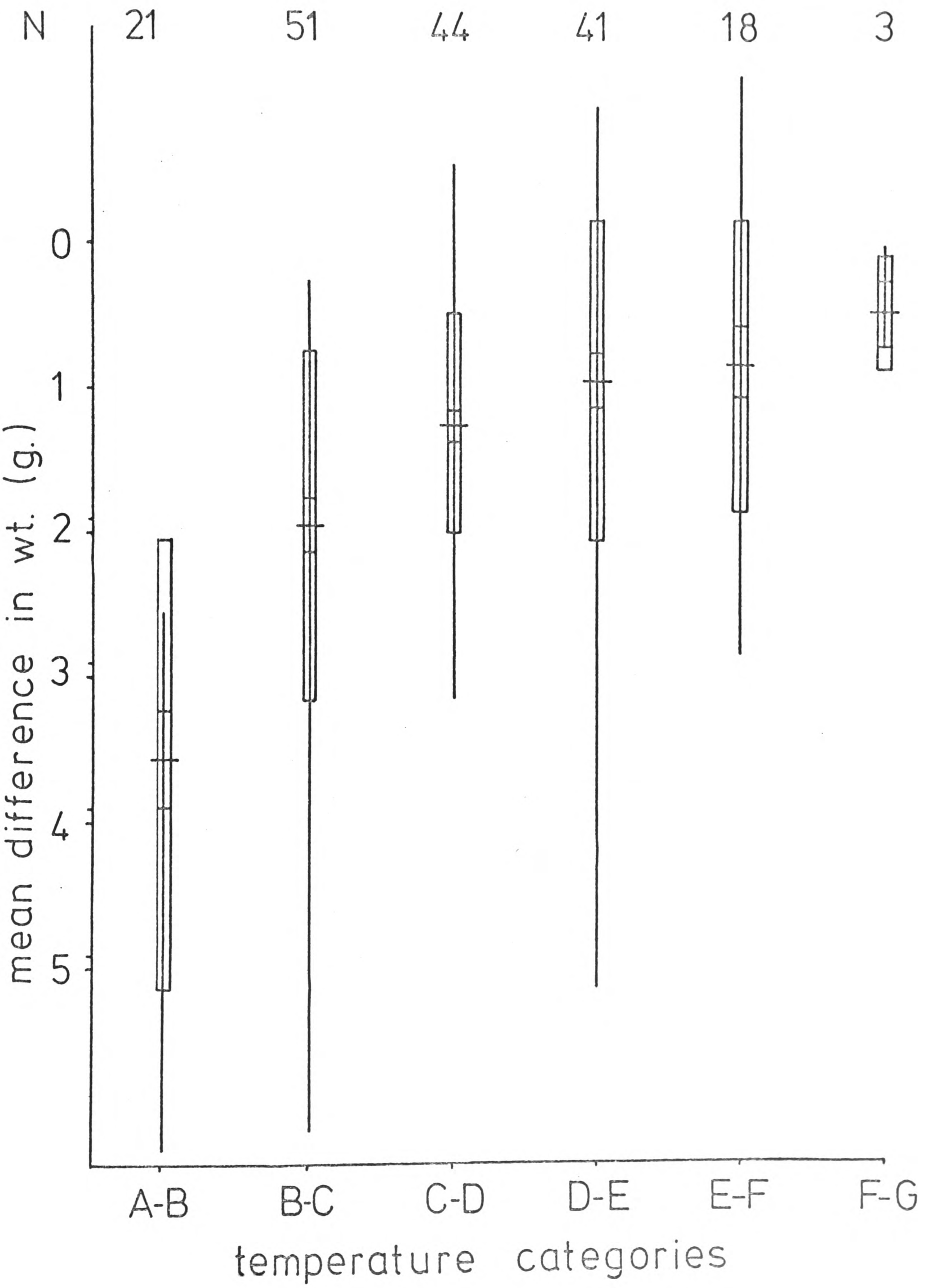
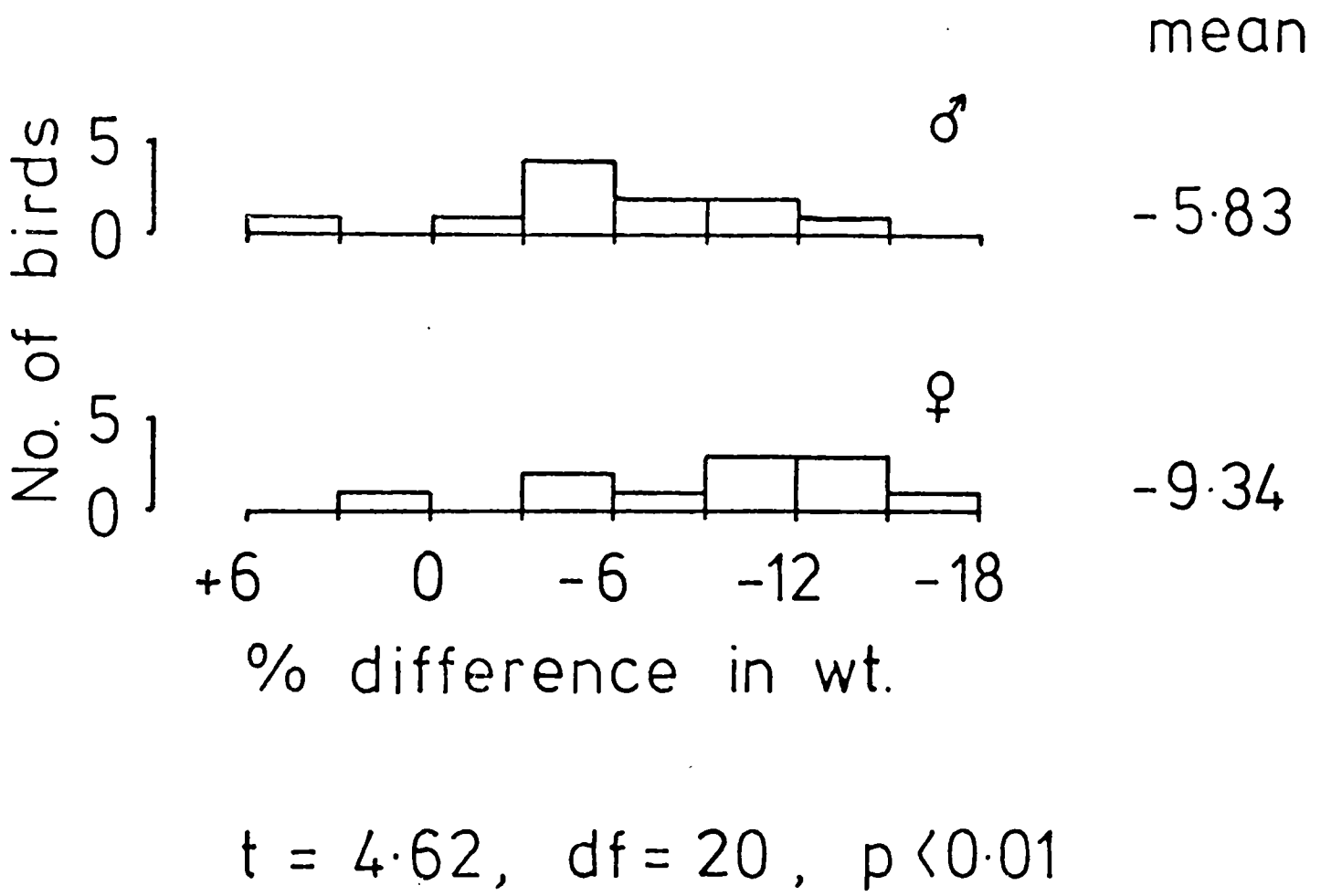


Figure 5c. Percentage difference in weight between trappings of the same bird at above and below 12°C. The difference is treated as negative if the weight in the lower temperature range was below that in the higher.



$t = 4{\cdot}62$, $df = 20$, $p < 0{\cdot}01$

at temperatures A and D, with a difference in weight of 3g, contributed 1g difference to each of categories A-B, B-C and C-D.

The figure suggests a steady decline in body weight with temperature, becoming steeper towards the lower end of the observed temperature range. The mean difference between weights in the highest and lowest temperature categories was 3.55g, 10% of mean male body-weight, and 11% of female. Calculations based only on birds of known sex, however, suggest that percentage weight loss with temperature is greater for females than for males. Figure 5c shows the percentage difference in weight between the means of weighings of the same birds at above and below 12 degrees. The mean difference for females is 9.3% and for males 5.8% of median body weight. Individuals included in this analysis are indicated in Appendix 8.

In January and February 1975 eleven Common Babblers were trapped at Dhok Pathan, in the Salt Range of Pakistan, just before going to roost. Overnight temperatures at the time were between $-1^{\circ}C$ and $+5^{\circ}C$ and the duration of the roost period was about 13 hours. Four of the birds were allowed to roost overnight and killed in the morning, the rest were killed immediately. All were preserved and later dried to constant weight and their fat extracted.

Extractable fat was found to constitute a mean of 9.25% of total body weight (30% of lean dry weight) for the seven birds killed in the evening and 6.85% (22%) for birds killed the next morning. These amounts are similar to those found by Evans (loc. cit.) in Yellowhammers Emberiza citrinella going to roost at similar temperatures near Oxford.

The Salt Range area experiences lower winter temperatures than Delhi and on average Common Babblers in this area are significantly larger in weight and wing-length than birds trapped around Delhi (Wing, $\bar{x}\ \sigma^{\prime} = 79.7$, $\bar{x}\ \varphi = 77.0$, cf. Table D). Despite this it seem unlikely that the capacity to deposit fat during the winter would differ between the two populations. It

therefore seems reasonable to assume that Common Babblers at Delhi survived overnight by metabolising fat stores, as has been demonstrated for temperate passerines. If this is the case it seems necessary to assume that observed weight changes between winter and summer were due to changes in lean weight, presumably muscle.

Discussion

Observed seasonal weight fluctuations of Common Babblers seemed to follow the pattern described by Ward and Fogden (loc. cit.) for birds in the non-seasonal tropics. Weights were high during the main breeding peak, and fell to their lowest during the period of low temperatures, scarce food, and short day-length which occurs in late winter. This decline in weight was probably due to a decrease in muscle weights, as observed for the bulbul Pycnonotus goavier by Ward (1969).

The shape of the curve produced in Figure 5b, if extrapolated to the lowest temperature recorded during the study ($0^{\circ}C$), suggests that the lowest mean weight might be about 5.5g (15% of body weight) below that maintained at the highest temperatures. Assuming variability similar to that observed at higher temperatures, some of the population might then be as much as 7g (20% of body weight) below maximum.

Ward (1969a) found that bulbuls (Pycnonotus goavier) which had been starved to death lost 22-24% of evening weight. This suggests that the kind of weight losses which can be predicted for Common Babblers at the lowest temperatures would be likely to cause severe stress, possibly resulting in death, for a proportion of the population. It therefore seems reasonable to hypothesize that availability of food during the cold season, affecting conditions and overnight survival could, at least at times, be a factor controlling population density in the Common Babbler.

Why the decline of body-weight with temperature should be greater for females than for males is not easily explicable. Most of the weighings made at below 12°C, however, took place in February, just prior to the breeding season, at which time there was probably intense rivalry between females to achieve breeding status. If aggression associated with this rivalry involved the expenditure of time and energy that might otherwise have been devoted to feeding, then this might explain the observed difference. Unfortunately the sample did not include any first year females, which under the above hypothesis might have been expected to show less weight loss as long as they remained in their natal group.

b) Reproductive success

Thirty-seven Common Babbler's nests were found during laying or incubation and details of the success of these nests are given in Appendix 8. Twenty-one (57%) of these succeeded in fledging at least one young, the mean number fledging per successful nest being 2.38. In 1972 and '73 estimates were made of the number of young fledged by 13 groups on the basis of nests found and birds seen just after fledging. These figures are shown in Table 5A, the mean estimates being 3.4 young per group in 1972 and 2.8 in 1973.

A comparison of some reproductive parameters for Common and Jungle Babblers is given in Table 5B. The smaller clutch size and lower hatching success of the Common Babbler, only partly offset by the higher survival rate of nestlings, led to a slightly lower productivity per nest. The mean number of young reared per group of Common Babblers in 1972 and '73, however, was higher than that observed for Jungle Babbler groups (Table 1E).

The number of young reared per group in 1971 was estimated from the proportion of juvenile and first year birds among those trapped in October

Table 5A. Estimated numbers of young Common Babblers reared per group.

Group	B	C	D	G	L	M	P	R	W	Y	A	F	O	Mean
1972	2	3	2	4*	5*	3*	3	2	6*	2	4*	7*	2	3.4
1973	5*	2	3	3	0	3*	4*	0	3*	2	2	6*	3	2.8

*two broods reared

Table 5B. Comparisons of some parameters of nesting success for Common and Jungle Babblers.

	Jungle Babbler	Common Babbler
Mean clutch	3.74	3.38
Nests predated before hatch	26%	35%
Mean no. hatched per nest	3.13	2.83
Total nests predated	45%	43%
Mean no. fledged per nest	2.56	2.38
Successful nests per year	1.09	1.31
No. fledged per group, per year	2.79	3.11
Sample size	42	37

and November (given in Table 5F), by which time the majority of nestlings would have fledged, and the known group sizes (given in Table 5F). This method must considerably under-estimate the number reared because it takes no account of possible mortality prior to trapping, by which time most juveniles were at least a month old. Evidence from ringing of pulli suggested that mortality was heavy during the first few weeks after fledging. Despite this the overall estimate for 1971 was 3.1 young reared per group; still higher than that found for Jungle Babblers.

The greater number of young reared per Common Babbler group per season was apparently due to their making a larger number of nesting attempts. The mean number of successful nesting attempts, estimated from nests found and juvenile birds trapped, was 1.35 per group in 1972 and '73, compared with 1.09 for the Jungle Babbler (see Appendix 5).

There was also some evidence that groups of Common Babblers varied less in their ability to nest successfully than groups of Jungle Babblers. In 1972 and '73 75% of all Common Babbler groups were known to have made at least two nesting attempts, whereas during the same years only 58% of Jungle Babbler groups made more than one attempt. The coefficient of variation in the number of successful nesting attempts made per year was 0.47 among Common Babbler groups and 0.72 among Jungle Babblers. For the number of young reared per year the coefficient of variation among Common Babbler groups was 0.54 and among Jungle Babbler 0.78. These differences seem more likely to be due to a greater uniformity in the quality of Common Babbler territories than to interspecific differences in the variability of reproductive performance between the two populations. The hypothesis that territories occupied by Common Babblers were relatively more uniform than those held by Jungle Babblers was also supported by observations on the vegetation. The amount and density of scrub varied between Common Babbler territories, but all contained some apparently optimal nesting habitat and no classification

was possible on the basis of different vegetation types, as was done for the Jungle Babbler.

Patterns of breeding within Common Babbler groups could be classified into three types:

1) Groups within which only one pair attempted to breed in a season (A1973, C1972, '73, G1973, L1972, '73, M1973, R1973, Y1972, '73 = 10 group-seasons).

2) Groups in which one male bred successively with two different females in the same season (B1972, '73, M1972, W1972, '73 = 5 group-seasons).

3) Groups in which two pairs attempted to breed simultaneously (D1972, '73, P1972, '73, R1972).

The mean group sizes for groups exhibiting each of the above patterns are shown in Figure 5d. Groups in which two pairs attempted to breed simultaneously were significantly larger than others ($U = 0$, $p < 0.01$).

A comparison of breeding success for these types of group is shown in Table 5C. The number of young reared by groups in which successive polygyny occurred (type 2) was higher than the number reared by other groups ($U = 16$, $p = 0.05$-0.1), although the number reared per female was lower than for type 1 groups. In situations in which two pairs attempted to breed only one was successful, and in all cases this was the earlier of the two pairs to initiate nesting.

A comparison of groups size with breeding success showed that there was a slight but insignificant correlation in both 1972 ($r^s = 0.176$), and 1973 ($r^s = 0.36$). Table 5D shows the number of young reared by groups of four size classes in 1972 and 1973. There is a suggestion from these figures that groups of an intermediate size may be more successful in rearing young than those that are either very small or very large.

Figure 5d. The number of Common Babblers per group in relation to the number breeding within the group territory.

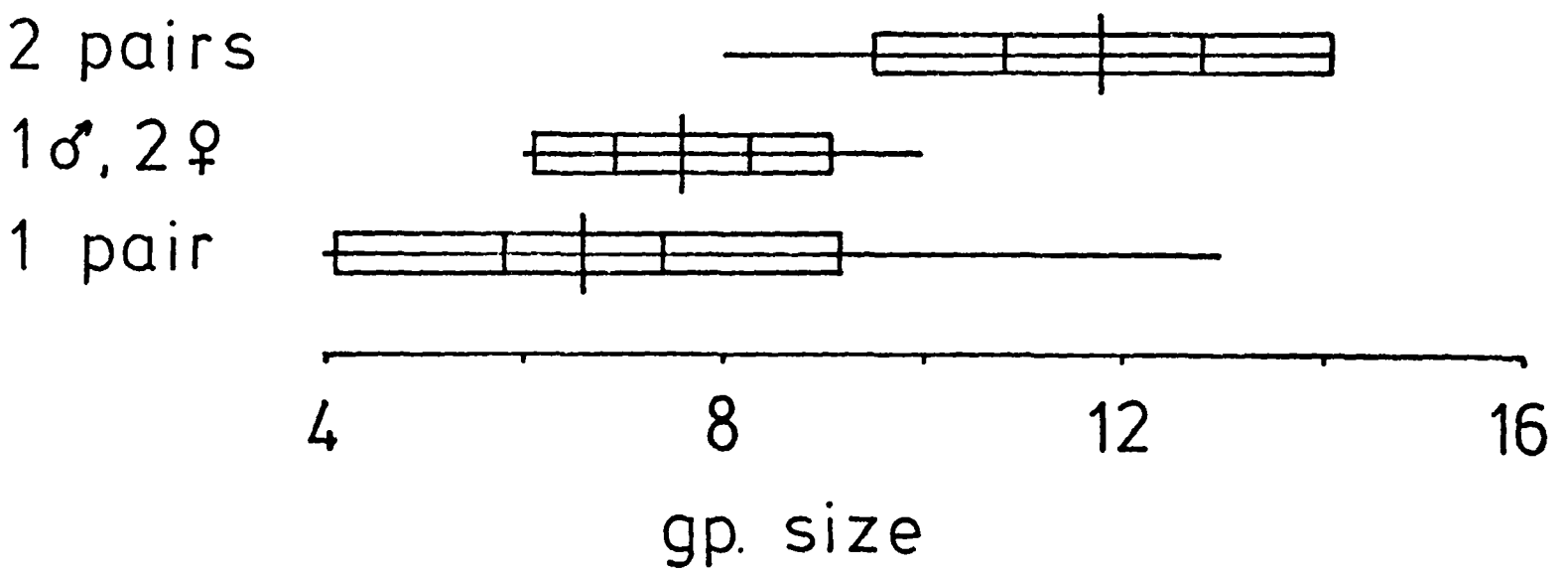


Table 5C. Reproductive success in relation to pattern of breeding within the group.

	Young fledged per season								
	0	1	2	3	4	5	6	7	Mean
Type 1	2		4	3		1			2.2
Type 2			1	2		1	1		3.8
Type 3			2	2	1				2.8

Type 1; only one pair attempts to breed

Type 2; one male breeds successively with two females

Type 3; two pairs attempt to breed

Table 5D. Numbers of young fledged by groups of four different size classes, 1972 and 1973.

	Numbers of birds per group (February)			
Number of young fledged	4-5	6-7	8-9	10+
7				1
6			1	1
5		2		
4			2	1
3	1	4	1	2
2	2	3		3
1				
0	1			
Mean	1.75	3.11	4.25	3.62

c) Survival of first year birds

The number of adult and first year birds trapped during September-November 1971 and '72 and their survival in subsequent years are shown in Table 5E. Full details are given in Appendix 9. First year birds constituted 31% of those trapped in October-November 1971, and 34% of those in 1972, giving a mean proportion of 32.5% at this season. Survival was estimated from subsequent sightings and recaptures. Seven cases of more than a year elapsing between sightings of the same bird were recorded. In three cases these were birds which had changed groups in the interim, and it is possible that they moved out of the study area temporarily, but the method clearly under-estimates survival.

Out of 17 birds of known sex recorded as still present in the group in which they had been reared at more than one year old, 16 were males. This suggests that nearly all females leave their native group during their first year. The timing of this departure could not be observed, but several females reared in July-September were still present in their native groups in the following February. No records of birds seen away from their native groups involved individuals less than six months old. These observations suggest that the bulk of female Common Babblers leave their native groups during their first summer.

There was a significant difference between the rates of survival of first year birds observed in 1971-72 and in 1972-73. The mean rate of survival was 55%. Assuming that 90% of all females disappeared during this period, owing to dispersal from their native groups, the survival of males can be calculated as 100%. This figure is clearly too high, but it does suggest that survival of first year males may be high relative to that of older males (see Section 5d).

Table 5E . Observed survival rates of Common Babblers.

	Sample	Surviving	Rate
1971-72 & 1972-73			
All adults	153	98	64%
1972-73 & 1973-74			
Breeding males	24	21	88%
Non-breeding males	59	38	64%
Breeding females	27	17	63%
Non-breeding females	29	19	65%
All adults			
1971-72	56	37	66%
1972-73	97	61	63%
1973-74	60	46	77%
First years			
1971-72	24	19	79%
1972-73	41	10	24%
1973-74	12	8	67%
Totals (first years)	77	37	48%

Table 5F . Estimates of the size of Common Babbler groups made in February

Group	B	C	D	G	L	M	P	R	W	Y	A	F	O	Total(B-Y)
1972	7	5	12	8	7	10	12	13	8	6	9	15		88
1973	7	6	8	7	4	6	14	13	7	5	5	13	6	77
1974	6	2	11	7	5	5	10	7	6	6				65(71)
1971 (Nov.)		6	13	8	7	11	14	14	8	6		15	8	

The figure in brackets after the total for 1974 includes two new groups of three established within the territories of groups B-Y.

Five cases of birds breeding in a group in which they had earlier been trapped as juveniles all involved males. Out of eleven cases where one member of a new breeding pair was ringed, and the other unringed, only one involved an unringed male ($p < 0.01$, binomial test). Since more than 50% of the population was ringed in 1972, and more than 70% in 1973, it seems likely that the higher proportion of unringed females indicates that some were immigrants from outside the study area. Six out of seven cases in which birds were observed to change groups involved females ($p = 0.06$, binomial test), and three of these were first year birds. One of them later bred in the group that it joined.

Combining observations on the relatively higher proportion of males persisting and breeding in their native groups, and the higher proportion of females changing groups and breeding outside their native groups, it seems likely that Common Babbler groups comprise male clans of a common lineage, with a variable number of immigrant unrelated females. It is possible that in some instances where two or more females joined a group simultaneously they may have originated from the same native group, in which case they would probably have been reared in the same year, being therefore siblings or half-siblings. No evidence for this was found.

d) Adult survival

Adult survival, calculated from retrappings and sightings during September-November of birds trapped or sighted in the previous September-November, is shown in Table 5E. This gives an overall adult survival of 63%. Calculations made on the same basis for birds of known sex, which involve only figures for 1972-73 and 1973-74, are also given. Those for 1973-74 are made on the assumption that birds present in June 1974 (when observations ceased) survived until September. Survival of non-breeders

is calculated as the proportion surviving from one year in which they did not breed to the next, irrespective of whether or not they bred in the second year. The survival of breeders is similarly calculated from one year in which they were known to have bred, at least to the stage of laying eggs, to the following year, irrespective of whether they bred in the second year.

The estimated survival of non-breeders of both sexes, and of breeding females, was very similar to that observed for the entire adult population. Breeding males exhibited a higher survival than other classes, however, and the difference between these and the non-breeding males approached significance ($chi^2 = 3.37$, $p = 0.05$-0.1). All three changes of breeding males observed were accompanied by changes of breeding female. This might be expected because of the chance that a female, remating within the same group, might do so with one of its own offspring.

e) Group size and composition

Minimum estimates of group size made in February-March are given in Table 5F. The variation within groups is considerably less than that between groups ($F = 7.65$, $p < 0.01$). To reduce the effect of group size in year x in determining group size in year y a comparison was made only between 1972 and 1974, but the between-group variation was still significantly greater ($F = 4.85$, $p < 0.01$).

No new groups became established in 1972 or '73 within the area covered by group B-Y (as listed in Table 5F). Some attempted establishments were probably overlooked. In 1974 several new groups became established, but the fact that they persisted may have been due to removal experiments carried out in February (see Section 6b). The totals of groups B-Y prior to removals showed a decrease of 19% in two years. Eight groups registered a decline between 1972 and 1974, one group remained the same size, and one rose by one bird. The factor causing a reduction in the population appears to have

operated rather uniformly.

The activity of graziers in cutting Zizyphus scrub, apparently in order to encourage the growth of grass, may have caused the observed decline in the Common Babbler population, since this species will not forage more than a few metres from cover. The cutting was not being practised in 1969-70 when I visited the study area on several occasions. The drought of 1972, following which the survival of first year birds was low, must also have had some effect.

Observed rates of adult survival were insufficient to maintain the population given the observed rate of reproduction (Section 5b). The difference must have been made up by immigration from outside the study area. This immigration could not be calculated accurately, but out of 41 birds more than one year old trapped from seven groups in the spring of 1974, ten were non-breeding females, and hence presumably unrelated to the groups in which they were trapped. Assuming that this mean of 1.4 foreign females per group was typical, the formula (1) given in Section 1f can be used to estimate the rate of immigration. For Common Babblers, however, it was not necessary to assume that foreign birds disappeared at the same rate as native ones, since the rate of disappearance of foreign birds (35% per annum, Table 5E) was known.

If x (total foreign birds per group) = $\frac{a \text{ (number joining per group per yr)}}{b \text{ (proportion disappearing per yr)}}$

then $a = bx$

Hence, substituting the above figures:

$a = 0.35 \times 1.4 = 0.5$ birds per group per year

The composition of the seven groups is shown in detail in Table 5G.

Calculation of the average group composition by the method used for Jungle Babblers (Section 1f) was not appropriate because of the declining population. The proportion of first year birds present in spring 1973 and '74

Table 5G. Composition of seven Common Babbler groups trapped during the spring of 1974.

Group	Date	1973 breeders	Ad males	Ad females	1Y	?
R	Feb. 3	2	2	2		1
G	Feb. 12	2	2	2	1	
D	Feb. 13	3(2m,1f)	3	3	1	
Y	Feb. 25	2		1	1	2
P	Feb. 27	2	1	1	3	2
M	Apr. 2	2	1		1	1
W	Apr. 17	3(1m,2f)	2	1	1	
Totals		16	11	10	8	6
Newly formed groups in the same area						
H (males from R gp.)			2	1		
I (male from P gp.)			1	1		1
J (male from W gp.)			1	1		1
Totals (new and established)		16	15	13	8	8

Proportion of 1Y birds = 8/60 = 13%

Adult sex ratio = 23m : 21f (with 8 unknown)

was probably lower than normal, and hence the proportion of non-breeding females may have been higher than usual. Assuming that the mean of 1.4 non-breeding females per group, observed in 1974, remained constant during the study, then their proportion ranged from 16-20% of the total population, double that for Jungle Babblers.

Summary

1) Seasonal weight changes among adult Common Babblers were strongly correlated with minimum temperatures. Weight losses during the cold weather indicated that mortality at this season might be a factor controlling population density.

2) Common Babbler groups reared a mean of three young per year, slightly more than Jungle Babblers. Groups in which successive polygyny occurred were more successful than others.

3) Breeding success was less variable among Common Babbler groups than among Jungle Babblers, and this was probably due to differences in the range of quality of the habitat occupied.

4) Most female Common Babblers left their group during their first summer to join other groups, whereas most males remained indefinitely in their native group, and several were observed breeding in the same group.

5) The proportion of unrelated females in established groups of Common Babblers is greater than that found in Jungle Babblers.

6) A decline in the population during the course of the study was possibly caused by changes in the habitat, reducing over-winter survival.

Chapter 6. Territory

Chapter 6. Territory

a) Territory size and population density

Common Babblers were absent from the wooded parts of the study area, except during March-May, when they were sometimes seen in closed-canopy woodland, although only in areas where there was a dense understorey of Prosopis or Lantana. Only one nest was recorded in woodland, all the rest being in scrub.

Outside closed-canopy woodland Common Babblers occupied all types of scrub, but avoided large areas of open ground. They would rarely forage more than a few metres from bushes, and retired into cover immediately on being disturbed. Figure 6a shows the distribution of 40m squares in which each group was recorded (home ranges), and their relationship to the main areas of closed canopy woodland.

Very little overlap between groups was observed. No instances of groups mixing together while foraging were recorded. No seasonal change in the utilisation of home ranges was detected, apart from the tendency to occur in closed-canopy woodland in March-May.

Contact between groups was very infrequent, and as a result overt territorial defence was rarely observed. In several cases where two groups, near the periphery of their home ranges, seemed to be moving in a way that might bring them into contact, one or other moved back towards the centre of their range. A few rather untidy encounters were seen in which two groups came into conflict. These were characterised by chases between individual birds and loud vocalisations, but fighting was seen only once.

The only piece of behaviour which suggested territorial advertisement was the tendency for groups to give brief bursts of calling from their roosts, both just after settling, and at dawn, just before leaving. Calls given on

Figure 6a. The Ridge study area, showing the position of Common Babbler group territories (diagonally hatched), nests and roosts. Stippled areas are closed-canopy woodland.

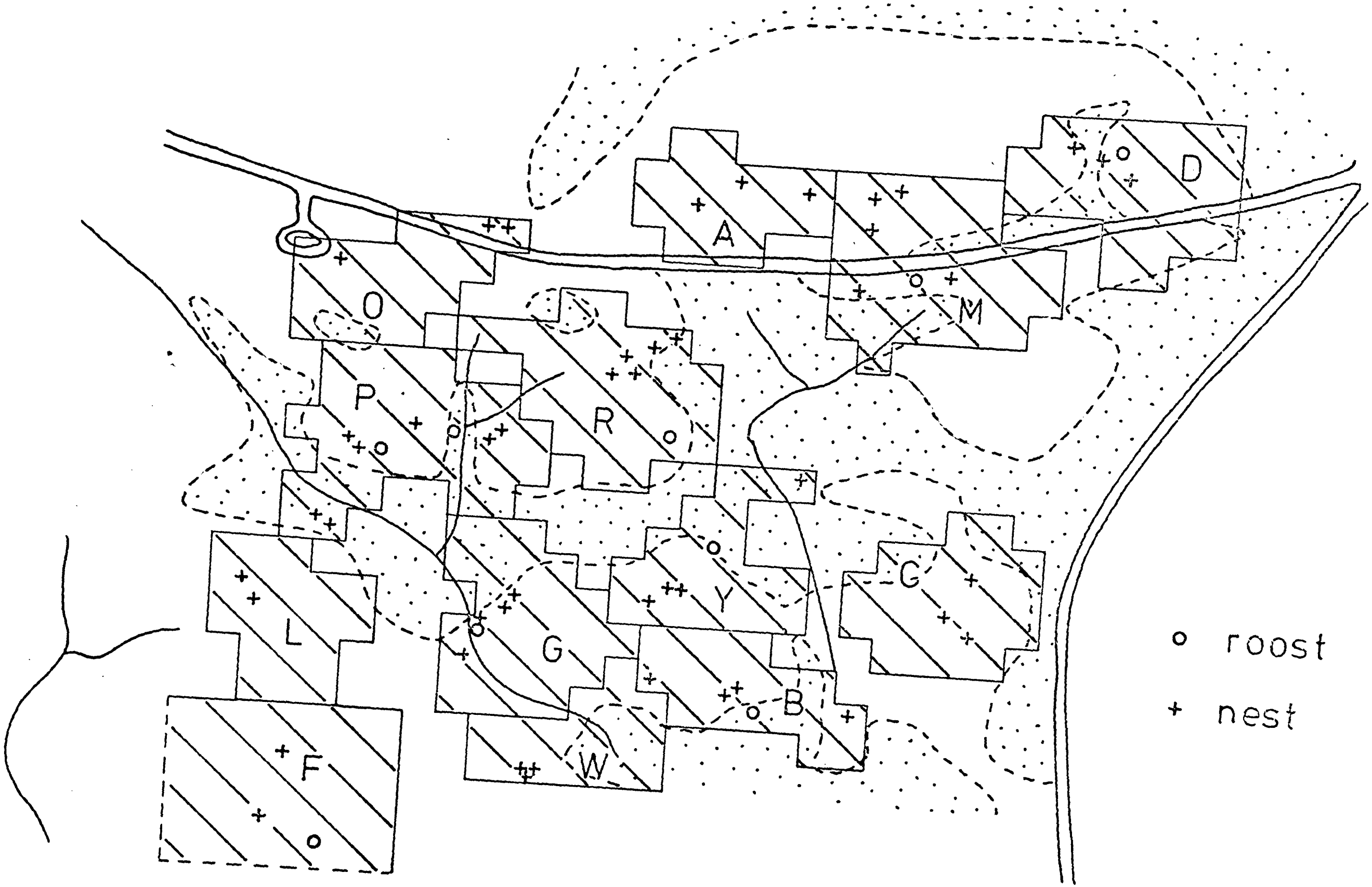
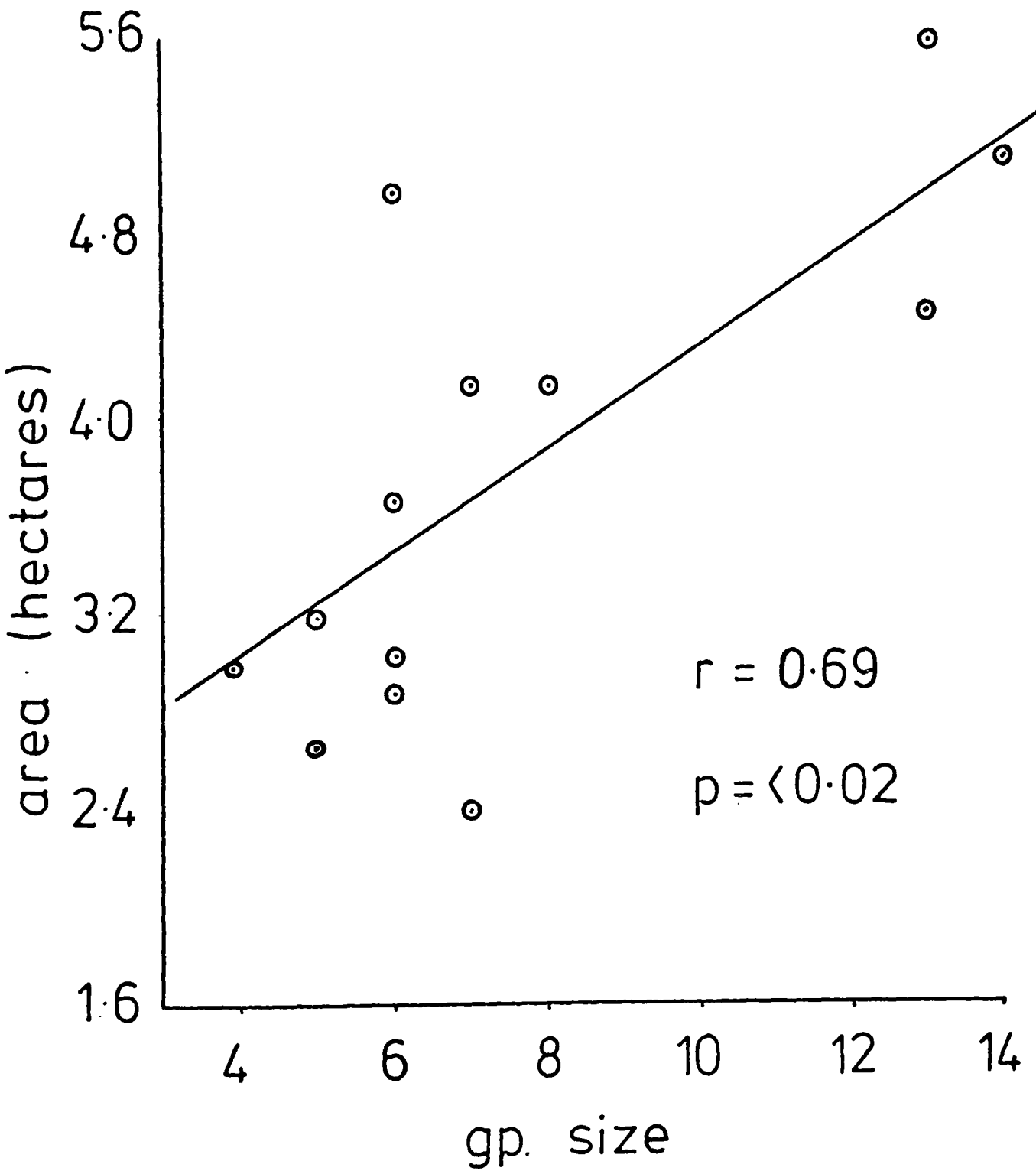

A
D
O
M
P
R
L
G
Y
G
B
W
F
o roost
+ nest

Figure 6b. The relationship between group size and the area of group territories among Common Babblers in the Ridge study area. Solid line is the regression of area on group size, 1973 only.



these occasions were of the alert/assembly type and several birds usually called together. When given in the evening they might have functioned to guide straying individuals towards the roost, but in the morning this could not have been the case. Most roosts were used regularly over many weeks, and must have been familiar to all members of the group, and it seems more likely that these regular vocalisations served to advertise the continuing presence of the group to their neighbours. These vocalisations were heard throughout the year and no seasonal fluctuation in their intensity was observed.

No attempts at establishing new groups resulting in successful breeding were observed during the study until after the experimental removals in the spring of 1974 (Section 6b). This may have been due to the steady decrease in population noted above. Two unsuccessful attempts observed involved three birds in each case, and included females from territories some distance away. The process of formation was not observed.

The size of home ranges, measured as the number of squares in which each group was recorded, was correlated with ~~the mean~~ group size in February 1973, and this relationship is shown in Figure 6b. [The increase in area did not bear a one-to-one relationship with group size, however, and a positive correlation was found between the density of birds per unit area within the home range and the mean group size in February, as illustrated in Figure 6c.] The solid line shows the regression of density on group size. This is significantly different from the horizontal line which would be expected if territories expanded in direct relation to the number of birds which they contained, assuming a uniform habitat.

The dotted line in Figure 6c shows the hypothetical relationship between group size and density assuming fixed territorial boundaries and

Figure 6c. The relationship between group size and the density of birds within the territory for Common Babblers in the Ridge study area. The dashed line shows the hypothetical relationship if territorial boundaries are fixed.

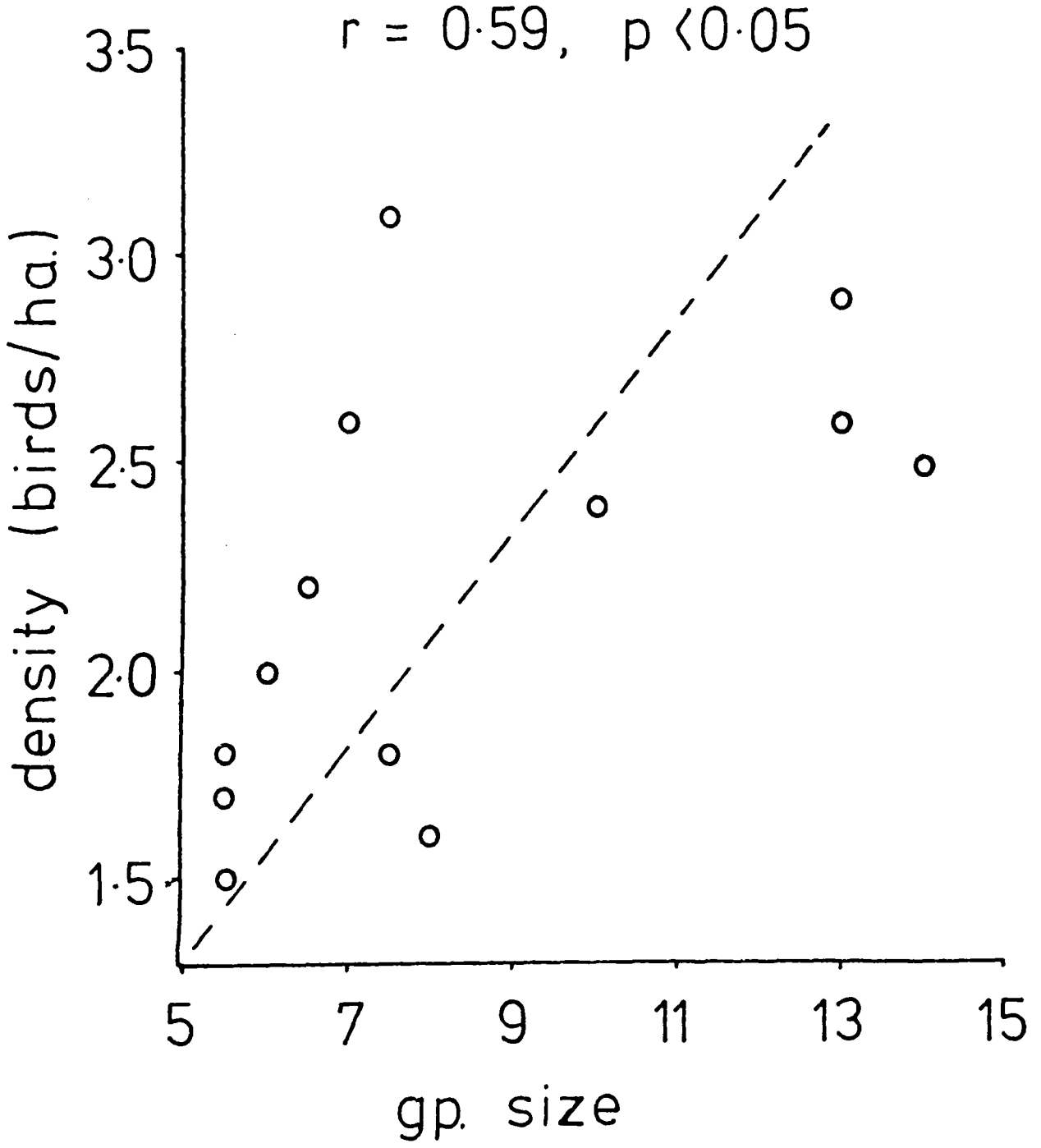
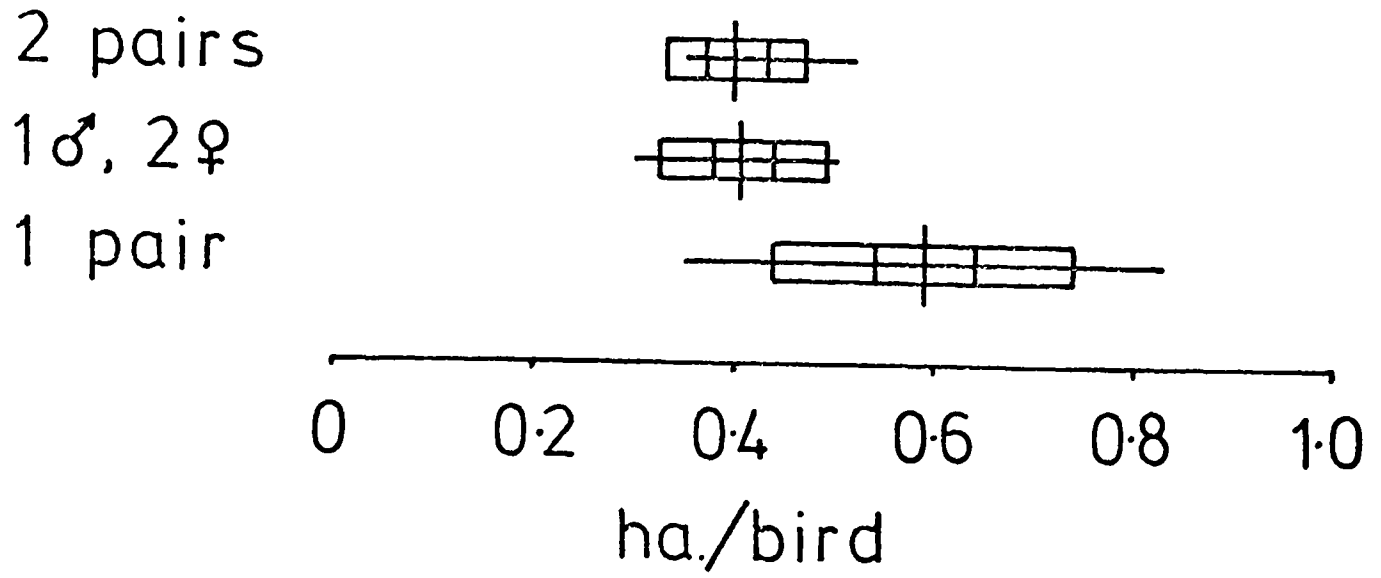


Figure 6d. The number of birds attempting to breed in relation to the density of birds within the group territory. Data for Common Babblers in the Ridge study area.



differences in group size created by random fluctuations. There is some resemblance between the slope of this line and the observed distribution of points. This hypothesis implies that food is likely to be scarcer in more densely populated territories. No evidence of this was found in the survival of first year birds, however, which showed a slight positive correlation with density ($r = 0.3$), instead of the negative correlation which might be predicted if densely populated territories contained less food per head than sparse territories. There was also a slight positive correlation between density and reproductive success over the years 1972 and '73 combined ($r = 0.2$).

Since counts made in February probably coincided with the critical period for food availability (Section 5a) it seems likely that larger groups occupied better quality habitat capable of supporting a greater density of birds. General observations on the vegetation suggested that scrub was denser in the territories of large groups, but no objective measurement was attempted.

Differences in the density of birds within territories were apparent between groups exhibiting the different patterns of breeding described in Section 5b. Territories in which only one pair bred during the season had a significantly lower density of birds than those in which two pairs attempted to breed, or those in which successive polygyny occurred, and this is shown in Figure 6d.

Counts of group size made in Pakistan in November 1973 supported the general hypothesis that group size increased with the density of birds, which was determined by the quality of the habitat. Table 6A gives details of counts of group size made in three different areas of the Salt Range, Campbellpur district, Punjab; at Chinji, Dhok Pathan, and Mahajan. At Dhok

Pathan groups were counted when going to roost, and the number of groups was determined by searching likely clumps of bushes for nests. Only a limited number of such clumps existed in the area and old nests, usually several in each clump, could be located easily. At Chinji the range of two ringed groups was estimated roughly by observing their movements over several days. The estimate of 0.5 km^2 for the area covered by these two groups, which totalled 23 birds, was deliberately generous. The species was very common at Mahajan but no measurement of density was made.

At Chinji and Mahajan Common Babblers inhabited bushy hillsides on the edges of cultivation. At Dhok Pathan the vegetation was similar in composition, but heavy over-grazing had made it very sparse. The area of cultivation was small and the hillsides largely bare rock. The density of Common Babblers at Dhok Pathan was very low, but despite this they were seen nearly everywhere in the area during the course of the study. One group was observed to travel one km in a straight line when moving to roost, emphasising the extent of territories in this area.

Movements of six females and one male Common Babblers from one established group to another within the Ridge study area and of five other birds from established groups to new ones, are shown in Figure 6e. The diagonal shading in the figure covers an area of woodland and bare rocky ground in which Common Babblers were very rarely observed. This seems to have acted as an effective barrier to dispersal since no interchange was observed between groups on opposite sides, despite the fact that at least one exchange occurred between nine out of the eleven groups to the east of the zone.

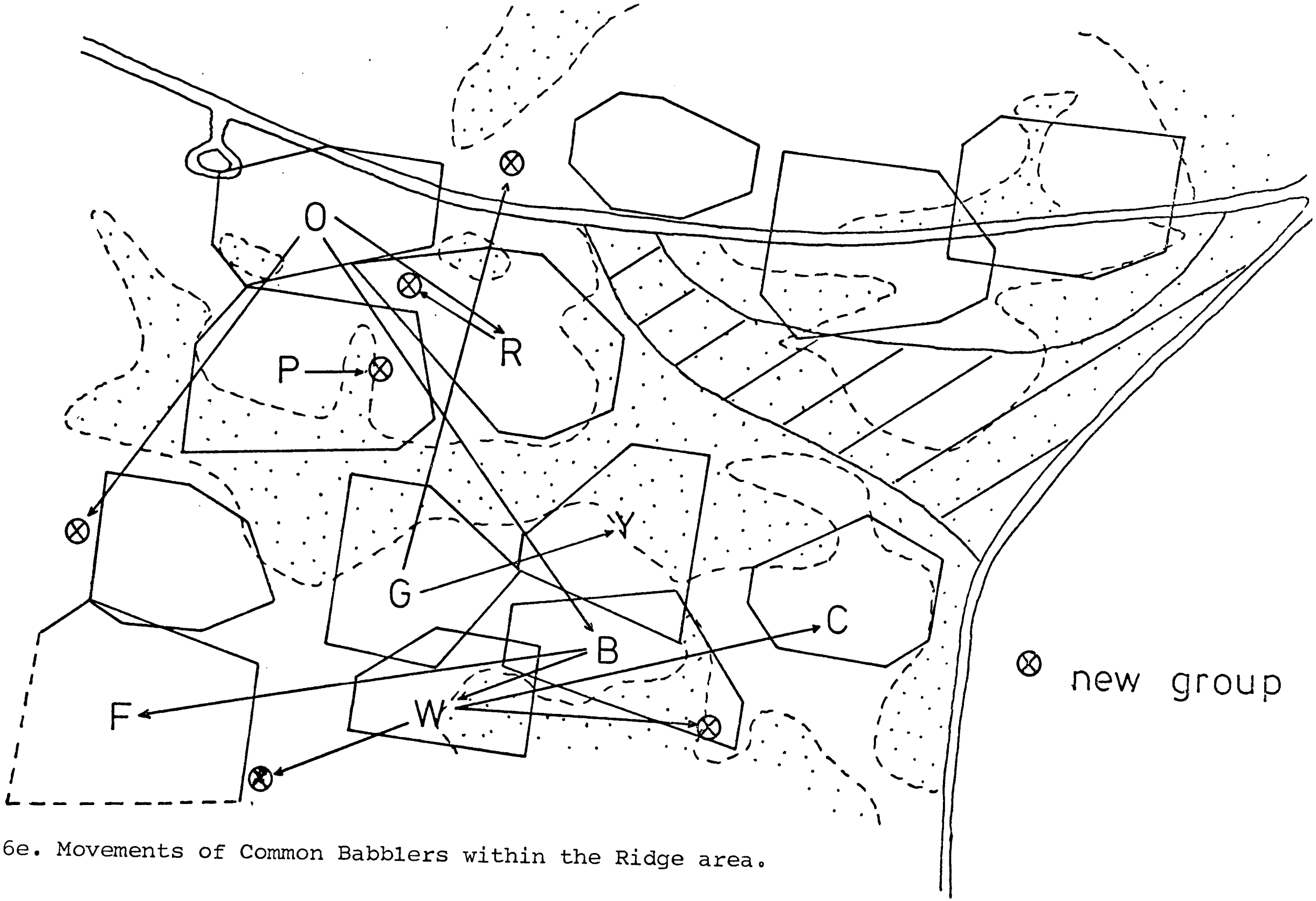


Figure 6e. Movements of Common Babblers within the Ridge area.

Table 6A. Densities of Common Babblers observed in Campbellpur district, Pakistan -

Locality	N. groups	Range	Mean gp.	Area(km^2)	Birds/km^2	Gps/km^2
Chinji	7	7-13	10.0*	0.5	46	4
Dhok Pathan	6	5-10	6.3*	6.0	6	1
Mahajan	3	10-18	13.7	?		

* Mann-Witney 'U' test for the difference between these two means, U = 5, p = 0.01

b) Removal experiments

During February 1974 permanent removals were carried out from several groups of Common Babblers to determine the effect of the following:

a) The removal of an entire group (G)

b) The removal of a breeding pair (Y)

c) The removal of several non-breeders (R, D, P)

Results

a) Group G, consisting of seven birds, was removed entirely on February 3. Their territory remained vacant until March 19 when L group, comprising five birds, was observed in the centre. From then onwards L group was observed regularly within the former territory of G group, and their own former territory was abandoned. This in turn was occupied by a newly formed group which was first seen near the periphery of L group's territory on February 23. Group L had been one of the smallest groups throughout the study, and in 1973 it failed to rear any young. The group was not observed to nest in its new territory before the termination of the study.

b) Four out of the six members of Y group were trapped and removed on February 25. These included the last season's breeding pair. The remaining two members, of unknown sex, continued to roost in the same area at least until March 5, but were not seen thereafter. A newly formed group was seen in the territory on March 27, and continued to visit the area until the end of the study, but it was also seen in other areas during the same period. In the area occupied by Y group, and the adjacent group B there were three groups established by April, including two formed that season. Group B and one of the newly formed groups attempted to breed. Although boundaries could not be exactly determined, it appeared that the area which had formerly contained two territories had been divided into three.

c) Six out of the seven members of R group were trapped on February 3 including the breeding pair of the previous season. All except the breeding pair of the previous season were removed. Two males formerly belonging to R group had previously established a new group (H) in conjunction with an unringed bird (presumed female) in a peripheral part of the R group range. This new group continued to exist until the termination of the study, but did not breed. The remaining three members of R group were joined by another unringed bird and continued to cover the same area which they had formerly held, excluding the portion occupied by group H. The same pair nested, laying about April 1.

Group R had been a large one throughout the study, and in 1972 two pairs attempted to breed simultaneously. At the end of the study it appeared that the former range had been divided into two, the bulk being retained by the former breeding pair.

On February 13 three adult females and two adult males were removed from group D, leaving six birds comprising the breeding pair from the previous season, two adult males, and one first year, and one adult of unknown sex.

The group continued to occupy the same territory, but a new group became established on the periphery, including at least one male from a neighbouring group, and this persisted. Another established group (M) appeared to encroach somewhat on the former range of D group. A great deal of habitat destruction had taken place in the former M group range.

The breeding male of D group in 1973 apparently paired with a new immigrant female, as they were seen nest-building on April 19, but the nest was not completed and no other sign of breeding was seen before the end of the study. Group M laid about March 25. This nest was destroyed but they relaid and four young were fledged on May 4, a record number of young Common Babblers reared from one nest.

In mid-February, a group of three birds (I group), including an adult male from P group (PY), became established in a peripheral part of P group home range. On February 27 four birds, an adult and a first year of each sex, were removed from P group, leaving six birds, all adult, including the subordinate pair from the previous season. The group continued to occupy the same home range as before, except the portion occupied by I group. No nesting activity was recorded during the subsequent two months, although an unsuccessful attempt may have been overlooked. Group I nested, and laid the first egg about April 18.

At the termination of the study the area formerly occupied by 13 groups contained 18, discounting one right on the periphery. The position of the re-organised groups in June 1974 are shown in Figure 6f. All established groups continued to use roughly their former ranges, and all the new groups occupied areas which had been peripheral to former group ranges, except those which took over the territories of L and Y groups.

The winter of 1973-74 was a comparatively dry one, and in the spring of 1974 the breeding activity of Jungle Babblers was somewhat reduced compared with 1972 and '73. The breeding activity of Common Babblers was greater in the spring of 1974 than had been observed in 1973, however (in 1972

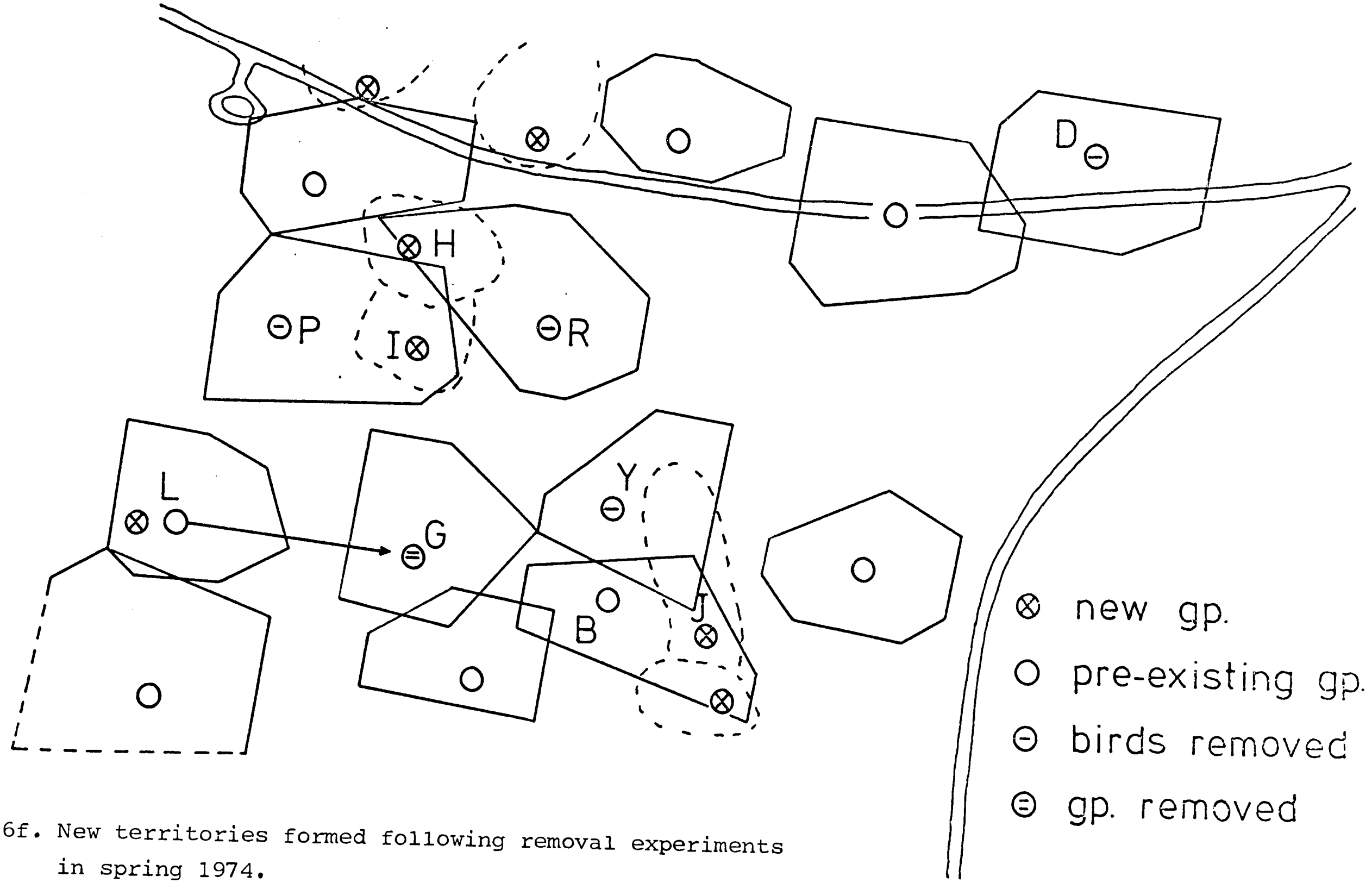


Figure 6f. New territories formed following removal experiments in spring 1974.

observations were incomplete) with nine groups laying eggs, compared to six in 1973, and a higher proportion laying clutches of four eggs, as shown in Table 6B. The initiation of nesting was also earlier in 1974, the mean date of first eggs being April 3 (n = 9), compared to April 9 in 1973 (n = 6).

Table 6B. Clutch sizes of Common Babblers in spring, 1973 and 1974

	Clutch size	
	3	4
1973	5	0
1974	3	4

p = 0.07, Fisher exact test.

Discussion

The removal of group G seems to have caused relatively little expansion on the part of adjacent groups. It may be significant that the group had occupied a fairly large territory at moderately low density (1.8 birds/ha), suggesting that the habitat within the territory may not have been optimal. Group L was smaller, and occupied a territory at slightly lower density. All the other adjacent groups were at a higher density (B, W, P), except Y from which removals were also made, and which had been effectively displaced by the end of March. The shifting of L group, rather than any of the others, therefore supports the hypothesis that groups living at higher densities occupied better quality territories.

The removal of the breeding pair from Y group was followed by the disappearance of the two remaining birds, but this is difficult to interpret since their sex was not known. Group Y was a small one, occupying a territory at comparatively low density (1.7 birds/ha), and the territory was probably not very attractive. This may account for why there was a re-arrangement of groups in the area instead of a simple replacement.

The removal of some non-breeding birds from D, P, and R groups seems to have had little effect on the status of these groups. All continued to use previous roosts and fed over roughly the same area. All suffered some encroachment from neighbouring groups, however, and it is possible that the persistence of the new groups formed in R group area (H), and on the borders of R and P groups (I), was made possible by the reductions brought about in the main groups. The general lowering of the population level, decreasing pressure on food supplies, may have accounted for the early nesting and large clutches observed, but other factors unrelated to the removals may also have played a part.

The increase in the number of groups within the study area following the removals suggested that there was nothing fundamentally indivisible about the pre-existing territories. The time-lag between the removals and the encroachment of other groups suggested that in the normal course of events traditional boundaries were rather infrequently transgressed. Because the removals were made at the end of the lean season, in a period when the availability of food was increasing, tendencies for expansion may have been lower than might have been the case in early winter.

Summary

1) Groups of Common Babblers held territories which overlapped very little, and contact between groups was infrequent.

2) Larger groups occupied larger territories than smaller ones, but the density of birds was higher in the territories of large groups.

3) There was some evidence that territories with a high density of birds were of a better quality than those with a low density.

4) Comparatively small areas of unsuitable habitat separating group ranges apparently reduced the frequency of interchange between them.

5) The artificial removal of birds from the population tended to promote the fragmentation of pre-existing groups and increased breeding activity.

Chapter 7. Behaviour during the breeding season

Chapter 7. Behaviour during the breeding season

a) Nest-building, laying, and incubation

Groups of Common Babblers, like those of Jungle Babblers, seemed less coherent during the summer than during the winter, and spread over a larger area while feeding. Despite this fragmented groups were rare and the breeding pair spent most of their time with the group, only leaving to attend the nest. No copulations were witnessed in this species.

Nest-building was carried out by both members of the pair, and in one case three birds were observed carrying material to the same nest. Building was quite difficult to observe and the participation of non-breeders may have been more frequent than it appeared. In two other cases non-breeders visited the nest during building without contributing to the construction.

Laying occurred between 0600-0900 hrs and no cases were observed of more than one egg laid on the same day. There were no clutches of more than four eggs (see Table E) and laying by more than one female therefore seems very unlikely. Continuous incubation began with the second or third egg, although the breeding female was sometimes found on the nest during the first day after laying commenced. Hatching always took place within 24 hours, suggesting that incubation during the first two days was not sufficient to initiate much development.

Incubation during the night was carried out by the breeding female. During the day the pair took turns, with some contribution from non-breeding birds. Two of the non-breeders observed to incubate were males, but the sex of the other four was not known. Out of 18 hours of observation at six different nests 53.5% of incubation was done by the breeding female, 31.5% by the breeding male, and only 15% by non-breeders. In two cases

non-breeding females were seen being driven off from the vicinity of the nest by the breeding female after they had approached it while she was incubating.

Calling from the nest was heard regularly during incubation. The call was similar to the assembly call of the species, but longer and more mellow in tone. Breeding females were heard giving this call on several occasions at all but one of the nests observed during incubation. Only one instance of calling from the nest by the breeding male, and one by a non-breeder, were observed during incubation. The call was generally given in the absence of other birds, often after 30 minutes or more of incubation.

Four non-breeding birds were collected during the incubation or nestling periods, two males and two females. Both of these males proved to have enlarged testes, but neither of the females showed any signs of ovarian development; the ovaries contained no oocytes more than 1mm in diameter and there were no signs of thickening of the oviduct.

b) Nestling period

The feeding of the nestlings was carried out by the parents and a variable number of non-breeders. Standard four-hour watches, from dawn on the 9-11 day after hatching, were carried out at thirteen nests, and at four of these watches were also performed earlier in the nestling period. At all four the proportion of feeding visits made by non-breeding birds increased with the age of the chicks, as did the overall rate of feeding.

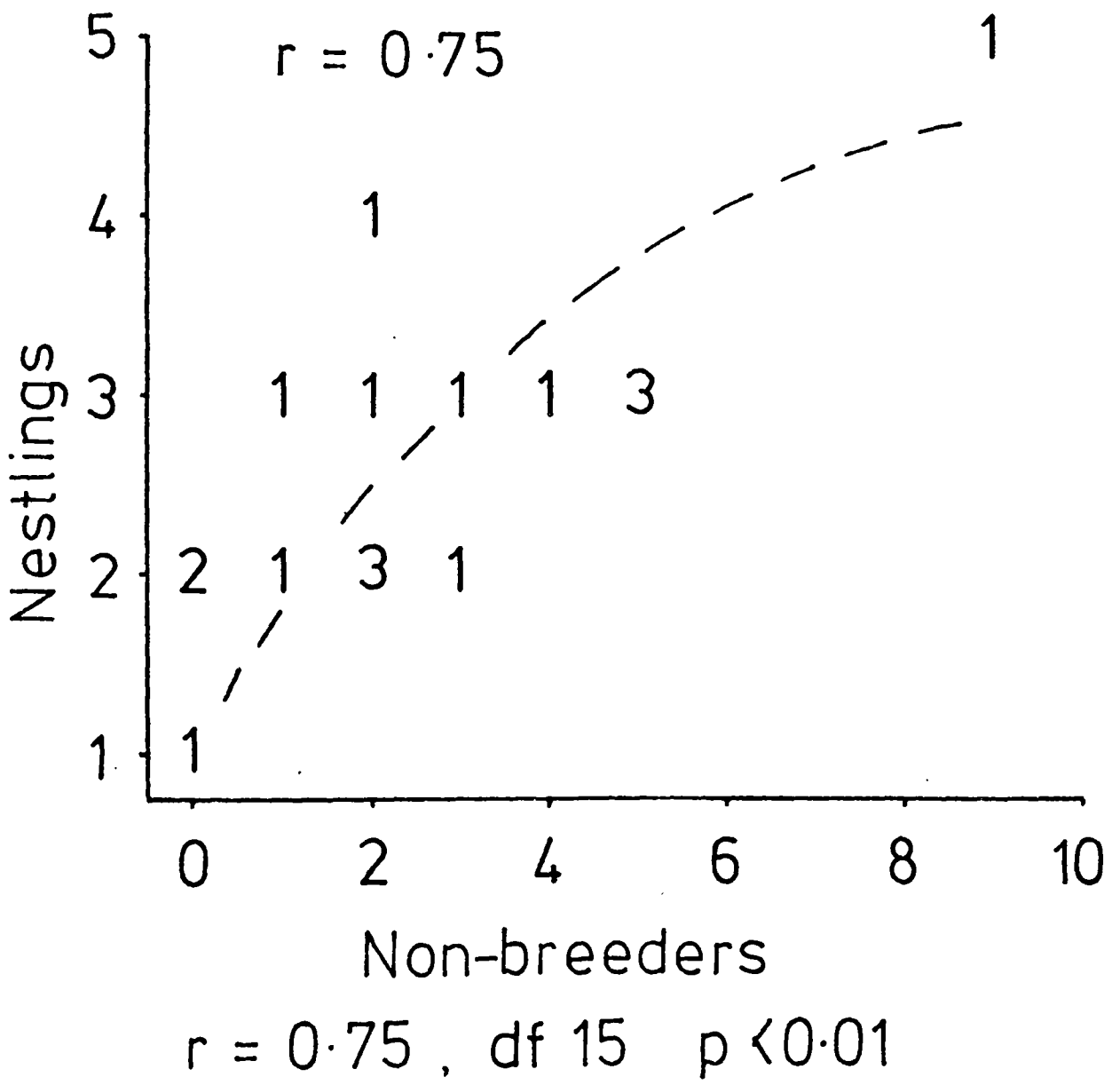
The results of the thirteen watches on days 9-11 are summarised in Table 7A. The number of non-breeders observed to bring food varied from 0-9 ($\bar{x}$ = 3.8). There was a positive correlation between the number of chicks in the nest during these watches and the number of non-breeders observed feeding. This is shown in Figure 7a, which includes four nests where observations were not made from a hide, but where prolonged watching of birds

Table 7A . Observations at Common Babblers' nests, made between 0600-1000 hrs on day 9, 10 or 11

NEST	NO. OF CHICKS (cuckoos in brackets)	VISITS	NON-BREEDERS	% OF VISITS BY BREEDERS	VISITS/CHICK*	VISITS/AD.
B1972/2	2	22	0	100%	11	11
Y1972/1	2	32	2	62%	16	8
R1972/2	3	36	5	44%	12	5.2
P1972/4	3(1)	93	9	31%	18.6	8.5
B1973/1	3	60	4	50%	20	10
B1973/3	2	70	3	60%	35	11
M1973/2	1(1)	27	1	59%	9	9
L1973/1	(1)	32	2	50%	16	8
E1973/3	1(1)	40	5	50%	13.3	5.7
A1973/2	2	29	0	100%	14.5	14.5
D1973/1	3	68	5	34%	22.7	9.7
W1974/1	3	39	2	50%	13	9.7
M1974/2	4	83	2	52%	20.7	20.7

* one cuckoo is counted as two babbler chicks

Figure 7a. The relationship between the number of nestlings in the nest on day 9-11 and the number of non-breeders recorded feeding them.



r = 0·75 , df 15 p <0·01

Figure 7b. Numbers of feeding visits recorded per nestling at nests watched on day 9-11, in relation to the size of the brood. Pied Crested Cuckoo nestlings are included and counted as two babblers.

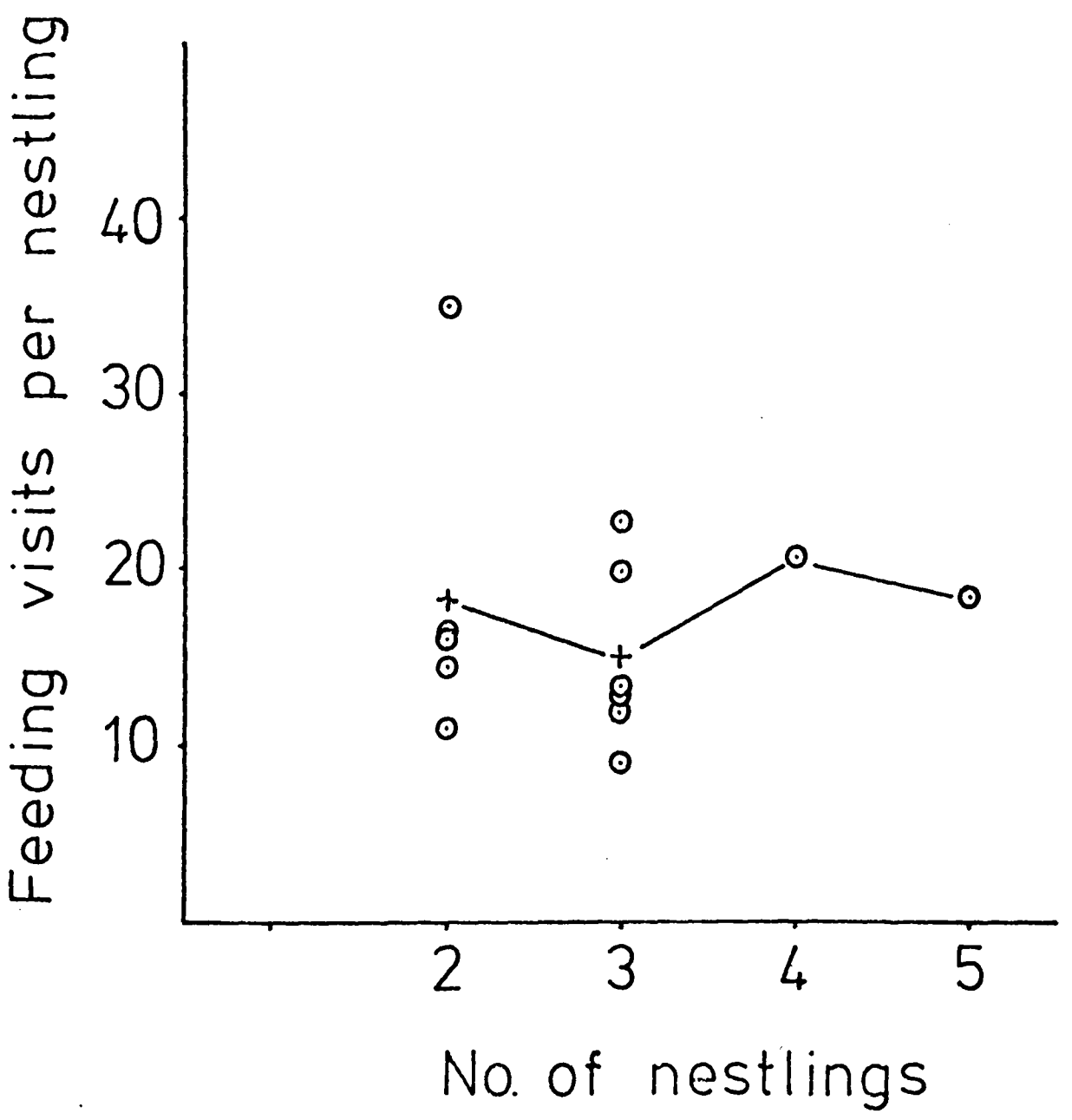
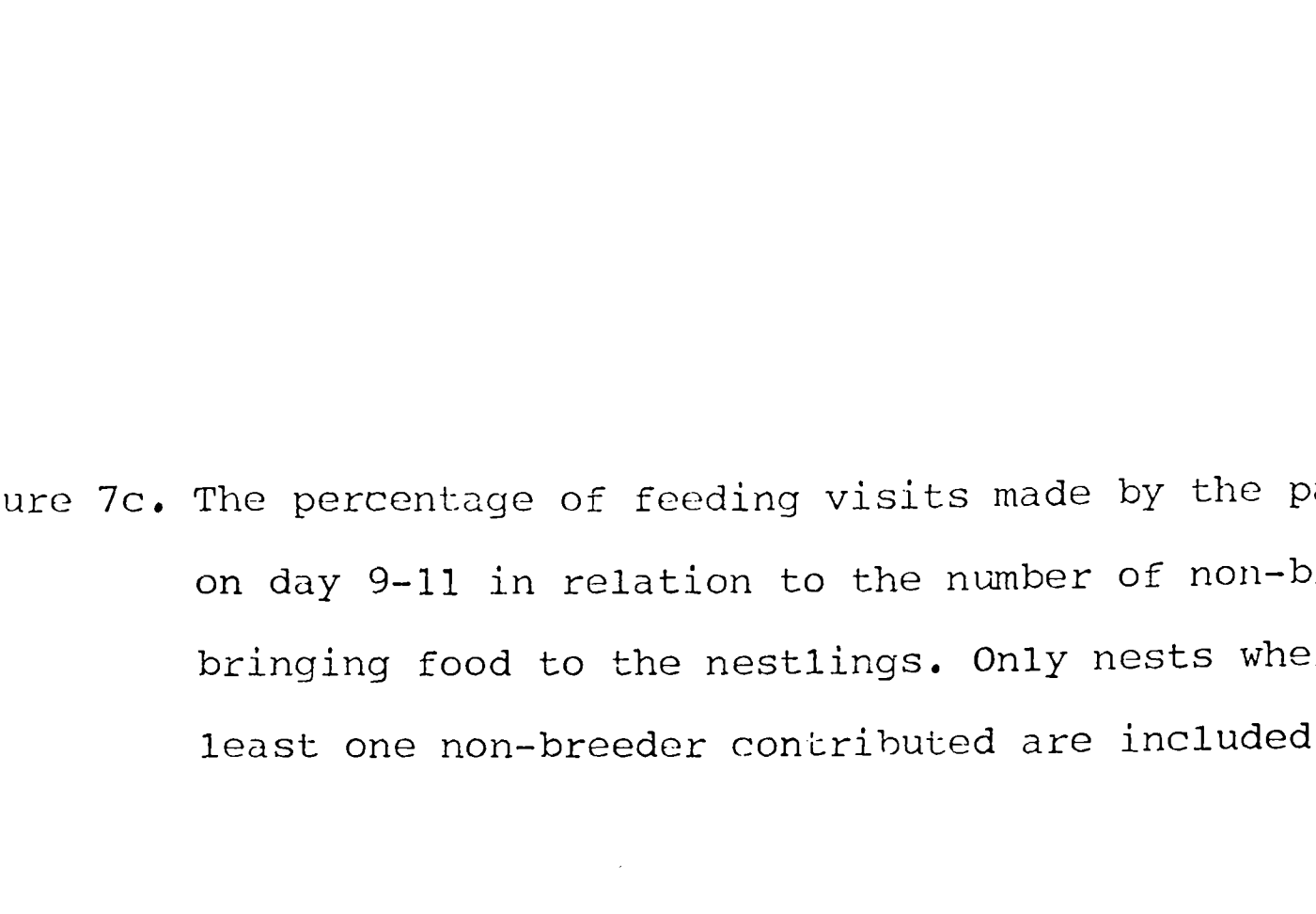


Figure 7c. The percentage of feeding visits made by the parents on day 9-11 in relation to the number of non-breeders bringing food to the nestlings. Only nests where at least one non-breeder contributed are included.



approaching the nest probably revealed all the non-breeders participating in feeding. No relationship was found between clutch size or hatching success and the number of non-breeders present.

As a result of the consistent relationship between the number of nestlings and the number of non-breeding birds participating in feeding there was no apparent correlation between the number of nestlings and the number of food items delivered per nestling, as illustrated in Figure 7b. The proportion of feeding visits made by the breeding pair at nest where at least one non-breeder participated showed a significant negative correlation with the number of non-breeding participants, and this is shown in Figure 7c.

The annual moult of the Common Babbler is initiated in July or early August. A number of breeding birds trapped during the incubation or nestling periods showed some new and some old primary feathers, but from the absence of any developing feathers they appeared to have arrested their moult. In a few cases birds were trapped again after two weeks in the same state, confirming that moult had been arrested. In other cases birds trapped during nesting exhibited partly grown feathers which suggested that moult was continuing. Table 7B gives the proportion of breeding birds showing arrested moult while breeding in relation to the size of their groups. Those in larger groups showed signs of arrested moult significantly less often than those in small groups. Breeding males showed arrested moult less often than females, but the difference was not significant.

Among non-breeding birds of known sex, a significantly higher proportion of males were seen feeding the nestlings. This is demonstrated in Table 7C. Of the three male non-breeders not recorded feeding nestlings, two were members of a group in which the breeding male nested successively with two different females. No non-breeders participated in the second nesting attempt.

Table 7B. State of moult of breeding birds trapped during the incubation or nestling periods, in relation to the size of their group, and their sex.

	Group size											
	2	3	4	5	6	7	8	9	10	11	12	13
Arrested	2	3	2	1	4		1		1			
Non-arrested				1	2		1		4			1

Median test, $chi^2 = 5.32$, $p < 0.05$

	Male	Female
Arrested	4	10
Non-arrested	5	7

Table 7C. Sex of non-breeders observed feeding nestlings.

	Observed feeding	Not observed feeding
Male	27	5
Female	5	7

$chi^2 = 8.0$, $p < 0.01$

full data are given in appendix 11.

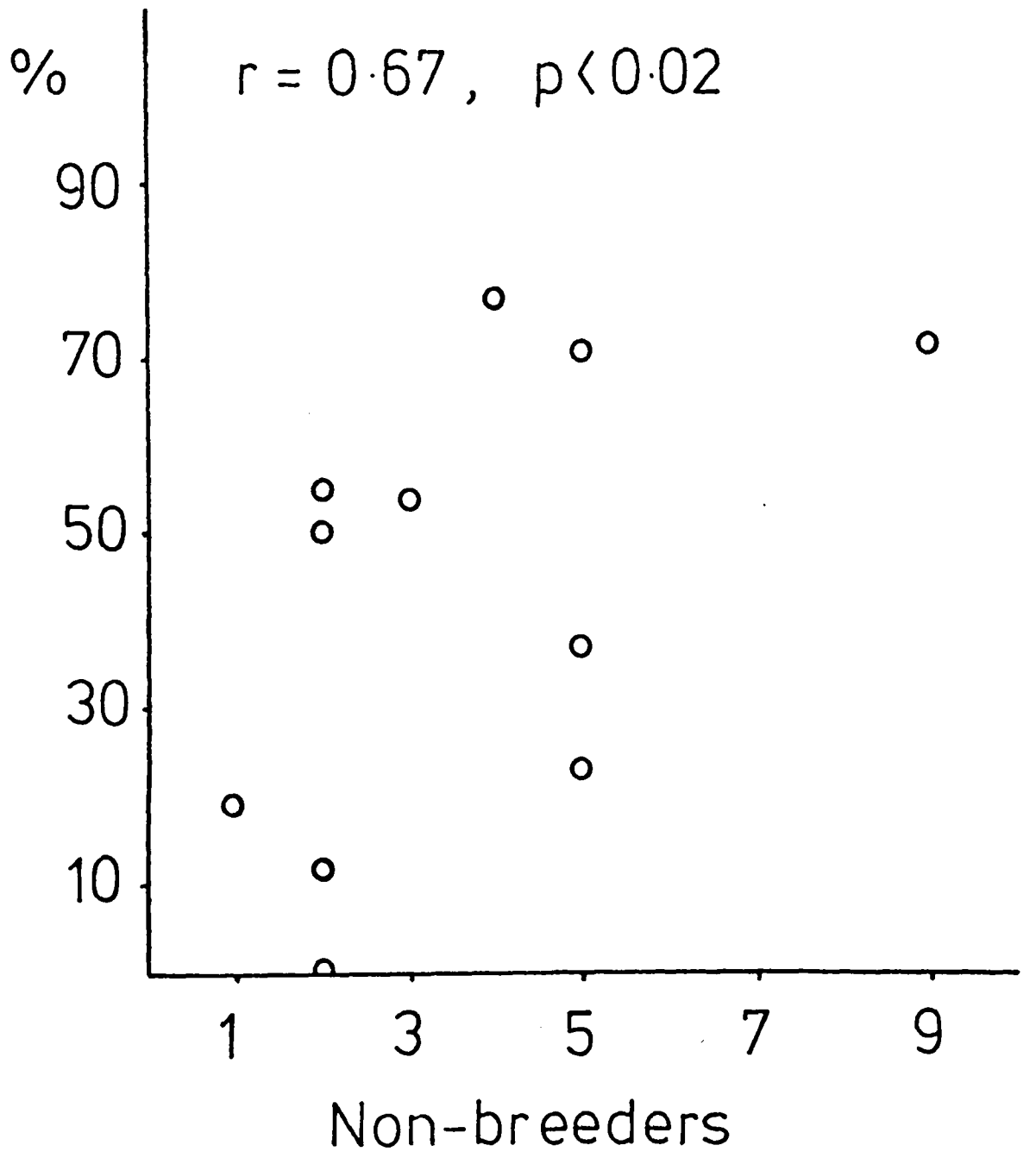
The larger number of males in the sample used to compile Table 7C may be partly due to a preponderance of this sex in the adult population, but must be due in part to the fact that many females were immigrants from unringed groups outside the study area, and since these could not be sexed they do not appear in the table. There is no reason to suppose, however, that the sample of females ringed prior to the observations were in any way unrepresentative.

Cases of non-breeding group members being chased away from the vicinity of a nest containing chicks were recorded at five nests. In all cases the chaser was the breeding female, and the bird driven off was also a female. In three instances the bird driven off was a member of a subordinate pair which had attempted to nest in the same territory. In one case it was a female which bred later with the same male in a polygynous situation. The other case involved a one year old female which had recently joined the group. This bird fed the nestlings on several occasions but was driven off twice. In groups where polygyny occurred one female (BB) fed the nestlings of its rival three times, but in others there was no feeding by the non-breeding female.

Removal of the faeces was performed by all birds which brought food to the nest. These were usually swallowed on the spot. The breeding female often carried out intensive nest sanitation, involving pecking inside and outside the nest, presumably to remove potential parasites. Sometimes non-breeders also performed this activity, but the breeding male was never seen to do so.

Birds which visited the nest during the latter part of the nestling period frequently performed a display, previously undescribed in the literature, which I have named the "shiver display". After feeding the nestlings the feeder would hop from twig to twig within a radius of about 25cm of the nest,

Figure 7d. The percentage of all feeding visits to the nestlings after which the 'shiver display' was performed, in relation to the number of non-breeding birds recorded feeding the nestlings.



rapidly shivering its wings. A low trilling call, similar to the follow call of the species, was normally uttered at the same time. The performance usually lasted for 10-20 seconds but sometimes continued intermittently for up to a minute.

At two nests where no non-breeders participated in feeding the nestlings no shiver displays were observed during watches on day 9-11. The proportion of visits during which shiver displays were performed increased with the number of non-breeders attending the nest, as shown in Figure 7d. The frequency also increased with the age of the nestlings at the four nests observed twice during the nestling period. The display was performed both by breeders and non-breeders, sometimes with other birds present, sometimes when the bird was alone in the bush containing the nest. In four cases the breeding male was the most frequent performer, and in three cases the breeding female, but the breeding pair were in any case the most frequent visitors at the nest. In two cases only non-breeders gave the display. At one nest the breeding female was twice seen to perform the display vigorously after chasing a rival female from the nest.

Discussion

The correlation between the number of non-breeders bringing food to the nestlings and the number in the nest at day 9-11 tends to support the hypothesis that the activity of the non-breeders makes a positive contribution to the reproductive success of the breeding pair. Other evidence, however, points to a modification of this conclusion. There was no difference in clutch size between groups with different numbers of non-breeders. If one nest which contained only one chick is excluded and cuckoos are ignored, then the correlation between the number of nestlings and the number of non-breeders depends on differences between nests with two and three chicks. Out of six nests with only two chicks at day 9-11 four cases were due to events

apparently independent of the presence of non-breeders; in one case two chicks starved immediately after hatching due to the presence of a cuckoo which was then removed, and in the three other cases brood sizes were determined by the infertility of one or two eggs.

Nest C1974/1, initiated in March, during the apparently less favourable spring breeding peak, was of particular interest. It was attended only by the breeding pair since there were no other birds in the group. All four eggs hatched and at four days weights ranged from 6-11g. Weight increases on day five were proportional to weight, as were overnight losses, and both were similar to those observed for another brood of four (M1974/2) two weeks later. On day six weights were 7.0, 7.8, 10.9, and 12.6g, and all appeared healthy, however on day seven only the largest chick remained. It seems unlikely that starvation could have accounted for the disappearance of the other three chicks and predation seems a more likely explanation. Four chicks were reared successfully from nest M1974/2, where only two non-breeders participated in feeding, and the weights of the nestlings on day nine were relatively high. Hence despite the observed correlation between the number of surviving nestlings and the number of non-breeders it is not clear which can be regarded as the independent variable. There was no definite evidence to suggest that a breeding pair alone are incapable of raising the maximum clutch to fledging.

The evidence from moult records suggests that the participation of non-breeders in incubation and feeding may reduce the strain of the breeding pair sufficiently to allow them to continue moulting while nesting. This could be of value to the breeders because loss of condition might lead to loss of dominance status. This may have been a contributory cause in the occurrence of successive polygyny. If the first female to attempt breeding loses condition as a result of this activity her dominant position may be

usurped by another. This would explain why the non-breeding female in this situation does not usually contribute to feeding the nestlings.

Successive polygyny was not observed in large groups where the number of non-breeders participating in incubation and feeding may have diminished the strain on breeding females sufficiently to allow them to retain their dominance. Nor was it observed in smaller groups where they occupied territories at low density, but these groups usually only reared one brood per year in any case, so there was no opportunity for polygyny to occur. The rivalry between females was illustrated by the frequency with which breeders drove others away from the nest, and the possibility of intra-specific predation, although it was not observed, may have selected for this behaviour. Breeding males occasionally exhibited antagonism towards other group members of both sexes, but the intensity of the interactions was much lower, and there was no case in which the intention of the aggression appeared to be directed at preventing the non-breeder from approaching the nest. The interactions observed may have constituted part of normal dominance behaviour.

General conditions affecting the strategies of non-breeders towards the reproduction of the breeding pair are discussed in Chapter 10. In the present context it seems relevant to point out that the behaviour of Common Babblers fulfils the prediction of kin-selection that altruism will increase with the degree of relatedness of the donor and the recipient (Eberhard 1975). Males, which must normally be related to the breeding male, feed the nestlings more frequently than females, which are probably not closely related to either parent.

In one instance of successive polygyny no non-breeders fed the nestlings at the second nest. A possible explanation for this observation is that the male non-breeders were offspring of the first female and made a distinction between bringing food to nestlings related to them through both parents and

those related through only one. More detailed studies of altruistic behaviour in relation to degrees of relatedness would be required to determine the importance of kin-selection in the origin and maintenance of these behaviour patterns. A situation in which the same male breeds successively with two females in the same season, however, provides an excellent natural control for this type of investigation.

The functions of the "long call" given from the nest and the shiver display are not clear. In the Arabian Babbler breeding adults frequently give a characteristic call when going to the nest at all stages of the nesting cycle (Zahavi, pers. comm.), and like the long call it is similar to the assembly call of the species. Zahavi has suggested that the call of the Arabian Babbler serves to assert the dominance of the breeders by advertising their breeding to other members of the group. This explanation seems less likely for the Common Babbler because the call is given much less frequently, and was not heard at all during nest-building or laying. From the far-carrying nature of the call it seems likely that it serves to communicate with the other members of the group but no satisfactory hypothesis concerning the content of the message has been devised.

The shiver display seems to be related to the participation of the non-breeders in the nesting effort. Because it is performed inside the dense bush containing the nest it is not visible at a distance. The call given with the display is low and hence probably not designed to communicate over any distance. It was sometimes hard to hear from the hide, less than ten metres away. Since the display was often performed in the absence of other adult birds, it seems likely that it is intended to communicate with the nestlings. This would also explain why it is given infrequently until the latter half of the nestling period, when the nestlings become more sensitive to outside stimuli.

Using the assumption that the shiver display is designed to communicate with the nestlings, a possible hypothesis to explain the origin of the display is that by drawing attention to themselves the parents and associated non-breeders familiarise the nestlings with the appearance and calls of their fellow group members, enabling them to identify these individuals after leaving the nest. Since most non-breeders at the nest are males they are likely to be related to the nestlings, and in this way it may be possible for nestlings to recognise those members of the group to which they are kin.

In one case where two non-breeding females contributed food to the nestlings both visited the nest twice without food but gave the shiver display. This could be explained as an attempt to become identified as kin by the nestlings. In cases where no non-breeders attended the nest shiver displays were not performed, and it is possible that the parents could be sufficiently readily identified without the performance of a display which might attract the attention of predators.

If the hypothesis that the shiver display is performed so that the nestlings are later able to identify their kin is correct, then some advantage should also accrue to the birds performing the display. Since non-breeding males may hope to succeed eventually to the position of breeder it may be in their interest to advertise their kinship with nestlings which may later, as non-breeders themselves, be in a position to assist them in reproduction. This theory assumes that non-breeders are able to modify the amount of assistance they provide in relation to their relatedness to the breeders.

Nothing equivalent to the shiver display was observed at Jungle Babbler nests. In this species the number of unrelated birds in the average group is lower than that observed in the Common Babbler (see Section 5f) and all members of the group attend the nest. Survival of the breeding adults is high, so that subsequent nests within the same group will, in most

cases, involve the nestlings' parents. For these reasons it may be less important for non-breeders to establish their relatedness with the nestlings, since a high degree of relatedness can be assumed, and the behaviour of the nestlings in later life must be adapted to this assumption.

The hover display of the Long-tailed Tit (see Chapter 9), given in circumstances very similar to those of the shiver display, might have a similar function. It is a noticeable feature of the hover display that it is performed very close to the nest opening, and usually late in the nestling period, when the chicks are old enough to look out. The display was performed only at nests where non-breeders were present, except in one instance where it was performed by the pair just after a non-breeder from another group had been driven off. Like the shiver display, it is performed both by breeders and non-breeders.

Conclusions

1) The contribution of non-breeding Common Babblers to incubation is less than that observed in Jungle Babblers.

2) The assistance of non-breeding birds probably reduces the strain imposed on the breeding adults.

3) Only male non-breeders make a significant contribution to rearing the nestlings. Females are actively discouraged from approaching the nest by the breeding female.

4) The number of chicks fledged is related to the number of non-breeders contributing food to the nestlings, but a casual relationship between these two parameters could not be established.

5) The shiver display is performed by adults to communicate with the nestlings, and this communication may concern their identity as related group members.

PART III

OTHER GROUP TERRITORIAL SPECIES

Chapter 8. Other species of Turdoides

Chapter 8. Other species of *Turdoides*

a) The Large Grey Babbler *Turdoides malcolmi*

This species occurred in small numbers in the Ridge study area, occupying open rocky ground with scattered trees. It is typical of farmland areas in NW India and in intensely cultivated plains of Punjab State it is often the most numerous species of the genus. Unlike all the other species, Large Grey Babblers forage well away from cover in open fields or grassland. They appear to be strong fliers and probably rely on this ability to escape predation. They are absent from completely treeless areas, however (Ali & Ripley 1971).

In breeding biology the Large Grey Babbler resembles the Jungle Babbler. Co-operative breeding has already been described by MacDonald (1959) and it appears that most or all group members take part in feeding the nestlings. MacDonald (1960) also recorded four birds participating in nest-building. The breeding seasons and nesting success of the species are dealt with in Appendix 1. It seems possible that the clutch size observed in the study area ($\bar{x}$ = 2.67, see Table E) was smaller than is typical of the species because the study area constituted marginal habitat. Ali and Ripley (loc. cit.) give three or four as the typical clutch size. The mean density of groups in the study area was 5 per km^2 and counts of group sizes in March are given in Table 8A.

Table 8A. Counts of groups of Large Grey Babblers present in the Ridge study area during March 1972-74.

	W	G	P	Y	F	Mean
1972	6	3	4	5		4.5
1973	6	2	4			4.0
1974	6	2	3		4	3.7
Means	6	2.7	3.7			4.1

In addition to the resident groups, nomadic groups of up to 11 Large Grey Babblers were sometimes encountered in the study area during February-April. These groups were vigorously attacked by resident groups and usually moved off within a few minutes. Their origin was not known, but their occurrence suggests that groups of Large Grey Babblers may travel some distance in attempts to establish new territories.

Groups of Large Grey Babblers encountered in February 1972 and '73 on farmland near the River Yamuna were larger ($\bar{x}$ = 7.6, n = 11) than those recorded at the same season in the Ridge study area (Mann-Witney 'U' = 3, $p < 0.002$). The species also appeared to be more common by the river, but no measurements of density were made. In March 1973 Large Grey Babblers were censused in Lodhi Park, New Delhi, an area of open grassland with scattered trees and shrubs, covering 0.37 km^2. Four groups were counted, totalling 23 birds ($\bar{x}$ = 5.75), a density of 62 birds per km^2, compared to the mean population of 15 birds in 0.8 km^2 in the Ridge area. Thus Large Grey Babblers showed a similar trend to that observed in the Common Babbler (section 6a) for groups to be larger in areas where the population was more dense.

A few groups counted on dry farmland south of Delhi were larger than any seen near the city, one group of 14 being recorded in March, a season when mixing of groups seems unlikely. In winter two or more groups probably forage together sometimes. Hutson (1954) mentions a group of 30 feeding together on a field of "gram" (chick-peas), and suggests that they had been attracted from a distance to a localised food source. Such congregations in the non-breeding season may account for the group sizes of up to 40 mentioned by Ali and Ripley (loc. cit.).

Allopreening and rough-and-tumble behaviour appear to be particularly frequent in the Large Grey Babbler, but this may be partly due to the fact that, feeding out in the open, it is more easily observed than the other species of

the genus. Table 8B compares the observed frequency with which different parts of the body were allopreened for four species of Turdoides. The proportion directed at parts of the body other than the head and neck is higher in the Jungle and Large Grey Babblers than in the Common and Striated Babblers, and this feature seems unlikely to be influenced by the relative visibility of the species concerned.

Table 8B. Comparison of the frequency with which allopreening is directed at different parts of the body in four species of Turdoides

	Parts of the body allopreened (see Fig. 3a)				
	Hn	Br	Ba	Ut	Total interactions
T. striatus	410(50%)	171	138	100	819
T. malcolmi	17(59%)	7	4	1	29
T. caudatus	46(75%)	8	6	1	61
T. earlei	14(67%)	2	5	-	21

Testing the frequency with which allopreening was directed at Hn (Head and neck) against the rest of the body, for all species, heterogeneity chi^2 = 16.9, df 3, $p < 0.01$.

A good description of rough-and-tumble behaviour in the Large Grey Babbler is given by Hutson (1954), and Dharmakumarasinhji (1954), who also describes this habit, mentions that birds may become so locked together that they can be caught by hand. Both Dharmakumarasinhji (loc. cit.) and Fletcher and Inglis (1924) describe the spirited attacks of Large Grey Babblers on Goshawks (Accipiter gentilis) and Shikras Accipiter badius which have succeeded in taking one of the group, pressing home their attacks "at risk of being killed" (Dharmakumarasinhji).

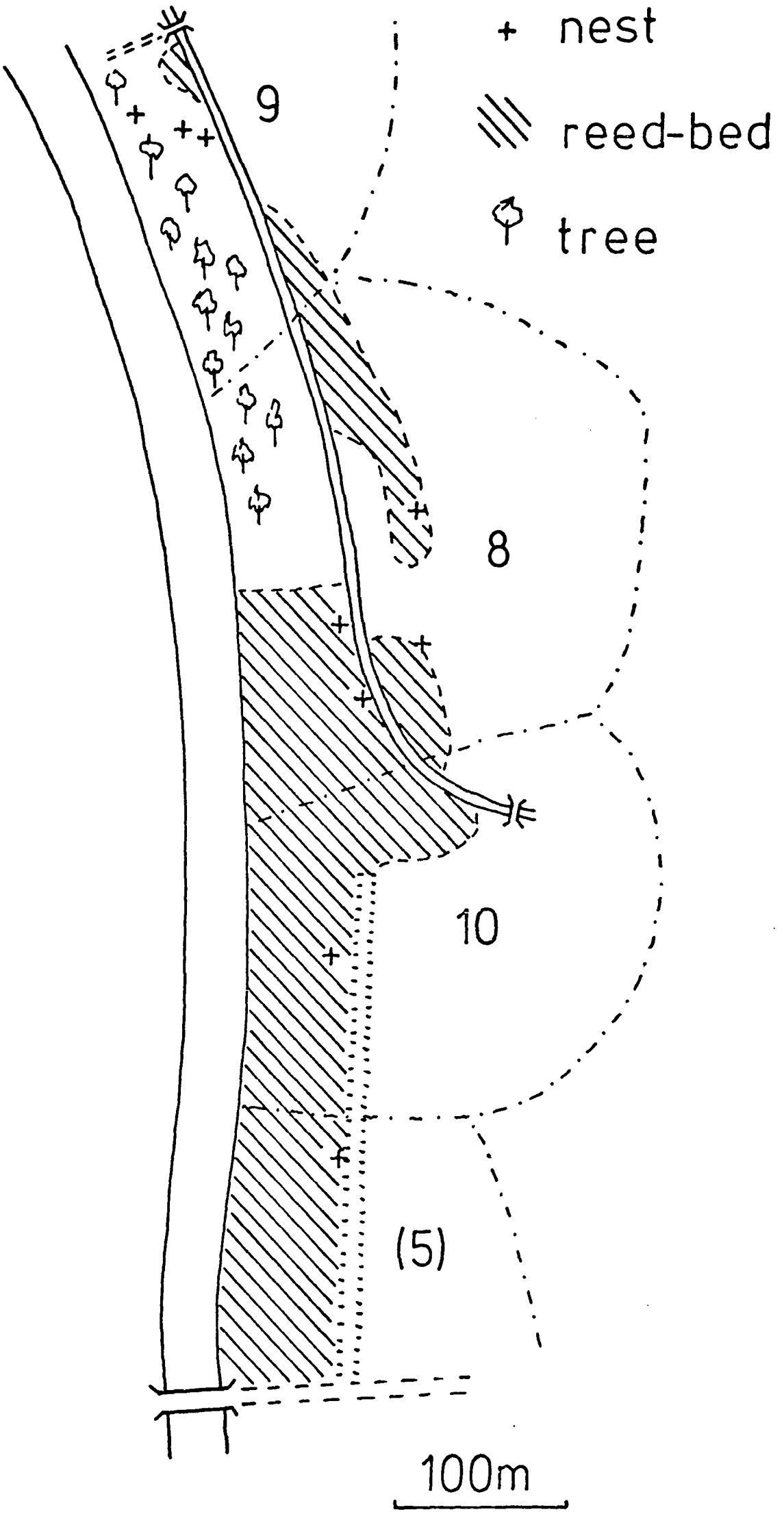
b) The Striated Babbler Turdoides earlei

This species was absent from the Ridge study area, but was observed in an area of reed-swamp (Typha) and water meadows close to the Yamuna canal, a few miles to the south of Delhi. A study area was mapped, and a few nestlings were colour ringed in this area, but no trapping was carried out. The position of nests and the approximate boundaries of the ranges of three groups are shown in Figure 8a. The area was visited on eleven occasions in February-May 1973, and twice in February and March 1974.

Four groups were present in the area in 1973, of which three were counted accurately (8, 9, and 10), and the fourth estimated as five birds. The size of groups and the position of their ranges were not determined accurately in 1974, but four groups were again present in the same area. All nests found were either 20-50cm above the ground in dense reeds, or 1-2m up in small palm trees, tucked in at the base of leaves. Only two out of nine nests located in 1973 succeeded in fledging young, and both of these were in reeds. The total number of birds in the area in 1973 was estimated as 32 in 0.24 km^2, giving a density of 133 birds per km^2 and 16 groups per km^2.

During the non-breeding season Striated Babblers appeared to be less confined to waterside habitats. Several groups were seen in dry fields close to the river in February, sometimes mixing with groups of Common Babblers, with which there appeared to be no interaction. On one occasion two groups which had been feeding separately were seen to merge. During the breeding season birds were often seen foraging singly or in small parties, and this also applied to members of a group which was feeding nestlings. Birds leaving the nest after bringing food would fly off in different directions, and although none of the birds were marked it was clear that members of the group were feeding over a wide area constituting most of the observed range.

Figure 8a. Map of the Yamuna study area showing the approximate boundaries of Striated Babbler group home ranges during the breeding season.



Intra-group behaviour in Striated Babblers differed from that observed in other species of the genus in several ways:

1) Allo-feeding was observed on several occasions in February. On each occasion the food was presented to a bird perched up on a reed stem, apparently undertaking sentinel duty, by a bird which flew up to present the food and then returned to feed on the ground. Allo-feeding is a common occurrence among members of Arabian Babbler groups (Zahavi, pers. comm.), where presentations are also usually made to a sentinel. Zahavi considers that this behaviour plays a role in the communication of dominance status but observations on this behaviour in the Striated Babbler were insufficient to provide evidence on this hypothesis.

2) Vocalisations included a loud, far-carrying call uttered by birds perched high up on reeds in situations where no source of alarm was apparent. This call, rendered "chirrup-ee, chirrup-ee-ee, chirrup-ee-ee, ..." was never given by more than one member of a group at a time. It usually continued for several minutes, being repeated after a short pause, and similar calls from birds in neighbouring territories could sometimes be heard simultaneously.

The function of this call would appear to be one of advertisement and the loud delivery from a prominent vantage point was reminiscent of a typical passerine song. The way in which members of different groups tended to call simultaneously suggested that it might have a territorial function. In that case the call would constitute the only instance of a territorial call given by only one member of the group, among the group territorial species of Turdoides, observed in the present study.

3) At two nests observed with half-grown chicks adult Striated Babblers maintained a constant sentinel watch nearby, taking turns at this duty after bringing food to the nest. The sentinel perched within 3m of the nest, and this close watch may relate to the fact that predators moving through the reeds could easily have approached the nest unseen.

The vocalisations of the Striated Babbler were generally similar to those of the Common Babbler, but in other aspects of behaviour the species appeared closer to the Jungle Babbler. During inter-group confrontations the body feathers were somewhat fluffed, and groups packed closely together, as seen in the Jungle Babbler. Interspecific interactions with groups of Large Grey Babblers were seen on two occasions.

c) The White-headed Babbler Turdoides affinis

This species is very similar to the Jungle Babbler in morphology, plumage, and habitat. Over large areas of South India the two species are sympatric, but where they occur close together Jungle Babblers are found in taller woodland and White-headed Babblers in scrub (Ali and Ripley 1971), usually 3-6m in height. The behaviour of White-headed Babblers is very similar to that of Jungle Babblers, but their vocalisations are distinctive, consisting of musical whistling notes, in contrast to the harsh cackles of Jungle Babblers. Co-operative breeding in this species has been described by Sanjeeva-Raj (1964).

The close similarity between White-headed and Jungle Babblers suggests that competition may be expected between the two species when they occur in similar habitat. Inter-specific territoriality has been reported from Kerala (K. N. Neelakantan, pers. comm.). An isolated population of Jungle Babblers found at Point Calimere, Tamil Nadu State,was observed to use vocalisations very similar to those of the White-headed Babbler, and this may also indicate convergence in calls to promote inter-specific territoriality, although interactions were not observed.

White-headed Babblers were censused over a portion of the grounds of the Theosophical Society in Madras during January 1974. Nine groups were recorded in an area of 0.32 km^2, consisting of coconut plantations and vegetable gardens, and all were counted while going to roost. Some groups contained juveniles, identified by their dark irides, which ~~must~~ were probably ~~have been~~ less than two months old. The rains in this area occur mainly in November and December, and nests from which the observed juveniles were reared would probably have been initiated at the beginning of these rains. Only seven juveniles were identified out of 76 birds in eight groups. The presence or absence of juveniles in the ninth group was not ascertained.

The mean size of the nine groups was 9.5 birds, and the density 264 birds per km^2. The size of individual territories, which did not appear to overlap significantly, was not measured exactly, but their density was 28 territories per km^2.

d) The Rufous Babbler Turdoides subrufus

The Rufous Babbler is a species endemic to the high-rainfall areas of the Western Ghats, along the west coast of the Indian peninsula. The species was observed at Ponmudi, Kerala State, during a visit made from 6-14 January 1974. It occupied two distince habitats in this area; overgrown tea-estates on steep hillsides, and grassy clearings in tall semi-evergreen forest, both at altitudes between 1000-1500m. In the tea estates the habitat consisted of dense rows of tea bushes trimmed to about 1.2m in height, with the rows spaced about 1m apart. Rufous Babblers appeared to be most numerous in areas where the tea bushes had not been trimmed for some years, and where thickets of Lantana and other shrubs grew among them.

A study area was chosen on the edge of an extensive tea estate. Groups were censused by plotting the position of calls given from the roost just before

sunset. An attempt was then made to watch these groups going to roost and to count them as they entered the roosting bushes. The positions of the roosts of seven groups were plotted in an area of 0.45 km^2, and five of these were counted accurately. The population was estimated from the number of groups multiplied by the observed mean group size (4.6 birds) as 32 birds, giving a density of 71 birds per km^2, and 15 groups per km^2.

Vocalisations were usually produced during the last half hour before going to roost, although they could be heard occasionally throughout the day. They consisted of explosive whistling trills, normally uttered in unison by two or more birds, although the exact number could not be determined. Not all groups called every evening, but on five evenings spent in the study area a mean of four out of the seven groups were heard calling at least once. Calls given by one group were often followed immediately afterwards by calls from an adjacent group, and it seems likely that these vocalisations had a territorial function.

Rufous Babblers were difficult to observe, keeping in dense vegetation, except briefly while crossing open spaces. During the day they could be induced to call by replaying tape-recordings of the evening call, and when this was done they would approach quite closely. They became habituated to this technique very rapidly, as had been observed in similar circumstances for Jungle Babblers. Nothing was observed of the nature of territorial interactions or intra-group behaviour.

e) The Spiny Babbler Turdoides nipalensis

The Spiny Babbler was thought to be extinct at the beginning of the 20th century and was only rediscovered in 1948 (Ripley 1950). It has since been discovered as widespread and locally common in the sub-montane tracts of Nepal. The behaviour and habitat of the species in the Kathmandu Valley, Nepal have been described by Proud (1959) and I visited the same area in June 1974 to make

some observations on the species.

Singing birds were located in two areas of dense scrub on the slopes of the Kathmandu Valley, at an altitude of about 1500m. A number of pairs were seen but no groups of more than two birds. Song was heard frequently in the early morning but also from time to time throughout the day. The song, quite unlike the vocalisations of other species of the genus, was a varied whistle similar to that of thrushes (Turdinae). A call similar to the mobbing call of the Jungle Babbler, given by the pair in unison, has been described by Proud, but I did not hear this.

Because maps of the area were not available I was unable to census Spiny Babblers satisfactorily. In one area of about 0.5 km^2 five or six pairs were located. In another area of similar size, but containing taller scrub, two birds were heard singing. The overall impression from observations of singing birds was that the density could not have been greater than 30 birds per km^2, but if some birds were not singing they would certainly have been overlooked since there was no other way to locate them. Proud's description suggests that they may be more numerous in other areas (loc. cit.).

Ali and Ripley (1971) suggest that Spiny Babblers may undertake seasonal movements to different altitudes, but within the Kathmandu Valley this seems unlikely, because the floor of the valley, just below the area where they were found, affords no suitable habitat. According to Proud they are present in the valley throughout the winter. Fleming (1952) recorded them in flocks of up to seven birds in winter, feeding at the edges of cultivation, and when in parties they kept up constant low vocalisations. Proud never saw more than two birds together.

f) Inter-specific comparisons

Several facts are readily apparent from a comparison of the species of Turdoides so far described. It is clear that any simple correlation with

habitat or climatic regime is unlikely to provide a clue to the factors involved in the evolution of the babblers' social system. Habitats occupied range from semi-desert to semi-evergreen forest. The Arabian and Fulvous Babblers T. fulvus occur in full desert conditions (pers. obs. in Algeria and Israel). The predictability of their environments varies from the stable, high-rainfall areas of western India to the unpredictable rainfall of semi-desert areas in NW India, where in some years rains may fail altogether (see Introduction d). The uniformity of the habitats occupied varies from the patchy heterogenous situation described for Jungle Babblers, with wide differences between different territories, to the artificial uniformity of the tea estates occupied by the Rufous Babbler or the coconut groves used by the White-headed Babbler.

In some aspects of their ecology all species are similar. All feed primarily on the ground by searching litter, and all except the Large Grey Babbler remain close to cover. The Jungle and White-headed Babblers, which have comparatively shorter tails than the other species, do some feeding in trees and shrubs, in the case of the Jungle Babbler, mainly on the boles and large branches. Food consists of a mixture of invertebrates, seeds and fruits, the latter taken mainly in winter (Mason & Maxwell-Lefroy 1912). All the four species observed feeding nestlings brought caterpillars during the first few days after hatching, and mainly Orthoptera thereafter.

From the observations made in the present study, social behaviour within the group appeared fairly uniform, with the exception of the Spiny Babbler. The repertoire of vocalisations used by Common Babblers appeared smaller than those of other species, but this may be partly an impression created by difficulties attendant on observing this species. Regular territorial vocalisations were performed by Large Grey and Rufous Babblers, and to some extent by Common and Striated Babblers. The importance of these vocalisations

may depend on the frequency with which groups come into contact with each other. The populations of Large Grey and Rufous Babblers studied were at rather low density, and hence inter-group encounters were infrequent, increasing the need to inform neighbouring groups of their continuing presence.

A comparison of the size of territories and the mean number of birds per group with population density for all the populations of Turdoides where these parameters could be measured, shows a remarkably close correlation between them. The figures are listed in Table 8C. The three parameters are inter-dependent in that if population density is fixed by external factors in the environment, such as availability of food, then group size and the number of groups per unit area must be inversely correlated.

Significant positive correlations were found between group size and population density (Fig. 8b), and between the number of groups per unit area and population density (Fig. 8c). There was also a significant positive correlation between group size and the number of territories per unit area ($r = 0.74$, df 8, $p < 0.02$), but when the partial correlation coefficient was calculated, partialling out the effect of population density on both parameters, a significant negative correlation was found ($r = -0.75$, df 8, $p < 0.02$). This supports the conclusion drawn from comparisons of group size with territorial area in the Jungle and Common Babblers, that larger groups occupy larger territories.

An analysis of variance showed that the variance of group size within populations was greater than that between populations ($F = 3.30$, df 9 and 63, $p < 0.01$). The range of group size observed in most of the populations studied was actually as large as that predicted by the regression of group size on population density over the observed range of population densities (predicted range 4.8-9.6). This suggests that though population density affects the mean group size found in a particular area, the factors controlling the range

Table 8C. Observed densities of Turdoides populations.

Species	District	Area(km^2)	Groups	Birds	Birds/km^2	Groups/km^2	Birds/gp.
1) striatus	Ridge	0.80	13	84	105	16	6.5(3-15)
2)	University	0.58	15(8)	154	266	26	10.25(7-16)
3)	Baroda	0.20	7	57	285	35	8.15(5-17)
4) malcolmi	Ridge	0.80	4	15	19	5	3.75(2-6)
5)	Lodhi Park	0.37	4	23	62	11	5.75(4-9)
6) caudatus	Ridge	0.50	13	104	208	26	8.0(2-15)
7)	Dhok Pathan	6.0	6	38	6	1	6.33(5-10)
8) earlei	Yamuna River	0.24	4	32	133	17	8.0(5-10)
9) affinis	Madras	0.32	9	86	264	28	9.5(6-15)
10) subrufus	Ponmudi	0.45	7(5)	32	71	15	4.6(3-8)

Figures in brackets in the groups column are the number for which an exact count was made, in cases where not all were counted exactly; the size of other groups in these areas was estimated as the the mean of those counted.

Figure 8b. The relationship of group size to population density in the genus Turdoides.

Dashed line; regression of mean group size on population density., (y = 4.6 + 0.017x).

Vertical bars; 95% confidence limits.

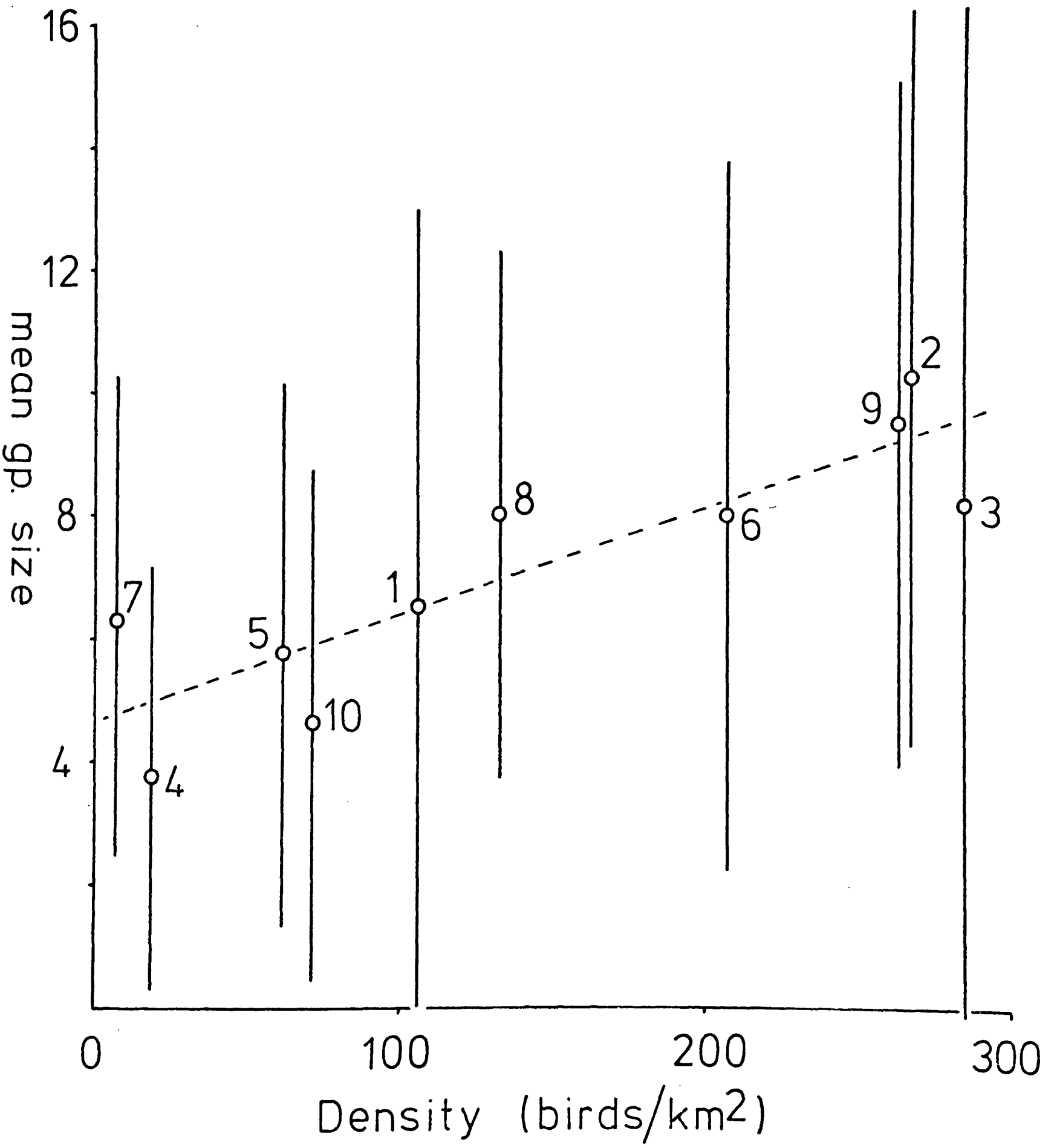
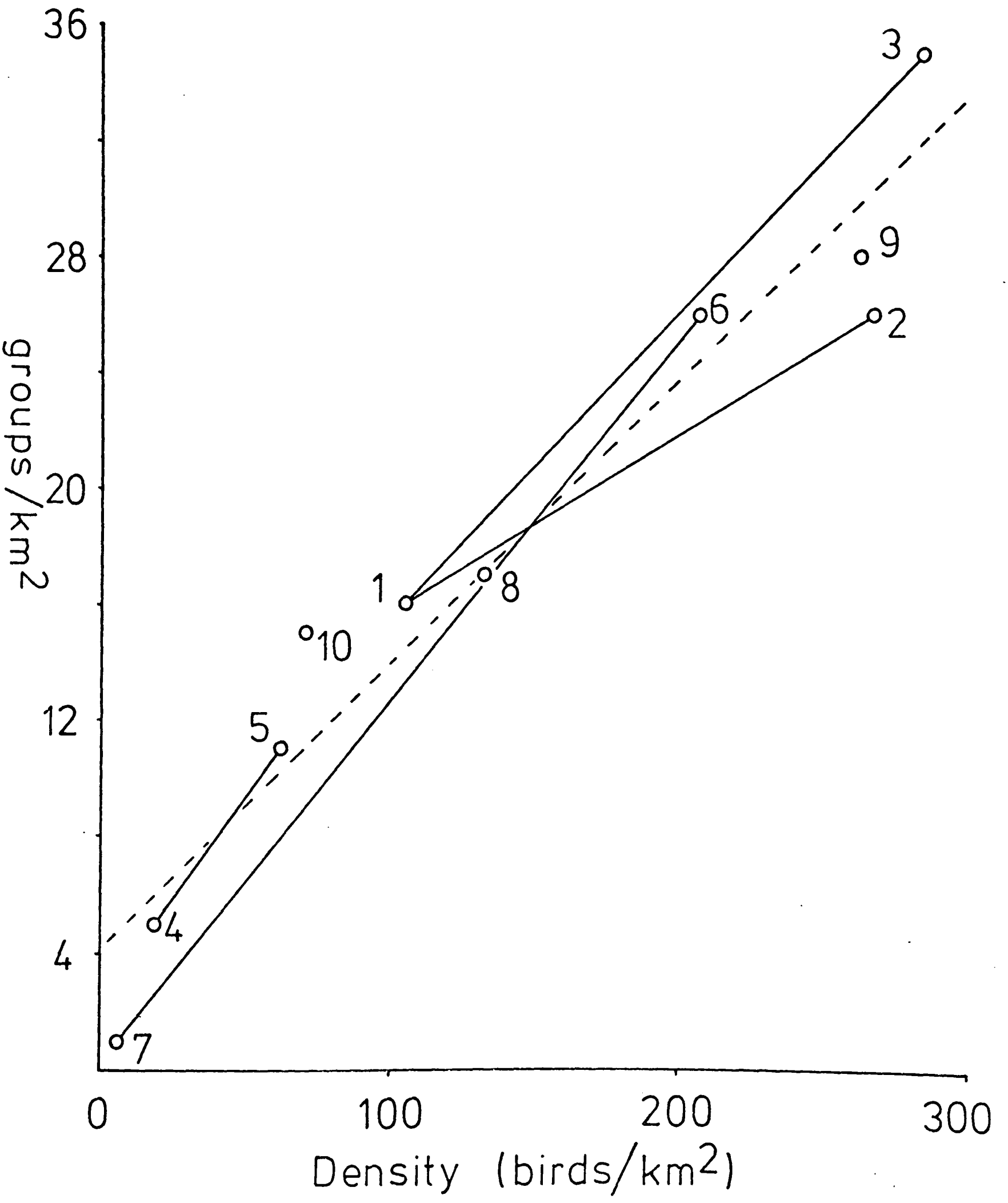


Figure 8c. The relationship of group density to population density in the genus Turdoides.

Solid lines connect populations of the same species.

Dashed line; regression of groups per km^2 against population density ($y = 4.2 + 0.097x$).



of group size are similar at all densities.

The close correlations between population density and group size, and between group size and territorial area, and the similarity in the range of group sizes between populations, suggest that factors influencing group size in Turdoides operate in the same way on all species and all populations of the genus. Further discussion of factors determining group size is set out in Chapter 10.

Species of Turdoides occupy all available habitats in lowland India. In addition to those observed in the present study the Slender-billed Babbler Turdoides longirostris occurs in tall grass plains in NE India. From the account of Ali and Ripley (1971), the behaviour of this species appears similar to that of the Striated Babbler. The White-throated Babbler T. gularis inhabits gardens and scrub in lowland Burma and its behaviour is apparently similar to that of the Common Babbler (Smythies 1953), which it resembles closely in overall morphology. In the forests of the Himalayan foothills the genus is replaced by a similar timalline genus Garrulax, of which 28 species occur in the Himalayas. One other is found in the hills of South India, where its habitat overlaps somewhat with that of the Rufous Babbler. Like Turdoides, species of Garrulax feed mainly on the ground amongst the litter of the forest floor, and those species observed in the present study appeared to hold group territories, and exhibited similar intra-group behaviour to that observed for Turdoides. A third genus, Babax, very similar in appearance to Turdoides, occurs in high altitude scrub in tibetan facies to the north of the Himalayas (Ali & Ripley, loc. cit.).

Summary

1) Intra-group behaviour and social behaviour and social organisation appear to be very similar in all species of Turdoides with the exception of T. nipalensis.

2) Habitats occupied by species of Turdoides range from desert to rain forest, and include all the major habitats of lowland India.

3) Despite differences in habitat the niches occupied by all species are quite similar.

4) Groups are larger in areas where population density is high, and larger groups hold larger territories.

5) Variances in group size within populations are similar, and greater than the variance between populations.

Chapter 9. The Long-tailed Tit Aegithalos caudatus

THE ECOLOGY AND BEHAVIOUR OF THE LONG-TAILED TIT

A. J. GASTON

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INTRODUCTION

The Long-tailed Tit *Aegithalos caudatus* is found throughout most of Britain, wherever there is woodland. In summer its feeding habits are similar to those of other species of British tits, but during the winter it is the only species which remains almost entirely insectivorous. The Goldcrest *Regulus regulus* and the Wren *Troglodytes troglodytes* are the only other sedentary small British passerines which remain insectivorous in woodland throughout the winter. A unique feature of Long-tailed Tits' behaviour, in comparison with other British passerines, is that outside the breeding season they are always found in small compact flocks.

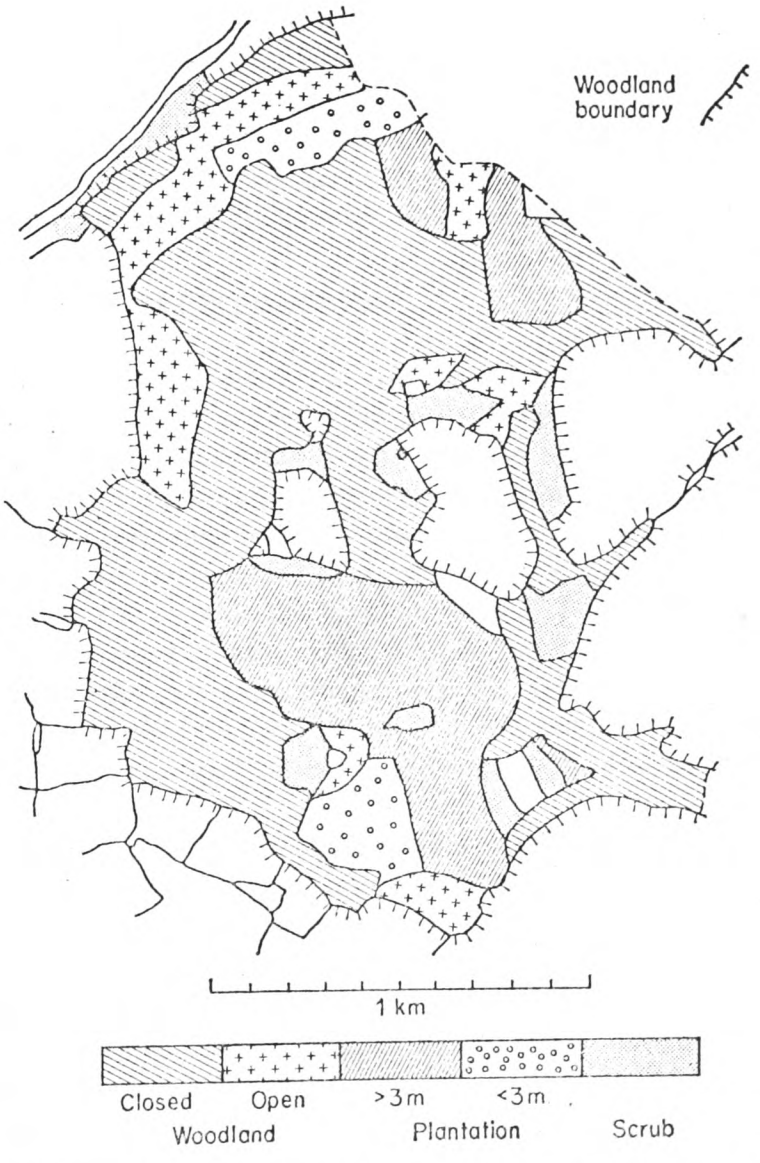


FIGURE 1. Wytham Great Wood: study area showing distribution of habitats.

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My interest in undertaking the present study was firstly to establish the degree of stability of Long-tailed Tit flocks, and secondly to discover the ecological significance of this behaviour. Differences between *Aegithalos* and the *Parus* tits have been detailed by Löhrl (1964). Feeding behaviour and feeding sites of both genera have been investigated by Gibb (1954). Lack & Lack (1958) have studied Long-tailed Tits in the breeding season, and recently two major studies have been published, by Nakamura (1969) in Honshu, Japan, on winter behaviour, and by Riehm (1970) in Germany, on all aspects of behaviour and breeding biology. The results of the present study are given in full, however, partly because they contribute much statistical information lacking in Riehm's study, and partly because my conclusions are rather different from those presented previously, and therefore require substantiation. In addition much information on nesting and nest-predation is given which amplifies the Lacks' study.

The work was carried out between October 1970 and June 1971 in Wytham Great Wood, near Oxford. This period is treated under three separate headings: (1) winter period (December–January); (2) pre-nesting period (mid-February–mid-March); (3) nesting period (mid-March–June). The pre-nesting period is the period between pair-formation and the initiation of nest-building. A total of approximately 650 hours was spent in the field and about a third of this was spent actually observing Long-tailed Tits.

A brief history, and much information about the present environment in Wytham Woods, is given by Elton (1966). Figure 1 shows the distribution of different vegetation types within the study area. Semi-natural woodland is dominated equally by Oak *Quercus*, Ash *Fraxinus* and Sycamore *Acer*, other broad-leaved species being of negligible importance. Scrub areas are dominated by Hawthorn *Crataegus* with some Elder *Sambucus* and Bramble *Rubus*. Plantations are mainly coniferous, including Spruce *Picea* and Pine *Pinus*. There are also some smaller Ash and Beech *Fagus* plantations.

WINTER PERIOD

FLOCK STRUCTURE

Outside the breeding season, Long-tailed Tits are almost invariably found in flocks which number from half-a-dozen up to about 30 individuals. In order to discover whether the composition of these flocks is stable over a period of time, as many birds as possible were colour-ringed with individually recognisable combinations. By the end of November 1970, 42 birds had been ringed within the central study area with individual combinations, and a further 17 with a single BTO aluminium ring. In addition a further 20 birds were colour-ringed on the far side of the study area (" Pond " flock).

The first group of 12 birds ringed (at site marked X on Fig. 2), and all birds trapped subsequently with birds of the first twelve, are known as Little Ash Hill (LAH) flock. All but one of the BTO-ringed birds were trapped together at the site marked Y on Figure 2 and these, along with three colour-ringed birds caught separately, but at the same site, form " Chalet " flock.

From 29 November to 12 December, daily observations were made in the central study area and an attempt was made to identify as many colour combinations as possible. During this period 74 separate sight records were made of birds in LAH group, on 16 occasions, in flocks in which two or more birds were identified. Of these 16 flocks only two contained individuals ringed as members of another group. In one case a single LAH bird was identified with six birds of another group; in the other case two birds from another flock were identified with five LAH birds, in a flock of at least 15 individuals. In the latter case the predominance of LAH birds suggests that it was the other birds which had changed flocks. If this is so, then only one out of the 74 records is of a bird which had changed its flock, and this bird was recorded once more in January when it was back with LAH flock.

The same consistency applies to the Chalet flock: out of 30 records of BTO-ringed birds or colour-ringed birds in the same flock, only two of BTO-ringed birds among a single flock of unringed birds show any evidence of mixture with other flocks.

" Doubles " flock was a party of six birds trapped with one member of Chalet flock (which was not seen with them subsequently but was seen regularly with Chalet flock). This flock was recorded twice later, when six and then five of the members were identified, in both cases with two members of another flock of eight, trapped earlier, which apparently broke up (" Broken " flock).

From the above observations it seems clear that Long-tailed Tit flocks are stable in composition during November and December. This is also indicated by observations on neighbouring flocks which were not trapped. Seven flocks recorded on the periphery of the main study area, comprising 85 birds in all, were observed closely enough to see whether or not they contained ringed birds. One flock contained a BTO-ringed bird, but no colour-ringed birds were observed.

The distribution of subsequent observations of birds in LAH flock, which was the one most frequently observed, suggests that all the birds ringed stayed within the area and the likelihood of my identifying them was the same for all individuals. Table 1 compares the number of birds which were seen on a certain number of occasions with the expected frequency derived from a Poisson distribution, assuming a consistently random chance of identifying any particular bird. Any event such as the disappearance of some individuals, or the presence of more than one flock, where the chance of finding one was higher than that of finding another, would tend to bias the observed distribution towards a larger number of individuals recorded often, and a larger number seldom or never recorded. In fact the result is surprisingly close to the expected distribution, surprisingly because some colour combinations seem harder to identify than others and this might have been expected to bias the observed figures.

TABLE 1

Number of observations of 21 individually marked birds in LAH flock

	Number of occasions that individuals were recorded					
	0	1	2	3	4	5
Expected from Poisson distribution	3·28	6·09	5·66	3·5	1·62	0·6
Observed	3	6	6	4	1	1

Variance: Mean ratio test gives $\chi^2 = 15{\cdot}8$, $P = 0{\cdot}75$ ($n = 20$).

The presence of more than one sub-group within the LAH flock would not bias the distribution if all sub-groups were equally likely to be encountered. The fact that most flocks containing LAH birds were estimated at between 15 and 25 birds makes the existence of sub-groups unlikely, however. This also applies to the Chalet group, where most flocks observed were estimated at between 10 and 20 birds.

VOCALISATIONS IN FLOCKS

Birds in flocks during November and December used three main calls:-

(1) a soft, slightly metallic *pit*. This is usually uttered while feeding, and is often accompanied by a short flight of up to a foot or by a brief wing-flick. The rate of calling varies enormously, but most feeding parties would utter this call from time to time even when apparently completely unexcited, and this was very valuable in locating them.

(2) a high-pitched *eez* or *eez-eez-eez*, rather " nasal ". This is usually uttered during a flight of more than 3 m and is particularly heard when a flock is in rapid movement. Isolated individuals used this call a great deal.

(3) A rattling *schnurr*, reminiscent of the alarm call of the Wren but less harsh in quality. It varies a great deal in length and intensity, and may be used while perched or in flight.

Birds using this call often seem excited, moving rapidly from twig to twig. It is often heard during flock movements over distances of more than 20 m, when it is interspersed with *eez* calls.

Another situation in which this call is used I have named the " plunge flight ". This consists of a rapid dive from the feeding site in the canopy into bushes below. Usually one bird initiates this display and is quickly followed by some or all of the flock. During this plunge, and subsequently while the birds are hopping about in the bushes, the *schnurr* call is uttered loudly. In some instances the initiating birds may begin *schnurr* calling before performing the plunge.

During inter-flock interactions an apparently high-intensity version of the *schnurr* call is used which sounds more like *schree*. This is very loud and uttered very frequently while two flocks are fighting.

DISPLAY

The behaviour of Long-tailed Tits in Japan has been summarised by Nakamura (1967). Winter flocks observed in Wytham Woods showed similar behaviour patterns, and most display observed was identical to that described for the Japanese population.

Courtship display was observed only once in December. Both birds flew with a slow, butterfly-like flight (similar to that of the courtship flight of the Blue Tit *Parus caeruleus*) the male following a foot or two behind the female as they twisted in and out of the branches of a tree. About every 10 seconds they paused to perch near one another for a few seconds before continuing. The whole display lasted only two minutes and was not seen again in the next half-hour.

Threat display was seen rarely within a flock, and supplanting another member of the same flock was seen on only eight occasions. In seven of these, the bird doing the supplanting was known to be a male, and in the other case the sex was not known. In two cases the birds supplanted were male, and in two cases female.

AGE STRUCTURE OF FLOCKS

Birds trapped for colour-ringing were aged on the presence or absence of unossified areas on the skull. This could be judged fairly accurately, in good light, by pulling the skin on the head forward so that the unfeathered area behind the ear is brought over the skull. Patches of unossified bone show up as pale pink areas. Details of this method for ageing small passerines in autumn are given by Svenson (1970).

Table 2 suggests that the ratio of first-year to older birds was about 2 : 1 in October and early November. Most birds identified as first-year showed quite large unossified areas on the skull and it seems unlikely that any but a very small proportion would have been fully ossified by that time.

TABLE 2

Age structure of Long-tailed Tit flocks trapped in October and November 1970

	Fully ossified	Not fully ossified
LAH flock	5	20
Broken flock	6	8
Doubles flock	2	4
Pond flock	10	8
	23	40

FLOCK RANGES AND MOVEMENTS

In order to determine whether individual flocks of Long-tailed Tits occupied regular home-ranges, all flocks encountered between mid-November and 12 December 1970 were followed for a minimum of 15 minutes and usually until lost. During October, following flocks proved more or less impossible because of the leaves on the trees, but during the winter conditions became progressively better, and flocks were followed for up to two hours on occasions.

The duration of the period in contact with a flock was timed, and the track of flock movements recorded on a map of the area, with notes on flock activity. The behaviour of the flocks fell into two categories: feeding, and rapid movement. Periods of more or less stationary feeding lasted from 2–15 minutes and were usually separated by periods of rapid movement.

Distance covered between periods of feeding varied up to 450 m with a mean of 216 m (n=35) for movements of more than 50 m. Such flights were not non-stop but involved brief rests at least every 30–40 m. Occasionally one bird was seen to hold the lead for a long period, but usually individuals "leap-frogged" one another, swapping the lead frequently. It was normally impossible, however, to identify colour combinations during these periods of rapid movement, so there remains a possibility that certain birds may be more prominent than others in initiating and orientating flock movements.

Rapid movements covered longer distances before noon than in the afternoon (Table 3). The average distance covered in unit time, however, including both feeding and moving, was actually shorter in the morning than in the afternoon, although this difference was not significant ($P>0{\cdot}1$). This means that periods of feeding must be longer in the morning than in the afternoon and suggests that the total time spent feeding remains fairly constant throughout the day. In the morning movements are longer and fewer, in the afternoon they are shorter and more frequent, as Nakamura (1969) also found for Long-tailed Tits in Japan. On the basis of the average speed (total distance covered divided by total time taken, all flocks combined), flocks move about 7 km per day during December.

TABLE 3

Rate of movement of Long-tailed Tit flocks, December

	Time of day (B.S.T.)			
	Before 12·00 (8 flocks)		After 12·00 (18 flocks)	
	Mean	s.e.	Mean	s.e.
Speed (m/min)	13·5	2·2	15·8	1·6
Distance between feeding sites (m)	265	27	177	16

The tracks of flocks followed during November and December are shown on Figure 2. From this map it would appear that the ranges of flocks tend to be discrete. The black arrows mark places where two flocks were observed to meet. In each case both flocks moved off rapidly towards the area in which they were normally found. On one occasion, when two flocks met on 8 December, there was a violent fight involving several members of both flocks (LAH and an unringed flock). One pair of combatants, one colour-ringed, the other unringed, fell through the air while grappling with one another and may have hit the ground (this could not be seen).

The fact that Long-tailed Tits are prepared to defend their home-ranges qualifies these as territories. Their boundaries seem to follow recognisable features such as roads or woodland/scrub edges. Nakamura (1969) also found the flocks to be territorial in Japan, but in his apparently more homogeneous study area there seems to have been a great deal of overlap between different flock territories. In Wytham, at least on the boundaries of the LAH flock, overlap seems to have been rather small.



FIGURE 2. Tracks of flocks containing identified individuals followed during December 1970.

BREAK-UP OF WINTER FLOCKS AND PRE-NESTING PERIOD

SOCIAL STRUCTURE

No observations were made in the second half of December 1970 or in January 1971, except on 29 January. On this date a flock of about 15 birds was encountered in the Little Ash Hill area and of five individuals recognised, all were birds which had been members of the LAH flock in December. This flock was seen twice during the course of the day, on both occasions within the December range of the LAH flock. The situation thus seemed to be similar to that in mid-December. The next day of observation, on 16 February, showed that the flocks had broken up, and from this date onwards no flock of more than seven birds was recorded. Because of the gap in observations, however, nothing was recorded of the actual process of flock disintegration.

From 16 February to 14 March, when nest-building was first observed, most records of Long-tailed Tits within the study area were of birds in pairs (Table 4). These records

TABLE 4

Size of Long-tailed Tit flocks during the pre-nesting period (16 Feb.–14 Mar.)

	Number of individuals in a flock						
	1	2	3	4	5	6	7
Number of flocks recorded	7	47	5	10	2	4	1

exclude sightings made after 18.00 hrs B.S.T. Towards dusk, pairs tended to join up into larger groups and to roost together. These roosting groups appeared to consist of the survivors of the winter flock which occupied the same area. In the case of the LAH area, all seven of the birds forming a roosting flock (LAH–LBW) during February were known to have been members of the LAH flock in December. In the Chalet area, four of the seven birds in a roosting flock were known to have been members of the Chalet flock, and the other three all had BTO rings, so they were almost certainly members of the same flock in December. The other known roosting flock (LAH–LGR flock) consisted of two LAH birds and two unringed birds, and this party occupied a segment of the total range of the LAH flock. The other seven LAH birds (LAH–LBW flock) never occurred in this area during the pre-nesting period, and it appears that the original LAH flock had at this stage divided into two sub-groups.

Figure 3 shows the occurrence of members of the three roosting groups (Chalet flock, and the two sub-flocks of LAH flock) within the study area. Plotted in this way, there is very little overlap between the home-ranges of the three groups and indeed no encounters between these groups were ever observed. The only inter-group interaction which was recorded during this pre-nesting period was on 14 March and involved LAH-LGR flock and a pair of unringed birds. The latter were feeding within LAH-LGR range and were chased about 300 m, after which there was an excited confrontation in exactly the same spot where LAH flock had fought with an unringed flock on 8 December. This was the only instance when more than a single bird was seen in an area which was known to be within the territory of another flock.

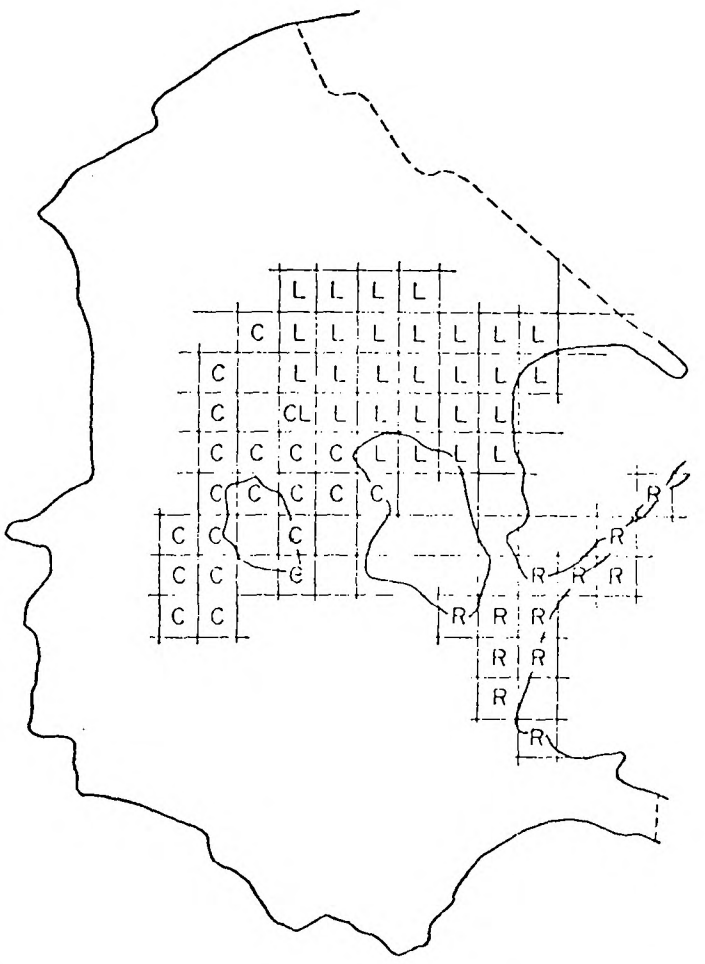


FIGURE 3. Distribution of flocks during the pre-nesting period. Grid squares are 100 m square. Flocks: L, LAH-LBW; R, LAH-LGR; C, Chalet.

When parties of more than two birds were seen together during the day (before 18.00 hrs) they were usually made up of recognisable pairs, sometimes accompanied by a single individual. These parties were more common in cold weather. The correlation coefficient (r) for flock size on maximum daily temperature was 0·4 ($n=75$, $P<0{\cdot}001$), a rather weak but highly significant correlation. On days when the maximum temperature was 7·5 °C or less, 6 out of 24 flocks recorded contained an odd number of individuals. On days when the maximum temperature was higher than this, only 3 out of 44 flocks of more than one contained an odd number of birds. A $2\times2\chi^2$ test on these figures gives $\chi^2=4{\cdot}01$, $P<0{\cdot}05$; hence there are significantly more odd-numbered flocks in cold weather.

If all odd-numbered flocks are assumed to comprise pairs plus a single bird then, from the number of flocks with an odd number of birds during cold weather, we can predict an expected number of solitary birds when the weather warms up. The expected number, 8, and the observed number, 7, tally so closely that the assumption seems justified. On this basis it is possible to work out the proportion of unpaired birds in the population during the pre-nesting period (Table 5). There is no suggestion from Table 5 that solitary individuals are gradually pairing up during this period, and the proportion of solitary birds is actually (though not significantly) higher during the second half of the period. Using the figures for the entire period, the proportion of unmated birds in the population can be estimated at 9%.

TABLE 5

Estimated numbers of unpaired and paired birds during the pre-nesting period

	Number of unpaired birds	Number of paired birds
16–22 February	3	56
23 Feb.–2 March	3	20
3–9 March	5	68
10–14 March	5	46

Single birds may wander between flocks. Thus two new birds were caught during January and February in the LAH area but not seen subsequently. One of these had been ringed in Marley Wood, about 1 km from the study area. Only one unringed bird was recorded in the range of the LAH–LBW sub-flock and this was chased for about 12 minutes by the male of one of the resident pairs. During this chasing, short periods of flight were interspersed with periods during which both birds sat with in a few feet of one another in the same tree. This behaviour was reminiscent of behaviour during the "pair-flight", but the actual flying was normal and rapid instead of butterfly-like. Both birds called a lot, using the *schnurr* and *eez* calls. The male of the resident pair also uttered a broken song consisting of a jangle of *schnurr* and *eez* notes with a few short *chirrups* mixed in, on five occasions. The intruder was not seen again.

Some single birds remain with their own flock and, in the case of both LAH–LBW sub-flock and the Chalet flock, these birds were present throughout the pre-nesting period. In the case of the LAH–LBW sub-flock, the odd individual eventually paired with one of its own flock after another bird had disappeared (presumed dead). The unpaired member of the Chalet flock, a male, was seen in late March with several different birds, some known to belong to other flocks. It later nested with a female from Pond flock.

Evidence from trapping in the Wytham area during 1959 also suggests that the pre-nesting period is the time of year when Long-tailed Tits are most likely to wander. Three birds, belonging to a flock of individuals which had been controlled regularly in Marley Wood between 24 January and 23 February 1959, were controlled in Wytham

Great Wood, 1·5 km away, in March. One of these returned to Marley, and the other two continued to be controlled in Wytham until the next winter. At the same period several unringed birds were trapped in Marley Wood along with members of the resident flock. This period probably corresponds to that described by Nakamura (1967) as " Spring instability phase ", on the basis of census data.

MOVEMENT OF BIRDS DURING THE PRE-NESTING PERIOD

Pairs and small flocks located during the pre-nesting period were followed in order to determine their rates of movement and home-range. An attempt was made to follow all birds located for at least 15 minutes. Flocks were found to move significantly faster than pairs, but this may have been due to the fact that many flocks were observed in the evening, just before going to roost. The rate of movement of both pairs and flocks was significantly lower at this season than that of the larger winter flocks (Table 6). The mean speeds for parties belonging to the three recognisable flocks LAH–LBW, LAH–LGR, and Chalet during the pre-nesting period were 10·2, 10·3 and 11·0 m/min respectively, which suggests that similar rates of movement apply to all flocks.

TABLE 6

Rate of movement of Long-tailed Tit flocks, winter and pre-nesting periods

	Winter (Dec.–Jan.)		Pre-nesting (mid-Feb.–mid-March)		
			Flocks		Pairs
Number of flocks	26		20		31
Mean speed (m/min.)	15·1	—†—	11·2	—*—	9·0
Number of birds/flock (mean and range)	14 (10–30)		4·8 (3–7)		2

* $t=2{\cdot}04$, $P<0{\cdot}05$.
† $t=2{\cdot}21$, $P<0{\cdot}05$.

During periods of concentrated feeding, flocks and pairs in the pre-nesting period moved at 1·6–7·3 m/min, with a mean speed of 4·0 m/min. There was nearly always some consistent direction to their movements during these feeding bouts, and birds rarely returned to a tree which they had just left unless there was another bird still feeding there.

The mean crown diameter of trees in Wytham Great Wood is about 8·5 m and this gives a mean searching time for each tree of 2–3 min, which corresponds well with direct observations. It seems certain that, in this period, no thorough search of a single tree could be made by a single bird or a pair. Instead a cursory search is made as the bird moves from twig to twig through the canopy and, if food is discovered, progress is halted while it is dealt with.

Changes in the direction of Long-tailed Tit movements were analysed from the maps of pair and flock movements during the pre-nesting period. Figure 4 illustrates the magnitude of changes in direction over 25-m intervals. Seventy-seven per cent of the changes were of 45° or less, and 35% were of less than 10°. The median change in direction was 18°. Although changes in direction over 25 m were usually small, flocks tended to circle around in the course of longer movements. This was tested by comparing observed frequencies of clockwise and anti-clockwise changes in direction with the 1 : 1 ratio expected on a hypothesis of random deviation. Summing the χ^2 values for 31 flocks or pairs gave $\chi^2=62{\cdot}4$ which with 31 degrees of freedom gives $P<0.005$. This suggests that parties tend to circle within their territories rather than flying in straight lines and then turning abruptly at the boundary of the territory.

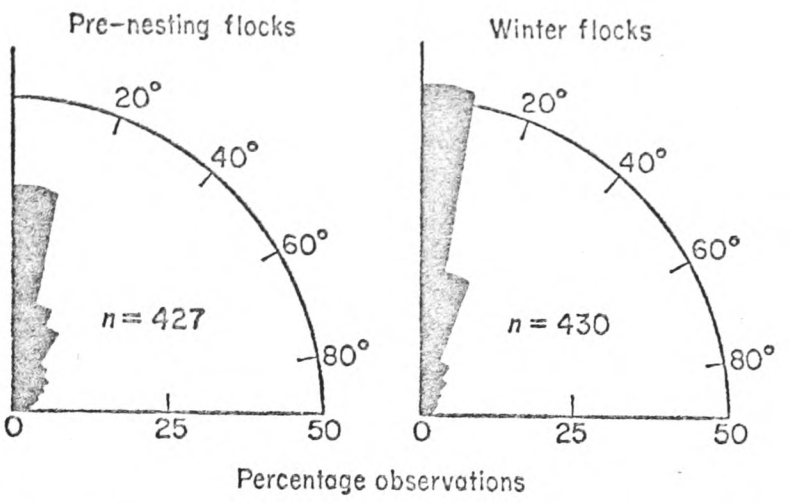


FIGURE 4. Angular change in the direction of flock movements over 25-m intervals.

A comparison of the pattern of movements seen in the pre-nesting period with that exhibited by flocks in December suggests that the latter range more evenly through the territory. Observations made in December were insufficient to show whether utilisation of squares within the territory was more equal than in the pre-nesting period, but an analysis of changes in the direction of flock movement (Fig. 4) shows that the deviation in heading over a 25-m interval was significantly smaller than that for pre-nesting flocks ($\chi^2=32$, $P<0{\cdot}005$), with a median deviation of 9° and 90·5% of all changes of direction being less than 45°.

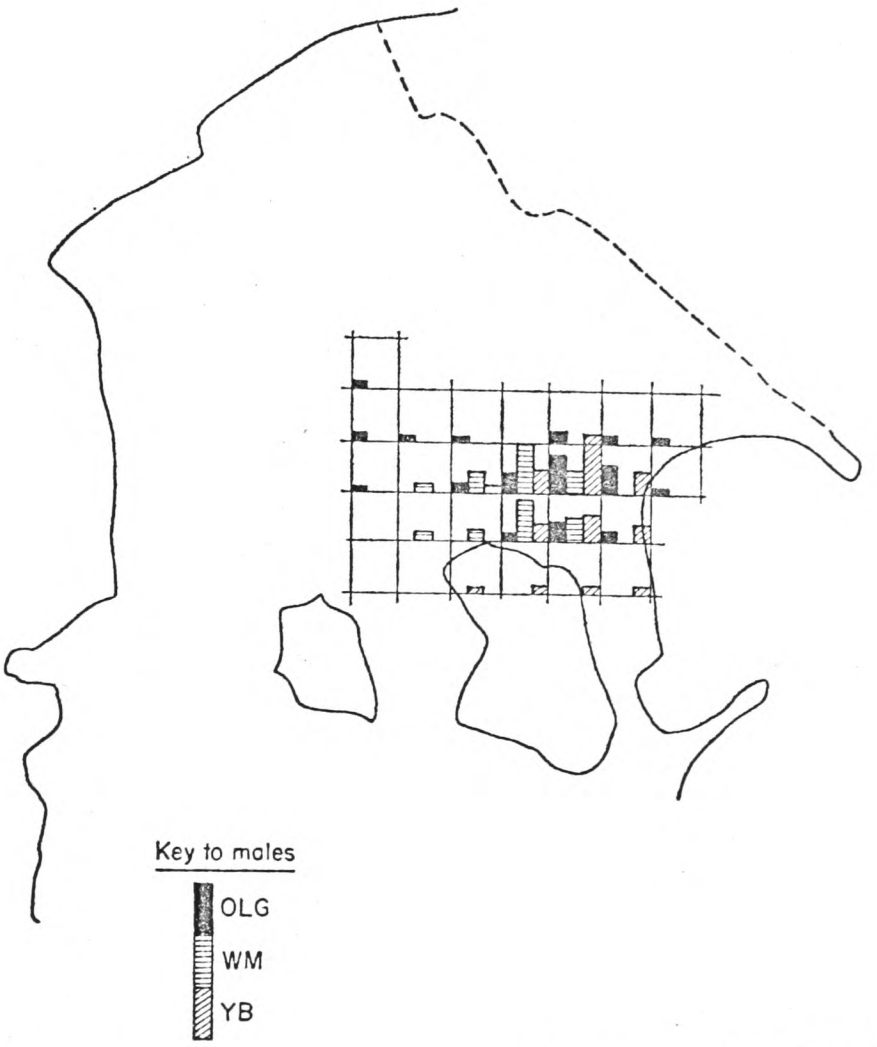


FIGURE 5. Flock LAH-LBW: distribution of males during the pre-nesting period. Columns show percentage observations in each 100-m grid square.

Continual ranging through a relatively large area ensures that no tree is searched twice in one day. Periodic rapid movements also have this effect. The reason that larger parties travel faster, on this principle, might be that the chance of searching a place where another bird has searched already becomes higher the more birds there are in the flock, and hence the period which it is profitable to spend in any one tree becomes shorter. The method of searching outlined above seems to be most advantageous for a species feeding on food which is not clumped but randomly scattered through the environment, as suggested by Richm (1970). Another factor which may be important in influencing the rate at which Long-tailed Tits move through their environment is the maintenance of the group territory. The long rapid movements already mentioned, which alternate with periods of feeding, may in part serve a function in patrolling the territory.

In fact, during the pre-nesting period, pairs tended to concentrate most of their activity in the centre of the flock territory. Figure 5 shows the percentage occurrence of the three males in LAH–LBW flock in each 100 m grid square of their territory. Out of 26 squares mapped as wholly or partially within their territory, the six most frequently used accounted for 65%, 70% and 71·5% of sightings for these birds. The actual time spent feeding in these squares, which surround the roosting place, was probably an even higher proportion of their total time.

Richm suggested that pairs divide up the flock territory into pair territories during the pre-nesting period, but no evidence of this was seen. Instead a tendency for pairs to spend more time in the area in which they eventually nested was discernible in the general pattern of occurrence, but the ranges of the pairs overlapped broadly, as Figure 5 shows. The mechanism by which nest-sites are spaced out is unclear.

BEHAVIOUR DURING THE PRE-NESTING PERIOD

During February Long-tailed Tits spent about 90% of daylight hours feeding. Other activities consisted mainly of social interactions with other members of the same flock and only one inter-flock encounter (already mentioned) was observed during this period. In March, display and a certain amount of nest-site investigation took place.

Pairs belonging to the same flock which encounter one another during the day usually become excited and call vigorously using the *schnurr* call. There is usually some chasing and all four birds become very agitated, hopping restlessly from twig to twig. This dies down after a few minutes and the two pairs feed side by side or gradually drift apart. A typical encounter is well described by Riehm (1970). Isolated individuals, even belonging to the same flock, tend to be chased much more by pairs, regardless of their sex. Encounters become more frequent in the evening as birds concentrate in the area of the roost, and the flock has usually combined by 45 minutes before they go to roost.

The call most commonly used during the pre-nesting period is the soft *pit* which pairs utter constantly while feeding, presumably to maintain contact. The rate of calling varied from 2 to 60 calls per bird per minute and high rates of calling seemed to be particularly associated with periods of agitation, although the cause of the agitation was not always apparent. The highest rate of calling was during an inter-flock confrontation, but birds were also recorded calling at a high rate when about to initiate a long flight, and when moving through low vegetation. Figure 6 shows the relationship between height and rate of calling in the pre-nesting period. The higher rate of calling at low levels might be explained in two ways: (1) while feeding low down the birds were often in thick bushes and therefore less able to keep in contact visually; (2) most nest-sites are low down and these sallies into low shrubs may have been related to nest-site selection.

Apart from the plunge flight, which was often performed when two pairs of the same flock came into contact, another display, named the flycatcher display, was seen a few times before nest-building commenced. This consisted of flying up rapidly a few feet into the air, then plummeting back with the tail held vertical and the wings somewhat

spread. This display lacks the hovering component which distinguishes the displays performed later while the young are being fed. The same movement was also performed while catching flies, but I consider that it must have a display function, because in some cases there were no flies apparent, and it was later seen often in the vicinity of nests, during building. This display was also associated with a high rate of *pit* calling, and often much *schnurr* calling.

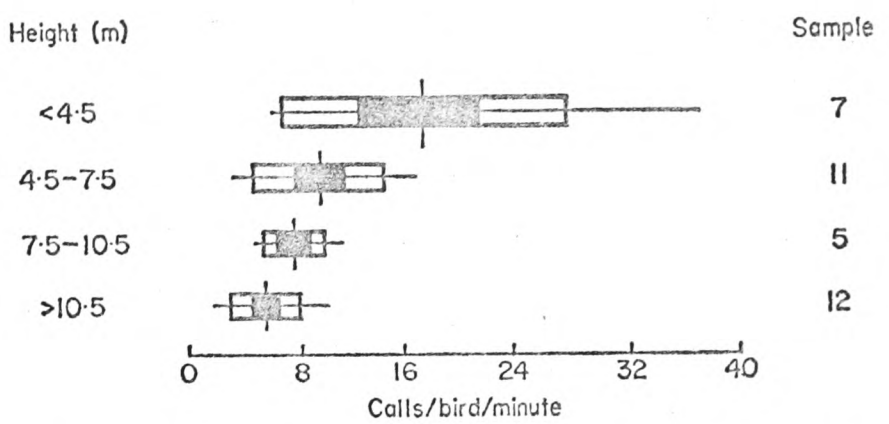


FIGURE 6. Rates of contact calling by pairs during the pre-nesting period in relation to height above ground. Horizontal line, sample range; vertical line, sample mean; open rectangle, ±1 standard deviation; black rectangle, ±1 standard error.

Riehm observed that pre-nesting flocks in her study area in south Germany usually bathed about 30–50 min before going to roost, but bathing was observed only once in my study, although many flocks were watched through the pre-roosting period. This may be because Wytham Great Wood has very few places suitable for bathing, although at least one apparently suitable spot did occur in each territory.

FEEDING TREES DURING THE PRE-NESTING PERIOD

During periods of observation on flocks and pairs from February to June 1971, the species of tree in which they were feeding was noted every 3 minutes (as has already been mentioned they change trees, on average, about once every 2–3 minutes while feeding). If several birds were feeding in the same tree it was recorded once only, but if birds of the same flock could be seen feeding in different trees then each was noted. The total number of observations was 481. Figure 7 summarises the results.

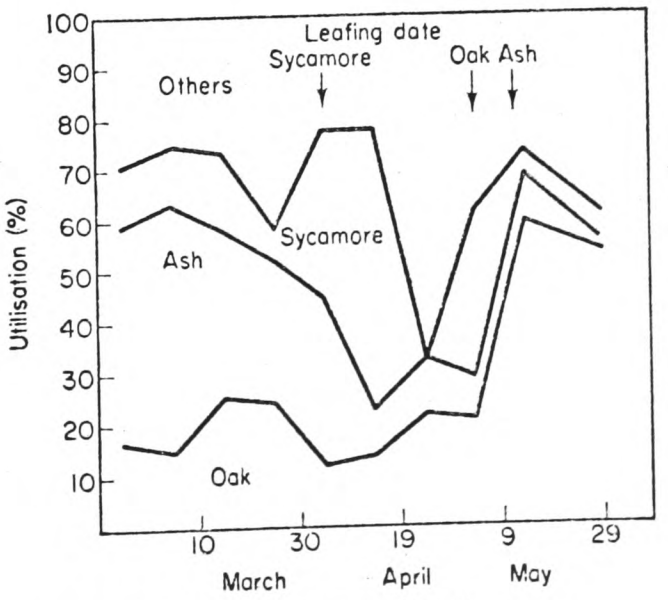


FIGURE 7. Utilisation of feeding trees.

Ash is the preferred feeding tree during February and early March, although over most of Wytham Great Wood it forms less than 30% of the canopy area. Sycamore, which forms about 50% of the canopy in the study area, comes into leaf in early April and there is a simultaneous increase in the proportion of time spent feeding in this tree. Once the oaks come into leaf, at the beginning of May, feeding becomes concentrated in these.

NESTING PERIOD

NEST-SITE IN RELATION TO FLOCK TERRITORIES

All birds known to have belonged to the Chalet, LAH and Pond flocks during the winter and pre-nesting periods nested either within the known flock territories or in hedges adjacent to them. All birds known to have belonged to Broken flock nested within the known pre-nesting period territory of the group. The extent of the winter territory of this flock was not known, but in the pre-nesting period the flock took over the winter territory occupied by Doubles flock and one pair nested in this area.

In two cases a female of one flock was mated to a male of a different flock, and in both cases the nest was within the territory of the male's flock. In seven other instances pairs were made up of a known male and an unringed female, and again, all nests were in the territory of the male's flock. There were no instances where a pair was made up of a known female and an unknown male. The probability of these pairings occurring purely by chance is less than 0·05, and it suggests that females move away from their flocks during the pre-nesting period and are more likely than males to be accepted into another flock.

TIMING OF BREEDING SEASON

An attempt was made to find all the nests within the study area. A total of 58 were found out of a probable total of 68 built in the area. The localities of three more were known but the nests were either deserted or predated before they could be found. All nests except two were found during building, by watching the birds carrying nest-material. At this stage the parents are very conspicuous, calling loudly in the vicinity of the nest. Within the main study area all nests were found during building, and most were followed from the first day or two. All nests were visited every other day in order to check their progress.

The first signs of nest-building in Wytham Wood were seen on 14 March in 1971, although a pair on farmland less than a mile away had begun building in February. Most first nests in the woods were well under way by the end of March and the first egg was laid on 9 April.

Early in the season, nest-building proceeded very slowly. The three earliest nests found took 26, 29, and 33 days respectively from initiation to the laying of the first egg. Nests are built much more rapidly later in the season (Fig. 8). It seems likely that an increased abundance of food and more hours of daylight allow the birds to spend more time per day in nest-building. Also, according to Riehm, later nests are less compact and lined with fewer feathers.

Most early nests were completed well before egg-laying began, although it was difficult to be certain that the lining was completely finished. It seemed likely that the factor holding up the onset of egg-laying concerned the ability of the female to lay, rather than delay in preparing the nest. Those pairs in which the female laid her first clutch soon after completing the nest were more likely to build a repeat nest after predation than those in which the laying of the first clutch was delayed. This is shown in Table 7. There is probably a seasonal decline in clutch size (Table 8).

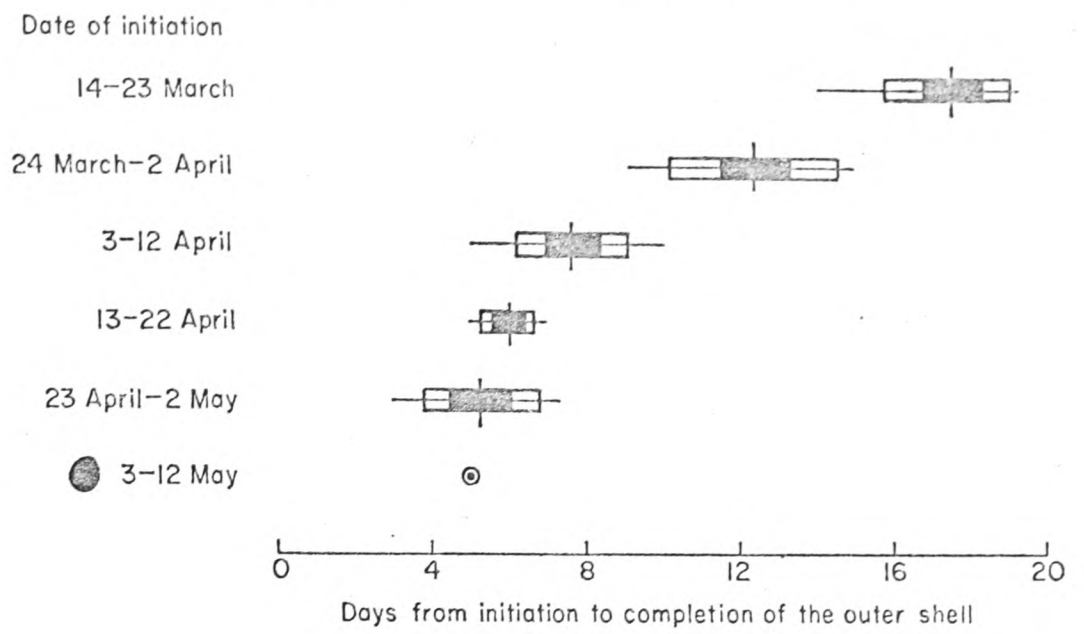


FIGURE 8. Rate of nest-building in relation to the date of initiation. Conventions as in Figure 6.

TABLE 7

Rebuilding in relation to date of laying first egg

	Date of laying of first egg of first clutch
Pairs which did not rebuild	April 18, 22, 26
Pairs rebuilding once	April 11, 12, 12, 14, 18, 22
Pairs rebuilding twice	April 11, 11

Note. The date of laying of the first egg in the earliest nest was 9 April.

TABLE 8

Clutch-size and date of laying of Long-tailed Tits, Wytham Wood 1971

	n	Mean date of laying	Mean clutch-size
First nests	20	14 April	9·4
Repeat nests	11	23 April	8·6 (7 clutches only)
Second repeat nests	1	10 May	6

Note. Eggs were removed from the nest with a plastic teaspoon in order to check their number, although feeling with the fingers was found to be fairly accurate.

NEST-SITE

The nest-sites utilised by Long-tailed Tits in Wytham Great Wood are discussed at length by the Lacks (*loc. cit.*), who emphasised the wide range of sites selected and their unusually broad vertical distribution. Table 9 compares the nest-sites used in Marley Wood during 1949–51, and in the Great Wood during 1955–57, with those found in the present study.

The Lacks found that a significantly higher proportion of nests were built 6 m or more above the ground in the Great Wood than in the nearby Marley Wood. Figures from the present study, however, show that this state of affairs has completely altered: a smaller proportion of nests in the Great Wood during 1971 were over 6 m than was found in the original Marley study. This switch in nest-height preference in the Great Wood between 1957 and 1971 is statistically significant ($P<0{\cdot}01$).

TABLE 9

Long-tailed Tit nest-sites in Marley Wood (1949–51) and Wytham Wood (1955–57 and 1971)

	Marley 1949–51	Wytham 1955–57	Wytham 1971
Site			
Low thorns	28	20	45
Thornless twigs	6	5	9
Bare forks	10	14	5
Height above ground			
0–3 m	29	21	51
3–6 m	4	0	3
>6 m	8	18	5

The difference in the proportion of nests above 6 m is significant between Marley 1949–51 and Wytham 1955–57 ($P<0.05$) and between Wytham 1955–57 and Wytham 1971 ($P<0.01$), but not between Marley 1949–51 and Wytham 1971 ($P<0.2$).

Only nests found during building have been used in compiling this table, which includes three nests built outside the study area but within the boundary of the Great Wood.

The observed change in nest-site preference over the last 14 years is understandable in view of the fact that the Lacks found nests built above 6 m to be invariably unsuccessful, and this was also true of the few attempts at this height in 1971. Evidence from both studies suggests that pairs which have their first nests destroyed tend to change the height of their nest-site when they rebuild (Table 10). In both cases the switch in nest-site between first and repeat nests is significant ($P=0.05$). The switch is in opposite directions in the two studies, however, because in 1955–57 the majority of first nests were more than 6 m above the ground, while in 1971 all first nests were below 3 m. Possibly a change in the height of the second nest decreases its chance of predation.

TABLE 10

Height of nest-sites above ground, Wytham Wood 1955–57 and 1971

		Height above ground <3 m	>6 m	
1955–57	first nests	4	7	$\chi^2=4.02$, $P=<0.05$
	repeats	12	4	
1971	first nests	25	0	$P=0.05$, Fisher exact test
	repeats	21	4	

SELECTION OF NEST-SITES IN RELATION TO HABITAT

Most of the study area, as shown in Figure 1, comprises closed-canopy deciduous woodland and mature or medium-aged plantations of conifers and beech. Open-canopy woodland, often created by thinning, occurs on the periphery of the main woodland blocks, along with areas of hawthorn and elder scrub. There are also some young plantations of conifers. Figure 9 shows the position of all Long-tailed Tits' nests found within the study area, in relation to the distribution of the different types of woodland.

During the winter the flocks fed mainly in the deciduous woodland but for nesting there was a strong preference towards scrub. In addition, 21 nests (36%) were built outside the wood in hedges and bushes near the woodland margin. Because areas of scrub are mainly peripheral to the woodland, nests have a tendency to be situated at the edges of the territories. Table 11 lists the number of nests in each type of woodland, and their density per km^2. Testing the number of nests in closed-canopy woodland against a theoretical number (29·6) derived from the proportionate area shows the observed number (10) to be significantly lower ($\chi^2=12.9$, $P<0.01$) than would be expected if the nests were distributed evenly.

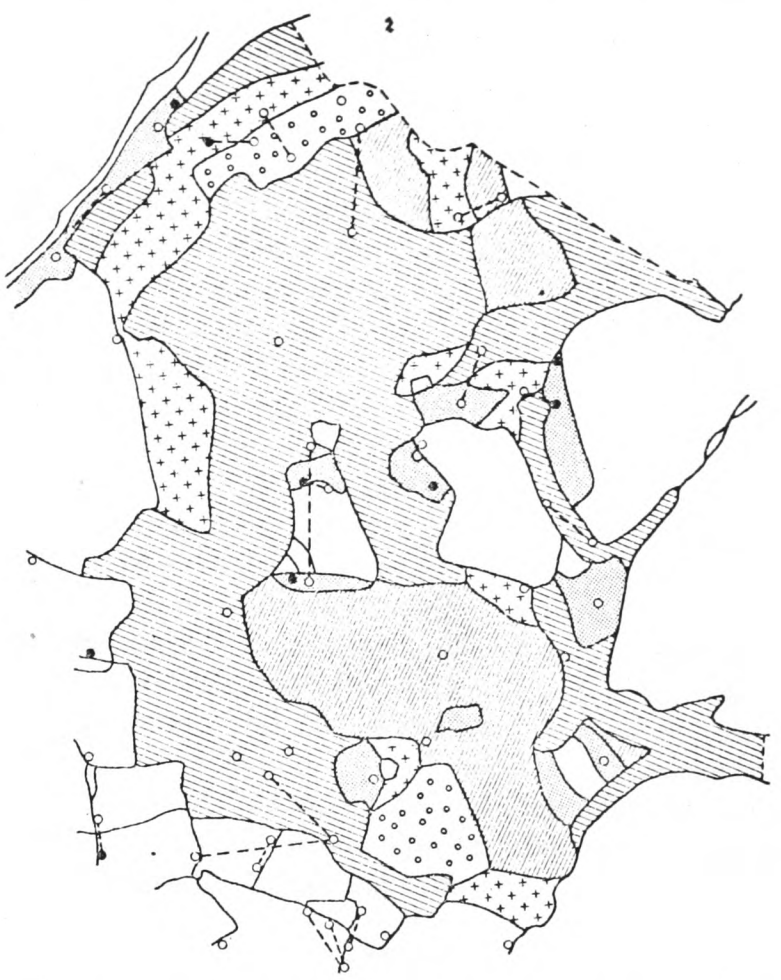


FIGURE 9. Distribution of nests in relation to habitat. Dotted lines connect nests of the same pair. Nest: ●, successful, ○, unsuccessful.

TABLE 11

Distribution of Long-tailed Tit nests in relation to woodland type, Wytham Wood, 1971

Woodland type	Area (km²)	No. of nests	No. successful	Nests/km²
Closed canopy	1·26 (51%)	10 (17·3%)	0	7·9
Open canopy	0·35 (14·2%)	4 (6·9%)	1	11·4
Plantation >10 ft	0·48 (19·6%)	3 (5·1%)	0	6·1
Plantation <10 ft	0·18 (7·2%)	4 (6·9%)	0	22·4
Scrub	0·20 (8%)	16 (27·6%)	5	80·0
Hedges or bushes outside the wood	—	21 (36·2%)	3	—

The observed preference for nest-sites in scrub, or hedges and bushes outside the wood, corresponds with the distribution of successful nests. In these two habitats 8 out of 36 nests found were successful in fledging young (22·2%), whereas in the other four areas only 1 out of 22 (4·5%) was successful. A similar effect was found by the Lacks, who divided nests in low thorn bushes into two categories: inside the wood, and on the edge of the wood. The second category was the more successful with 8 out of 17 nests (47%) surviving, while in the first group only 3 out of 26 (12%) survived ($\chi^2=3{\cdot}88$, $P<0{\cdot}05$).

PREDATION OF NESTS

Predation is by far the most important cause of nest-failure. The signs of predation are usually of two kinds: either the nest is torn to pieces and the lining scattered around, or the nest is more or less intact with either an enlarged entrance or a hole in the bottom or

side and perhaps a little lining pulled out. Predation of the first kind was ascribed by the Lacks to Jays *Garrulus glandarius* and this seems the most likely explanation in the case of woodland nests. In the case of hedgerow nests, Carrion Crows *Corvus corone* or Magpies *Pica pica* may be responsible.

The second category of predation seems likely to be caused by some mammal, perhaps weasels or mice. No definite evidence was found of either, but in some nests the entrance hole was pulled closed, so that there was apparently no way in, and it seems possible that this might be done by mice, adapting the structure for their own nest.

Of those nests showing typical symptoms of either form of predation 25 were of the Jay type, and 15 of the mammal type. The figures for April and May were, respectively, 14 : 6 and 11 : 9, which suggests that Jay predation may be higher earlier in the season, but the difference is not statistically significant.

Table 12 compares the number of nests predated at each stage of the nesting cycle with the total number of nest-days for which they were exposed to predation. The degree of predation in each period is calculated as an index, derived from 100 × no. nests predated ÷ total no. nest-days. From the number of nest-days in any period an expected number of predations can be calculated from $Nd_x/Nd_t \times 37 + 49$, where Nd_x is the number of nest-days in a given period and Nd_t is the total number of nest-days. Testing the period of nest-building, $\chi^2 = 3{\cdot}95$ and $P < 0{\cdot}05$ ($n = 1$). The same level of probability is obtained testing the two sets of data separately and then multiplying the two probabilities obtained. The rate of predation would appear from this to be higher during nest-building than at other stages in the nesting cycle.

TABLE 12

Nest predation at different stages of breeding in relation to duration of exposure to predation. Data from present study and Lack & Lack (1958)

	Duration of exposure (nest-days)		Number predated		Index of predation	
	1971	1955–57	1971	1955–57	1971	1955–57
Building	267	475	16	25	6·0	5·25
Laying	207	264	9	4	4·35	1·52
Incubation	227	345	8	16	3·52	4·64
Fledging	152	208	4	4	2·62	1·92
Totals	835	1292	37	49	4·44	3·79

Figure 10 shows the index of predation for five 16-day periods covering the entire breeding season of the Wytham Long-tailed Tits in 1971. This shows a build-up in periods A–C followed by a sharp drop in the last two periods. The peak predation during period C (29 April–4 May), tested against an expected predation, assuming a constant rate of predation throughout the season, gives $\chi^2 = 6{\cdot}4$. $P < 0{\cdot}02$; hence predation is definitely highest in mid-season. There is no apparent reason why nests in late April and early May should be more vulnerable than those earlier in the season. A possible explanation is that predators may become more adept at recognising nests, due to the development of a search-image.

The pattern of predation revealed in this analysis may help to explain why Long-tailed Tits build their nests so early in the season. Nest-building is the most critical period, so that it may be advantageous to complete this stage before the activity of the predators reaches its peak. This idea assumes, however, that the visits made to the nest by the birds during the course of construction are the factor which increases the vulnerability of the nest at this stage. An alternative explanation is that some nests are very badly sited and are extremely vulnerable to predation, so that they are inevitably destroyed during building. This possibility is difficult to eliminate.

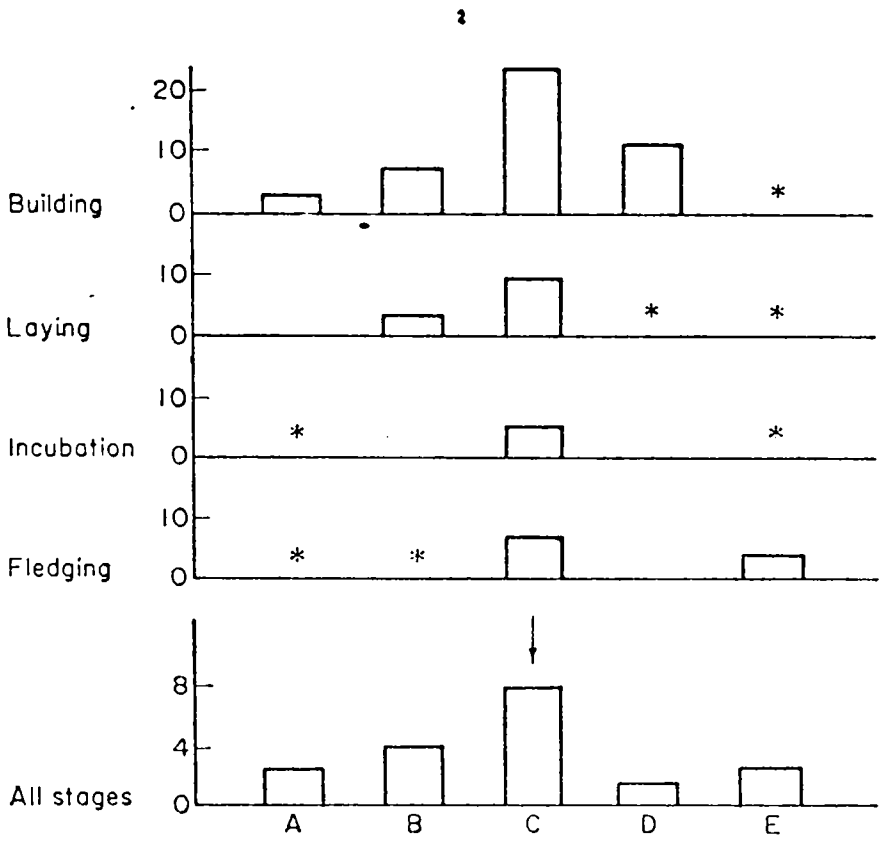


FIGURE 10. Rates of predation in relation to time of year. The vertical axis represents the index of predation (for derivation see text, p. 346); A–C represent the five periods into which the breeding season is divided. ↓ = peak significance at 0·05% level; * = no nests at risk.

The sharp drop in predation after 15 May (periods D and E) is probably due to the growth of vegetation and the leafing of trees and bushes. In 1971 hawthorn in Wytham began leafing about 10 April and blackthorn about 18 April. By early May both were almost completely leafed. Brambles also thicken up considerably, starting about the middle of April and continuing into May. The thickening of the vegetation from mid-April onwards might be expected to cause a decline in predation from this point on, and the fact that this does not happen strengthens the idea that predators become progressively better at finding nests as the season proceeds.

SUPERNUMERARY BIRDS AT THE NEST

One feature of Long-tailed Tit nesting habits which has been commented on often (see Lack & Lack 1958 for references) is the high incidence of extra birds assisting the parent pair during the rearing of the young. Most accounts on record involve only a single nest, however, and it is difficult to assess from these just how common the habit is. Of the 10 pairs in the present study which reared young to at least 7 days old, six were known to have had supernumerary birds bringing food to the young. In addition supernumerary birds were seen feeding the recently fledged young of two of the other four pairs.

The sex of the supernumerary birds helping at the nest was determined in three cases, the birds involved being two males and a female. Of these one male and the female had belonged to the same pre-nesting flock as the pair that they assisted. The other male had definitely not belonged to the same pre-nesting flock as the pair which it assisted. The supernumerary birds assisting after fledging were a pair and they fed both broods of two pairs from the same pre-nesting flock. In another case two supernumerary birds began

assisting a pair immediately after a nearby nest had been predated and it seems likely that these were the unsuccessful pair.

The earliest supernumerary bird to be recorded was one helping on the fourth day after hatching, but this bird was not seen again and another helper appeared at the same nest on the 13th day. The arrivals of the supernumerary birds at the other nests were recorded 8, 10, 10, 13 and 15 days after hatching.

At 3 nests, due to the presence of colour-ringed birds, it was possible to assess the number of visits made by each bird to feed the young. In one case the supernumerary bird, a female, visited the nest 28 times, against 18 and 21 visits respectively by the male and female parent. At another nest the supernumerary, a male, made 57 visits against 68 by the male and 151 by the female parent. In the third case the two unringed birds made 22 visits to the ringed male's 6 visits. No pattern is discernible from such a small sample of observations and it seems likely that the contribution of the supernumerary bird varies considerably.

The importance of this assistance at the nest is not clear. Several factors (including age of nestlings and time of day) influence the rate at which nestlings are fed and the present data are not adequate to show whether nestlings were fed more frequently in nests where a supernumerary bird assisted. The supernumerary birds assisted mainly in the later stages of the fledging period, when the rate of feeding would be expected to be higher in any case. The mean rate of feeding at nests where three or more birds were involved was 21·4 visits/hr (10·5 hrs). The mean rate of feeding at nests with only the parent pair was 20·5 visits/hr (7·5 hrs). This difference was not significant ($t=0{\cdot}32$ for 54 degrees of freedom, $P>0{\cdot}3$). The rate of feeding by the parent pair at nests where there was a helper was only 16·3 visits/hr (12·5 hrs) and this is lower than the rate of visits by parents without helpers ($t=1{\cdot}76$, $P=0{\cdot}05$–$0{\cdot}1$ for 42 degrees of freedom). These figures include only observations on nests with chicks at 10 days or older between 09.00–17.00 hrs BST.

The fact that the presence of a supernumerary bird may reduce the feeding rate of the parents, so that the young are fed with the same frequency as at nests without helpers, might be true only when food is in any case abundant. It does not exclude the possibility that assistance may be useful under less favourable conditions.

THE HOVER DISPLAY

This display has been recorded previously by Nakamura (1962) and Riehm (1970). It consists of flying steeply upwards one or two feet from a perch, or during a short flight between perches, and hovering for about a second before descending with a flutter to the same or another perch. The display is sometimes accompanied by a *tic* call, but is often silent. It occurs both before and after feeding the young, and may be performed with the beak full of caterpillars, and even occasionally while the bird is carrying a faecal sac.

The onset of this behaviour, which occurs only within a few yards, often a few feet, of the nest, was recorded on the following days after hatching: 2, 4, 5, 5, 7, 8, 10 (mean 5·8). Both sexes perform the display. In some pairs the male does so more frequently, in others the frequency is more or less equal. The female ceases to brood the young about day 5.

The frequency of the display varied between pairs and was highest at nests where a supernumerary bird was helping to feed the young (Table 13). The arrival of these supernumerary birds in no case occurred until the onset of the hover display. The supernumerary birds performed the display to about the same extent as the parents.

Riehm suggests that the hover display serves to distract predators, but this seems rather unlikely. If so, then it would surely be employed earlier in the breeding period

TABLE 13

Relationship of the hover display to the presence of supernumerary birds at the nest

		Number of visits with hover display	without display
Nests without supernumerary helper	a	2	24
	b	7	10
	c	1	20
	d	10	0
	Total	20	54
Nests with supernumerary helper	e	19	6
	f	6	4
	g	27	0
	h	14	2
	Total	66	12

Testing the totals, $\chi^2 = 51$, $P < 0{\cdot}001$.

Counts at eight nests with young more than 7 days old, made between 11.00 and 15.00 hrs.

when the nest is more at risk. In addition it seems unlikely that potential predators use the behaviour of the parents to locate nests, as the Lacks (1958) pointed out.

The display is extremely conspicuous, and being performed right beside the nest, would appear to provide an accurate guide to the position of the nest to any extra bird which might be in a state to assist in the rearing of the young. On a few occasions the display appeared to be specifically provoked by the intervention of an intruder bird near the nest (not one which was seen to feed the young), but in these instances it was apparently coupled with aggression, since the intruder was chased off.

The display is so distinctive that it is difficult to believe that it does not have an important function. As it pinpoints the whereabouts of the nest very accurately, and exposes the adult itself to predation, it must have some compensatory value. The attraction of supernumerary helpers to the nest might provide such compensation.

POST-FLEDGING BEHAVIOUR

The two broods reared by pairs of the LAH–LBW flock joined up three days after the fledging of the second brood and were fed jointly by both pairs and the supernumerary female which had assisted one pair. Two of the broods reared by pairs of Chalet flock joined up two days after the fledging of the second brood and were fed by both pairs and a supernumerary pair already referred to. The third successful nest in the Chalet flock territory, which had an unringed female and supernumerary helper, fledged two weeks later than the other two broods and was not known to have joined up with them.

The fledged young continued to be fed for at least two weeks after leaving the nest. A flock watched 10 days after the fledging of the younger brood was being brought largely caterpillars by the adults, but the juveniles seemed to be catching aphids and other adult insects for themselves.

During the period from one to three weeks after fledging, parties of juveniles call persistently, using the *eez* call. There is also a great deal of chasing among juveniles after the second week after fledging and this may be related to the establishment of a linear dominance hierarchy, as suggested by Riehm.

POPULATION DYNAMICS

The approximate population of the study area during October, estimated from counts of flock size and the extent of territories subsequently discovered, was 150 birds. The distribution of these is shown in Figure 11. Evidence from the random sighting of

colour-ringed birds during December suggests that the population remained stable until then. In mid-February the population was difficult to assess because of movements, but it was probably little larger than the subsequent breeding population of 78. A reduction of nearly 50% took place, therefore, between mid-December and mid-February.

With a total of 78 young reared the breeding population was doubled by the reproductive effort. If the October population in 1971 was similar to that in 1970, then losses between June and October were probably negligible, the bulk of post-fledging mortality being concentrated between mid-December and mid-February.

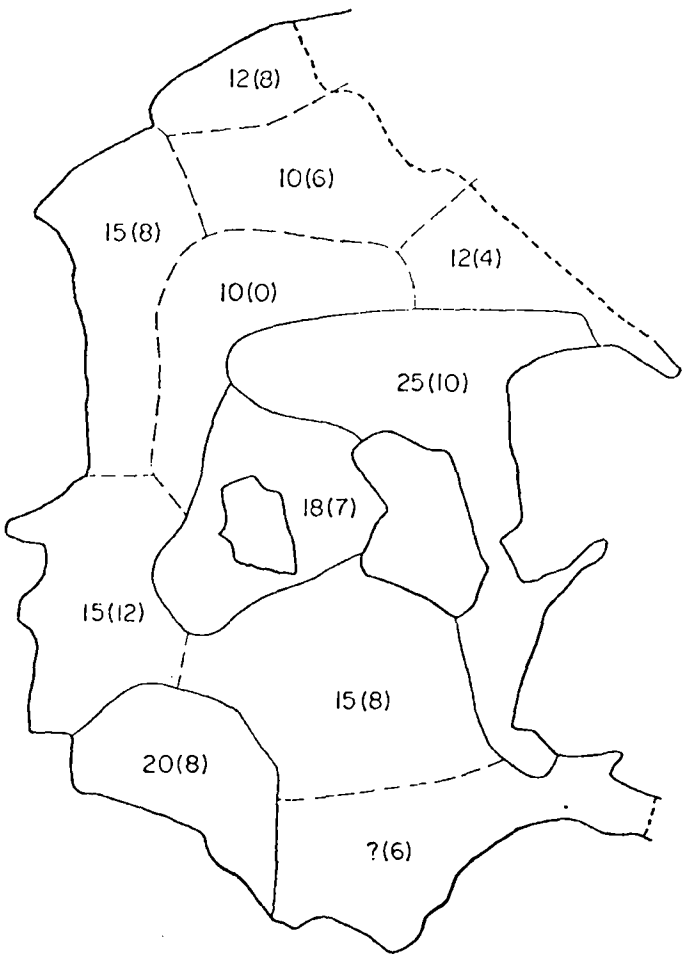


FIGURE 11. Probable distribution of flock territories, October–December 1970. Numbers give flock sizes in October, bracketed numbers flock sizes in March.

Within the territories of LAH, Chalet and Pond flocks the population density in October was calculated as 79/km^2. The density over the whole study area was 61/km^2. In March the density in LAH, Chalet and Pond territories had fallen to 34/km^2 and the overall density in the study area to 31/km^2.

In the Tenryu area of Honshu, Japan, Nakamura (1967) recorded fluctuations in density between 30–140 Long-tailed Tits per km^2. In the Keito area fluctuations were between 30–50/km^2. The mean area of five flock territories in Japan was 0·21 km^2. The mean area of LAH, Chalet and Pond territories was 0·25 km^2

Both Nakamura and Riehm discussed changes in the social structure and population density of Long-tailed Tits through the year. Both of these studies showed significant differences from the situation at Wytham. In the Japanese study there was a decline in population throughout the autumn instead of the rapid crash in late winter observed in Wytham. In south Germany, Riehm found that juveniles and adult flocks split up in

July and only adult flocks defended territories. In Wytham, however, all flocks trapped in October contained both adult and first-year birds, and all helped to defend the joint territory.

SUMMARY

The behaviour and ecology of a population of Long-tailed Tits in Wytham Great Wood, Oxford, were studied between October 1970 and June 1971. Flocks were found to have a stable composition in autumn, and to occupy fairly discrete territories which they defended against other flocks.

In spring the population was reduced by about 50% and in the pre-nesting period flocks formed only in cold weather or just before going to roost. These flocks occupied the same territories as the autumn flocks and the individuals composing them eventually nested within the flock territory.

Predation of nests was heavy, increasing to a peak in the first half of May. Only nine pairs out of 36 managed to rear young successfully. At six out of these nine nests, supernumerary birds helped to feed the young, but it seems unlikely that this increased their success, since all young hatched fledged successfully. The presence of supernumerary birds at the nest was accompanied by frequent hover-displays by all the adults.

The distribution of nests in relation to habitat shows that there is a preference for scrub rather than mature woodland, although the latter is used extensively for feeding during the winter. There appears to have been a radical change in the height of nest-sites in Wytham Great Wood between 1955–57 and 1971, and this is probably due to predation.

REFERENCES

ELTON, C. 1966. The pattern of animal communities. London.

GIBB, J. A. 1954. Feeding ecology of tits, with notes on Treecreeper and Goldcrest. Ibis 96: 513–543.

LACK, D. & LACK, E. 1958. The nesting of the Long-tailed Tit. Bird Study 5: 1–19.

LÖHRL, H. 1964. Verhaltensmerkmale der Gattung *Parus* (Meisen), *Aegithalos* (Schwanzmeisen), *Sitta* (Kleiber), *Tichodroma* (Mauerläufer), and *Certhia* (Baumläufer). J. Orn. 105: 153–181.

NAKAMURA, T. 1962. Observations on the breeding biology of Long-tailed Tits, *Aegithalos caudatus trivirgatus*. Misc. Rep. Yamashina Inst. 3: 155–173.

NAKAMURA, T. 1967. Studies on the fluctuations in numbers of Long-tailed Tits (*Aegithalos caudatus*) along the slopes of the River Tenryu, Nagano. III. Seasonal changes in the mode of life. Japan. J. Ecol. 16: 17–22.

NAKAMURA, T. 1969. Structure of flock range in the Long-tailed Tit, I. Winter flock, its home range and territory. Misc. Rep. Yamashina Inst. 5: 1–29.

RIEHM, H. 1970. Ökologie und Verhalten der Schwanzmeise (*Aegithalos caudatus*). Zool. Jb. Syst. Bd. 97: 338–400.

SVENSON, L. 1970. Identification guide to European passerines. Stockholm: Naturhistoriska Riksmusect.

A. J. Gaston, Edward Grey Institute, Department of Zoology, South Parks Road, Oxford OX1 3PS

Chapter 10. The evolution of group territorial behaviour and co-operative breeding

Chapter 10. The evolution of group territorial behaviour and co-operative breeding

Introduction

This chapter considers factors influencing the evolution of group territorial behaviour and co-operative breeding in birds. In many species of tropical birds there is a prolonged period of post-fledging care (Fogden 1972), but for the present analysis only cases where groups of more than two birds persist during the following breeding season will be discussed. Instances of group territoriality in which groups form outside the breeding season, such as that described by Glase (1973) for the Black-capped Chickadee Parus atricapillus, and those where breeding groups form from the coalition of unrelated birds, as in the Anis Crotophaga (Vehrencamp-Bradbury 1974), are also excluded.

A number of authors have discussed correlates of group territorial behaviour (Skutch 1961, Fry 1972, Ricklefs 1975, Grimes 1976) but only one general model has so far been attempted (Brown 1974, elaborated by Wilson 1975). The intention of this chapter is to present another model, taking into account some factors not discussed by Brown and Wilson and to examine some of its implications in the light of current knowledge.

a) Factors influencing the evolution of group territorial behaviour

Evidence from the present study and from several others (Rowley 1965, Brown 1972, Parry 1973, Zahavi 1974) suggests that most groups consist of a pair plus the offspring of one or more previous seasons. From these observations it appears likely that group territorial behaviour in these species evolved through prolonging the period during which offspring remained in the parental territory (Brown 1974). The following assumptions are made:

1) That the parents could drive their offspring out of the territory if they chose.

2) That the parents cannot prevent the offspring from leaving if they choose to do so.

The first assumption is based on observations that adult birds usually fare better than first year birds in competition for territories (Tompa 1964, Delius 1965, Watson & Moss 1970, Dhondt 1971, Klomp 1972) and that dominance within groups is usually related to age (Rowley 1965, Ridpath 1972, Zahavi & Woolfenden pers. comm. and also data from the present study). The second assumption is based on the physical impossibility of any such constraint being imposed. The crucial process in the evolution of group territorial behaviour, therefore, is considered to be selection for tolerance in the breeding pair towards the continuing presence of offspring within their territory.

When considering factors affecting the evolution of group territorial behaviour priority will be given to those affecting the fitness of the breeding adults, since an increase in fitness to the non-breeder must presumably occur (assumption 2). Effects on the inclusive fitness (Hamilton 1964) of breeders will be divided into direct effects; those which affect their own survival and reproductive success, and indirect effects; those affecting the survival and reproductive success of non-breeders allowed to remain in their territory. Since initially these non-breeders are likely to be the offspring of the breeders, there is no clear line between the two effects, but for the present purpose all effects operating on the offspring after the initiation of a further nesting attempt by their parents will be considered to affect their parents indirectly.

Factors I believe to influence the selective value of group territorial behaviour to the breeders are considered below.

Indirect effects

1) As the survival rate of the breeding adults increases, the chances of young birds finding a vacant territory are diminished, if reproductive success and survival of young remains unchanged. In this situation, if the competitiveness of the young birds increases with age then postponement of departure from the parental territory increases the chance of establishing a territory elsewhere. The circumstances necessary for the evolution of deferred maturity have been formulated by Wiley (1974) for the case in which the danger of mortality due to reproduction decreases with age. In the present case it can be assumed that non-breeding birds will remain in the parental territory as long as: $\Delta z.s > 1$,

where 'Δz' is the increase in the reproductive value of the individual due to increased competitiveness.

's' is the survival rate over the same period.

2) As the reproductive success of the breeders, or the survival of their offspring increases, the chances of young birds finding territories is also diminished, assuming constant adult survival. This and the preceding factor combine to create the excess potential reproductive population noted by Ricklefs (1975) as an important factor in the evolution of group territories.

3) As the survival of non-breeders in marginal areas, or in areas suitable for feeding but not for breeding decreases, so the increase in fitness likely to be derived from remaining within the parental territory increases.

4) As the availability of vacant territories decreases, the value of being in a position to succeed to the parental territory increases, assuming that the presence of the non-breeder in the territory increases its competitive ability compared to birds from outside, in the event of the death of the incumbent breeder. This effect will be called the 'patrimony

factor', since only the male non-breeders of most group territorial species eventually breed within the parental territory (Woolfenden 1975, Zahavi pers. comm. and data from this study), and the effect should only operate on the non-dispersive sex.

The dispersal of female offspring reduces the possibility of inbreeding. Since dispersal is likely to carry higher risks to individual survival than remaining within the natal group it seems necessary to assume that inbreeding leads to a reduction in the inclusive fitness of the birds involved. Little is known of the effects of inbreeding among natural populations of birds but evidence from Great Tits (Bulmer 1973) suggests that it can cause a considerable decline in reproductive success. The fact that the female sex disperses among babblers presumably results from the fact that males were the territorial sex originally, as is the case for most birds. In a situation where group territorial behaviour became adaptive for a species of bird in which females were the territorial sex we might anticipate male dispersal and matrilineal succession within territories.

Direct effects

5) The ways in which living in groups may increase the fitness of the individuals involved have been discussed at length by Wilson (1975). Those advantages which seem most applicable to group territorial birds are improved detection of predators, combined defence against them (mobbing), and increased foraging efficiency. The latter might be achieved both through imitative foraging, or by increased efficiency in the way in which the food supply is cropped. In a heterogenous environment a larger group, holding a larger territory, is likely to have a greater diversity of resources under its control, and hence be more able to cope with environmental fluctuations such as unpredictable rainfall or the local failure of certain food supplies.

It seems worth noting that most group territorial species studied so far are insectivorous or feed on small vertebrate prey during the breeding season, and hence exploit relatively uniformly dispersed food supplies. Wintering insectivores which utilise the same habitat as the Jungle Babbler adopt individual territories (pers. obs.), and most models of foraging predict that flocking is most adaptive when food is clumped (Horn 1968, Thompson, Vertinsky & Krebs 1974). For this reason it is not permissible to assume that feeding efficiency is necessarily enhanced by the adoption of group territorial behaviour. Certain feeding strategies may be adversely affected by the presence of conspecifics nearby. Group territory would increase this interference unless limited by some second order spacing mechanism.

6) The presence of a non-breeder in the territory might have an adverse effect on the fitness of the breeders in a number of ways. Its presence might cause depletion of food resources in the territory, or might attract the attention of predators and brood-parasites to the nest. The breeders also run the risk that by allowing a non-breeder to remain within the territory it may later improve its competitive ability to the point where it is able to usurp their dominance.

7) Adaptations in the behaviour of the non-breeder which reduce the effects listed under section 6 above are ~~altruistic~~ kin-selected, since they enhance the fitness of the breeders while they improve the fitness of the non-breeder only through its relatedness to them. Such adaptations would include the avoidance of conspicuous behaviour in the vicinity of the nest, and assisting with the enlargement of the territory so that sufficient food was present to compensate for the presence of the non-breeder. Other apparently altruistic behaviours which have been observed among group territorial birds include the participation of non-breeders in incubation,

the feeding of the nestlings, and joint defence of the nest against predators. This conspicuous and much discussed feature of group territorial behaviour is known as co-operative breeding (Lack 1968).

Co-operative breeding occurs in a wide range of species of diverse ecology (Skutch 1961) and it is probably found in all species which maintain group territories throughout the year. Examination of the literature suggests that in some cases the activities of non-breeders make a positive contribution to the reproductive success of the breeders (Rowley 1965, Parry 1973, Woolfenden 1975), while in other cases they may not (Zahavi 1974, and this study). Where a positive contribution is made this must affect the value of group territorial behaviour to the breeders.

Effects resulting from competition

8) The discussion of altruism in the preceding section (7) does not consider the case in which competition exists between the donor (the non-breeder) and the recipient (the offspring of the breeding pair). Real or potential competition must exist in all cases (Alexander 1974, Eberhard 1975). For many group territorial species which have low dispersive powers this competition is likely to be quite severe.

The effects of reproductive competition on the strategy of the non-breeder depends on the likelihood that an offspring reared later than itself could become established as a breeder before it. The extent to which this occurs is known in very few instances. In the Florida Scrub Jay Aphelocoma c. coerulescens Woolfenden (pers. comm.) found rigidly age-related hierarchies, but in the Common Babbler several instances of males achieving breeding status before older members of the same group were observed.

The individual non-breeder is affected by competitive relations with all other non-breeders, and hence the effect of competition must increase with group size. Where the patrimony factor is high there may be strong competition between male non-breeders to succeed to the common territory. As Woolfenden (quoted by Wilson 1975) has pointed out, however, if increase in group size leads to expansion of the common territory then one of the non-breeders may eventually be able to split off a portion for itself. In that case the help rendered to the breeders is not entirely altruistic.

Competition may also create differences in strategy between the sexes in relation to co-operative breeding. Because females disperse they do not come into such direct competition with other group members as males which compete for succession to the parental territory. At the same time males are likely to have more at stake in the continued maintenance of the group territory, and this may depend partly on recruitment into the group. If enlargement of the group, leading to enlargement of the territory, gives non-breeders an opportunity to split off a portion for themselves then direct benefit accrues to males through increases in group size. In Mexican Jays Aphelocoma ultramarina (Brown 1972) and in Common and Jungle Babblers Turdoides caudatus and T. striatus male non-breeders were found to contribute more feeding visits to nestlings than females of the same age, supporting the idea that strategies may differ between the sexes. In the case of the Jungle Babbler both the males and the females concerned were known to be the offspring of the breeding pair.

b) Factors affecting the evolution of co-operative breeding

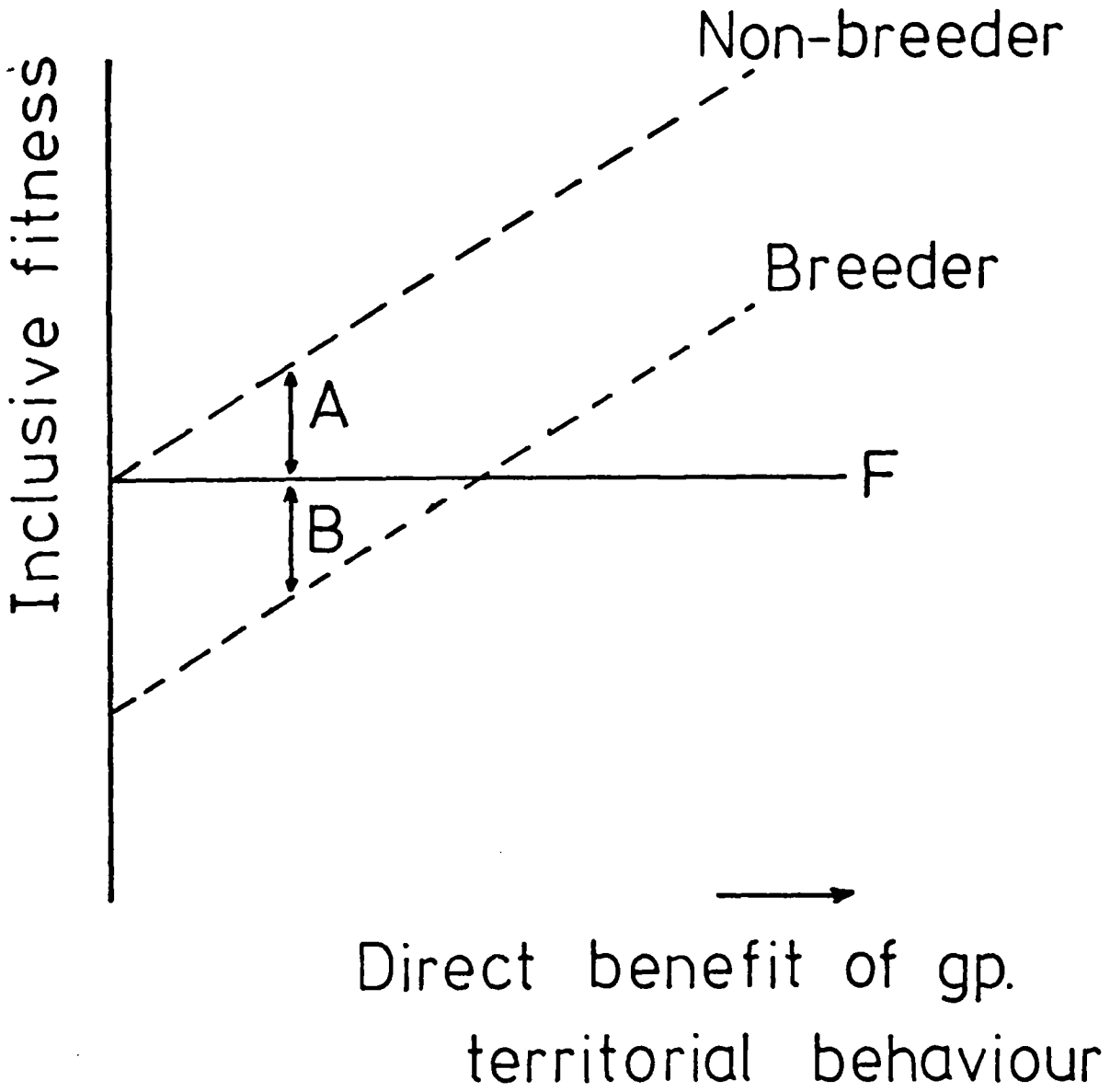
It is now possible to compare the increase in fitness of the breeders and the non-breeders resulting from the non-breeders remaining in the parental territory. Direct improvements to the fitness of the breeders, such as

feeding enhancement, predator detection, etc., operate equally for breeders and for non-breeders, though in practice they might be expected to operate preferentially for the non-breeders since breeders are likely to be more experienced at finding food or detecting danger. Indirect effects, by definition, accrue to the breeders only through the increased fitness of the non-breeder, and hence cannot increase the fitness of the breeders more than that of the non-breeder. On the other hand the interference and competition created by the presence of the non-breeder affects the breeders directly, and by the same argument the reduction in the fitness of the breeders through these effects must be greater than the reduction in the fitness of the non-breeder.

Because of these inequalities it is reasonable to suppose that a situation might arise in which remaining in the parental territory would increase the fitness of the non-breeder, but would not increase that of the breeder. In that case we might expect the non-breeder to assist the reproduction of the breeder to the extent that the breeders' fitness is raised by its continuing presence. Otherwise, under assumption 1, we should expect the non-breeder to be driven out of the territory. Assistance rendered to the breeders in this situation increases the fitness of the non-breeder both indirectly, through increasing the reproduction of the breeders, but also directly, by improving its own chance of being allowed to remain in the territory. A portion of the assistance rendered to the breeders can then be regarded as 'payment' for the right to remain.

The idea of payment is summarised in Figure 10a. The hypothesis is that the non-breeder should provide sufficient assistance to the breeders to raise their fitness to a level greater than that attainable by driving the non-breeder away. The non-breeder can afford to reduce its own fitness in providing this assistance so long as its fitness does not fall below that attainable

Figure 10a. Diagram illustrating the situation in which 'payment' may occur.
F; inclusive fitness of breeders in a pair territorial situation.
A; amount by which the non-breeder can afford to lower its own inclusive fitness in assisting the breeders.
B; amount by which the breeder's fitness must be raised through assistance, for the non-breeder to be allowed to remain in the territory (= payment).



outside the parental territory. The loss of fitness to the non-breeder need not be as great as the gain to the breeder because as Eberhard (1975) points out, under the theory of kin-selection the value to the receiver of a donation may be greater than the loss to the donor. In the case of food provided to nestlings, this inequality is likely to be large because in a period of food abundance there may be relatively little cost to the non-breeder in making sufficient feeding visits to increase the number of young fledged.

In a situation where the direct benefits of group territorial behaviour are large we should expect payment to be unnecessary for the non-breeder to be allowed to remain in the territory. In this case the non-breeder still stands to increase its inclusive fitness through kin-selection by assisting the breeders. This is only true, however, as long as the increase in fitness due to kin-selection exceeds the decrease in fitness due to the competition created.

The potential direct benefit to the breeders of having a non-breeder in their territory can be expected to be smaller in situations where group territorial behaviour has only recently evolved, since in these populations behavioural mechanisms for coping with aggression and other forms of social indiscipline are likely to be less effective. This may account for the considerable positive assistance rendered to the breeders by the non-breeders in the case of the Florida Scrub Jay Aphelocoma c. coerulescens (Woolfenden 1975), and the Superb Blue Wren Malurus cyaneus (Rowley 1965), species in which groups are generally small and include many pairs without non-breeders in attendance.

As the benefits of group territorial behaviour increase we should expect groups to become larger and this will reinforce the benefit which might be derived from increased predator detection and enhanced feeding.

Competition is also likely to increase, however, thereby reducing the potential increment in the fitness of the non-breeders gained through assisting the reproduction of the breeders. In the Arabian Babbler Turdoides squamiceps (Zahavi 1974), and the Jungle Babbler no positive assistance by the non-breeders to the reproductive success of the breeders could be detected, suggesting the presence of strong intra-group competition. In both of these species groups are larger and solitary pairs do not occur. Overt aggression within groups is rare and adaptations such as mobbing and sentinel behaviour which involve co-operation for mutual benefit, are well-developed.

It can be argued that the process of 'payment' could not influence the evolution of group territorial behaviour, since a non-breeder must be allowed to remain within the territory before it can contribute to the fitness of the breeders by helping them to reproduce. This difficulty can be avoided if we postulate a population occupying a habitat of varying quality. In good quality areas the fitness of the breeders may be increased by allowing non-breeders to remain within the territory irrespective of whether they assist in reproduction. In this situation tolerance towards non-breeders would increase the fitness of breeders in good quality areas, and decrease it in poor quality areas. Since reproduction and survival are higher in good quality areas, traits selected for there are likely to be exported to lower quality areas, and in these areas tolerance towards non-breeders will only be selected for if a payment is forthcoming.

In the absence of evidence that non-breeders render positive assistance to the reproduction of the breeders in species such as the babblers, where groups are large and non-breeding status lasts for several years, it seems necessary to conclude that in some cases where 'payment' is not required the increase in fitness of the non-breeders due to kin selection is insufficient

to offset the direct disadvantages created by the resulting competition within the group. Under this reasoning the feeding of the nestlings carried out by non-breeders in such species as the Mexican Jay and Jungle Babbler is a contribution directed at maintaining a continuing advantage to the breeders. It therefore represents a compromise between the interests of the breeders and the non-breeders concerning their rate of reproduction and the consequent group size.

An increase in intra-group competition among males can be predicted as group size increases because of the patrimony factor. Once a situation is reached in which all territories contain non-breeding males with priority to succeed to the territory the importance of the patrimony factor becomes very large, since finding a new territory, except in a marginal area, becomes almost impossible, and the best chance of breeding is to remain in the parental territory. The inter-relation of the payment effect, kin-selection, and intra-group competition in determining the strategy of a non-breeding bird is summarised in Figure 10b. Group size is assumed to increase with increase in the direct benefits of group territorial behaviour, and competition is assumed to increase with group size up to the point where all territories contain non-breeders.

As Figure 10b is designed three stages can be predicted in the evolution of co-operative breeding behaviour:

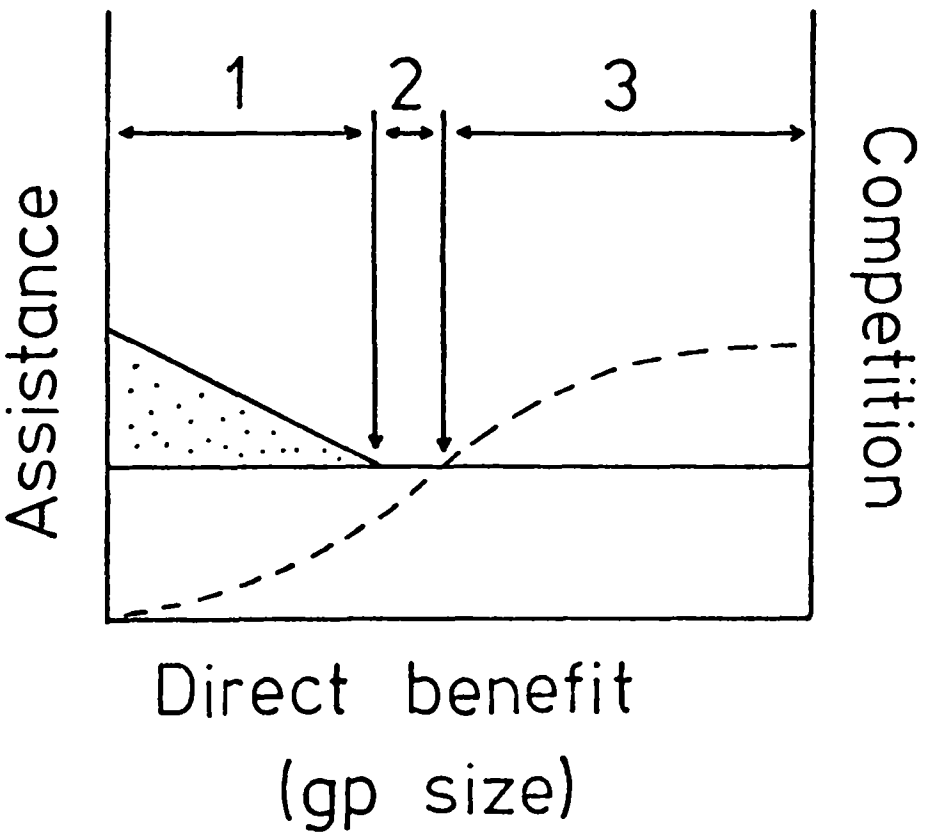
1) Positive assistance rendered to the breeders due to a combination of the payment effect and kin-selection.

2) Positive assistance rendered due to kin selection only.

3) No positive assistance rendered because the decrease in fitness resulting from the competition created would exceed the increase in fitness through kin selection.

Species such as the Superb Blue Wren and the Florida Scrub Jay can be assumed to be at stage 1 or 2, while the Arabian and Jungle Babblers are

Figure 10b. Diagram illustrating the proposed relationship between the direct benefits of group territoriality, the amount of assistance rendered by non-breeders and the amount of competition thus created.
Assistance (solid line); the amount of assistance provided to the breeders by the non-breeder which maximises the fitness of the non-breeder in the absence of competition.
Competition (broken line); the potential decrease in the inclusive fitness of the non-breeder due to the competition created by the predicted amount of assistance.
Stippled area; amount of assistance contributed due to the payment effect.



probably at stage 3. The sophisticated behavioural adaptations of the babblers to group existence suggest that they have been adapting to group territorial life for a long period.

c) Factors affecting the rate of emigration from groups

Only the case in which the breeders choose between driving one non-breeder out of the territory or allowing it to stay has been considered thus far. It seems reasonable to assume that if permitting one non-breeder to remain in the territory raises the fitness of the breeders, then allowing more to remain should compound this benefit. Hence no opposition to increases in group size should be anticipated from the breeders once group territoriality has become an adaptive strategy. Group size is therefore likely to be controlled by the emigration of non-breeders in their own interest, rather than by active expulsion by the breeders.

Since we assume that non-breeders will be allowed to remain in the territory only as long as their presence increases the inclusive fitness of the breeding pair, we can also assume that attempts by some non-breeders to drive out others will not be in the best interests of the breeders and may be resisted by them. On this issue competition is likely to cause a difference between the optimum strategies of breeders and non-breeders, but under the assumpiton that breeders are dominant we can assume that the conflict is resolved in their favour.

Factors which affect the rate of emigration are likely to be the same as those controlling the evolution of group territories. In a situation with more than one non-breeder, however, where differences in status exist between them, the optimum strategies of lower ranking birds may be different from those of the highest non-breeder. Where the patrimony factor is large, for instance, most males can expect to attain breeding status through succession to the natal territory. For birds of the same age the chance of

breeding will be lower for those lower in the hierarchy as long as they remain in the natal group. In some circumstances it may be more adaptive for these birds to attempt to establish new territories, even if these are inferior to their natal territory. This strategy will be adopted if,

$$C.r_1 > r_2 \qquad (2)$$

where C is the chance of eventually succeeding to the natal territory, and r_1 and r_2 are its reproductive potential in the natal and the new territory respectively. If the difference between the territories is large (i.e. if the natal territory is of good quality) then the chance of succeeding can be smaller before trying to establish a new territory becomes an adaptive strategy.

The chance of a non-breeding male succeeding as the breeder in its natal territory (C) can be calculated using the formula below:

$$C = \sum_{n=0}^{\infty} S_{NB}(1-S_B).(S_{NB}S_B)^n \qquad (3)$$

where S_B is the survival of the breeder and S_{NB} the survival of the non-breeder. The derivation of this formula is given in Appendix 12.

If a situation is envisaged in which senility inevitably reduces the ability of the breeder to retain its dominance, then this can be introduced into the equation as a constraint on 'n', and the chance of succeeding through the senility of the breeder ($S_{NB}^{\ n}$) added to the chance of succeeding due to random mortality to give the equation below:

$$C = \sum_{n=0}^{a} S_{NB}(1-S_B).S_{NB}.S_B \quad + S_{NB}^{\ a} \qquad (4)$$

where 'a' is the average period between the non-breeder reaching maturity and the breeder reaching senility. That such an age-related decline in competitive ability may occur in passerine birds with survival rates similar to those observed for the Jungle Babbler is suggested by the work of Lill (1974) on White-headed Manakins Manacus manacus in Trinidad

Using the above formula (4) we can predict the chance that the highest ranking non-breeder will survive to take over the natal territory for some hypothetical values of S_B, S_{NB} and a. In a situation in which the survival of the breeders and non-breeders is equal and no senility occurs, the chance of the non-breeder surviving to succeed to the territory increases with increasing survival, as illustrated in Figure 10c, to approach 0.5 as survival approaches 1.0. Senility increases the chance of succeeding and the difference increases with survival (Figure 10d). If the survival of the non-breeder is lower than that of the breeder then the chance of succession is lowered (Figure 10e). In practice it seems likely that the non-breeder survives as well as the breeder as long as it does not attempt to leave its natal group.

For a second-ranking non-breeder the chance of succeeding is considerably lower and it can be shown that, where senility is not taken into account:

$$\frac{C_2}{C_1} = \frac{1-S_{NB}}{1}$$

where C_2/C_1 is the ratio of the chance that the second-ranked non-breeder will succeed (C_2) to the chance that the first will succeed (C_1). Hence where the survival of the non-breeders is 0.8, the chance that the second ranking bird will succeed is only one fifth that of the first-ranking bird. Where there is a difference in age between the two non-breeders senility might affect this ratio, but in most circumstances it seems permissible to assume that the chances of a second-ranking bird are likely to be less than half those of the first-ranking bird.

The simple model described above gives some indication of the complexity of factors affecting the strategy of second and lower ranking non-breeders. Although the role of senility in determining dominance has not been reported

Figure 10c. Chances of a non-breeder surviving to succeed to its natal territory in a situation where the survival of breeder and non-breeder are equal and no senility occurs.

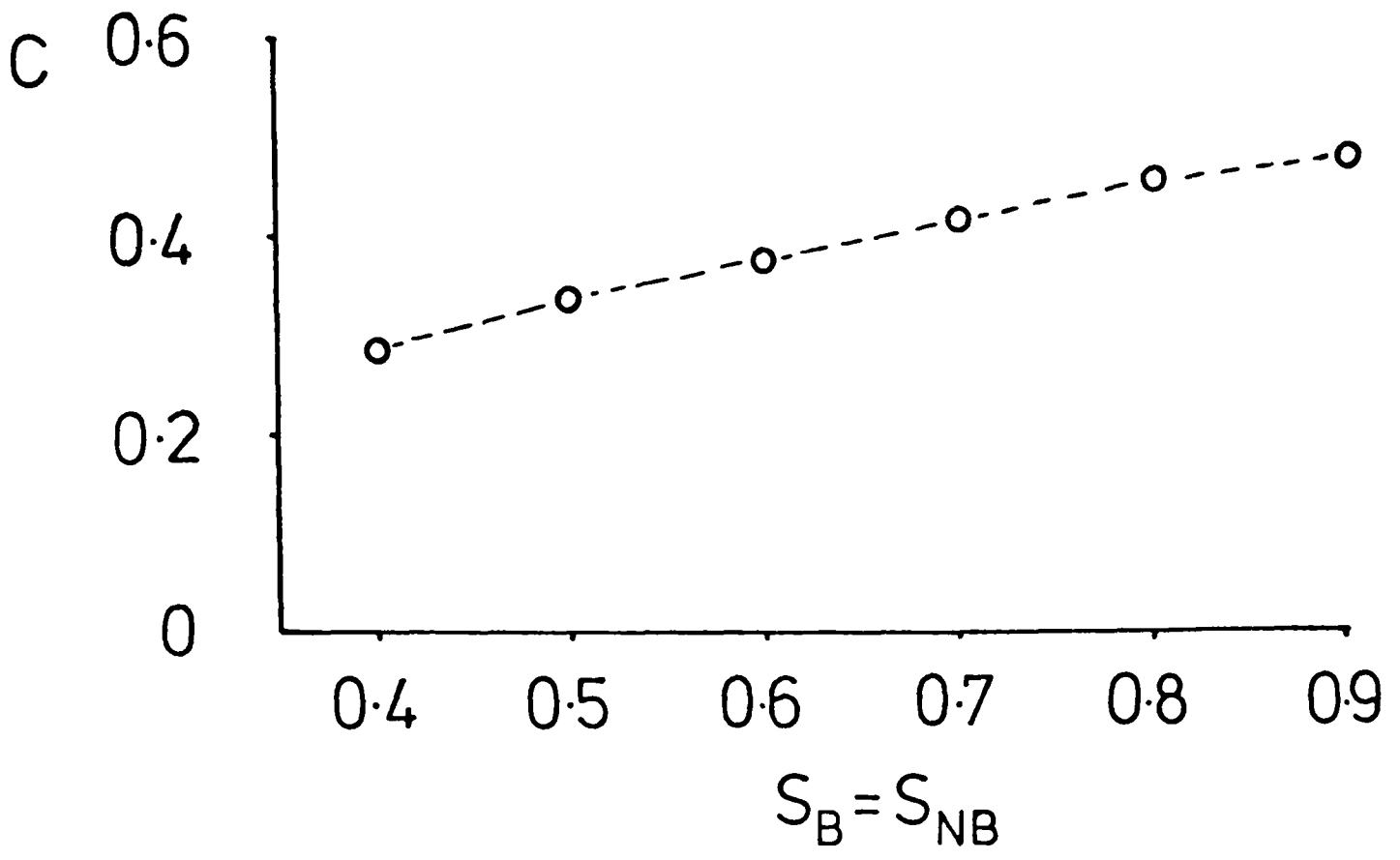


Figure 10d. Chances of a non-breeder succeeding where survival of breeder and non-breeder are equal, in relation to the timing of the onset of senility in the breeder.
1, S = 0.9 ; 2, S = 0.8 ; 3, S = 0.7

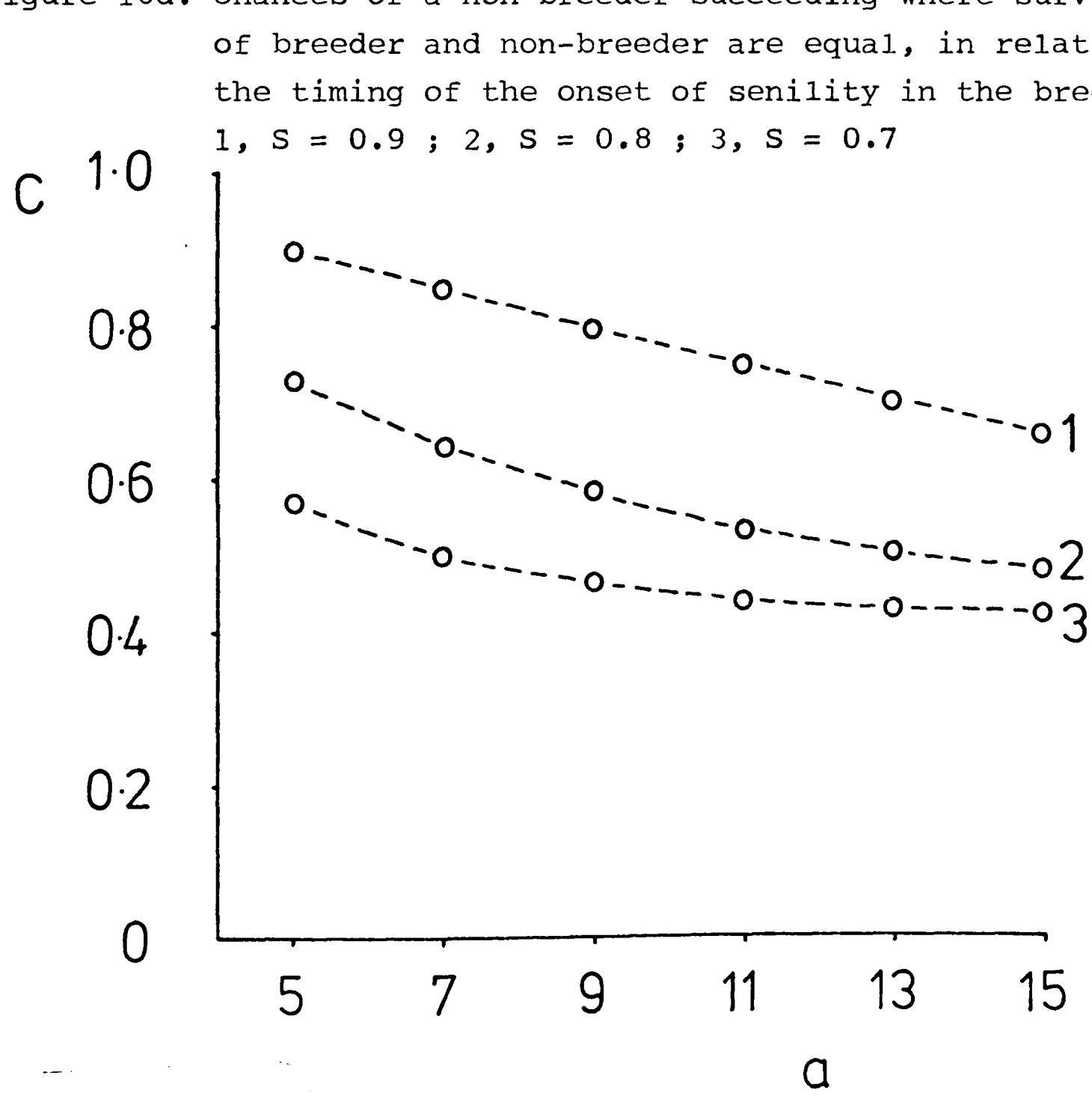
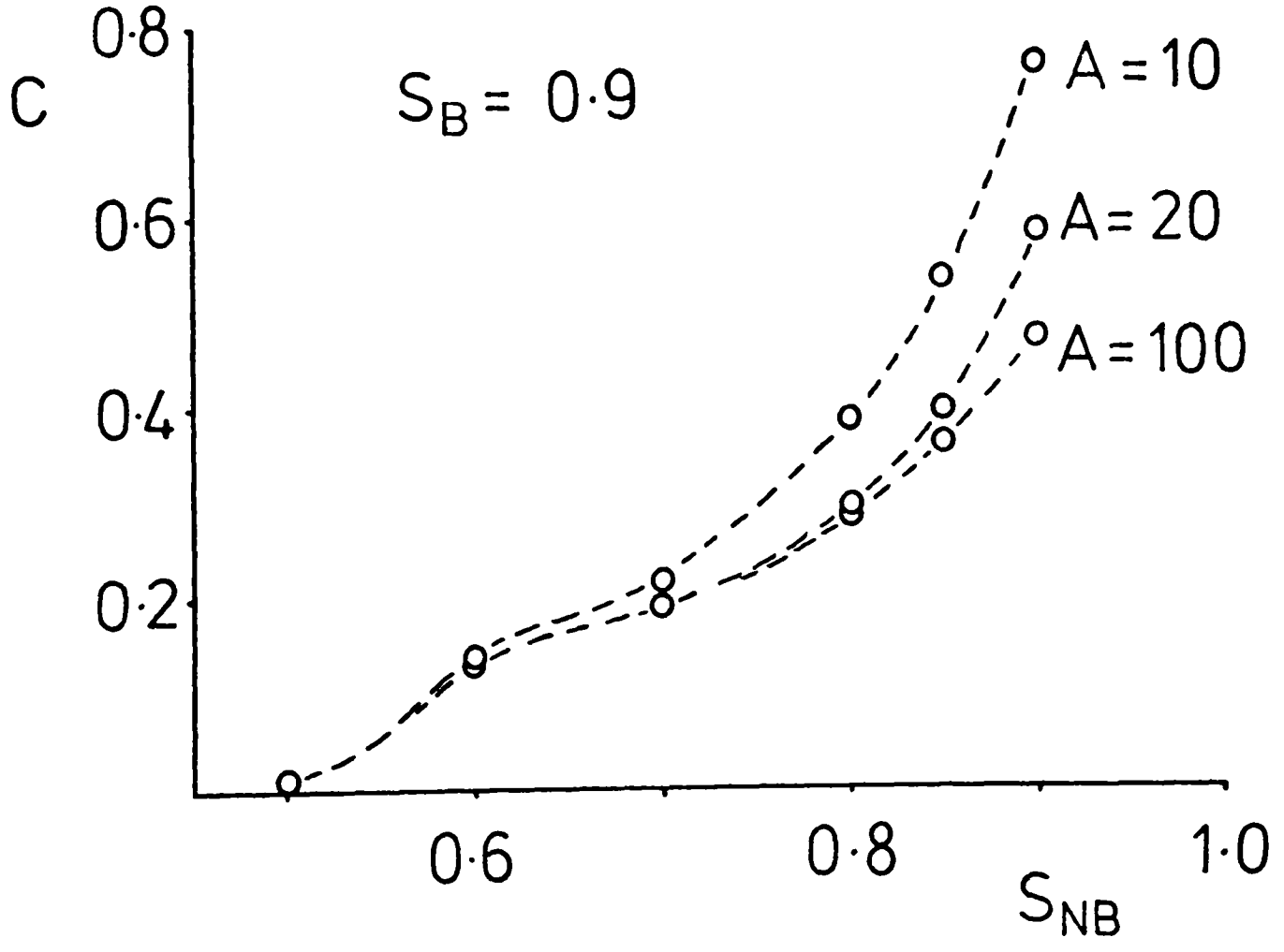


Figure 10e. Chances of a non-breeder succeeding where the survival of the breeder exceeds that of the non-breeder, in relation to the survival of the non-breeder. Survival of the breeder is fixed at 0.9.
A = 10, period before the onset of senility in the breeder = 10 years ; A = 20, = 20 years ; A = 100, = 100 years.



for any species of group territorial bird, it seems likely that senility may well have an effect in such long-lived species, as has been argued in the case of mortality by Botkin and Miller (1974.

One effect predicted by a consideration of the options of non-breeders in relation to their social status, is that a lower ranking bird stands less chance of succeeding than a higher ranking bird of the same age. This is true even if the difference between the quality of the two birds is very small. If lower ranking birds are more likely to attempt to establish new territories then this may affect the reproductive success observed in low quality territories, since part of the lowering of reproductive success compared to better quality territories may be due to the quality of the birds themselves.

The occurrence of groups containing several non-breeding males, which has been observed among several species of group territorial birds apart from babblers (Corcorax, Corvinella, Aphelocoma) raises the question of why two or more non-breeders should not combine to usurp the dominance of the breeder. The reason that these non-breeders do not form a coalition is easily demonstrated mathematically if it is assumed that the quality of each bird, in terms of its ability to defend a territory, is fixed and quantifiable. The qualities of the breeder, the second, third, etc., will be assigned the values of a, b, c ... It is now possible to examine some possible coalitions.

If $a < b + c$ we can assume that the second and third ranked birds could combine to get a larger share of the territory than the breeder. There is no advantage in this coalition to the third ranked bird, however, because by remaining with the breeder it can do better still, $a + c$ being greater than $b + c$ by definition. By similar arguments it is possible to show that the territory obtained by coalitions of non-breeders will always be inferior to that part retained by the breeder, provided that all members

of the hierarchy behave in accordance with their optimum strategy.

In a situation where the non-breeders are both offspring of the breeding pair a coalition of the second and third ranked males to oust the breeding male completely would not be in the best interests of the third ranked bird for kin-selective reasons. Assuming that the second ranked bird, on becoming breeder, would not mate with its mother but with an unrelated female, the offspring reared would be related to the third ranked bird as first cousins (0.25). In the former situation, however, offspring reared within the territory were full siblings of the third ranked bird (0.5), and hence its relatedness to them was twice as large.

Arguments concerning the adaptiveness of establishing a new territory apply only to male non-breeders in species where succession is patrilineal. The rate of emigration of females is likely to be partly determined by the optimum strategies of the male non-breeders, however, because the number of new territories which are established will be one factor determining the number of opportunities for females to breed. In species where breeding females survive as well as breeding males the opportunities for females to become breeders in established groups is the same as that for males. The risk involved in doing so is greater for females however because they have to expose themselves to predation in marginal areas and away from their natal group. The option of attempting to establish a new group is therefore likely to be more attractive to females than to males, and in such a case females may be expected to initiate new territories.

Summary of factors affecting the evolution of group territoriality and co-operative breeding.

1) The persistence of young birds within their parents' territory is viewed as an adaptation to defer maturity, in a situation where extra-territorial survival is poor, and high adult survival is considered to be the most important factor selecting for deferred maturity.

2) The development of tolerance in the parents towards the persistence of non-breeders in their territory is thought to be a crucial stage in the evolution of group territories.

3) The benefits to the breeder of offspring remaining within the territory are divided into two categories; indirect, accruing only through the increased fitness of the offspring; and direct, enhancing the individual fitness of the breeders.

4) Arguments are put forward to suggest that non-breeders always stand to benefit more from remaining in the parental territory than do their parents.

5) This inequality is used to provide an explanation for the origin of co-operative breeding, food fed to nestlings by non-breeders constituting a 'payment' for their right to remain in the territory.

6) Differences between the strategies of male and female non-breeders are considered to derive from a situation in which males were originally the territorial sex.

d) Discussion of the model in the light of Babbler studies

Jungle Babblers fulfil several of the criteria proposed for the evolution of group territorial behaviour. They have a relatively high rate of survival as long as they remain in their natal group, the rate of reproduction is sufficiently high to produce a considerable non-breeding surplus, and survival in areas outside those defended by permanent groups appears to be lower than that inside the group territories. Babblers are poor fliers and the benefit of group feeding in enhancing predator detection may be high. Whether feeding is enhanced by flocking during the breeding season was not determined.

These points also apply to the Common Babbler, although survival was found to be somewhat lower. This may have been due in part to the general decline in the population taking place in the study area. The survival of

breeding males, however, which determines the opportunities for new territories to be established in good quality habitat, was still quite high.

A difference between Common and Jungle Babblers which may have been important in determining the strategies of non-breeders in the study area was the degree of variability in their preferred habitats. Because optimal nesting habitat for Jungle Babblers covered only a small part of the area, and because much feeding during the winter was carried on outside the nesting habitat, the expansion of range necessary to support a larger group during the critical period for food did not cause an expansion in the area of nesting habitat under the group's control. Hence the expansion did not increase the opportunities for a non-breeder to split off part of the natal territory. Because Common Babbler territories contained a large amount of suitable nesting habitat non-breeding males could, in some circumstances, split off portions, hence there was greater incentive to render assistance to the breeders which might result in an increase in group size.

Data given in section 1i suggests that new Jungle Babbler territories in the Ridge study area were generally of type 3, and that the reproductive success in terms of young surviving their first winter was only a quarter that in type 1 territories. If adult survival is also less in type 3 territories, then the value of achieving breeding status in a type 3 territory is probably less than a quarter that in a type 1 territory. Using this assumption we can predict on the basis of Figure 10e that with the survival of the breeding adults greater than 0.9 the survival of the first non-breeding male would have to be less than 0.77 for establishing a new territory to be an adaptive strategy for it. Since the survival of birds between 6-18 months was 0.94 it seems likely that the survival of non-breeders is as high as that of breeders as long as they remain in the natal territory, and if this is true then we might also expect the second ranking non-breeder to remain.

Because non-breeders of either sex do not begin to leave their natal group until 18 months of age we can predict on the basis of the model a mean group composition in type 1 territories on March 1 as follows; the breeding pair, two non-breeding males, 2 first years (see Table 1E), 2 second years, plus perhaps one other bird, either an immigrant female, another non-breeding adult male, or a persistent native female. The number of non-breeding adult males should depend on the quality of the territory; if it is very good there might be three, if rather poor then only one.

The range of group size predicted by the model depends on the reproductive success of the groups during the previous two years. The lower limit would be three; a pair plus one adult non-breeding male. The upper limit is about 15 comprising the breeding pair, three adult non-breeding males, eight first and second year birds (the maximum recorded), and two immigrant or persistent females. These figures are very close to those observed for the mean and range of group size for type 1 groups in the Ridge study area.

The similarity demonstrated in section 8f between the ranges of group size among different populations of Turdoides probably results from similar potential rates of reproduction. All species of Turdoides lay clutches of three or four eggs (Baker 1932), and probably all have the opportunity to make at least two successful nesting attempts per year. The steady increase in mean group size with population density must be the result of increased mean reproductive success and possibly decreasing opportunities to establish new territories.

The reason for the adoption of pair territorial behaviour by the Spiny Babbler may lie in the rarity of the species in relation to the available habitat. If the breeding population is being controlled by factors such as predation, unrelated to the extent of the breeding habitat, and if other benefits of group territorial behaviour are insufficient for it to be maintained, a regression to pair territoriality should be expected.

It is also possible that the Spiny Babbler, which was previously placed in a separate monotypic genus (Ripley 1950) represents a form descended from a pair territorial babbler stock.

Figures from the Florida Scrub Jay (Woolfenden 1975) also coincide well with the predictions of the model. The annual survival of breeding adults is 0.8, and the reproductive rate is such that on average only one yearling is produced per group per year. As would be anticipated from the model the mean group size of four birds at the start of the breeding season is considerably lower than that observed for Jungle Babblers except in the worst quality habitat. The population density in birds per km^2 is not given, but the territory size of 4-16 ha suggests a density of 25-100 birds per km^2. The group size of the Florida Scrub Jay therefore conforms quite well to that predicted by the regression of group size on density shown in Figure 8b.

Among the species listed in Table A of the Introduction the following appear to have adopted group territorial behaviour similar to that observed in Turdoides; Tribonyx mortierii, Dacelo gigas, Aphelocoma coerulsescens and A. ultramarina, Corcorax melanorhamphus, Malurus cyaneus and Corvinella corvina. The situation in Gymnorhina dorsalis provides several noteworthy differences which can be easily explained in terms of the model outlined above. In this species the survival of non-breeders in extra-territorial areas appears to be high and the average reproductive success of breeding groups is only one young per year. As a result breeding groups are small, averaging about three birds. Male offspring disperse from their natal territory before the female offspring. This is probably because many groups consist of a male and two breeding females (35%). If the male offspring were allowed to remain in this situation they would have the opportunity of pairing with the female which was not their mother. The male offspring are therefore evicted from

the territory by the breeding male.

The habitat in which Carrick's study was carried out consists of range land with scattered trees, created by the felling of natural woodlands. It seems likely that the density of the population studied and the large surplus of non-breeding birds may be a recent phenomenon resulting from the changes in the environment, in which case the observed behaviour of Gymnorhina may not represent the optimum potential strategy for the population.

Although the exact breeding system occuring in groups of Acorn Woodpeckers Melanerpes formicivorous has not yet been established (MacRoberts & MacRoberts 1974) it seems likely that this species also has a pattern similar to that of babblers. The operation of the patrimony factor can be seen particularly well in this species, where the stores of acorns which are wedged into holes drilled in trees represent a particularly tangible benefit which non-breeders can hope to become heir to by remaining within their natal territory.

Many aspects of babbler behaviour are best explained by regarding them as adaptations to a group territorial strategy. Most of the social behaviour reflecting hierarchies within the group can be viewed in this way. It seems most plausible to suggest that contact behaviour, allopreening, and rough-and-tumble are behaviour patterns that reduce and ritualise the aggressive content of intra-group interactions. Sentinel behaviour also seems best regarded as an adaptation evolving as a result of group territorial behaviour. The present behaviour of Turdoides seems likely, therefore, to be the result of a prolonged period of adaptation to group territoriality.

The present ecology of Turdoides species can be considered to be modified by a number of feedback systems operating as a result of the adoption of a group territorial strategy. For instance, if non-breeders which remain in the territory assist the breeders this may lower the cost

of reproduction to the breeders, and hence increase their survival. Retention of non-breeders in the territory throughout the population tends to increase the patrimony factor. The fact that young birds normally do not get a chance to breed in their first year may cause selection for less rapid development of those abilities which determine reproductive success. All of these effects of group territoriality tend to reinforce the selection pressures which brought about its evolution in the first place. The line between pair territoriality and group territoriality can be thought of as an adaptive watershed. Once selection for group territories has begun it tends to intensify through a process of self-reinforcement.

e) Discussion of group territoriality in the Long-tailed Tit

Whether the evolution of group territorial behaviour in the Long-tailed Tit can be explained along the lines of the model proposed for babblers is not clear from research conducted so far. It is likely, but not proven, that Long-tailed Tit groups constitute essentially male clans, and that assistance at the nest is generally provided by members of the same group. There is only a small non-breeding population, however, so that while group territoriality in the babblers can be thought to have evolved through competition for breeding territories this seems unlikely to apply to the Long-tailed Tit which, in Britain at least, suffers periodic population reductions which must create many vacancies in the subsequent breeding seasons (Dobinson & Richards 1964).

A more plausible hypothesis for the social behaviour of the Long-tailed Tit is that the direct benefits of group territorial behaviour in promoting feeding enhancement and an optimal cropping of the food supply are sufficient to account for the observed pattern. Because the food and foraging strategies of the Long-tailed Tit remain similar throughout the year, except while breeding (Gibb 1954), it is advantageous for the family flock to remain

together during the post-breeding period. The consequent potential for kin-selection within these groups of closely related birds has brought about adaptations in social behaviour similar to those observed in babblers.

The behaviour of the Long-tailed Tit cannot be thought of as incipient group territoriality because in many aspects of its behaviour, such as clumping, the lack of a territorial song during the breeding season, and the lack of overt aggression between birds feeding close together, the species appears well adapted to a group territorial existence. This is in contrast, for instance, to the group territoriality observed by Glase (1973) and Smith (1976) in the Black-capped Chickadee (Parus atricapillus) where behaviour included clear dominance interactions within groups, and behaviour during the breeding season was similar to that in other species of the pair territorial genus Parus. It seems likely that group territorial behaviour in the Black-capped Chickadee has evolved only recently as an adaptation to improve foraging efficiency.

The other four asiatic species of the genus Aegithalos all occur in the temperate zone of the Himalayas and associated mountains (Vaurie 1959), where they probably experience a more stable climatic regime than that experienced by the Long-tailed Tit in Britain. Casual observations of the Red-headed Tit (Aegithalos concinnus) in NW India showed that this species tends to occur in parties of 10-20 birds (cf. also Ali 1949), and may well hold group territories similar to those observed in the Long-tailed Tit.

If the Long-tailed Tit has colonised its present range from an original centre in the temperate zone of the Himalayas then some of its behaviour may have evolved as a result of selection pressures not operating in all parts of its present range.[1] This is not to suggest that the Long-

[1] A similar hypothesis was proposed by Kunkel (1974) to account for some aspects of the behaviour of the Bullfinch Pyrrula pyrrula, another palaearctic member of a genus otherwise confined to the Himalayas.

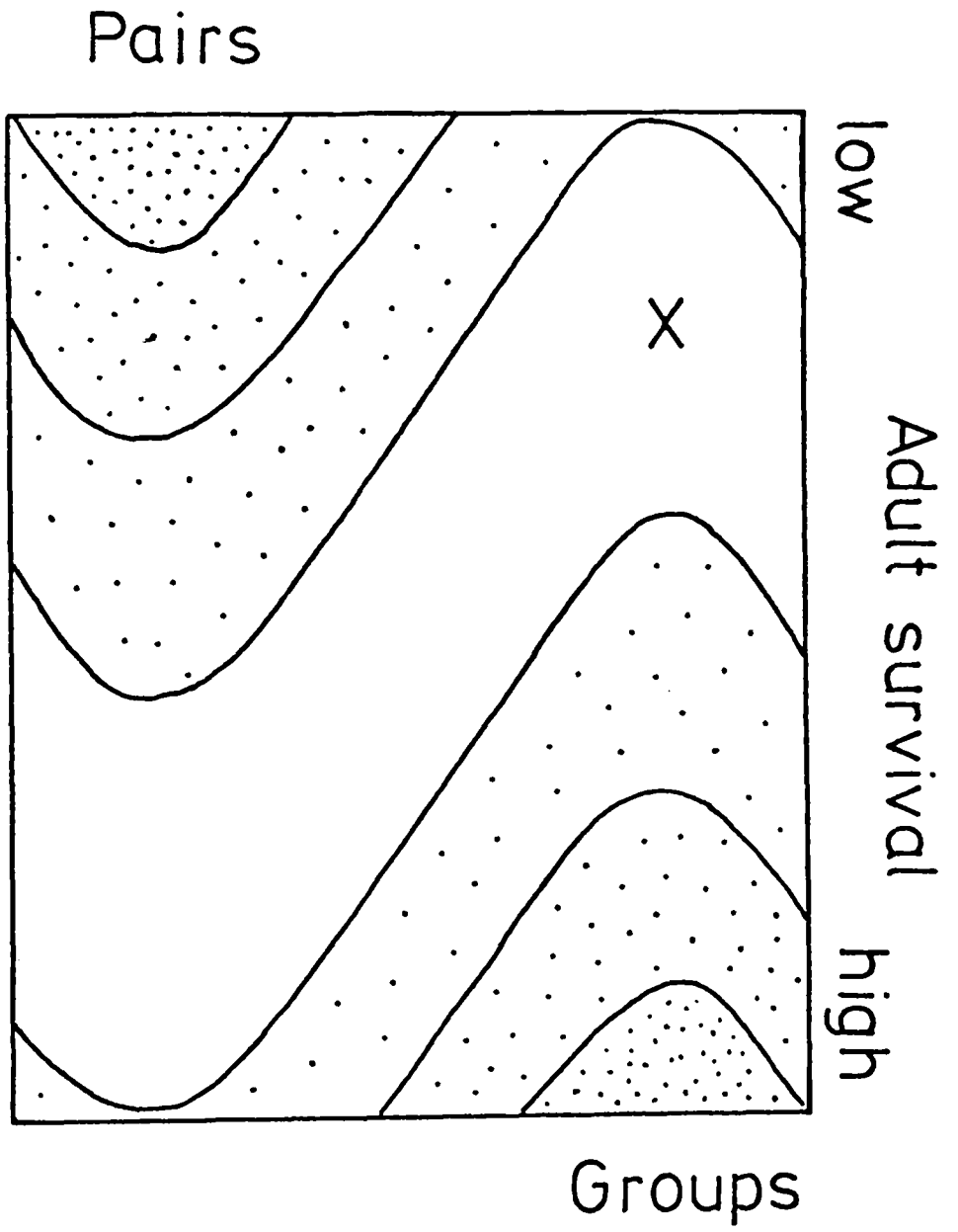
tailed Tit is anywhere adopting a sub-optimal strategy. As has already been discussed, the effects of group territorial behaviour tend to be self-reinforcing. Adaptations such as sentinel behaviour, for which selection could not occur in a pair territorial species, may confer sufficient advantage once acquired so that a group territorial system can be maintained in conditions where it could not originally have evolved.

The concept of post-adaptive expansion can also be applied to explain the diversity of habitats occupied by babblers. It is not necessary to assume that a pair territorial species with the same physical limitations as those of the genus Turdoides would eventually evolve a group territorial system if introduced into all those areas now occupied by babblers. Group territorial behaviour may have evolved in a single proto-Turdoides population which then expanded into other habitats as the genus diversified.

Figure 10f summarises the idea of interpenetration of habitats by species with different territorial systems. The contours represent an adaptive landscape as proposed by Simpson (1953), with the higher altitudes representing areas of optimum adaptation and selection operating uphill. The right hand species, pre-adapted to group territory, is forced into a smaller adaptive zone (i.e. a narrower choice of habitats, foods, feeding strategies) as it moves North towards areas of lower adult survival, but selection, provided that it narrows its niche in this way, still maintains group territorial behaviour. Once the point 'x' is reached, however, selection is neutral regarding the social system, and any further expansion northwards can only be achieved by adopting pair territorial behaviour.

A pair territorial species which appears to occupy a niche very similar to that of the babblers in parts of the Indian peninsula is the Blackbird Turdus merula which occurs in forested country down to 900m (Ali & Ripley 1973), and in some areas exists side by side with the Jungle

Figure 10f. Hypothetical adaptive landscape, showing the interpenetration of different zones of adult survival by species with group territorial and pair territorial social systems.



Babbler. The Blackbird is widespread in the Palaearctic region (Snow 1958) where it is probably pair territorial throughout its range. The penetration of the Blackbird into lowland India can perhaps be compared with the penetration of the Long-tailed Tit into cool-temperate Eurasia. A similar example of contrasting life history strategies adopted by animals with very similar ecologies is given by Schaffer (1974) who compares the semelparous salmonid genus Oncorynchus with the closely related iteroparous genus Salmo which often spawns in the same rivers.

f) Group territorial behaviour as a life history strategy

One obvious factor of group territorial behaviour is the reduced size of the breeding population. Since, as pointed out by Skutch (1961), group territorial species do not lay larger clutches than similar non-group territorial species, there is a consequent decrease in the per capita reproductive rate of the population. This has led some authors to suggest that the need for population regulation is a factor causing selection for group territorial behaviour (Fry 1972, Parry 1973). The model presented here for the evolution of group territories suggests that a decrease in the per capita reproductive rate is simply a result of strategies aimed at maximising individual fitness, and that it does not in any case regulate the population, something which has not been demonstrated for any group territorial species.

Several aspects of group territorial behaviour in babblers qualify it to be considered the result of K-selection, as defined by MacArthur and Wilson (1967) and elaborated by Pianka (1970). These include a reduced r (intrinsic rate of increase), slow development, deferred maturity, and long life, compared to temperate passerines of similar size. Although practically

all discussion of life history strategies agree that the stability of the environment is a crucial determining factor, there are some differences in the predictions resulting from different models. MacArthur and Wilson, Pianka (loc. cit.), Gadgil and Bossert (1970), and Brockleman (1975), all suggest that greater environmental stability increases K-selection, and greater instability promotes r-selection. A different approach by Murphy (1968) and Schaffer (1974a) prefers to distinguish between environmental fluctuations which affect reproduction and those which affect adult survival. In conditions where adult survival is unpredictable they are in agreement with other authors that r-selection will occur. In conditions where adult survival is predictable and high, but reproductive success is unpredictable they suggest that K-selection should occur.

The ecology of Common and Jungle Babblers at Delhi appears to fall into the latter category relative to temperate passerines. Although adult survival is high, opportunities for reproduction are partly dependent on rainfall which is relatively unpredictable. The same is even more true of the Arabian Babbler for which, in some years, no breeding is possible at all (Zahavi, pers. comm.). The reverse is true of resident temperate passerines. Adult mortality is generally assumed to be dependent on fluctuating food crops and unpredictable weather during the non-breeding season, whereas reproduction is guaranteed by the predictable flush of insects and other invertebrates in the temperate spring (Lack 1950).

As Southwood et al (1974) have pointed out, K-selected strategies may involve the risk of extinction in the long term. Progressive adaptation to stable conditions may result in a lack of flexibility to change when it does occur. A possible example of this among the babblers is the rather exposed nest sites adopted by the Jungle and Large Grey Babblers. Selection for cryptic nest sites may have weakened because of the success of joint nest defence by all group members. A change in conditions which reduced the density of the population might lead to a rapid switch to pair

territorial behaviour. If nest site selection procedures could not adapt sufficiently quickly this could lead to a decline in the overall fitness of the population despite the fact that all individuals were pursuing their optimum strategy.

REFERENCES

Alexander, R. D. 1974. The evolution of social behaviour. Ann. Rev. Ecol. Syst. 5: 325-383.

Ali, S. 1949. Indian Hill Birds. Oxford University Press, London & Bombay.

Ali, S. & S. D. Ripley 1968. Handbook of the Birds of India and Pakistan, Vol. 1. Oxford University Press, London.

Ali, S. & S. D. Ripley 1971. Handbook of the Birds of India and Pakistan, Vol. 6. Oxford University Press, London.

Ali, S. & S. D. Ripley 1973. Handbook of the Birds of India and Pakistan, Vol. 9. Oxford University Press, London.

Andrews, M. I. & R. M. Naik 1965. Some observations on flocks of the Jungle Babbler, Turdoides striatus (Dumont) during winter. Pavo 3: 47-54.

Andrews, M. I. & R. M. Naik 1970. The biology of the Jungle Babbler. Pavo 8: 1-34.

Anon. Monthly and Annual Rainfall, and Number of Rainy Days. Period 1901-1950, Part II. Indian Meteorological Office, New Delhi.

Armitage, K. B. 1962. Social behaviour of a colony of the Yellow-bellied Marmot (Marmota flaviventris). Anim. Behav. 10: 319-331.

Bailey, N. T. J. 1959. Statistical Methods in Biology. English Universities Press.

Baker, E. C. S. 1932. The Nidification of Birds of the Indian Empire, Vol. 1. Taylor and Francis, London.

Baldwin, S. P. & S. C. Kendeigh 1938. Variations in the weight of birds. Auk 55: 416-467.

Barnett, S. A. 1963. A Study in Behaviour. Methuen, London.

Basil-Edwards, S. 1926. A contribution to the ornithology of Delhi. J. Bombay Nat. Hist. Soc. 31: 261-273, 567-578.

Bernstein, I. S. 1970. Primate status hierarchies. In L. A. Rosenblum (ed.) Primate Behaviour. Academic Press, New York.

Bernstein, I. S. & L. G. Sharpe 1966. Social roles in a rhesus monkey group. Behaviour 26: 91-104.

Botkin, D. B. & R.S.Miller 1974. Mortality rates and survival of birds. Amer. Natur. 108: 181-192.

Brockelman, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. Amer. Natur. 109: 677-699

Brown, J. L. 1963. Social organisation and behaviour of the Mexican Jay. Condor 65: 126-153.

Brown, J. L. 1963a. Aggressiveness, dominance and social organisation in the Steller Jay. Condor 65: 460-484.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160-169.

Brown, J. L. 1972. Communal feeding of the nestlings of the Mexican Jay (Aphelocoma ultramarina): interflock comparisons. Anim. Behav. 20: 395-403.

Brown, J. L. 1974. Alternative routes to sociality in jays - with a theory for the evolution of altruism and communal breeding. Amer. Zool. 14: 63-80.

Bulmer, M. G. 1973. Inbreeding in the Great Tit. Heredity 30: 313-325.

Burt, W. H. 1940. Territorial behaviour and populations of some small mammals in Southern Michigan. Museum Zool. Univ. Mich. Misc. Pub. 45: 1-58.

Carpenter, C. R. 1964. Naturalistic Behaviour of Non-human Primates. Pennsylvania State University Press.

Carrick, R. 1972. Population ecology of the Australian Black-backed Magpie, Royal Penguin and Silver Gull. Bureau of Sport, Fisheries and Wildlife, Wildlife Research Report 2, Population Ecology of Migratory Birds, 41-99.

Chance, M. R. A. & C. J. Jolly 1970. Social groups of monkeys, apes and men. Jonathan Cape, London.

Cody, M. L. 1971. Ecological aspects of reproduction. In D. S. Farner and J. R. King (eds.) Avian Biology, Vol. 1. pp. 461-512 Academic Press, New York & London.

Crook, J. H. 1965. The adaptive significance of avian social organisations. Symp. zool. Soc. Lond. 14: 141-218.

Cullen, J. M. 1963. Allo-, auto- and heteropreening. Ibis 105: 121.

Dakshini, K. M. M. 1968. Vegetation of Delhi State: Mehrauli region, 1. Analysis of pattern. Proc. Nat. Inst. Sci., India 34: 127-133.

Davis, D. E. 1940. Social nesting habits of the Smooth-billed Ani (Crotophaga ani). Auk 57: 179-218.

Davis, D. E. 1940a. Social nesting habits of Guira guira. Auk 57: 472-484.

Dawson, D. G. 1972. The Breeding Ecology of House Sparrows. D. Phil. thesis, Oxford University.

Delius, J. D. 1965. A population study of Skylarks Alauda arvensis. Ibis 107: 466-492.

DeVore, I. & K. R. L. Hall 1965. Baboon ecology. In I. DeVore (ed.) Primate Behaviour, pp. 20-52. Holt, Rinehart & Winston, New York.

Dexter, R. W. 1952. Extra-parental co-operation in the nesting of Chimney Swifts. Wilson Bull. 64: 133-139.

Dharmakumarsinhji, R. S. 1954. Birds of Saurashtra. Private, Bombay.

Dhont, A. A. 1971. Some factors influencing territory in the Great Tit (Parus major L.) Gerfaut 61: 125-135.

Dobinson, H. M. & A. J. Richards 1964. The effects of the severe weather of 1962/63 on birds in Britain. Brit. Birds 57: 373-434.

Donahue, J. P. 1967. Notes on a collection of Indian birds, mostly from Delhi. J. Bombay Nat. Hist. Soc. 64: 410-429.

Eberhard, M. J. W. 1975. The evolution of social behaviour by kin selection. Q. Rev. Biol. 50: 1-39.

Evans, P. R. 1969. Winter fat deposition and overnight survival of Yellow Buntings (Emberiza citrinella L.) J. Anim. Ecol. 38: 415-423.

Fleming, R. L. 1952. Notes on the Nepal Koklas Pheasant (Pucrasia macrolopha nipalensis) and the Spiny Babbler (Acanthoptila nipalensis). J. Bombay Nat. Hist. Soc. 50: 658-661.

Fletcher, T. B. & C. M. Inglis 1924. Birds of an Indian Garden. Thacker, Spink & Co., Calcutta & Simla.

Fogden, M. P. L. 1970. Some Aspects of the Ecology of Bird Populations in Sarawak. D. Phil. thesis, Oxford University.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307-343.

Fry, C. H. 1972. The social organisation of Bee-eaters (Meropidae) and co-operative breeding in hot-climate birds. Ibis 114: 1-14.

Gadgil, M. & W. H. Bossert 1970. Life historical consequences of natural selection. Amer. Natur. 104: 1-24.

Ganguli, U. 1966. Some observations on the Jungle Babbler (Turdoides striatus) Peacock 3: 139-143.

Gibb, J. 1954. Feeding ecology of tits with notes on Treecreeper and Goldcrest. Ibis 96: 513-543.

Glase, J. C. 1973. Ecology of social organisation in the Black-capped Chicadee. Living Bird 12: 235-267.

Grimes, L. 1975. Co-operative breeding behaviour and family relationship within groups of the Long-tailed Shrike Corvinella corvina. Emu 74: 309-310.

Grimes, L. 1976. The occurrence of co-operative breeding behaviour in African birds. Ostrich 47: 1-15.

Hall, K. R. L. 1967. Social interactions of the adult male and adult females of a Patas monkey group. In S. Altmann (ed.) Social Communication among Primates, pp. 261-280. University of Chicago Press, Chicago & London.

Hall, K. R. L. 1968. Social organisation of old-world monkeys and apes. Symp. zool. Lond. 14: 265-290.

Hall, K. R. L. & I. DeVore 1965. Baboon social behaviour. In I. DeVore (ed.) Primate Behaviour, pp. 53-110. Holt, Rinehart & Winston, New York.

Hamilton, W. D. 1964. The genetical theory of social behaviour. J. Theoret. Biol. 7: 1-52.

Hamilton, W. J. & K. E. F. Watt 1970. Refuging. Ann. Rev. Ecol. Syst. 1: 263-286.

Hardy, J. W. 1974. Behaviour and its evolution in neotropical jays (Cissilopha). Bird Banding 45: 253-268.

Harrison, C. J. O. 1965. Allopreening as agonistic behaviour. Behaviour 24: 161-209.

Harrison, C. J. O. 1969. Helpers at the nest in Australian passerine birds. Emu 69: 30-40.

Helms, C. W. & W. H. Drury 1960. Winter and migratory weight and fat field studies on some North American buntings. Bird Banding 31: 1-40.

Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis 98: 340-369.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (Euphagus cyanocephalus). Ecology 49: 682-694.

Hutson, H. P. W. 1947. Observations on the nesting of some birds around Delhi. Ibis 89: 569-576.

Hutson, H. P. W. 1954. The Birds about Delhi. Delhi Bird Watching Society, New Delhi.

Jolly, A. 1972. The Evolution of Primate Behaviour. Macmillan, New York.

Kalela, O. 1958. Uber ausserbrutzeitliches Territorialverhalten bei Vögeln. Ann. Acad. Sci. Fennica, IV Biologica 42: 1-42.

Kaufmann, J. H. 1962. Ecology and social behaviour of the Coati (Nasuta narica) on Barro Colorado Island, Panama. Univ. Calif. Publ. Zool. 60 (3): 95-222.

Kaufmann, J. H. 1967. Social relations of adult males in a free-ranging band of Rhesus monkeys. In S. Altmann (ed.) Social Communication among Primates, pp. 73-98. University of Chicago Press, Chicago & New York.

Kepler, K. 1972. A Comparative Study of Todies (Aves, Todidae) with Emphasis on the Puerto Rican Tody, Todus mexicanus. D. Phil. thesis, Cornell University.

Klomp, H. 1972. Regulation of the size of bird populations by means of territorial behaviour. Netherlands J. Zool. 22: 456-488.

Kruuk, H. 1972. The Spotted Hyaena. University of Chicago Press, Chicago.

Kühme, W. 1965. Freilandstudien zur Soziologie des Hyänenhundes (Lycaon pictus lupinus Thomas 1902). Z. Tierspychol. 22: 495-541.

Kummer, H. 1968. Social Organisation of Hamadryas Baboons. S. Karger, New York & Basel.

Kunkel, P. 1974. Mating systems of tropical birds. Z. Tierspychol. 34: 265-307.

Lack, D. 1950. The breeding seasons of European birds. Ibis 92: 288-316.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford University Press, Oxford.

Lack, D. 1966. Population Studies of Birds. Oxford University Press, Oxford.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Lack, D. & R. E. Moreau 1965. Clutch size in tropical passerine birds of forest and savanna. Oiseau 35, No. Special: 76-89.

Lancaster, D. A. 1964. Biology of the Brushland Tinamou, Nothoprocta cinerascens. Bull. Amer. Mus. Nat. Hist. 127: 269-314.

Lancaster, D. A. 1964a. Life history of the Boucard Tinamou in British Honduras. Condor 66: 165-181, 253-276.

Lill, A. 1974. Social organisation and space utilization in the lek-forming White-bearded Manakin, M. manacus trinitatis Hartert. Z. Tierpsychol./ 36: 513-530

Loizos, C. 1967. Play behaviour in higher primates: a review. In D. Morris (ed.) Primate Ethology, pp. 176-218. Weidenfeld & Nicolson, London.

MacArthur, R. H. & E. O. Wilson 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

MacDonald, M. 1959. Communal nest feeding in babblers. J. Bombay Nat. Hist. Soc. 56: 132-133.

MacDonald, M. 1960. Birds in my Indian Garden. Jonathan Cape, London.

MacRoberts, M. H. 1970. Notes on the food habits and food defence of the Acorn Woodpecker. Condor 72: 196-204.

MacRoberts, M. H. & B. R. MacRoberts 1975. Social organisation of Acorn Woodpeckers, Melanerpes formicivorus. Emu 74 (supl.): 310-311.

Mackworth-Praed, C. W. & C. H. B. Grant 1957. African Handbook of Birds, Series 1, Vol. 2. Birds of Eastern and North Eastern Africa. Longmans, London.

Maheshwari, J. K. 1963. The Flora of Delhi. Council for Scientific and Industrial Research, New Delhi.

Marchant, S. 1960. The breeding of some Southwest Ecuadorean birds. Ibis 102: 349-382, 584-599.

Marler, P. 1965. Communication in monkeys and apes. In I. DeVore (ed.) Primate Behaviour, pp. 544-584. Holt, Rinehart & Winston, New York.

Mason, C. W. & H. Maxwell-Lefroy 1912. The Food of Birds in India. Memoirs of the Agricultural Department of India, Entomological Series, no. 3.

Maynard-Smith, J. & M. G. Ridpath 1972. Wife sharing in the Tasmanian Native Hen, Tribonyx mortierii: a case of kin selection? Amer. Natur. 106: 447-452.

Meher-Homji, V. M. 1971. Bio-climatic variability with special reference to India. Tropical Ecology 12: 155-176.

Morley, A. 1943. Sexual behaviour in British birds from October to January. Ibis 85: 132-158.

Morris, D. 1956. The feather postures of birds and the problem of the origin of social signals. Behaviour 9: 75-113.

Mulligan, J. A. & K. C. Olsen 1969. Communication in Canary courtship calls. In R. A. Hinde (ed.) Bird Vocalisations, pp. 165-184. Cambridge University Press, Cambridge.

Murphy, G. I. 1968. Pattern in life history and the environment. Amer. Natur. 102: 391-403.

Naik, R. M. & M. I. Andrews 1966. Pterylosis, age determination and moult in the Jungle Babbler. Pavo 4: 22-47.

Naik, R. M. & A. Razack 1967. Studies on the House Swift, Apus affinis (G. E. Gray) 8. Breeding seasons and their regulation. Pavo 5: 75-96.

Nakamura, T. 1969. Structure of flock range in the Long-tailed Tit 1) Winter flock, its home range and territory. Misc. Rep. Yamashina Inst. 5: 433-461.

Nakamura, T. 1972. Structure of flock range in the Long-tailed Tit 2) Home range and territorialism in the breeding season. Misc. Rep. Yamashina Inst. 6: 424-488.

Newton, I. 1966. The moult of the Bullfinch Pyrrhula pyrrhula. Ibis 108: 41-67.

Nice, M. M. 1941. The role of territory in bird life. Amer. Midl. Nat. 26: 441-487.

Odum, E. P. & E. J. Kuenzler 1955. Measurement of territory and home range size in birds. Auk 72: 128-137.

Parry, V. 1973. The auxilliary social system and its effect on territory and breeding in Kookaburras. Emu 73: 81-100.

Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit, Parus major L. J. Anim. Ecol. 34: 601-647.

Pianka, E. R. 1970. On r and K selection. Amer. Natur. 104: 592-597.

Pielou, E. C. 1969. An Introduction to Mathematical Ecology. Wiley-Interscience, New York.

Proud, D. 1959. Notes on the Spiny Babbler, Acanthoptila nipalensis (Hodgson) in the Nepal Valley. J. Bombay Nat. Hist. Soc. 56: 330-332.

Rana, B. D. 1975. Breeding biology of the Indian Ring Dove in the Rajastan desert. Auk 92: 322-332.

Richards, S. M. 1974. The concept of dominance and methods of assessment. Anim. Behav. 22: 914-930.

Ricklefs, R. E. 1973. Fecundity, mortality and avian demography. In D. S. Farner (ed.) Breeding Biology of Birds, pp. 366-447. National Academy of Sciences, Washington.

Ricklefs, R. E. 1975. The evolution of co-operative breeding in birds. Ibis 117: 531-534.

Ridpath, M. G. 1972. The Tasmanian Native Hen, Tribonyx mortierii, II The Individual, the group and the population. CSIRO Wildlife Research 17: 53-90.

Riehm, H. 1970. Okologie und Verhalten der Schwanzmeise. Zool. Jb. Syst. Bd. 97: 338-400.

Ripley, S. D. 1950. Birds from Nepal 1947-1949. J. Bombay Nat. Hist. Soc. 49: 355-417.

Rowell, T. E. 1966. Hierarchy in the organisation of a captive baboon group. Anim. Behav. 14: 430-443.

Rowell, T. E. 1967. A quantitative comparison of the behaviour of a wild and a caged baboon group. Anim. Behav. 15: 499-509.

Rowell, T. E. 1972. The Social Behaviour of Monkeys. Penguin, Harmondsworth.

Rowley, I. 1965. The life history of the Superb Blue Wren Malarus cyaneus. Emu 64: 251-297.

Rowley, I. 1965a. White-winged Choughs. Australian Natural History 15: 81-85.

Rowley, I. 1968. Communal species of Australian birds. Bonn zool. Beitr. 19: 362-368.

Rowley, I. 1976. Co-operative breeding in Australian birds. Proc. XVI Int. Orn. Cong. 1974 (in press)

Sanjeeva Raj, P. J. 1964. Communal breeding in the White-headed Babbler (Turdoides affinis (Jerdon)) in Tambaram, Madras State. J. Bombay Nat. Hist. Soc. 61: 181-183.

Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age-structure. Ecology 55: 291-303.

Schaffer, W. M. 1974a. Optimal reproductive effort in fluctuating environments. Amer. Natur. 108: 783-790.

Schaller, G. B. 1972. The Serengeti Lion. University of Chicago Press, Chicago.

Schifferli, L. 1976. Factors affecting weight and conditions in the House Sparrow, particularly while breeding. D. Phil. thesis, Oxford University.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123-141.

Siegal, S. 1956. Non-parametric Statistics. McGraw-Hill, New York.

Simpson, G. G. 1953. The Major Features of Evolution. Columbia University Press, New York.

Skutch, A. F. 1935. Helpers at the nest. Auk 52: 257-273.

Skutch, A. F. 1961. Helpers among birds. Condor 63: 198-226.

Smith, S. M. 1976. Ecological aspects of dominance hierarchies in Black-capped Chickadees. Auk 93: 95-107.

Smythies, B. E. 1953. The Birds of Burma, 2nd edition. Oliver & Boyd, London.

Snow, D. W. 1955. The breeding of the Blackbird, Song Thrush and Mistle Thrush in Great Britain. Pt II; clutch size. Bird Study 2: 72-84.

Snow, D. W. 1958. A Study of Blackbirds. Allen & Unwin, London.

Snow, D. W. 1962. A field study of the Black and White Manakin Manacus manacus in Trinidad. Zoologica 47: 65-104.

Snow, D. W. & A. Lill 1974. Longevity records for some neotropical land birds. Condor 76: 262-267.

Southwick, C. H., M. A. Beg & M. R. Siddiqi 1965. Rhesus monkeys in North India. In I. DeVore (ed.) Primate Behaviour, pp. 111-159 Holt, Rinehart & Winston, New York.

Southwick, C. H. & M. R. Siddiqi 1967. The role of social tradition in the maintenance of dominance in a wild rhesus group. Primates 8: 341-354

Southwood, T. R. E. 1966. Ecological Methods, with Particular Reference to the Study of Insect Populations. Methuen, London.

Southwood, T. R. E., R. M. May, M. P. Hassell & G. R. Conway 1974. Ecological strategies and population parameters. Amer. Natur. 108: 791-804.

Sparks, J. H. 1964. Flock structure of the Red Avadavat with particular reference to clumping and allopreening. Anim. Behav. 12: 125-136.

Sparks, J. H. 1965. On the role of allopreening initiation behaviour in reducing aggression among Red Avadavats. Proc. zool. Soc. Lond. 145: 387-403.

Sparks, J. H. 1967. Allogrooming in primates: a review. In D. Morris (ed.) Primate Ethology, pp. 148-175. Weidenfeld & Nicolson, London.

Struhsaker, T. T. 1966. Auditory communication among Vervet Monkeys (Cercopitheous aethiops). In S. Altmann (ed.) Social Communication among Primates, pp. 281-324. University of Chicago Press, Chicago.

Thompson, W. A., I. Vertinsky & J. R. Krebs 1974. The survival value of flocking in birds: a simulation model. J. Anim. Ecol. 43: 785-820.

Tinbergen, N. 1957. The functions of territory. Bird Study 4: 14-27.

Tompa, F. S. 1964. Factors determining the number of Song Sparrows Melospiza melodia (Wilson) on Mandarte Island, British Columbia. Acta Zool. Fennica 109: 1-73.

Trewartha, G. T. 1954. An introduction to Climate. McGraw-Hill, New York.

Vaurie, C. 1959. The Birds of the Palaearctic Fauna. Order Passeriformes. H. F. & G. Witherby, London.

Vehrencamp-Bradbury, S. 1975. Adaptive advantage of communal nesting in Groove-billed Anis. Emu 74: 312.

Ward, P. 1969. The annual cycle of the Yellow-vented Bulbul Pycnonotus goavier in a humid equatorial environment. J. Zool. Lond. 157: 25-45.

Ward, P. 1969a. Seasonal and diurnal changes in the fat content of an equatorial bird. Physiol. Zool. 42: 85-95.

Watson, A. & R. Moss 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. In A. Watson (ed.) Animal Populations in Relation to their Food Resources, pp. 167-220. Blackwells, Oxford & Edinburgh.

Watts, C. R. & A. W. Stokes 1971. The social order of Turkeys. Sci. Amer. 224 (6): 112-118.

Wiley, R. H. 1974. Evolution of social organisation and life-history patterns among grouse. Q. Rev. Biol. 49: 201-227.

Willis, E. O. 1961. A study of nesting Ant-tanagers in British Honduras. Condor 63: 479-503.

Willis, E. O. 1967. The behaviour of Bicolored Antbirds. Univ. Calif. Publ. Zool. 79: 127 pp.

Willis, E. O. 1973. The behaviour of Ocellated Antbirds. Smithsonian Contrib. Zool. 144.

Wilson, E. O. 1975. Sociobiology. Harvard University Press, Cambridge, Mass.

Wood-Gush, D. G. M. 1955. The behaviour of the domestic chicken: a review of the literature. J. Anim. Behav. 3: 81-110.

Woolfenden, G. E. 1974. Nesting and survival in a population of Florida Scrub Jays. Living Bird 12: 25-49.

Woolfenden, G. E. 1975. Florida Scrub Jay helpers at the nest. Auk 92: 1-15.

Wynne-Edwards, V. C. 1962. Animal Dispersion in Relation to Social Behaviour. Oliver & Boyd, Edinburgh.

Zahavi, A. 1974. Communal nesting by the Arabian Babbler. Ibis 116: 84-87.

Zahavi, A. 1976. Co-operative nesting in Euroasiatic birds. Proc. XVI Int. Orn. Cong. 1974 (in press).

APPENDIX 1

Brood Parasitism by the Pied Crested Cuckoo *Clamator jacobinus*

Brood parasitism by the Pied Crested Cuckoo (*Clamator jacobinus*)

Introduction.

The Pied Crested Cuckoo (*Clamator jacobinus*) occurs throughout the Indian sub-continent, from the plains up to an altitude of 2600m. in the Himalayas (Ali & Ripley 1969). Within this range it parasitises a number of host species, in the plains mainly babblers of the genus *Turdoides*, and in the hills Laughing Thrushes (*Garrulax* spp.).

Two sub-species of Pied Crested Cuckoo are found in India; *C. j. jacobinus* in the southern part of the peninsula, where it is a local migrant, and *C.j.serratus* which is a summer visitor to the north, wintering apparently in Africa (Whistler 1928). The present paper describes studies carried out on the northern sub-species around Delhi, in the North Indian plains, concentrating on the effects of parasitism on the host species, and the adaptations of the parasite for its particular breeding strategy. The hosts involved were the Jungle Babbler (*Turdoides striatus*), the Common Babbler (*T.caudatus*), and the Large Grey Babbler (*T.malcolmi*). All these species live in groups of 3-20 individuals, of which only one pair breed at a time, and all adult members of the group assist in incubation and feeding the nestlings.

One other species of brood parasite, the Hawk-cuckoo (*Cuculus varius*) was also found in the study area, but only two eggs were found in babbler's nests. Elsewhere in India this species parasitises the nests of all the above-mentioned hosts (Baker 1942).

This study on Pied Crested Cuckoos and their effect on the breeding of *Turdoides* species was carried out as part of a general study on the ecology of *Turdoides*, and experimental work on cuckoo problems was limited by the necessity to cause as little disturbance as possible to the babblers.

Methods.

Observations were carried out from August 1 1971 to October 15 1973, and hence covered two complete breeding seasons and part of a third. The area selected for the study formed part of the reserved forest near Delhi, known as the Ridge. It consisted of mixed Acacia/Prosopis woodland, intermingled with low scrub dominated by Zizyphus nummularia, with scattered Butea monosperma trees.

Ten groups of Jungle Babblers, totalling about 75 birds, were selected for intensive study, and all nests of these groups were found. An attempt was made to find all nests of Common Babblers in the same area, but this was unsuccessful. Observations of fledged young and trapping of birds in juvenile plumage, suggested that about 70% of nests were found in 1972, and perhaps 80% in 1973. Only a few nests of the Large Grey Babbler were found, as this was less common than the other two species in the study area.

Not all nests were located at the same stage. Only a few were found during building and laying, during the period when cuckoos were present, and most were found during incubation or the early nestling period. Sample sizes vary for different statistics because not all nests yielded the same kind of information.

Dates of laying were calculated for nests found with incomplete clutches (1 or 2 eggs), or nests in which the young were seen and aged by weight. In the latter case the date was calculated by estimating the incubation period as fifteen days from the laying of the first egg for the babblers, and twelve days for the Pied Crested Cuckoos (12 days in four cases, 11 or 12 in another). Jungle Babblers began incubation from the laying of the first egg, whereas in Common Babblers incubation was only intermittent until the third egg. Hatching of the first chick was about day 15 for both

species, however. A nest found containing a cuckoo nestling and one or more babbler nestlings was used to calculate the date of laying for both the babblers and the cuckoo, but not for recording the clutch size, as some babblers might have died and been removed.

Nests found during building were checked daily in order to record the laying of the first egg, and each egg was individually marked with a felt-tipped pen as soon as possible after laying, which took place generally 2-4 hours after sunrise. Cuckoos' eggs were also marked to check whether they were sometimes removed. Nests were again checked daily about the time of hatching, but were otherwise checked every two days.

During the nestling period the young in some nests were weighed at two day intervals, beginning on day two (hatching of the first egg = day 1), in order to measure the growth rate of young cuckoos, and to compare the growth rates of babblers with and without cuckoos. In cases where nests were difficult to climb up to, checks were made only as often as was necessary to determine the dates of laying and hatching, and the subsequent success, and no weighings were made.

Close observations were made from a hide at a number of nests during the incubation and nestling periods, in order to observe the behaviour of the parent babblers and of other group members. This was always done between dawn and mid-day.

Many young cuckoos were removed from the nest ten days after hatching so that their gizzard contents could be examined as part of a study on the food of the babblers. These birds were already capable of scrambling out of the nest, and they were counted as having fledged. They were not removed in cases where the cuckoo was the only surviving nestling, as this would have released the babblers to nest again immediately, and hence upset the concurrent study of babbler population dynamics. In some other cases nestling

cuckoos were allowed to fledge in order to observe the date of fledging, the behaviour of the babblers towards the cuckoo after fledging, and the period of post-fledging dependance.

Pied Crested Cuckoos' eggs closely resemble those of their hosts in colour and size, although the eggs of the Common Babbler are somewhat smaller. Baker (1942) gives the mean weight of 167 North Indian Pied Crested Cuckoos' eggs as 4.58 g., measurements 23.9 x 18.6 mm., and the measurements of 100 Jungle Babblers' eggs averaged 25.2 x 19.6 mm. (Ali & Ripley 1971). In the present study Jungle Babblers' eggs were found to average slightly smaller than those of the cuckoo, but there was no significant difference in weight. Common Babblers' eggs average 21.1 x 16.1 mm (Baker 1932-35). All are turquoise blue.

Intact cuckoos' eggs could be identified from those of their host by their less glossy texture, as mentioned by Whistler (1935). When broken they were easily identified by the thick chalky shell, much thicker than a babbler's shell. Both Hume (1890) and Ali & Ripley (1969) mention that the cuckoo's eggs can be identified from those of their host by their more rounded oval shape, but this criterion was not found to be satisfactory in all cases because babblers' eggs varied considerably between different females, and more than one female may occasionally lay in the same nest. Babblers eat the shells of their own eggs completely after the young have hatched, but apparently find the cuckoos' eggs too difficult to cope with, because on several occasions these were found on the ground 20-60m from the nest.

The adult size of the cuckoo falls in the middle of the range of its hosts. The weights of two trapped at Delhi, and of four given by Ali & Ripley (1969) fall between 61-74 gms., exactly the same range of weights as are found in the Jungle Babbler. Common Babblers trapped in the Delhi area weighed 28-43 g., and Large Grey Babblers 72-82 g..

Behaviour of the Pied Crested Cuckoo.

Immediately after their arrival in the breeding area Pied Crested Cuckoos perform noisy courtship chases, often involving several birds, and carrying them over long distances. Individuals also call loudly, either perched prominently in the top of a tree, or in flight. The intensity of the chases, and the amount of vocalisation, falls sharply after the end of July, and the birds are rather silent in the second half of the season. Apart from the courtship chases they are usually seen alone or in pairs. The chases and vocalisations are presumably concerned with pairing, and perhaps with the establishment of territories.

While feeding or resting the cuckoos are not generally molested by babblers, although Pied Crested Cuckoos flying over usually elicited an alarm call. If they approached within 20m of a babbler's nest, however, they were vigorously chased off. The Hawk-cuckoo, on the other hand, perhaps because of its close resemblance to an Accipiter hawk, elicits an immediate mobbing response from babblers wherever it is encountered.

Pied Crested Cuckoos were seen feeding mainly in open scrub, taking large hairy caterpillars from on or near the ground, and sometimes feeding on fruit. Single birds were regularly found perching in the woodland canopy, and although sexes are indistinguishable in the field, it seems likely that these birds were females searching for nests of the Jungle Babbler. One bird, followed for an hour, perched frequently for periods of up to five minutes, before shifting 20-50m. At one point it examined the unused nest of a Jungle Babbler, perching beside it for a minute before moving on.

During observations at babblers' nests Pied Crested Cuckoos were seen to approach on a number of occasions. Usually a non-incubating bird perched nearby would chase off the cuckoo, but when no other bird was present the incubating bird would give chase as soon as the cuckoo approached within 3-4m.

In the course of one continuous watch from dawn on the eighth day of incubation a cuckoo approached the nest at 0730, and the incubating bird (the female) took off in pursuit. Because of the restricted view from the hide, the two birds were immediately lost from sight. About 30 seconds later the cuckoo, or another, re-appeared, perched briefly in the thorny twigs which curved over the nest, and then flew off. The time spent above the nest was not more than five seconds, and the cuckoo did not settle into the cup, but remained perched at least 15cm. above it. The babbler returned about a minute later and settled onto the eggs.

At 1000 I inspected the nest, which at dusk the previous day had contained four babbler's eggs, and found that it now contained four babbler's eggs and one cuckoo's egg. One of the babbler's eggs showed a circular depressed crack on the upper side, which was probably caused by the impact of the cuckoo's egg falling on it. The depression was similar to several that had previously been observed on babbler's eggs in nests parasitised by cuckoos. Most eggs cracked in this way did not hatch, but at least one did, although the crack was sustained on the third day after laying.

If this observation reveals the habitual laying technique of the Pied Crested Cuckoo then it would explain not only the number of depressed circular cracks, but also the ability of the cuckoos to lay in apparently inaccessible nests of the Common Babbler, built in dense thorn bushes. As Lack (1968) has suggested, the function of the very thick egg shell is probably to protect the egg when falling into the nest. In three cases cuckoos' eggs were found, after hatching, to have double shells, the inner being separated from the outer by a duplicate egg membrane. The occurrence of this abnormality may be encouraged by the necessity for very strong shells. Liversidge (1971) found that the eggs of C.jacobinus serratus sometimes escaped predation when those of their host were eaten, and this might also be due to the greater thickness of their shells.

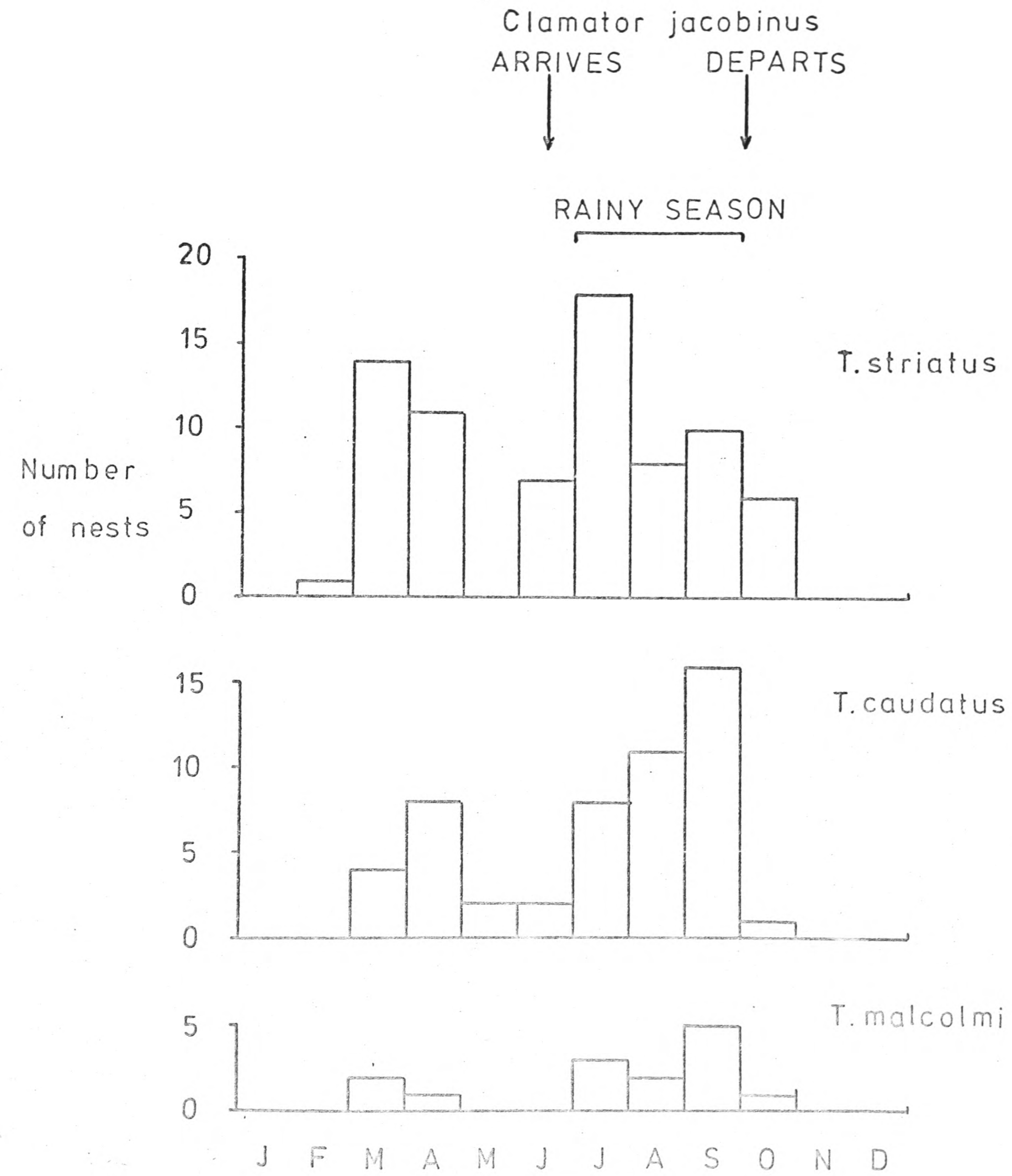
No evidence of egg removal by the female cuckoo was recorded, although this occurs in the Great Spotted Cuckoo (Clamator glandarius) (Mountfort & Ferguson-Lees 1961), and Ali and Ripley (1969) suggest that it also occurs in the Red-winged Crested Cuckoo (C. coromandus). A comparison of babbler clutch size in nests with and without cuckoos' eggs showed that clutches without tended to average larger than those with, in the case of the Jungle Babbler (see later, Table 5), but this was not observed in the Common Babbler.

In nests where eggs were marked immediately after they had been laid none subsequently disappeared simultaneous with the arrival of a cuckoo's egg. It is possible that some or all of the difference in observed clutch sizes is due to the removal by babblers of eggs cracked in the course of egg laying by the cuckoos, which was recorded once, but the difference is not statistically significant, and may be due to chance.

Ali and Ripley (loc. cit.) also suggest, very tentatively, that young Pied Crested Cuckoos may remove the eggs or young of their host from the nest, in the same way that young European Cuckoos (Cuculus canorus) do, but no evidence of this habit was found, either in the present study, or in Liversidge's observations on the same species in South Africa. In 8 out of the 27 nests from which cuckoos fledged successfully at least one babbler was also fledged, and this was also true for two of the four cases in which two cuckoos were fledged from the same nest. Young babblers disappeared only in cases where the cuckoo hatched two or three days before the first babbler, and was large enough to monopolise the food supply. Dead babbler chicks, clearly starved, were found in several nests containing young cuckoos.

Pied Crested Cuckoos continued to be fed for two-three weeks after leaving the nest. When fledged from a nest without young babblers the cuckoo followed its foster group, uttering continual begging calls. These seem to have had only a weak attraction for Jungle Babblers, however, because birds

Figure 1. Seasonal distribution of nesting attempts for three species of Turdoides at Delhi in 1972 and 1973.



rarely flew more than a few metres to feed a young cuckoo. Instead the cuckoo flew down, begging loudly, as soon as it saw a babbler find an attractive food item. Young babblers generally remained perched inside dense vegetation during the first week after fledging, the adults bringing food to them from surrounding areas. When they were present the cuckoo remained perched nearby, begging from the adults as they arrived.

There was some suggestion, from the relatively poor condition of cuckoo nestlings in nests where no babbler nestling survived, that the adult babblers began to lose interest in the young cuckoo in the last few days before it left the nest, by which time the black and white plumage of the adult was becoming conspicuous. Sanjeeva Raj (1964) mentions an instance in which a young cuckoo was ignored by its foster group (of Turdoides affinis) after fledging, and disappeared within two days, although in this instance one young babbler was also fledged.

At night the babbler group roost in contact with one another, side by side along the branch of a tree. The juvenile cuckoo does not attempt to join the huddle, perching alone a few metres away, and flying to join the group again when it sets out the next morning.

Timing of breeding in host and parasite.

Figure 1 shows the distribution of egg laying dates among the three species of babblers during 1972 and 1973. The length of the breeding season is variable, and apparently depends on the rainfall. In 1972, a relatively dry year, only one Jungle Babbler clutch was laid in October, whereas in 1973, after a prolonged rainy season, there were five October nests.

Rainfall in Delhi occurs mainly in the months July-September, as a result of the SW monsoon, but some also falls during the winter, and this

produces a flush of vegetation and insect life in spring (March). The two breeding peaks shown in Fig.1 will be referred to respectively as the spring and the rainy season peaks, the second beginning quite abruptly with the arrival of the first heavy monsoon showers.

The first Pied Crested Cuckoos arrived in Delhi about the end of the first week of June, a date roughly coinciding with the arrival of the SW monsoon front on the west coast of India. The rain does not usually reach Delhi until almost a month later. Whistler (1928) gives the first dates of arrival for Pied Crested Cuckoos all over North India. The earliest is May 15, but for most places the date is in the last week of May or the first of June.

The airstream over the Arabian Sea during May is generally WNW, but in June it changes to WSW, making it favourable for migration from the coast of East Africa. The onset of this change is controlled by the northward movement of the inter-tropical front (Ramakrishnan, Sreenivasaiah, & Venkiteshwaran 1958). The absence of isolated early records of Pied Crested Cuckoos suggests that birds may await the onset of the favourable WSW winds before undertaking the crossing of the Arabian Sea.

Adult Pied Crested Cuckoos disappeared from the study area by the end of September. No cuckoo's egg was recorded being laid later than September 14, which means that the latest that a young cuckoo might become independent would be about the end of October. The departure of the cuckoos again coincides with a change in the direction of the airstream over the Arabian Sea, which switches to easterly in October.

Table 1 shows the number of babblers' nests available to be parasitised during the 1972 and 1973 seasons (figures for the Common Babbler were estimated by assuming that 70% of nests were found in 1972 and 80% in 1973). The observed rate of parasitism in cuckoos' eggs per nest is also shown for all

Table 1. Comparison of numbers of cuckoos' eggs laid and intensity of parasitism in three breeding seasons, June-September only. For Jungle and Large Grey Babblers all nests were found. Figures for Common Babblers were estimated on the assumption that 70% of nests were found in 1972 and 80% in 1973. Figures in brackets are numbers of nests.

	Jungle Babbler	Common Babbler	L.G.Babbler	Totals
1971				
Cuckoos' eggs per nest	2.0(5)	-	0.5(4)	
1972 Nests available (A)	24	21.5	5	50.5
Cuckoos' eggs per nest (B)	0.85(20)	0.31(13)	0.2(5)	
Total cuckoos' eggs (B x A)	20.4	6.7	1.0	28.1
1973 Nests available (A)	19	28.8	5	52.8
Cuckoos' eggs per nest (B)	1.31(13)	0.5(18)	0.2(5)	
Total cuckoos' eggs (B x A)	24.8	14.4	1.0	40.2

Table 2. Numbers of babblers' nests available in each month and numbers of cuckoos' eggs laid per nest for the 1972 and '73 seasons only. Estimates of Common Babbler nests calculated as for table 1. Figures in brackets are numbers of nests.

	Jungle Babbler	Common Babbler	L.G.Babbler	Totals
June. Nests available	7	2.5	0	9.5
Cuckoos' eggs per nest	1.2(5)	0(2)	-	
Total cuckoos' eggs	8.4	0	-	8.4
July. Nests available	18	11.8	3	32.8
Cuckoos' eggs per nest	1.06(17)	0.6(5)	0(3)	
Total cuckoos' eggs	19.1	7.1	0	26.2
August. Nests available	8	14.4	2	24.4
Cuckoos' eggs per nest	0.5(4)	0.6(10)	0(2)	
Total cuckoos' eggs	4.0	8.6	0	12.6
September. Nests available	10	21.4	5	36.4
Cuckoos' eggs per nest	1.14(7)	0.29(14)	0.4(5)	
Total cuckoos' eggs	11.4	6.2	2.0	19.6
Proportion in nests of each spp.	42.9(64%)	21.9(33%)	2.0(3%)	66.8

nests which could be examined, and which were available to cuckoos for at least eight days after the laying of the first egg. From these figures it is possible to estimate the total number of cuckoos' eggs laid in the study area as 27.1 in 1972 and 37.3 in 1973.

The intensity of parasitism in cuckoos' eggs per nest was lowest for all three host species in 1972, a year of below average rainfall for North India. General observations suggested that fewer cuckoos were present in the study area in that year, and it is possible that cuckoos were concentrating further South, in areas of adequate rainfall.

Table 2 shows the intensity of cuckoo parasitism for the four months during which the cuckoos were present. Only the 1972 and '73 seasons are included because the 1971 season was incomplete. In the Jungle Babbler peak intensity of cuckoo parasitism occurred in July and September, the months in which most nests were initiated. In August more eggs were laid in Common Babblers' nests than in other months, and it is possible that there is a tendency for cuckoos to switch their attention to this species while there is a hiatus in the initiation of Jungle Babbler nests.

The monthly totals also suggest that the cuckoos reduce their laying rate in August, compared to July and September, and this is even more true when the fact that laying finishes in the middle of September is taken into consideration. Payne (1973) showed that Clamator jacobinus breeding in South Africa lay in clutches of 1-4 eggs with a pause between each. It is possible that in the Delhi area cuckoos find a prolonged pause in egg laying necessary in mid-season, which may be reflected in the reduced intensity of parasitism in August.

Density of cuckoos in relation to their hosts.

It was not possible to make an accurate census of the number of Pied Crested Cuckoos in the study area at any one time. In June, soon after their

arrival, parties of three and four birds were seen commonly, but after the beginning of August only pairs or solitary individuals were observed. Sexes were not distinguishable in the field, but parties of two seen after the beginning of July were assumed to be mated pairs. General observations over the whole study area in 1973 suggested that at least three pairs were present throughout the breeding season.

The estimated number of cuckoos eggs laid in the two full seasons seems well within the capabilities of three female cuckoos, since Payne (1973) has shown that female Clamator jacobinus lay at a rate of 1.9-2.5 eggs per week. There were no periods recorded when this rate was being exceeded within the study area, assuming the presence of three female cuckoos.

During the rainy season the study area contained about 115 Jungle Babblers in 20 groups, 120 Common Babblers in 15 groups, and 16 Large Grey Babblers in 4 groups. As only one pair bred at a time in each group the ratio of parasite to hosts in terms of pairs can be estimated as about 1 : 13, assuming three pairs of cuckoos.

Young cuckoos were easily found by their persistent calls, and probably all those fledged in the study area were noted. Nine were seen in 1972 (33% of eggs laid) and 18 in 1973 (49% of eggs laid). Assuming the presence of three pairs of cuckoos in 1973, this suggests a reproductive rate of six fledged young per pair.

Availability of nests.

For the cuckoos the maximum rate of laying can only be maintained as long as suitable nests are available to parasitise. Some evidence suggests that babbler groups which are particularly affected by cuckoo parasitism tend to synchronise their nesting; a factor which would reduce the chances of a cuckoo's egg being laid in any particular nest.

Figure 2. Numbers of nests initiated per 10-day period by Common Babblers, Jungle Babblers holding woodland territories (1) and Jungle Babblers holding non-woodland territories (2&3). The solid lines show Poisson distributions calculated for the observed means.

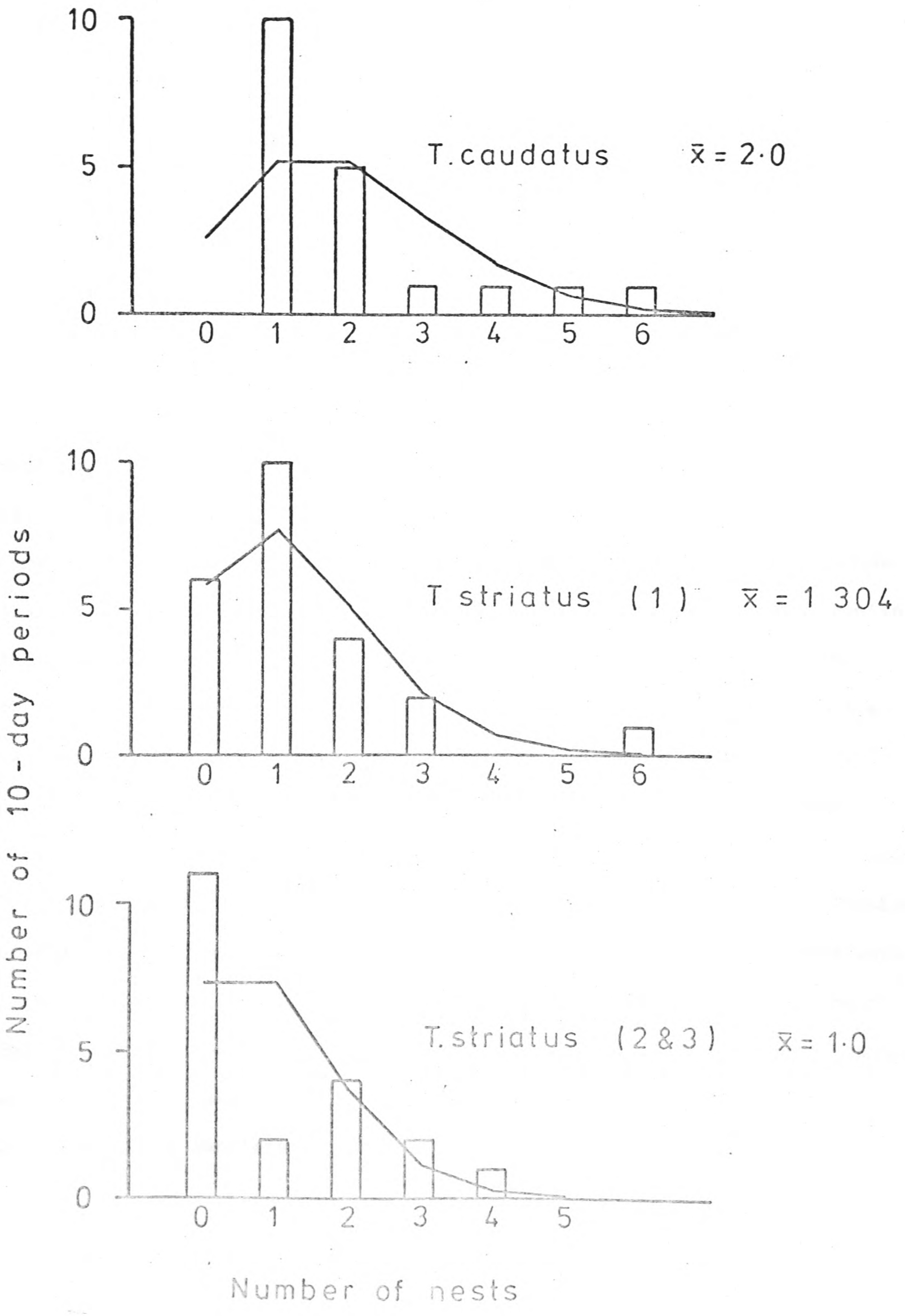


Figure 2 shows the distribution of egg laying by babblers in ten-day periods during the 1972 and '73 seasons. Jungle Babbler groups are divided into two categories on the basis of the type of habitat which they occupy (1) holding territories largely within closed canopy woodland, (2 & 3) holding territories partly (2), or wholly (3) outside closed canopy woodland. A study of the breeding success of Jungle Babblers shows that groups with territories outside closed canopy woodland make fewer nesting attempts than those with woodland territories, and that the nesting of non-woodland groups is more concentrated in the season when cuckoos are present, presumably because of lack of suitable food in these territories at other times. Because of this non-woodland groups suffer more drastically from the effects of cuckoo parasitism.

If cuckoo parasitism causes selection for synchronisation of nesting the effect should be most noticeable in the host population which is most affected. A comparison of the histograms in Fig. 2 shows that Common Babblers, which suffer less reduction in recruitment due to cuckoos than do Jungle Babblers (see below), have the least tendency to synchronise their nesting, and that the Jungle Babblers nesting in woodland (1) are less synchronised than those outside (2 & 3). The difference between the two categories of Jungle Babbler is statistically significant ($\chi^2 = 6.67$, df = 2, $p < 0.05$), and that between Common Babblers and the woodland Jungle Babbler groups approaches this level ($\chi^2 = 5.93$, df = 2, p = 0.1-0.05). The black line in each histogram is calculated from the Poisson distribution having the observed mean, and shows the expected distribution if nests were initiated randomly throughout the season. In comparison with this Common Babblers' nests appear to be overdispersed in time, though not significantly, woodland Jungle Babblers (1) are more or less randomly dispersed, and non-woodland Jungle Babblers show a tendency to clump their nests.

Timing of egg laying in relation to the host's clutch.

Table 3 shows the timing of egg laying by Pied Crested Cuckoos in relation to the laying of their host's clutch, for the nests of Jungle and Common Babblers. Twenty out of 38 (52.5%) were laid during the host's laying period, but one was laid as late as the 21st day, when the nest contained half grown nestling babblers. Nestling cuckoos hatched from eggs laid later than the eighth day from the laying of the first Jungle Babbler's egg did not survive to fledging, apparently because the young babblers were able to monopolise the food supply, and selection against late laying is therefore strong.

Chance (1922, 1940) has shown that European Cuckoo females locate the nests of their hosts during the building stage. This enables them, almost invariably, to lay their eggs during the host's laying period. The large proportion of Pied Crested Cuckoos' eggs laid after the end of their host's laying period suggests that they may not be able to find enough nests during the building stage. Jungle Babblers tend to be rather inconspicuous while nest building, much of the work being done in poor light just before going to roost, and this may cause difficulty for the cuckoo.

Resistance from the babblers may also prevent cuckoos from depositing their eggs at the optimum time, although this implies that the cuckoo is capable of retaining an egg if frustrated. On several occasions Jungle Babblers were seen to successfully drive off cuckoos which had approached to within a few metres of their nest, although in these instances it is possible that the cuckoo was merely making an inspection. Several babblers usually combined during these interactions and it seems unlikely that the cuckoo could have succeeded in laying in the face of opposition from a number of birds of its own size.

Table 3. Timing of cuckoos' eggs laid in babblers' nests.

	Days from laying of first babblers' egg (day 1)					
	1-4	5-8	9-12	13-16	17-20	21-24
Jungle Babbler	16	7	4	1	1	1
Common Babbler	4	3	1			
Totals	20	10	5	1	1	1

Table 4. Numbers of cuckoos' eggs per nest, all seasons.

	Number of nests with 0,1,2..eggs					Proportion of nests parasitised
	0	1	2	3	4	
Jungle Babbler	11	13	12	1	1	71%
Common Babbler	19	11	1			39%

Table 6. Ways in which cuckoos affect the reproductive success of babblers.

	Jungle Babbler	%loss	Common Babbler	%loss
Mean clutch without cuckoo	4.2	14.3	3.37	
Mean clutch with cuckoo	3.6		3.44	
No. fledged, assuming normal survival (J.Bab.62%, C.Bab.77%)	2.14	34.8	2.6	24.4
Observed mean number fledged	1.14	23.8	1.14	42.5
Total loss due to cuckoos		38.1		42.5

Liversidge (1961) showed that in one case an egg of Clamator jacobinus collected immediately after laying, had developed to a stage equivalent to 17-20 hours after the beginning of incubation in the domestic fowl. There was no suggestion that this egg had been delayed abnormally, but it indicates that retention can occur. Perrins (1967) suggested that eggs are normally retained up to 24 hours by the European Cuckoo, and that this explains, in part, the very short incubation period observed for this species. Two eggs removed in the present study on the day of laying showed no signs of premature development to the naked eye, although both had been laid in unsuitable nests already containing nestling babblers.

Eggs laid well beyond the end of the host's laying period may result from females being frustrated at their first choice nest. Accidental hosts are uncommon for the Pied Crested Cuckoo, and it seems probable that the species prefers to lay in the nest of the correct host at the wrong time, rather than that of the wrong host at the right time, the apparent preference of the European Cuckoo when frustrated (Chance 1922).

Multiple laying by cuckoos in the same nest was quite frequent in the study area. The following intervals were observed between successive eggs laid in the same nest; 1,2,2,2,3,3,4,4,7,7 and 12 days. The preponderance of two and three day intervals over nil and one day intervals suggests that the same female may often be involved if, as is true for the majority of parasitic cuckoos (Payne 1973), the eggs are laid at two-day intervals. Two young cuckoos were reared successfully from the same nest on four occasions, out of the eleven, which indicates that there is little disadvantage in laying at least two eggs in the same nest. In two cases, however, two eggs laid in the same nest were sufficiently dissimilar in shape to suggest the presence of two females.

Table 4 shows the distribution of the number of Pied Crested Cuckoos' eggs per nest for the Jungle and Common Babblers. Out of 44 eggs laid in Jungle Babblers' nests 17 were laid in nests already containing one or more cuckoos' eggs, but the same ratio for Common Babblers' nests was 12 to 1. The fact that for both species nests containing only one egg predominated suggests that double laying occurred only when no suitable unparasitised nest was available.

Relative growth rates of babbler and cuckoo nestlings.

In addition to having an incubation period three days shorter than that of their hosts, nestling Pied Crested Cuckoos also develop more rapidly after hatching, being ready to leave the nest at 11-12 days old compared to 14-16 days for the Jungle Babbler. The mean maximum rate of growth recorded for eight nestling cuckoos was 6.5g. per day, compared with a mean of 5.2g. per day for Jungle Babblers (n = 21), which have the same sized egg, and 2.7g per day (n = 5) for Common Babblers. The burden of rearing a cuckoo, therefore, appears to be about twice as great for Common as for Jungle Babblers, and a proportionately higher loss of nestling babblers was noted in the former species.

Figure 3 shows two examples of the growth curves of nestling Pied Crested Cuckoos, and those of the Jungle Babbler nestlings in the same nest. Not only do the cuckoos achieve a higher maximum rate of growth, but this rate is reached earlier, and carried on to a higher weight level before slowing down. This is despite the fact that the adult weights of the two species are the same. The rate of growth during the first few days after hatching was appreciably slower for the cuckoo in nest BLB2, hatching 2-3 days behind its three babbler nest-mates, than for the other cuckoo which had only one babbler to compete with on hatching. In nest P2 it was the

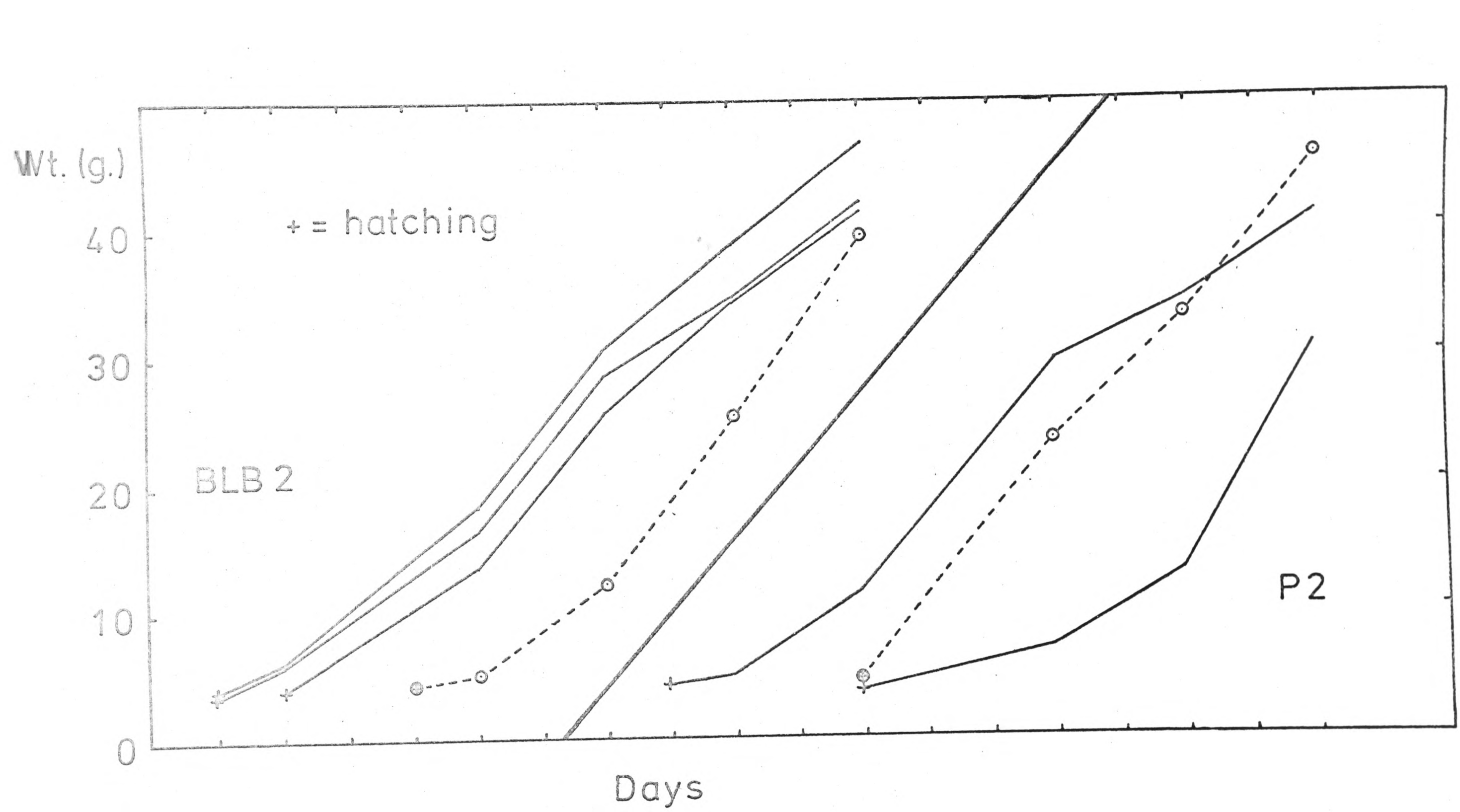


Figure 3. Growth rates of Jungle Babbler and Pied Crested Cuckoo nestlings in two nests. Solid lines connect weighings of babbler nestlings, broken lines, cuckoos.

late hatching babbler which was slow to accelerate its growth rate, a pattern seen in late hatching nestlings irrespective of the presence of a cuckoo. All nestlings shown in fig. 3 fledged successfully.

No difference was found between the rates of growth of babbler nestlings with and without cuckoos. Disappearance of nestlings due to starvation occurred only during the first few days after hatching, usually in the first day, and this applied equally to babbler and cuckoo nestlings. Those which survived beyond this point developed normally, and at the normal rate, regardless of their size in relation to that of other nestlings. The cuckoo nestlings can apparently monopolise the attention of the adult babblers only when the babbler nestlings are very small.

At one nest, containing a six day old Common Babbler nestling, and a seven day old cuckoo nestling, both were fed with equal frequency, despite the fact that the cuckoo cutweighed the babbler by 41g to 16g. The babbler chick had difficulty in accepting some of the larger food items presented, however, and these were then passed on to the cuckoo, which must, in this way, have received a greater weight of food.

The effect of parasitism by the Pied Crested Cuckoo on the reproductive success of its hots.

Pied Crested Cuckoos were found to affect the rate of increase of their hosts populations in the following ways.

1) A cuckoo's egg may crack one of the hosts eggs during laying, so that it fails to hatch.
2) If the cuckoo hatches early one or more of the host's nestlings may die of starvation.
3) Where a cuckoo is the only fledgling its dependence delays the initiation of another nesting attempt.
4) Young babblers reared during the period when cuckoos are present have a higher survival during the first three months after leaving the nest than those reared at other times, and hence losses due to cuckoos have a disproportionate effect on numbers surviving the following season.

Table 5 shows the mean number of eggs laid, and young fledged, in nests with and without cuckoo parasitism. The mean number of young babblers fledging from Jungle Babbler nests containing a young cuckoo was 1.14 young per nest, compared with 2.65 young per nest from nests without cuckoos. These represent 32% and 62% respectively of the mean number of eggs laid per nest. In the Common Babbler 33% of eggs laid in nests parasitised by cuckoos were reared to fledging, against 77% in nests without cuckoos.

The relative contribution made by Pied Crested Cuckoos to the decreased breeding success of Jungle and Common Babblers is estimated in table 6. In the Jungle Babbler breeding success is reduced 26% by decreased fledging success, while in the Common Babbler this contributes 42.5% to the loss of breeding capacity. This difference is probably due to the fact that Common Babblers nestlings are smaller at hatching than those of the Jungle Babbler, and therefore less able to compete with a young cuckoo.

Table 7 shows the proportion of babblers' nests parasitised by Pied Crested Cuckoos, during June-September 1972 and '73. The effective decrease in the production of the babblers during this period can be calculated from this and Table 5 as 38.75% for Jungle Babblers, and 23.5% for Common Babblers. Out of 39 Jungle Babblers reared during the study and surviving until March 1 in the following year, 29 were from clutches laid during June-September, and this means that the overall decrease in recruitment due to cuckoo parasitism can be calculated at 32% (this calculation is given in the appendix). For the Common Babbler survival to the following spring is not known, but 37 out of 52 nests (71.2%) were begun during June-September, and assuming equal survival for the

Table 5. Clutch size and fledging success in parasitised and non-parasitised nests, June-September only.

Jungle Babbler	1971	1972	1973	together	%loss
Without cuckoo					
Mean clutch		4.25(8)	4.0(2)	4.2(10)	
Mean no. fledged	2.33(3)	2.8(10)	2.14(7)	2.5(20)	40.5
With cuckoo					54.4
Mean clutch		3.67(9)	3.5(6)	3.6(15)	
Mean no. fledged	0.84(6)	1.0(5)	1.4(10)	1.14(21)	68.4
Common Babbler					
Without cuckoo					
Mean clutch		3.28(7)	3.44(9)	3.37(16)	
Mean no. fledged		2.75(8)	2.43(7)	2.6(15)	23
With cuckoo					56
Mean clutch		3.33(3)	3.5(6)	3.44(9)	
Mean no. fledged		2.0(3)	0.5(4)	1.14(7)	67

Table 7. Proportion of babblers' nests parasitised by cuckoos.

	1971	1972	1973	together
Jungle Babbler	5/5	12/20	10/13	27/38 = 71%
Common Babbler		4/13	9/18	13/31 = 42%
Large Grey Babbler	2/4	1/5	1/5	4/14 = 29%

birds fledging at different seasons, the overall decrease in recruitment due to the cuckoos is 18.1% (see appendix).

The total effect of cuckoo parasitism on the babblers is certainly more complex than the simple calculations above would suggest. No assessment was possible of factors such as increased predation of fledglings due to the conspicuous calls of the young cuckoo, the long-term effects of nestling deprivation on birds which succeeded in fledging, or of density dependent mechanisms operating on the babbler population. General ecological factors affecting the breeding success of babblers are beyond the scope of this paper, but as mentioned under 'availability of nests', it appears that groups living in optimum habitat (woodland) are large, and make several nesting attempts during the season. Smaller groups, living outside woodland, usually nest only during the rainy season breeding peak, and the effect of cuckoo parasitism will be greatest on these, since they are not capable of rearing young outside the period in which the cuckoos are present.

A comparison of the number of Pied Crested Cuckoos' eggs laid in the nests of groups holding territory inside and outside closed-canopy woodland showed that woodland groups of Jungle Babblers averaged 1.08 cuckoos' eggs per nest ($n = 25$), while the nests of groups living outside woodland averaged 1.2 eggs per nest ($n = 18$). This suggests that pressure from cuckoos is roughly equal in both habitats.

Discussion.

Friedmann (1964) and Liversidge (1971) have compared the adaptations of the genus Clamator to brood parasitism with those of the better known genus Cuculus. Species of Clamator differ chiefly in not possessing sympatric gentes laying eggs adapted to different host species, and in the fact that the nestling Clamator does not evict the eggs and young of its host.

The first requirement in becoming a successful parasite is to adopt a successful host. The range and population density of the parasite are inevitably controlled by the distribution and abundance of its hosts. The European Cuckoo maintains a wide distribution by parasitising a wide range of host species, and this had led to the evolution of distinct gentes with eggs closely mimicking those of their hosts. Southern (1954) has pointed out that a certain degree of habitat isolation is necessary for those gentes to evolve, and in places such as Britain, where this is lacking, mimicry is rather poor, despite the fact that individual cuckoos are faithful to a single host species (Chance 1922).

The evolution of egg mimicry depends on the ability of the host species to discriminate the eggs of the parasite (Baker 1923). Once such behaviour begins there is selection pressure for the parasite to evolve eggs which resemble those of the host and, having done so, to parasitise only that species. New gentes can be initiated only by eggs laid in the nests of species which are not normally parasitised, and the fact that such casual hosts are quite common in the case of the European Cuckoo helps to explain the proliferation of gentes in this species.

No cuckoos' eggs were found in nests other than those of Turdoides spp., although nests of Pycnonotus spp., hosts of Clamator jacobinus in Africa, were common during the period when cuckoos were present. In addition no juvenile cuckoos were seen being fed by other hosts, suggesting that, at least in the

Delhi area, there is little scope for the initiation of new gentes. Perhaps assisted by the absence of sympatric gentes, the Pied Crested Cuckoo in India has evolved an egg which is virtually indistinguishable from that of its hosts, all of which lay eggs of a similar colour. Conversely the nestling shows no trace of mimicry, being distinguishable easily, even before the feathers develop, by its rather blackish skin, and later by the black-and-white plumage, contrasting strongly with the dull brown of the babblers.

The occurrence of mimicry in the egg, but not in the nestling, probably results from the relatively greater strength of the feeding drive in the parent birds. The evolution of desertion behaviour in response to an alien egg being laid in the nest can occur fairly easily because the loss in time and energy to a bird deserting during egg-laying, or the early incubation period, is quite small, particularly in a species with a long breeding season. The corresponding loss if desertion occurs during the nestling period is much higher, both in terms of energy expended, and in lost opportunity in a species subject to heavy nest predation, so that a mistaken rejection carries a correspondingly heavy penalty. The evolution of rejection behaviour towards a chick is likely to be much slower, therefore, than the evolution of egg-desertion. Both rates of evolution are likely to be slower where some of the host's own offspring may survive despite the presence of a cuckoo, because in this situation, even if the presence of a cuckoo is correctly detected, the host may reduce its reproductive potential by resorting to desertion.

Eviction behaviour, as manifest in the genus Cuculus, may be partly an adaptation to parasitising hosts much smaller than themselves, for which the rearing of a single nestling cuckoo is equivalent to rearing a whole brood of their own offspring. In the genus Clamator most species parasitise hosts similar to, or larger than, themselves in size, and hence eviction is unnecessary, provided that the female cuckoo removes or destroys one of the host's eggs while laying. At the same time, by a llowing

some of the host's young to be reared the Clamator cuckoos are acting as "prudent parasites" in minimising the amount of damage that they do.

Owen (1933) records a case where the European Cuckoo apparently brought a local population of Sedge Warblers (Acrocephalus schoenobaenus) close to extinction. Such an outcome would be unlikely in the case of Turdoides species which rear some young outside the period when the cuckoos are present, but for the same reason the cuckoo needs to avoid having too drastic an effect on its hosts. If all cuckoos eggs laid had hatched and evicted their nest mates, only 0.9 Jungle Babblers would have been reared per nest during June-September. Babblers have a high adult survival rate, and under these circumstances the option to breed at all while cuckoos were present might become evolutionarily unprofitable.

Removal of one of the host's eggs at the time of laying is not invariable in Clamator; it was not observed in the present study, and was not recorded in Liversidge's study on South African C.jacobinus (loc. cit.). In the present study one egg was often damaged when the cuckoo laid, and as these eggs did not usually hatch the result was equivalent to egg removal. In the Clamator studies where egg removal was observed (Jensen & Jensen 1969, Mountfort & Ferguson-Lees 1961) the populations involved were ones where multiple laying by the cuckoos was the rule, and under these circumstances it becomes imperative that some eggs are removed to ensure that the brood does not become too large. Mountfort & Ferguson-Lees describe Great Spotted Cuckoos (Clamator glandarius) parasitising Magpies (Pica pica) and mention that Magpies' eggs in nests where cuckoos' eggs had been laid often appeared "slightly dented". They attributed this to careless feet or deliberate pecks, but the damage sounds rather like that caused by the impact of a falling egg.

Although multiple laying in the same nest must be greatly influenced by the relative densities of host and parasite, their relative sizes may also be important. Cases of more than one egg in a nest are quite rare for the European Cuckoo (Baker 1942), which parasitises hosts between 10-20% of its own adult wieght. South African Clamator jacobinus, parasitising bulbuls (Pycnonotus spp.) which weigh about half their own weight, laid 21.6% of their eggs in nests which already contained one (Liversidge loc. cit.). In the present study 17 out of 44 (39%) cuckoos eggs were laid in Jungle Babblers nests which already contained one, and for the Great Spotted Cuckoo parasitising Magpies the proportion was 60% (Friedmann 1964), the Great Spotted Cuckoo being smaller than its host. Multiple laying is also the rule in the Red-winged Crested Cuckoo (Clamator coromandus) which parasitises hosts larger than itself (Ali & Ripley 1969). Thus the genus shows a steady increase in the amount of multiple laying with increase in the relative size of the host.

One feature of the behaviour of the Pied Crested Cuckoo which contrasts with that of most other parasitic cuckoos is the relatively small amount of vocalisation. In the genera Cuculus, Cacomantis, and Eudynamys persistent vocalisation by the male continues throughout the breeding season, whereas Pied Crested Cuckoos are relatively quiet after the first month in their breeding area. This suggests a difference in social structure between Clamator species and the other parasitic cuckoos, and it is possible that pairing is more permanent in this genus. Liversidge (loc. cit.) describes how the male Clamator jacobinus distracts the host pair, while the female slips in to lay an egg; von Frisch (1973) observed similar behaviour in captive Clamator glandarius and the same tactics are probably used by Clamator levaillantii (Steyn 1973). This possibility was also suggested for the Pied Crested Cuckoo by Ali (1930) and fits the observation of laying recorded in the present study. If co-operation by the pair is the normal

strategy for egg laying in Clamator species, this would explain the need for a durable pair bond.

A number of factors probably contribute to making the genus Turdoides particularly suitable as cuckoo hosts.

1) Species of the genus are common everywhere in lowland India, and occupy all types of habitat, from semi-desert to tropical evergreen forest.
2) In Delhi, and probably over most of the drier parts of India, Turdoides spp. have comparatively long breeding seasons, spanning the entire period during which the Pied Crested Cuckoos are present.
3) All species lay unmarked eggs, which are probably easier to mimic than marked eggs.

The effect of parasitism by Pied Crested Cuckoos on their babbler hosts cannot be assessed completely. It varies with the habitat, and with the seasonal rainfall, and probably also geographically, because in some areas the peak of babbler breeding comes before the arrival of the cuckoos (Andrews & Naik 1970). At Delhi the fact that cuckoos are more common in years of heavy rainfall leads to the surprising fact that more young babblers are reared in seasons of low rainfall because of the lower rate of parasitism.

It is unlikely that cuckoo parasitism has much effect on the general level of babbler populations, which are probably limited by food supply at the critical season, but, depressing breeding success, it may affect group size. Young babblers do not begin to leave their natal group until half way through their second year, so that an increase in breeding success should lead to an increase in group size, and a shift in the age structure of the population towards more younger birds. If the population level is fixed by other factors an increase in group size would mean a decrease in the number of groups, and hence the number of breeding pairs

per unit area. Cuckoo parasitism, by reducing group size, may actually increase the number of nests available to be parasitised, another factor which might make babblers attractive hosts.

Summary.

1) In the course of a study on the behaviour and ecology of babblers (Turdoides spp.) near Delhi, North India, a number of observations on parasitism by the Pied Crested Cuckoo (Clamator jacobinus) were made.

2) The behaviour of the cuckoo, the timing of its breeding in relation to that of its host species, the relative densities of parasite and hosts, the intensity of parasitism, and the effect of the parasitism on the breeding success of the host species are described. Measurements of the growth rates of cuckoo and host nestlings are compared.

3) The adaptations of the genus Clamator to brood parasitism are compared with those of the genus Cuculus, and the differences related to the type of hosts selected.

4) General strategies for brood parasitism are also discussed, and reasons advanced to suggest that the genus Turdoides is particularly suited to exploitation by brood parasites in India.

Appendix. Derivation of the theoretical reduction in the recruitment rate of babblers due to parasitism by the Pied Crested Cuckoo.

Jungle Babbler

Decrease in number fledged from parasitised nests	54.4%
Proportion of nests parasitised, June-September	71.0%
Proportion of young surviving on March 1 following which were reared from clutches laid in June-September	74.4%
Reduction in numbers fledged, June-Sept., 54.4% x 71.0% =	38.6%

Effect on annual recruitment

Theoretical increase without cuckoos

June-September $\frac{100}{100-38.6} - 1 \times 100 = 62.9\%$

Theoretical increase without cuckoos

No. surviving following March 1 $\frac{100}{100-38.6} - 1 \times 74.4\% = 46.8\%$

Hence percentage reduction in the number surviving

due to cuckoo parasitism $\frac{46.8}{100+46.8} \times 100 = 31.9\%$

Common Babbler

Decrease in number fledged from parasitised nests	56.0%
Proportion of nests parasitised, June-September	42.0%
Proportion of nests found where clutches were laid during June-September	71.2%
Reduction in numbers fledged, June-September 56.0%x42.0% =	23.5%

Effect on annual recruitment

Theoretical increase without cuckoos

June-September $\frac{100}{100-23.5} - 1 \times 100 = 31.0\%$

Theoretical increase without cuckoos

over the entire season $\frac{100}{100-23.5} - 1 \times 71.2 = 22.0\%$

Hence percentage reduction in the number reared during the entire season due to cuckoo parasitism

$\frac{22.0}{100+22.0} \times 100 = 18.1\%$

References.

Ali, S.	1930	Notes on the Pied Crested Cuckoo (Clamator jacobinus) in Alibag Taluka (Kolaba District). J. Bombay Nat. Hist. Soc. 34: 1071-72
Ali, S. & Ripley, S. D.	1969	Handbook of the Birds of India and Pakistan, Vol. 3, O.U.P.
	1971	Handbook of the Birds of India and Pakistan, Vol. 6, O.U.P.
Andrews, M. I. & Naik, R.M.	1970	The biology of the Jungle Babbler. Pavo 8: 1-34
Baker, E. C. S.	1923	Cuckoos' eggs and evolution. Proc. zool. Soc. Lond. : 277-294
	1932	The Nidification of the Birds of the Indian Empire. Taylor and Francis.
	1942	Cuckoo Problems. Witherby
Chance, E.	1922	The Cuckoo's Secret. Sidgwick and Jackson.
	1940	The Truth about the Cuckoo. Country Life.
Friedmann, H.	1964	Evolutionary trends in the avian genus Clamator. Smithson. misc. Coll. 146, 4.
Frisch, O. von	1973	Ableukungsmanöver bei der Eiblage des Häherkuckucks. J. Orn., Lpz. 114: 129-131
Hume, A. C.	1890	Nests and Eggs of Indian Birds (2nd ed.). R. H. Porter.
Jensen, R. A. C. & Jensen, M. K.	1969	On the breeding biology of southern African cuckoos. Ostrich 40: 163-181
Lack, D.	1968	Ecological Adaptations for Breeding in Birds. Methuen.
Liversidge, R.	1961	Pre-incubation development of Clamator jacobinus. Ibis 103a: 624
	1971	The biology of the Jacobin Cuckoo Clamator jacobinus. Ostrich suppl. 8 117-137
Mountfort, G. & Ferguson-Lees, I. J.	1961	The birds of the Coto Donana. Ibis 103a: 86-109

Owen, J.H.	1933	The cuckoo in Felsted District. Felsted School Scientific Soc. 33:25-39.
Payne, R.B.	1973	Individual laying histories and the clutch size and numbers of eggs of parasitic cuckoos. Condor 75:414-438.
Perrins, C.M.	1967	The short apparent incubation period of the cuckoo. Brit. Birds 60: 51-52.
Ramakrishnan, K.P., Sreenivasaiah, B.N. & Venkiteshwaran, S.P.	1958	Upper air climatology of India and neighbourhood in the monsoon seasons. in Symposium on "Monsoons of the World". New Delhi.
Sanjeeva Raj, P.J.	1964	Communal breeding in the White-headed Babbler Turdoides affinis (Jerdon) in Tambaram, Madras State. J. Bombay nat. Hist. Soc. 61:181-183.
Southern, H.N.	1954	Mimicry in cuckoos' eggs. in "Evolution as a Process", ed. Huxley, J., et.al. Allen & Unwin.
Steyn, P.	1973	Some notes on the breeding biology of the Striped Cuckoo. Ostrich 44: 163-169.
Whistler, H.	1928	The migration of the Pied Crested Cuckoo (Clamator jacobinus). J. Bombay nat. Hist. Soc. 33: 136-146.
Whistler, H.	1935	Popular Handbook of Indian Birds, (2nd ed.). Gurney & Jackson.

APPENDIX 2

Change of iris colour during the post-fledging period in the Common Babbler (Turdoides caudatus). J. Bombay Nat. Hist. Soc. 72: 548-551.

Introduction

During the course of ringing operations in an area of mixed Prosopis/Acacia woodland and Zizyphus scrub adjacent to New Delhi notes were kept on the colour of the iris and the state of moult among Common Babblers. During the period between fledging and the completion of the post-juvenile moult Common Babblers were found to undergo two changes of iris colour and at close range these make it possible to age birds in the field up until four or five months old.

Methods

About 200 Common Babblers were trapped between August-November 1971 and between July-November 1972, of which 70 were birds in their first year which had not yet completed their post-juvenile moult. Juvenile birds could be identified by the blunt, rounded tips to their primary feathers, particularly the tenth, as mentioned by Naik and Andrews (1966) for the Jungle Babbler.

The state of moult was recorded for each bird according to the system used by Newton (1966), where each new or growing primary feather is assigned a rank score from 0 (feather missing) to 5 (growth complete). Secondary moult was scored in the same way and the state of moult in the rectrices, wing coverts and body tracts was noted in general terms. The colour of the iris was also noted.

During 1972 a number of nestlings were ringed and six of these were retrapped during their post-juvenile moult. A total of 13 birds in the two seasons were trapped two or more times during the course of their post-juvenile moult and from these the mean rate of moult was calculated in points per day.

This rate was then used to calculate a date of commencement for the moult of the six birds trapped after being ringed as nestlings and hence to find the mean length of time between fledging and the onset of the post-juvenile moult.

Results

The course of the post-juvenile moult is similar to that of the adult moult, which in turn resembles that of adult Jungle Babblers described by Naik and Andrews (loc. cit.). In contrast to the adult moult, however, the moult of the greater coverts usually begins before the primary moult, and the moult of the rectrices lags behind that of the primaries so that birds are found with a complete set of adult primaries, but most, or in some cases all, of the juvenile rectrices. Because of abrasion the juvenile rectrices tend to become difficult to identify after a few months and do not provide much help in ageing.

The mean rate of post-juvenile moult in points per day was found to be 0.95(n = 13, 95% confidence limits 0.61-1.29), giving a mean duration for theprimary moult of 105 days (95% conf. limits 77-164 days).

Using the six birds for which the date of fledging was known, and the mean rate of primary moult, the periods between fledging and the commencement of the primary moult were calculated as 30.5, 31.5, 36.5, 39.5, 47 and 47 days ($\bar{x}$ = 38.7) Thus the mean duration of the period between fledging and the completion of theprimary moult is about 144 days.

The colour of the iris in the adult Turdoides caudatus was found invariably to be a warm, dark brown, sometimes with a narrow white rim. No birds in juvenile plumage, or in post-

juvenile moult possessed exactly this colour of iris. Table 1 shows the different categories into which irides were classified and the number of birds at each stage of post-juvenile moult recorded in each class.

Table 1. The relationship of iris colour to primary score during post-juvenile moult.

Iris colour	No. of birds trapped in each moult score category						
	0	1-19	20-39	40-59	60-79	80-99	100
1. Dark grey + olive tint (nestlings and birds with juvenile remiges not fully grown)							
2. Dark grey	4(all moulting greater coverts)						
3. Pale hazel brown	3	12	9	12	7	4	1
4. Dark brown centre, grading to hazel margin		1	2	1	1		
5. Dark brown, traces of hazel at the margin					2		7

The majority of birds trapped during the course of the post-juvenile primary moult (88%) showed a pale hazel iris. The coincidence of this colour with the duration of the post-juvenile moult suggests that the change in iris colour might be linked to the same hormones that initiate and control the course of the moult.

A few birds reared late in the season did not commence their post-juvenile moult until the following spring, but these birds lost their juvenile iris colour, the irides becoming hazel as in those undergoing moult. The exact timing of the colour change was not observed. One bird, reared in early October,

was still in juvenile plumage the following February and had a hazel iris at 120 days old. Another, reared in September, showed arrested moult at P3 when trapped in February and had a hazel iris at 150 days old.

The occurrence of the transitional stages between hazel and the dark brown adult colour in only 14 out of the 66 birds in table 1 suggests that this change must be quite fast, probably less than a month. The transition from the dark grey juvenile colour to hazel must be even more rapid, since no transitional states were observed at all.

In the field a bird which had not yet started the post-juvenile moult could be easily recognised by its yellow, fleshy gape. This disappeared soon after the start of the moult and during that period the pale hazel iris provided a useful guide to the age of the bird at close range.

Discussion

Among Indian species of its genus, the Common Babbler is alone in having a dark iris when adult. In the Jungle Babbler, the Rufous Babbler, the White-headed Babbler, the Ceylon Rufous Babbler, the Spiny Babbler and the Slender-billed Babbler the adult iris is white, and in the Large Grey Babbler and the Striated Babbler it is bright yellow (Ali & Ripley 1971). The colour of the nestling and early juvenile iris is very dark grey throughout the genus. It seems likely that the dark adult iris of the Common Babbler has recently evolved and that the pale iris which appears during the post-juvenile moult represents a recapitulation of the former adult colour.

In the Arabian Babbler the female iris colour is similar to that of the adult Common Babbler, but the adult male has a pale iris similar to that of the Common Babbler during its

post-juvenile moult. The colour of the nestling and early juvenile iris is the same as that of the rest of the genus.

The Arabian Babbler is very similar to the Common Babbler in overall morphology, differing from it mainly in its larger size. Since the western races of the Common Babbler are larger than the Indian race, it seems possible that the Arabian Babbler may represent the speciation of the western end of a former cline running from India to the Near East.

In bill colour, adult male Arabian Babblers resemble first year birds of both sexes, whereas the bill changes colour in adult females, and in this respect the adult male character can be considered neotonous (A. Zahavi, pers. comm.). If this is the case then it seems likely that sexual dimorphism in the Arabian Babbler must have evolved through retention of the juvenile iris colour in the male.

Appendix 3. Monthly counts of ten groups of Jungle Babblers made on the 1st of each month.

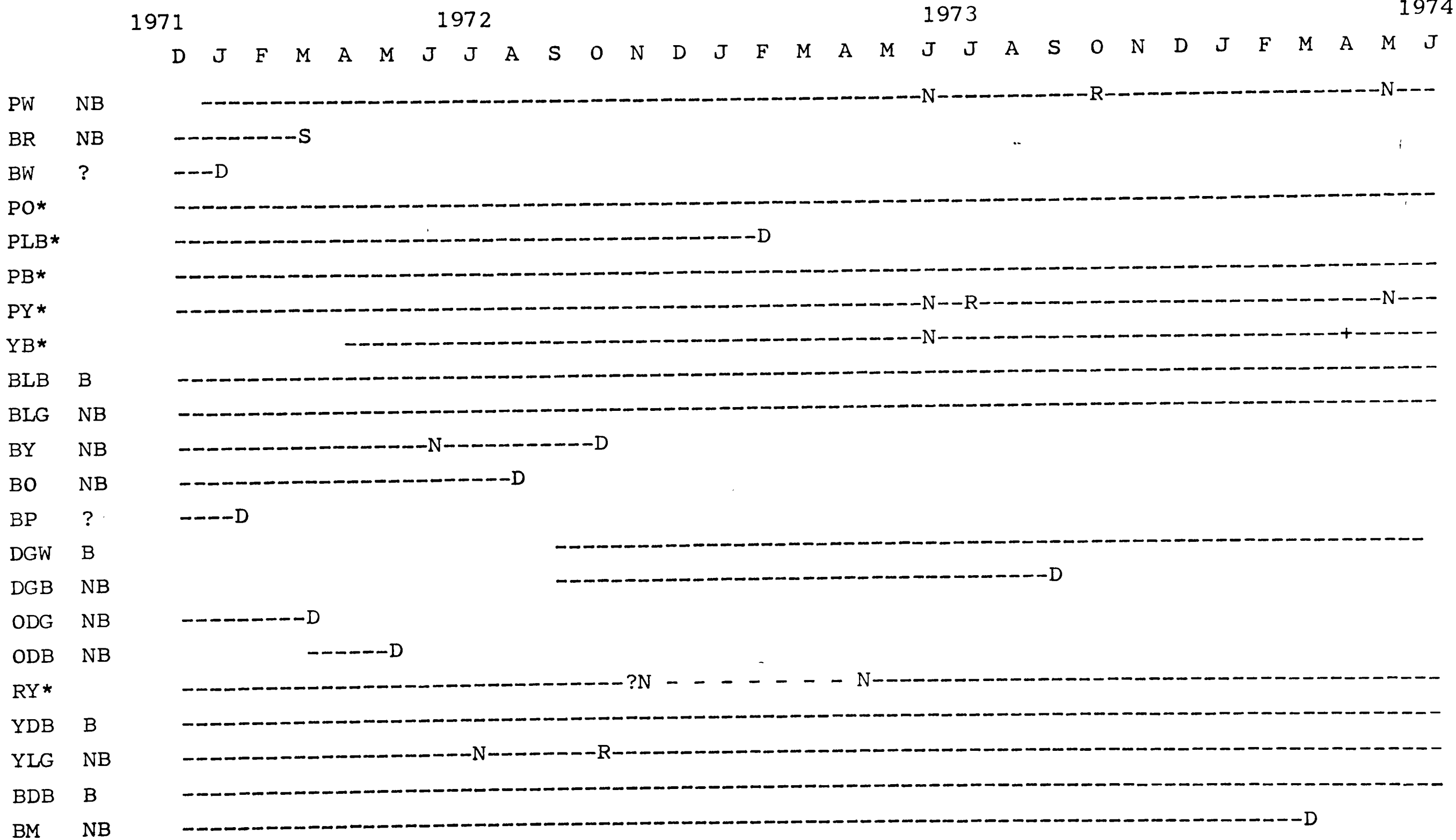
		P	L	M	O	D	B	R	G	F	J	Total
1971	Dec.	13	9	10	8	6	6	6	6	6	7	77
1972	Jan.	13	9	10	8	5	6	6	6	6	6	75
	Feb.	12	9	10	9	8	6	6	5	6	5	76
	Mar.	12	9	10	5	8	6	6	4	5	5	70
	Apr.	11	9	10	8	7	7	6	4	5	5	72
	May	12	9	10	8	7	6	8	4	5	5	74
	June											
	July	12	9	7	9	7	6	7	5	5	4	71
	Aug.	12	13	9	10	7	9	7	5	5	4	81
	Sep.	12	13	9	9	5	8	7	5	8	3	79
	Oct.	12	13	7	9	9	7	7	5	8	3	80
	Nov.	12	15	7	9	9	7	6	5	8	3	81
	Dec.	12	14	7	8	10	6	7	4	8	3	79
1973	Jan.	12	14	7	8	10	5	6	4	8	4	78
	Feb.	12	14	7	8	10	5	6	2	8	4	76
	Mar.	10	13	7	8	8	5	6	3	7	5	72
	Apr.	10	13	7	8	8	5	6	3	7	4	71
	May	11	13	7	10	8	7	6	3	7	4	76
	June											
	July	7	13	7	9	8	6	6	4	7	4	71
	Aug.	8	13	9	9	8	6	6	4	7	4	74
	Sep.	10	16	9	9	7	8	6	4	7	4	80
	Oct.	10	16	9	9	7	8	6	3	7	7	82
	Nov.											
	Dec.	14	15	9	6	7	7	9	4	8	6	85
1974	Jan.											
	Feb.	10	16	9	8	7	6	7	3	8	5	79
	Mar.	9	15	9	8	7	6	7	3	7	5	76
	Apr.	9	12	9	7	7	5	6	3	7	5	70
	May	9	14	9	10	7	5	6	3	7	5	75
	June	6	11	8	8	4	5	6	3	7	5	63

Appendix 4. Survival of birds trapped as post-juveniles.

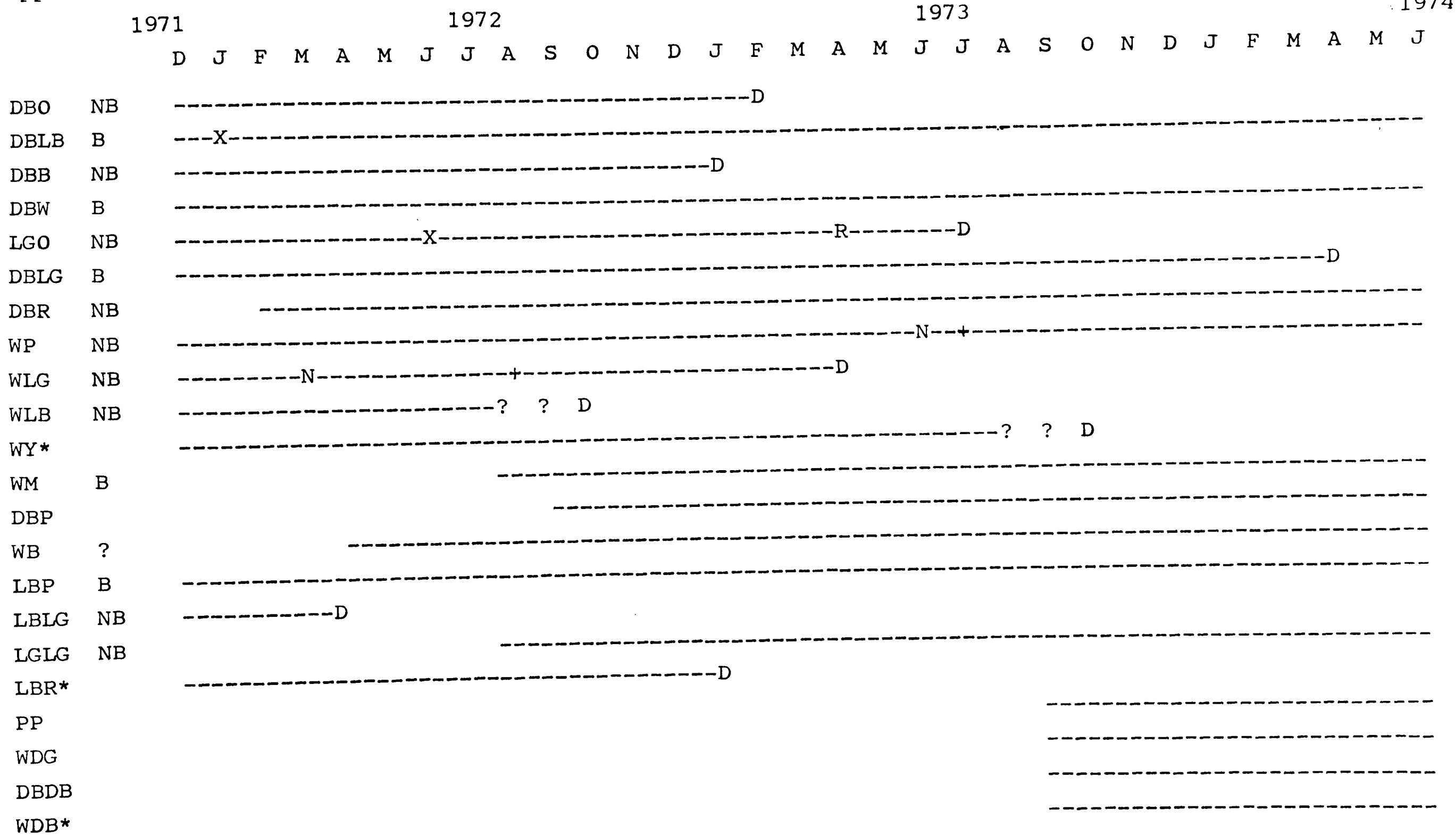
N = joins new group, X = changes to another established group, R = returns to former group, D = disappears, S = shot, *1Y when trapped, + attempts to breed in new group. Breeding status given in the first column refers to the 1972 season.

		1971						1972								1973												1974	
		D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J
LBO	B	----------																														
LBB	NB	----------																							N	--	R	----------			D	
LBDB	NB	----------																										N	--	R	--	D
LBW	NB	----------																													D	
LBY*		----------																														
LBM*		----------																														
MDB	B	----------																														
MB	B	----------																														
MR	NB	----------						D																								
MLG	NB	----------						N	--	+	--------	D																				
MW	NB	----------									X	----------								N	--	+	----------								
MY*		----------									D																					
MO*		----------																														
MP*		----------																														
PDB	B	----------																														
PDG	B							----------																						N	---	
PM	B							----------																								
PLG	NB	----------																														

Appendix 4 (continued)



Appendix 4 (continued)



Appendix 5. Reproductive success of Jungle Babbler groups in the Ridge study area, 1972 and 1973.

1972

Group	Size March 1	Territory type	Number fledged/nest Spring	Rains	Surviving Mar. 1 1973
P	12	1	0,1	0,0,0,0	1
L	9	1	0,0	4,0,3	5
M	10	1	0,0	2	2
O	5	1	3	1	4
D	8	1	0	0,4	4
B	6	1	1,0	3	0
R	6	1	2	0,2	2
G	4	1	2	0,0	1
F	5	2	0	3	3
J	5	2		0,0	0
Y	8	2		0	0
H	(4)	3		3	1
I	(4)	2		2	1
A	(5)	3		0	0
Z	(5)	3		2	2
U	4	2	0	0	0
ZA	5	3			
ZC*	(4)	3			
ZD*	(3)	2		(1)	0

All nests in which eggs were laid are included. Group sizes given in brackets are counts made in July.

* ; not included in the preparation of tables 1E and 1F

Appendix 5 . (continued)

1973

Group	Size March 1	Territory type	Number fledged/nest Spring	Rains	Surviving Mar. 1 1974
P	10	1	2	2,3	0
L	13	1	0,0	0,4	3
M	7	1	0	2	2
O	8	1	3	1	2
D	8	1		0	0
B	5	1	0,3	2,1	1
R	6	1		3	1
G	3	2		1	0
F	7	2	2	0,1	1
J	5	2		3	2
Y*	4	2	0	?	?
H	4	3		2	0
I	5	2		4	0
A	5	3	0	3	1
z*	5	3	?	?	?
K	(5)	2		1	1
ZB	8	1	2	3	4
Q	(3)	3		0	0
V	3	3		1	0

All nests in which eggs were laid are included. Group sizes given in brackets are counts made in July.

* ; not included in the preparation of tables 1E and 1F

Appendix 6. Events observed during the establishment of new groups.

1) K group

September 1972. MW(female) disappears from M group.

April 1973. MW seen feeding nestlings at the nest of W group. It was definitely not one of the breeding pair.

July 1973. MW and WP(a male from W group) nest in an area located between the home ranges of M and W groups. The new group also contains three unringed non-breeders, at least two of which were probably derived from W group. The nest fledged one young and the group persisted until the end of the study.

2) S group

July 1973. PW, PY and YB(all females from P group) form a group with two unringed birds in an area adjacent to the territory of P group.

July 29. PY leaves the new group, returns to P group.

September 18. PW leaves the new group and is not seen again before October. It rejoined P group before December 1, however.

March 1974. YB nests with an unringed male. The group, which contains two other unringed birds, still occupies the same area, and persists until the end of the study.

3) N group

March 11, 1974. OLB(male), OY, OLG, OM(females), and OR(first year of unknown sex), all from O group, mix with RDG(female) and an unringed bird from the same group (I). After some time the two from I group are driven off and DGLG(male) from L group joins the birds from O group. They feed in a peripheral area used by both L and O groups.

March 12. DGLG is with L group, OLB is with O group.

March 15. DGLG, OY, OR, and some unidentified birds move rapidly through parts of L group range. Later DGLG, OY, OLG, RDG and two

unringed birds are together where seen on the 11th. This group has a territorial confrontation with L group. DGLG does not roost with L group.

March 18. RDG is seen with one unringed bird. DGLG, OY, OLG, and OM, with one unringed bird are in the same area as before. This group continues to confront other groups in the same area.

March 31. LBDB(male) joins DGLG et. al. (LBDB is also from L gp.)

April 19. OY, OLG, and OM return to their natal group where the nestlings have just hatched. All are seen bringing food to the nestlings. LBDB and DGLG rejoin L group.

4) T group

March 7, 1973. PDG(female) gives contact calls about 100m away from its group (P), but rejoins them five minutes later.

March 10. LBDB(male non-breeder) believed on circumstantial evidence to have destroyed the eggs in its group's nest.

March 13. 0745 PDG leaves its group briefly. 0755 LBW(female) and an unringed male from L group arrive near P group but are chased back towards the core area of L group 0803 High intensity confrontation between L and P groups.

March 15. High intensity confrontation between L and P groups in the morning. 1755 L and P groups feeding 60m apart 1803 PW(female) approaches L group. It is chased off but remains alone nearby giving the contact call. When abird in P group replies PW moves away from it and closer to L group. 1810 A bird in L group gives a single contact call and PW moves closer to them. PDG also contact calls 50m away but the rest of P group has moved off into their core area. 1815 PW, PDG and an unringed bird from L group are within 10m of one another (L group contains two unringed birds, the breeding male and a non-breeding adult male).

1824 PW and PDG perch close together and give contact calls. The

unringed bird also gives contact calls 10m away. PW and PDG allopreen. Both are chased by the unringed bird which snaps its bill. They assume a horizontal posture, necks stretched forward and bills held level, giving hoarse "schurr" calls. Unringed assumes an upright position with its bill raised and the neck stretched up. Following these displays, during which the three birds were about 5m apart, PW and PDG repeatedly approach unringed, pressing together flank to flank, as though trying to form a roost, while unringed moves about in a rather uncertain fashion, sidling along the branches.

1830 LBO, the breeding female of L group, LBY(2Y male) and an unringed bird (almost certainly the breeding male) chase the three birds about 100m and then return to their roost. PW and PDG do not return to their group's roost that night.

March 16. 0740 PW and PDG not with P group. 0800 LBO with two others chases PW away from L group core area. LBO presses closest. 0806 PW, PDG and an unringed in the same area as the previous night. LBO again chases off PW which continues to approach L group. P group arrives and there is a confrontation. 0814 PW and YB(then a second year) and unringed remain in the same area, the rest move off. 0819 L group drive off the trio but after the chase they move back to the same area.

0830 PDG arrives and contact calls, then PDG, PW and YB have a brief confrontation with L group. 0850 unringed joins PW and gives the contact call, then PW moves towards L group core area and exchanges contact calls with a bird in that direction. 0900 LBO, LBY and two others chase PW away from L group core area.

0901 LBDB joins PW and PDG giving hoarse contact calls and some squeaky notes. It procedes to display by flapping its wings loosely, as though injured, uttering a gurgling call with its bill

half open. Following this display LBDB attempts to mount PW, which flies off, and there is a brief chase.

0921 PDG and PW allopreen. 1002 all three alert call, then LBDB gives the head-up display given by unringed the previous evening. It then flicks its wings and tail. 1014 PDG returns twice to the fork of a tree which appears to have some traces of nest foundation. PDG and LBDB visit the site of a nest of L group in a previous year and hop about in the adjacent twigs. 1035 LBDB gives the wing-flapping display again while hopping about in a bush giving low chuckling calls with the bill half open. PW follows and begins to manipulate twigs. LBDB attempts to copulate but PW flies off. 1100 the trio is still together.

March 17. 1030 LBDB with OM, OY, OLG, and an unringed bird in the same area that PW and PDG had occupied the previous day. 1031 they confront L group, then LBDB and unringed allopreen. A count suggests that unringed is from L group.

March 18. 0740 LBDB, OM, OY, OLG and unringed confront PW and PDG in the same area, then the larger group moves off. 0750 L group is feeding in its core area, then LBO arrives, gives a feather-fluffing display and confrontation call, then flies off towards the area where PW and PDG were last seen, followed by the rest of the group which had gathered around it.

March 19. 0725 L group chase off PW and PDG, then confront LBDB, OM, et. al. which were nearby. 0730 LBDB joins PW and PDG and then they are again chased off by L group including LBO, LBW(female), LBB(male) and LBY(male). 0930 P group confront LBDB, OM, OY, OLG and unringed. Following the confrontation the groups mix and then P group return to their core area.

March 20. 1045 LBDB, OY, et. al. have a mild confrontation with PW and PDG in the usual area, then LBDB and unringed allopreen.

1055 The breeding pair of P group chase PW and PDG away from their core area. Their eggs hatch.

1805 LBDB contact calls on the edge of L group's core area. LBO and two others arrive and perch beside LBDB after some brief vocalisations. LBDB autopreens, then all four move to join L group roost.

March 21. PW and PDG feed nestlings in P group nest.

March 24. LBDB joins two others in chasing a solitary intruder away from the core area of L group.

March 28. OY, OLG, OM help to feed the nestlings in O group nest, where they hatched on the 22nd.

NB

The displays and vocalisations recorded during the formation of new groups have not been recorded previously.

Appendix 7. Weights and measurements of Common Babblers trapped in the Ridge study area. Wing and tarsus were measured at each trapping, means are given. All weighings are included, those made in the evening are marked thus;**. Birds marked thus; PLG* were trapped in their first year.

Bird	Wing	Tarsus	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May
PDB	78	30.7	38.0	36.5,36.0	35.5**	
PM	75	29.0	35.0,33.0	32.0		
PR	77	29.0	38.0,37.0		36.0**	
PLG*	78	30.0	34.5,36.0 36.5	35.5	34.5**	
PY	78	30.0	37.0	38.0**	35.0**	
PLB	75	29.0	32.0,33.0 32.5,32.5		31.0**	
PB*	78	30.3	35.5	35.0		36.5
PDG	78	30.0	36.0		34.0**	
PO*	72	29.0		31.0	30.0**	
PW*	79	31.5	36.5	36.0,37.0 35.5		
BP*	77	30.2		34.5,36.0		
PP	78	29.5		37.5		
YM*	76	31.0		37.0	34.5**	
YDG	73	29.3	31.0	30.0		29.0
BDG	77	31.0	37.5			
PRP*	80	31.0		35.0		
OPO	78	29.0	33.0	33.5		
DBODB	75	30.0	34.5			
LGPLG	74	29.2	37.0		32.0	34.0
LGMLG	77	30.2	32.5		29.0	
DBLGDB	75	30.2			28.0,27.0	

Appendix 7 (continued)

Bird	Wing	Tarsus	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May
RW	74	29.7	32.0,32.5	31.0	27.0	
RLB	80	30.0	36.0,37.0			
RY	76	29.0	35.0			
RM	76	30.0	36.0,35.0 34.0,34.0			
RDB	77	31.5	36.0,38.0			
RO*	73	29.0	32.0			
RB*	78	31.7	37.5,40.5	38.0	37.0	
RLG*	74	28.0	31.0			
RP	74	29.0		33.5		
RR	77	30.0		34.5,33.0		
RDG*	74	29.0		31.0		
OW*	77	31.0	38.0		38.0*	
OB	73	30.0	35.0,34.5		31.0,31.0	
RM^2	74	29.0		32.0		
OLG	73	31.0			32.5	
LBR	80	30.0	37.0,34.5 36.5			
LBLG	79	30.0	37.0,37.5 36.0			
LBW	76	30.0	33.0			
DGP	73	29.5	36.0,38.0			
RDGR	73	30.0	33.0**			
LBYLB*	79	32.0			35.5	
MR	73	29.0	33.0,28.0			
MY	73	29.2	33.0,33.5** 34.0			30.0
MW*	76	30.7	35.0,36.0	35.5		
MDB	74	28.5	30.0,30.0			

Appendix 7 (continued)

Bird	Wing	Tarsus	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May
LGO*	76	31.0	36.0			
MO	74	30.0	31.0			
MLG	77	31.0	36.0			
MP	79	30.0	34.0			
MLB*	77	30.8	35.0,34.0	36.5		34.0
			36.0			
BB[2]	79	30.0	33.0			
MB	78	30.0	36.5			
MDBM*	74	30.0	34.5			
DB	72	29.0	34.0			
DG	79	31.0	39.5			
B	76	31.0	35.0			
YR	81	30.0	38.0		36.0	
YLB	73	29.3	32.0,34.0	31.0		
YW	76	29.2	35.0,36.0	35.0	30.5	
			35.0			
YLG	77	31.5	36.5	37.5		
YB*	77	32.0	40.0	38.0		
YP*	74	31.0		35.5		
YLBY	73	30.0	30.5			
YPY	77	30.0	36.0			
YOY	79	32.0	40.0			
YMY						
YR[2]	75	30.0				31.5
LBLB*	74	29.0		33.5		
LBDB	75	29.5	32.5	33.0		
LBO	73	29.0	32.5,35.0	33.5		

Appendix 7 (continued)

Bird	Wing	Tarsus	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May
DBWDB*	72	28.0	30.0			
DBPDB	75	30.0		32.0	29.5	
DBLBDB	74	29.0		30.5	30.5	
DB?	76	30.0			34.5	
BR	76	30.0		32.0		
BLG	80	30.0		37.0		
BY	76	30.0		35.5		
BW	72	29.0	31.5,33.5			
BO	79	30.3	36.0,34.5	35.5		
BDB	78	30.0	35.0			
BLB	77	30.0	32.0			
BM	77	30.0	38.0			
BB	75	31.0	32.0,33.0	32.0		
BLBB	80	29.0			37.5	
BDGB*	79	31.0	36.0			
BMB	80	31.0	39.5			
BLBB[2]*	77	30.0	35.0			
OM	79	31.0	35.0			
OLG[2]	74	29.0	36.5			
WO	?	29.0	37.0			
WDB*	77	30.5	36.5,38.0			
WY	81	31.0	42.0			
WB*	79	31.0	39.0			
WM*	74	29.0	34.0			
WP*	79	30.0	36.5			
WR	74	29.0	35.5,33.0			
			34.5			
WLB	79	30.0	37.5			

Appendix 7 (continued)

Bird	Wing	Tarsus	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May
WOW	76	32.0	36.5			
DGMDG	75	31.0	33.0			
DGODG	74	29.0	32.0			
LGW	74	29.0	33.5			
LGLB	77	31.0	35.5,37.0 37.0		35.0,33.0	
LGR	74	29.0	34.0,33.5 33.0,34.5		29.5	
LGY[2]	74	28.1	33.5,32.0 30.0			
LGP	76	29.0	36.5			
DGDB	74	28.3	31.0		30.0,29.0	
LGM*	76	30.0	31.5	33.5	31.0,32.0	
DGLB	79	30.0	38.0			
DGY*	76	30.0	30.0,32.5	33.5		
LGDBLG*	76	30.0	35.0	35.5		
LGDG*	76	28.5		35.0	34.0	
LGWLG	76	29.5			32.5,31.0	
LGRLG*	76	31.0			32.0	
DBR	77	30.3	35.5,37.5		33.0	
DBDB	73	30.0	36.5,35.5			
DBLB	78	29.0	36.5	37.0		
YDB	77	30.0	30.0,33.5	35.0	31.0	
DBDG*	76	29.5		34.0,35.5		
DBM	77	29.0	40.5**	35.5		
DBO	77	27.0	32.0	32.5		
DBP	76	31.0		39.0,40.0		
DBRDB*	76	30.5	39.5**		35.0	

Appendix 7 (continued)

Bird	Wing	Tarsus	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May
DBWDB*	72	28.0	30.0			
DBPDB	75	30.0		32.0	29.5	
DBLBDB	74	29.0		30.5	30.5	
DB?	76	30.0			34.5	
BR	76	30.0		32.0		
BLG	80	30.0		37.0		
BY	76	30.0		35.5		
BW	72	29.0	31.5,33.5			
BO	79	30.3	36.0,34.5	35.5		
BDB	78	30.0	35.0			
BLB	77	30.0	32.0			
BM	77	30.0	38.0			
BB	75	31.0	32.0,33.0	32.0		
BLBB	80	29.0				37.5
BDGB*	79	31.0	36.0			
BMB	80	31.0	39.5			
BLBB[2]*	77	30.0	35.0			
OM	79	31.0	35.0			
OLG[2]	74	29.0	36.5			
WO	?	29.0	37.0			
WDB*	77	30.5	36.5,38.0			
WY	81	31.0	42.0			
WB*	79	31.0	39.0			
WM*	74	29.0	34.0			
WP*	79	30.0	36.5			
WR	74	29.0	35.5,33.0			
			34.5			
WLB	79	30.0	37.5			

Appendix 7 (continued)

Bird	Wing	Tarsus	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May
WPW	78	30.0	36.0			
WDG	75	29.5	36.0			37.0,33.5
RBR	80	30.5	37.5	36.5		
RPR	80	29.0		36.5		
RYR	73	29.0	35.0	32.5		
RMR*	78	30.5	32.5	32.5		
Y	74	29.0			32.0**	
RLBR	82	30.5	38.5**			
RWR*	78	30.0	35.0**			
ROR	73	28.0	30.5**			
RDBR	80	32.0	40.5			
R	79	29.0		35.0**		
MLBM	78	30.0			38.0**	
MBM	78	29.0			33.0**	
BWB	82	32.0	37.0			
BOB	77	28.0	32.5			
CAU-2	75	29.0	33.5			
3	75	28.0	31.5			
4	76	29.0	34.5			
8	78	31.0			34.5	
13	74	30.0			31.0	
16	72	30.0			29.5	
17	76	30.0			31.5	
22	78	29.5			30.5	
23	76	32.0			34.5	
24	73	29.5			32.0	
27	74	30.0				29.5

Appendix 7 (continued)

Bird	Wing	Tarsus	Jul-Oct	Nov-Dec	Jan-Feb	Mar-May
CAU-28	79	30.0				35.5
29	75	29.5				29.0
30	75	30.0				30.5
31	75	31.0				34.0

Appendix 8. Details of clutch size, and hatching and fledging success for all Jungle Babblers' nests found in the Ridge study area.

Rains 1971

Nest	Clutch	Hatched	Fledged
P1971/1	?	?	3
P1971/2	?	?	2
L1971/1	?	?	2*
M1971/1	?	?	2*
D1971/1	?	?	0*
F1971/1	?	?	0*
Y1971/1	?	?	0*

Spring 1972

P1972/2*	4	4	1
L1972/2*	4	-	
O1972/1	?	?	3
B1972/1	?	2	1
B1972/2*	3	3	-
R1972/1*	4	4	2
G1972/1*	4	2	2
U1972/1*	3	3	-

Rains 1972

P1972/3*	4	4	-*
P1972/4*	4	3	-
P1972/6	3	?	0*
L1972/4*	4	4	4*
L1972/6*	4	3	3
M1972/3*	4	3	2*
O1972/2	4	?	1
D1972/4*	5	-	
D1972/5*	4	4	4
B1972/3*	3	3	3
R1972/2	?	?	0*
R1972/3	?	?	2
G1972/2*	4	0	0*
F1972/2*	4	3	3*
J1972/2*	4	3	-*
J1972/3*	4	-	
Y1972/1	?	?	1
H1972/1*	4	3	3*
I1972/1	?	?	2
A1972/2*	4	3	-
Z1972/1*	3	2	2*
ZD1972/1	?	2	1*
U1972/2	?	?	2

Spring 1973

P1973/1*	3	2	2
M1973/1*	3	2	-
O1973/1*	3	3	3
B1973/1*	4	3	3
Y1973/1	?	3	3
A1973/1*	3	2	-
W1973/1	?	2	-
ZB1973/1	?	?	2
E1973/1	?	4	-

* ; in the first column signifies nest included in table 5

* ; in the fourth column signifies nest parasitised by cuckoo

- ; nest predated 0 ; no babblers, but at least one cuckoo fledged

Appendix 8 (continued)

Rains 1973

Nest	Clutch	Hatched	Fledged
P1973/2*	4	2	2*
L1973/3	?	?	-*
L1973/4*	4	4	4*
M1973/2	?	?	2
O1973/2	?	?	1
D1973/1*	4	-	
B1973/3*	4	4	2*
B1973/4	?	?	1
R1973/1	?	?	1
G1973/1	?	?	1
F1973/1	?	2	0*
F1973/2	?	?	1
J1973/1*	7	6	3
H1973/1	?	?	2*
I1973/1	?	?	4
A1973/2*	4	3	3*
K1973/1*	3	2	1*
ZB1973/2*	4	4	3
Q1973/1*	3	0	0*
V1973/1	?	?	1
C1973/2	?	?	0*

Spring 1974

P1974/1*	4	-	
L1974/3	4	?	?
O1974/1	?	?	2
B1974/1*	3	-	
B1974/2*	3	3	2
R1974/1*	3	3	2
ZB1974/1*	4	-	
S1974/1*	3	-	

* ; in the first column signifies nest included in table 5 .

* ; in the fourth column signifies nest parasitised by cuckoo.

- ; nest predated 0 ; no babblers, but at least one cuckoo fledged

Appendix 8. Details of clutch size and hatching and fledging success for all Common Babblers' nests found in the Ridge study area.

Rains 1972				Rains 1973			
Nest	Clutch	Hatched	Fledged	Nest	Clutch	Hatched	Fledged
B1972/1*	4	-	-*	A1973/2*	4	2	2
B1972/2*	3	3	2	B1973/1*	3	3	3
C1972/1	?	?	3	B1973/2*	3	-	
F1972/1*	4	4	4	C1973/1*	3	-	
F1972/2	?	?	3	D1973/2*	4	2	-
G1972/1*	3	3	3	E1973/2	4	?	0*
L1972/1	?	?	2	E1973/3*	4	4	1*
L1972/2	?	?	3	F1973/1	?	?	3
M1972/1*	3	1	1*	G1973/3	?	?	3
M1972/2	?	2	2	K1973/1*	3	-	-*
P1972/2*	4	-		L1973/1	?	?	0*
P1972/3*	3	-		M1973/1	3	?	0*
P1972/4*	3	3	3*	M1973/2*	3	3	1*
R1972/1*	3	2	2*	P1973/1*	4	4	2*
R1972/2*	4	-		P1973/2*	3	3	-
W1972/1*	3	3	3	R1973/1*	4	1	-
W1972/2	?	?	3	U1973/2*	3	3	2
Y1972/1*	3	2	2	C1973/2*	4	2	2
Spring 1973				Spring 1974			
D1973/1*	3	3	3	C1974/1*	4	4	1
E1973/1*	3	3	3	I1974/1*	3	-	
G1973/2*	3	-		M1974/1*	4	-	
O1973/1*	3	3	3	M1974/2*	4	4	4
U1973/1*	3	-		O1974/1*	4	-	
				R1974/1*	3	-	
				W1974/1*	3	3	3

* ; in the first column signifies nest included in table 5 .

* ; in the fourth column signifies nest parasitised by cuckoo.

- ; nest predated 0 ; no babblers, but at least one cuckoo fledged.

Appendix 9 . Details of birds ringed and subsequent survival in 13 groups of Common Babblers.

Group	Status	1971	1972	1973	1974
A	B male			LGOLG	?
	B female			WDBW	WDBW
	1972 AD		3	2	?
	1Y		4	1	?
B	B male		BO	BO	BO
	B female		BW,BLB	BW,BB	BW
	1972 AD		7	6	3
	1Y		2	0	
C	B male			YMY	YMY
	B female			WM	YR2
	1971 AD	2	0		
	1Y	1	1	0	
	1972 AD		4	1	1
	1Y		2	0	
D	B male		DBM(YDB)	YDB(DBRDB)	YDB/DBRDB
	B female		? (DBO)	DBPDB(?)	?/UN
	1971 AD	7	7	2	2
	1Y	5	3	0	
	1972 AD		3	3	3
	1Y		1	1	0
	1973 1Y			3	1
E	B male			RBR	
	B female			RYR	
	1972 AD		3	2	?
	1Y		1	1	?
	1973 AD			4	?

Appendix 9 (continued)

Group		Status	1971	1972	1973	1974
F		B male			?	
		B female			LBY	
	1971	AD	8	4	4	?
		1Y	3	3	2	?
	1972	AD		3	3	?
		1Y		7	2	?
G		B male		LGLB	LGLB	LGLB?
		B female		LGR	LGR	LGR?
	1971	AD	3	2	2	2
	1972	AD		4	3	2
		1Y		4	2	2
	1973	AD			1	1
		1Y			2	1
L		B male		LBLG	LBLG	LBLG?
		B female		DGP	RDGR	RDGR?
	1971	AD	3	2	2	1
	1972	AD		1	0	
		1Y		3	0	
	1973	AD			2	2
M		B male		MLB	MLB	MLB
		B female		MB,MY	MY	MY
	1971	AD	5	3	2	2
		1Y	4	2	1	1
	1972	AD		2	1	1
		1Y		4	0	
	1973	1Y			2	1

Appendix 9 (continued)

Group	Status	1971	1972	1973	1974
O	B male				OYO
	B female				UN
1971	AD	4	0		
1972	AD		2	0	
	1Y		2	2	2
1973	1Y			4	4
P	B male		PDB(PY)	PDG(PB)	PB?
	B female		PLB(?)	DBODB(YDG)	YDG?
1971	AD	7	6	2	2
	1Y	5	4	3	3
1972	AD		4	2	1
	1Y		3	0	
1973	AD			2	1
R	B male		OW(?)	OW	OW
	B female		OB(ODB)	OB	OB
1971	AD	10	9	5	3
	1Y	4	4	3	3
1972	AD		1	0	
	1Y		2	1	1
1973	AD			2	1
	1Y			1	1
W	B male		WLB	WLB	WLB
	B female		WR,WDG	WR,WDG	WDG,WR?
1971	AD	4	1	0	
	1Y	2	2	2	1
1972	AD		4	4	3
	1Y		4	0	

Appendix 9 (continued)

Group	Status	1971	1972	1973	1974
Y	B male		YR	YR	YR?
	B female		YLG	YLG	YW?
1971	AD	3	3	3	2
1972	1Y		2	0	

Conventions

Breeding birds listed in brackets were members of subordinate pairs. Where two females are listed in the same year with only one male this signifies successive polygyny. Those breeders listed with question marks in 1974 were birds which had shown evidence of pairing, but which did not nest.

Appendix 10 The relationship of body weight to minimum over-night temperature in the Common Babbler

	Temperature categories, degrees C.						
	5.0-9.0	9.1-13.0	13.1-17.0	17.1-21.0	21.1-25.0	25.1-29.0	29.1-33.0
LGMLG*		29.0			32.4		
RB*		37.5		39.0			
RW*		27.3	31.0	32.5	32.0		
DGDB*	29.1	30.0			31.0		
LGM*	32.0	31.0	32.5				
DBLBDB*	30.7		30.5				
YDB*	31.1	35.0		30.0	31.5		
DBR*	33.2		35.5		35.5		
LGLB*	32.8	35.0	37.0		35.5		37.0
YW*		30.7	35.0	35.5			
LGR*	29.7		34.5		33.5		33.5
PLB*		31.0	33.0	32.2	32.5		
PDG*		32.0	36.0				
BP*		36.0	34.5				
RBR*	36.5				37.4		

Appendix 10 (continued)

	5.0-9.0	9.1-13.0	13.1-17.0	17.1-21.0	21.1-25.0	25.1-29.0	29.1-33.0
RYR*	32.5				35.2		
BB*		30.0			32.5		
LGY*		28.3	30.0		32.0		33.5
YR*		35.8		38.0			
OB*		30.9		34.7			
OW*		36.0		38.0			
LGPLG*	32.0				34.6		
RM				34.5	35.0		
LGWLG	31.2	32.5					
PB			35.0	35.5	34.5		
BO		35.5			35.2		
LGYLG		37.0		37.3			
YDG			30.0		30.0		
OPO		33.5	33.0				
LGOLG			32.0			33.2	
RMR	32.5					32.4	
LGDB		34.0		37.0			

Appendix 10 (continued)

	5.0-9.0	9.1-13.0	13.1-17.0	17.1-21.0	21.1-25.0	25.1-29.0	29.1-33.0
LBRLB		34.0		33.0			
DGR		37.0			34.5		
LGB		37.5			38.0		
LBDB		33.0			32.5		
LBO		33.5			32.5	35.0	
LBM		38.0			37.0		
LBY		36.0		38.5	36.6		
DBPDB	29.4		32.0				
DBRDB	35.2					39.5	
DBM		35.5				40.5	
DBO		32.5				32.0	
DBLB		37.0		36.5			
DBDB		35.5			36.5		
MR				28.0	33.0		
MLB		36.5		34.0		35.6	
MW		35.5		36.0	35.0		
MDB				30.0	30.0		

Appendix 10 (continued)

	5.0-9.0	9.1-13.0	13.1-17.0	17.1-21.0	21.1-25.0	25.1-29.0	29.1-33.0
LBLG				36.5	37.5		
LBR				36.7	34.5		
LGDG		34.0	35.0				
RR	33.0		34.5				
RLB					37.0	36.0	
RDB				38.0		36.0	
YM	32.5	37.0					
PW		35.7	36.7				
PO	28.0	31.0	31.0				
PY	33.0	38.0		37.0			
PR	34.0			37.0		38.0	
PDB	33.5	36.2				38.0	
PLG	32.5	35.5		36.0	36.5	34.5	

Appendix 11. The composition of groups of Common Babblers observed at the nest.

Nest	Breeders	Non-breeders	
		observed feeding	not observed feeding
B1972/2	BO, BLB	-	BW♀, BB♀, BM♂, BDB♂
Y1972/1	YR, YLG	YW♀, UN?	-
R1972/2	OB, OW	RLB♂, RDB♂, RM♂, RY?, RR?	RB♂, RW♀, ODB♀
P1972/4	PDB, PLB	BP♂, PB♂, PLG♂, PDG♂, YDG♀, PM?, YM?, BDG?, UN?	-
B1973/1	BO, BW	BM♂, BB♀, ORO♀, UN?	-
B1973/3	BO, BB	BM♂, BLBB♂, BLGB♂	-
M1973/2	MY, MLB	MOM♂	MP♂
L1973/1	LBLG, RDGR	LBYLB♂, LBR♂	-
E1973/3	UN, RYR	RLBR♂, RDBR♂, RMR♂, RWR♂, UN?	
A1973/2	LGOLG, WDBW	-	c4?
D1973/1	YDB, DBPDB	DBRDB♂, DBR♂, DBDG?, UN?	-
W1974/1	WLB, WDG	BDGB♂, UN♂, UN♀	WR♀
M1974/2	MY, MLB	MOM♂, MP♂	-
L1972/1	LBLG, DGP	LBR♂	-
W1972/1	WLB, WR	WDB♂	
P1973/1	PDG, DBODB	LGMLG♂,	PB♂, YDG♀, LGPLG♀
Totals		♂ 27, ♀ 5	♂ 5, ♀ 7

Appendix 12. Derivation of formulae for calculating the chances of a non-breeding male succeeding in breeding as long as it remains in its natal territory.

In a situation in which there is only one non-breeding male in year 0, the chance of its becoming the breeder in year 1 is the product of S_{NB}(the chance that the non-breeder will survive to the next season) and $1-S_B$(the chance that the breeder will not survive).

Hence $C_{0-1} = S_{NB}(1-S_B)$

The chance that both birds will survive is $S_{NB} \cdot S_B$

The chance of succeeding in year 2 is the product of the chance that both birds will survive to year 1 and the chance that the non-breeder will survive to year 2 but the breeder will not.

Hence $C_{1-2} = S_{NB}(1-S_B) \cdot S_{NB} \cdot S_B$

The chance of eventually succeeding in a situation where no senility occurs is the sum of the series $C_{0-1} + C_{1-2} + C_{2-3} \cdots$

Hence $$C = \sum_{n=0}^{\infty} \left[S_{NB}(1-S_B) \cdot (S_{NB} \cdot S_B)^n \right] \qquad (3)$$

In a situation where there are two non-breeding males the chance of the second ranked non-breeder succeeding depend on the chance that both the breeder and the first ranked non-breeder die. Assuming that the survival of the non-breeders is equal then for the second ranked non-breeder;

$$C_{0-1} = S_{NB} \cdot (1-S_B) \cdot (1-S_{NB})$$

The chance of the second non-breeder surviving and the first non-breeder dying are $S_{NB} \cdot (1-S_{NB})$.

Appendix 12 (continued)

Comparing the chances of the first and second ranked non-breeders succeeding during the first year (C_{0-1}) we obtain the following relationship;

$$\frac{\text{Second}}{\text{First}} = \frac{S_{NB}.(1-S_B).(1-S_{NB})}{S_{NB}(1-S_B)} = 1-S_{NB}$$