THE GREY TIT
(*PARUS MAJOR CASCHMERENSIS*)
IN NORTHERN INDIA:
BEHAVIOUR AND ECOLOGY
IN THE NON-BREEDING SEASON

DISSERTATION SUBMITTED TO SAURASHTRA UNIVERSITY, RAJKOT,
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CERTIFICATE

This is to certify that Suhel Quader of the Wildlife Institute of India has carried out an original piece of research work entitled "The Grey Tit (*Parus major caschmerensis*) in northern India: behaviour and ecology in the nonbreeding season" in partial fulfilment of the M.Sc (Wildlife Science) degree of Saurashtra University. These investigations were carried out under our supervision at the Wildlife Institute of India from November 1994 to June 1995. We also certify that this work has not been submitted for any other degree of any university.

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SUMMARY

I studied the grey tit (*Parus major caschmerensis*) in Naina Devi Sanctuary, in the Shivalik hills of the Himachal Pradesh Himalaya. This is a subspecies of the well-studied great tit which ranges over a large part of Eurasia. The study had two main components:

a. to investigate the non-breeding behaviour and ecology of this bird in India, and to interpret the findings with respect to what is known about the species from more northern areas (a comparative approach).

b. to study the behaviour of individuals in the context of short- and long-term processes (in the winter, examples of these might be survival and reproduction, respectively).

I collected data on colour-banded grey tits by following individuals, and recording behaviour using the point-sampling technique with one-minute intervals. Field work was carried out between December 1994 and April 1995.

Throughout this thesis, I refer to the subspecies in India as grey tits, those studied in Europe and Japan as the great tit, and to the species as a whole as *Parus major*.

In a comparison with what is known about great tits, the following points emerge:

--- Grey tits do not spend the winter in flocks of conspecifics; instead, they are either solitary or in pairs. This is associated with comparatively high winter temperatures, and may be the result of a low seasonality in resource abundance allowing for greater territorial site-fidelity.

--- Sexual dimorphism in bill shape mirrors that found in a previous study on great tits in England, where males have deeper and shorter beaks than females, tend to forage more on beech seeds, and are more efficient at doing so than females. Grey tits show a sexual dimorphism in beak shape paralleling this, and males exhibit a strong tendency to forage

more on *Acacia catechu* (from which largely pods are taken) than females, implying that similar ecomorphological processes can operate in populations widely separated in space.

- Grey tits use a wider variety of foraging substrates than their more northern counterparts, and correspondingly spend less time foraging on the ground. This is associated with the absence of any congeners, although whether it is a case of competitive release is open to dispute.
- The Indian birds seem to spend more time feeding than what has been reported for English great tits. The greater time spent feeding is perhaps unexpected given the comparatively higher winter temperatures, and longer day-lengths in Naina Devi than in northern Europe. While a strict comparison of different studies may not be entirely valid, the solitary/pair-living habit of grey tits may result in lower levels of aggression, and this may allow for more feeding time.

The date of laying is related to the duration for which the male and female have been together (i.e pairing date). Birds which paired early bred early, though this is based on a limited sample of four pairs. If this relationship is causal, and if reproductive success decreases through the breeding season (as has been shown for many temperate species), it would imply a strong selection pressure for early pairing in the great tit.

As breeding approached, males spent less time feeding than in the winter, and were involved in greater territorial activity such as singing. Female time budgets showed a similar, *though non-significant* trend over the season. Pooling sexes, the proportion of time spent tended towards a decrease as summer drew near. This decrease approached statistical significance.

1. INTRODUCTION

1.1 Geographical variation in birds

One of the defining features of biological systems is variation (Mayr 1982). Species differ from each other; so do populations of the same species, and individuals within a population. Before a comprehensive theory of evolution based on variation was advanced, most variation below the species level was considered noise (Mayr 1982, Lott 1991). Darwin changed this perception with his view of evolution: variation is one of the pillars on which Darwinism stands. With the widespread acceptance of Darwinism, the study of variation garnered unprecedented attention. Differences between species and populations were sought to be integrated into the framework of the biological species concept. Increasingly, adaptive explanations for this variation began to emerge and studies on selective pressure often confirmed them (e.g. industrial melanism in *Biston betularia*: Ford 1975).

The study of variation between populations of the same species has received increasing attention. Whereas traditionally the emphasis was on morphological variation, the ubiquity and significance of behavioural variation is now recognized. That the song of many birds varies with distance (as 'dialects') is well-known, as also other aspects of behaviour. Whereas dialects may have arisen purely due to cultural transmission without any adaptive value (but see Hunter and Krebs 1979), many behavioural traits that vary consistently with ecological factors (e.g. Crook 1965) are thought to be adaptations to that environment. Studies on within-species variation in social system (Lott 1991) have become increasingly common since Brown's (1964) paper which provided a general theoretical framework for work on territoriality. Despite all this attention, the study of variation, especially in an evolutionary perspective, still has much to offer (Zink and Remsen 1986). Indeed, adaptation is an essentially comparative idea (Harvey and Pagel 1991).

This study looks at variation in the behaviour and ecology of a small bird, the grey tit, by comparing quantitative information from India with what is known about the same species elsewhere. In addition, it investigates some individual 'strategies' in the nonbreeding season with respect to short- and long-term advantages.

1.2 The great tit (*Parus major*)

Parus major is a small (13-21 g), omnivorous passerine of the family Paridae. It is interesting for a variety of reasons. It is a remarkably adaptable species, occurring over a large part of Eurasia in open woodland, and, to a lesser extent, forests. A consequence of this wide distribution is that *P. major* occurs in a wide variety of climates and habitat types - from the coniferous forests of northern Europe to the tropical forests of south-east Asia, and across Eurasia from the Atlantic to the Pacific coasts. The species is distributed throughout the Indian subcontinent wherever open forests exist (Ali and Ripley 1983). Within India, four subspecies are recognized: these are commonly called grey tits. This work deals with the non-breeding behaviour and ecology of the Kashmir grey tit (*Parus major caschmerensis*). This subspecies is found along the lower elevations of the Himalaya from Himachal Pradesh west to Pakistan, and is abutted on the east and west of its range by other races. Throughout this thesis I shall retain local usage by calling the Indian subspecies **grey tits** in order to distinguish them from other subspecies (largely the European and Japanese), which will be referred to as **great tits**. The species as a whole will be called *Parus major*.

1.3 Geographical variation in *Parus major*

Perhaps as a consequence of its distribution, the species has undergone a considerable degree of differentiation in various characters of which the best documented are plumage and morphology. For example, 30 subspecies have been recognized, and these are often divided into four broad groups or 'allospecies'. While the allospecies *major* has yellow underparts and green upperparts, *cinereus* and *bokharensis* are whitish and greyish in these places, and *minor* is intermediate. The four Indian subspecies of grey tits belong to the allospecies *cinereus*. Differences in body size within these allospecies are related to geographic differences in climate following Bergmann's rule (Snow 1953, 1954). Another character which varies dramatically is song. Although the physical properties of the song are similar across large distances (but within the same habitat type: Hunter and Krebs 1979), European great tits do not respond to playback of the song of Asian birds (Gompertz 1968).

The widespread range of the species provides a perfect opportunity for the comparison of various characters across different climates and patterns of seasonality in resources. Since such comparisons would be intraspecific, the problems with the comparative approach when applied between species (Clutton-Brock and Harvey 1984) are minimized. In this thesis, I present behavioural and ecological information about the species in the non-breeding season from northern India, and show that this differs substantially from what has been described for *Parus major* in more northern latitudes. However, since demonstrating cause is difficult in any comparative study, my approach will be to describe patterns, and suggest processes which might explain them.

Apart from being a comparative study, this work also attempts to investigate non-breeding social organization from the point of view of long-term fitness effects. Studies on social behaviour tend to be focused either on breeding seasons (see review in Møller 1986), or on short-term factors (e.g. predation or weather) influencing gregariousness outside reproductive seasons (see Pulliam and Millikan 1982 for a review). More long-term factors which might be important to overall evolutionary fitness, like spatial defence and prolonged social bonds have received less emphasis (Matthysen 1990). This study was initially inspired by the observation that grey tits along the outer Himalaya are usually found in pairs over the winter (rather than in flocks). I set out to determine whether this indeed is the case, and to investigate the behaviour of individuals by following individually identifiable birds.

1.4 Review of literature

Perhaps more has been written about this species than any other bird (Gosler 1993). There are so many papers relevant to even the limited scope of this work, that mentioning all of them is impossible. The following account is based on the more important and influential studies from this vast literature. For a more comprehensive (but still by no means complete) bibliography of the species see Perrins (1979) and Gosler (1993).

Parus major has garnered a remarkable amount of research attention over the past fifty years, largely due to its hole-nesting habits and willingness to accept artificial nest-boxes as surrogates for natural holes (Gosler 1993). This attention has been mostly centred around populations in northern Europe and has resulted in an impressive body of knowledge regarding population dynamics, interactions with other species, foraging ecology, breeding, social organisation and so on. *Parus major* has also contributed in many ways to conceptual advances in theories of clutch size (Liou *et al.* 1993), timing of breeding (Perrins 1970), territoriality (e.g. Krebs 1971, 1982), and dominance (de Laet 1985), and in experiments in optimal foraging (e.g. Cowie 1977, Krebs *et al.* 1977, Kacelnik *et al.* 1981, Ydenberg 1984). This compendium of knowledge is, however, heavily biased towards populations in northern Europe, some work having also been done in Japan (Saitou 1988), and, more recently, in Israel and Turkey (Gosler 1993, E.Curio pers. comm.).

1.4.1 *Social organization and ranging:*

Great tits are territorial in the breeding season (Krebs 1971, 1982), while in the non-breeding season, they move around in non-territorial flocks (Matthysen 1990), whose structure is site-dependent (Saitou 1978). These flocks may consist of up to fifty individuals (Gosler 1993). The basic units of such flocks are pairs (or small groups containing pairs). It is not clear whether these pairs consist of birds which have bred together, or will breed together, and Hinde (1952) considered most pair-formation to take place towards the end of winter, since he found no apparent close association of birds in winter flocks. However, studies by Drent (1983) in Holland, and Saitou (1988) in Japan, indicate that adult birds do possess pair bonds over the winter (though these are not necessarily breeding pairs; see below). Neither found any evidence of pairing among juveniles in the winter. Saitou (1988) found that the 'basic' flocks are comprised of a pair of adults which may be accompanied by two to four unrelated juveniles. The centre of activity (up to 4 ha in area; Saitou 1979a in Gosler 1993) of each basic flock differs from one another, but home ranges may overlap substantially (Saitou 1978 in Matthysen 1990). Basic flocks may form large, temporary aggregations with neighbouring flocks forming 'compound' flocks in zones of overlap. Thus the whole area over which a basic flock ranges might be from 0.7 to 15.9 ha (Saitou 1979a). Hinde (1952), however, did not find evidence that small flock units preferred certain areas.

Most *Parus* species, including the great tit, also occur in mixed-species foraging flocks (Perrins 1979). These flocks typically contain several tit species, and often include other species, such as the treecreeper *Certhia familiaris* and the goldcrest *Regulus regulus*.

Thus, in all northern populations studied so far, great tits spend the winter in flocks, and group sizes of two occur only at a low frequency (Gompertz 1961, Saitou 1978). Morse (1978) found the average number of great tits *within a heterospecific* flock to be 1.8, but Matthysen (1990) suggests that these birds may be just subunits of a larger stable group. Adult great tits do not defend territories against use by conspecifics; rather, they defend their dominance rights within their ranges. In this, they are different from most other *Parus* species, where pairs are often territorial, and flock ranges exclusive. The ranges of great tits flocks are usually restricted to the area surrounding former or future breeding territories (Brian 1949, Webber 1975, Drent 1983, De Laet 1984, Saitou 1988), though this will depend on local conditions and food supplies (Gosler 1993). The exact time when *breeding* pairs are formed is open to dispute. Some pairs are already formed when they join the winter flocks, and some pairs might form within these flocks, but most pairs form after the basic flocks disintegrate (Hinde 1952, Saitou 1979b). Hinde (1952) feels that pairs are usually formed by the end of February, and pair-formation precedes territory establishment.

In the spring, the majority of birds reoccupy their previous territory, especially after producing a successful brood the previous year (Harvey *et al.* 1979). Territorial boundaries are usually defined by the end of March, with song playing an important role in their establishment (Gosler 1993). Although territoriality reaches a peak in spring, it may emerge in the winter if the weather is mild, so song can be heard at any time during the winter (Perrins 1979, Gosler 1993).

1.4.2 *Time budgets and foraging*:

Great tits are omnivorous, though they prefer invertebrates when presented together with seeds (Gibb 1957, Gosler 1987). Gibb (1954, 1960) studied the winter foraging of the great tit and its congeners (in heterospecific flocks) in England. In Marley Wood, Gibb (1954) used point observations to estimate proportion of time spent in different activities, as well as on different foraging substrates. Since I used methods similar to his, I will compare my results mostly with what he found.

Between December and January, great tits spend 65 to 81% of their time foraging, and Gibb (1954, 1960) provides evidence that food is scarce during the winter. Gibb (1954) showed that great tits occupy a substantially different foraging niche from their congeners. They are the largest of sympatric Parids almost throughout their range, and forage closer to the ground, and closer to the boles of trees than other, smaller species (Gibb 1954, Suhonen *et al.* 1994). On the ground, they forage largely on the seeds of beech, hazel and oak trees (Gibb 1954, Gosler 1993). Seeds are especially important when temperatures drop, and the supply of invertebrates decreases; consequently, in December, plant material can comprise 90% by volume of the ingested food, up from 10% in October (Van Balen 1980). However, there are indications that, where winter temperatures are higher, as in Spain, plant food is of less importance (Gosler 1993). Tracking the availability of food, the time great tits spend on the ground increases sharply to a peak in mid-winter (December), and decreases thereafter, although the exact figures vary widely from year to year and depend on the supply of seeds. Gosler (1987) documents a sex difference in foraging in English great tits, with males feeding more on the ground and on seeds than females. This is associated with a sexual dimorphism in bill shape, males having shorter and deeper beaks than females, especially during the winter, when these seeds are available. Gosler (1987) has also shown in an experiment that birds with shorter and deeper beaks are more efficient at exploiting seeds than those with long, thin beaks. He postulates that since seeds are an important food resource to tits in the winter, this pattern can be explained by dominance: males are socially dominant to females (Gosler 1993), and simply exclude them from preferred feeding sites. Since good crops of beechmast are variable in time and often clumped in space, usual home-range boundaries may break down temporarily and large aggregations may occur at the food source (Gosler 1993).

1.5 Objectives

Some specific objectives of this study were to

a. to determine the social organization of the grey tit in northern India, and compare this, and other behaviours with what is known about the species from elsewhere.

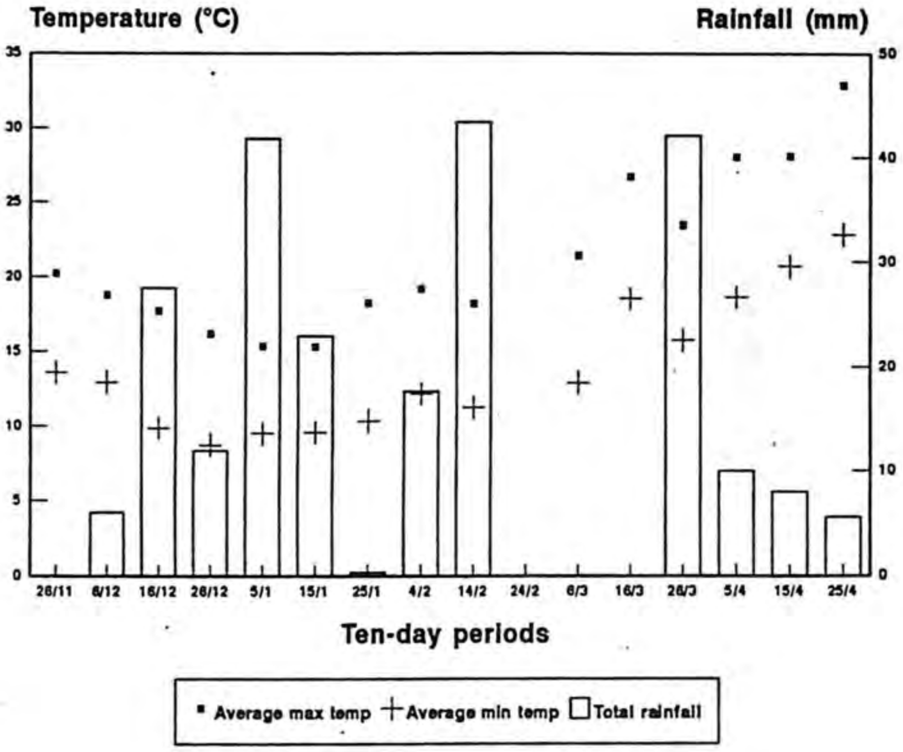
b. to investigate the long-term consequences of social behaviour by following individually identified birds.

2. STUDY AREA

Grey tits were studied at an altitude of approximately 600 m in Naina Devi Sanctuary, in the Shivalik hills of Himachal Pradesh. The Shivaliks are a low range of hills which fringe the Himalaya on the south. Naina Devi sanctuary was established in 1962. It is 123 km' in area, and lies between 31°16'40" and 31°24'36" N, and 76°25'54" and 76°35'38" E. Most of the precipitation in this area occurs during the southwest monsoon, between July and September, but winter rain is regular, though occasional. Forest Department records indicate that the temperature varies from -2 to 40°C, and the mean annual rainfall is 1155 mm (Singh *et al.* 1990). However, during my stay, I never recorded temperatures below 4.5°C. The temperature and rainfall data I recorded between December 1994 and April 1995 are given in Figure 1. Snow never falls in this area, and frost is uncommon. The dominant forest type in this area has been classified as Northern Dry Mixed Deciduous Forest 5B/C2 by Champion and Seth (1968).

I worked in the area immediately below the Forest Rest House, Saloa. This area straddles the boundary between Khal and Saloa villages. The general aspect is North-Eastern, the whole area facing the greater Himalaya. The study area consisted of open deciduous woodland, interspersed with small terraced agricultural fields and houses. *Acacia catechu* is easily the most common tree. Other trees include *Dalbergia sissoo* and *Mallotus philippensis* in the flatter areas, and *Syzygium cumini*, *Ficus rumphii* and *Ficus glomerata* along the *nalas* (stream-beds). The vegetation was much thicker along the nalas then away from them. A more formal description of the vegetation of the study area is given in Appendix A. A general pattern in the phenology of different trees over the winter is apparent. Most trees are bare, or progressively shed their leaves as winter progresses (e.g. *Dalbergia sissoo, Lannea coromandelica*). These species bud fresh leaves from March. Evergreen species like *Acacia catechu, Mallotus philippensis*, *Syzygium cumini*, and the *Ficus* spp replace their leaves as the season changes in March. During the study about 20% of the available land was under wheat cultivation.

Figure 1. The weather at Saloa
December 1994 to April 1995



Dates on the X-axis represent the start of the ten-day period in question. No data were collected for the period starting on 24th February

3. METHODS

Data were collected from December 1994 through April 1995, although most of December was spent in mist-netting birds (see below) and preliminary observations.

3.1 Mist-netting, banding and morphological measurements

Grey tits were caught with mist-nets and were banded using unique colour-combinations of plastic rings. Tits were sexed according to the width of the breast-stripe (Gosler 1993) and standard morphological measurements were taken. In this context it is worth noting that no publications on Indian birds mention any plumage dimorphism between the sexes (Ali 1949, Bates and Lowther 1952, Ali and Ripley 1983, Roberts 1992), although such a dimorphism is well established for the European subspecies (Svensson 1970, Perrins 1979, Gosler 1993). Nevertheless, I found it possible to distinguish males and females with ease, both in the field and in the hand, with males showing an enlarged breast-stripe from the belly downwards, the black of the stripe always joining the base of the legs. In contrast, the breast-stripe of females often thins out at the belly, and never joins the base of the legs (Gosler 1993). I tested the accuracy of sexing by observing five pairs of banded tits during nest-building and breeding. My prior classifications turned out to be accurate in all cases.

I measured the wing, tail, and tarsus of each bird caught using a wing-rule. Bill length, as well as width and depth (at the front of the nostril) was recorded to 0.02 mm using a vernier calliper. Bill length was taken from the base of the skull, as well as the anterior edge of the nostril. Weight was recorded to the nearest 0.5 gm on a Pesola scale. All morphological variables were assumed to be normally distributed for analysis. Basic statistics of morphological measurements of males and females separately are given in Table 1, along with tests for intersexual differences. In the text and tables, individual birds will be referred to by their colour-code; an explanation of this code is given in Appendix B.

Table 1 : Morphological measurements on grey tits. All linear measurements are in mm; weight is in grams.

	MALES			FEMALES			t-test (♂ vs ♀)	
Character	Mean	S.E.	n	Mean	S.E.	n	t	p
Wing length	70.43	0.39	15	66.18	0.38	11	7.47	<0.01
Tail length	65.20	1.07	15	60.00	1.28	11	2.97	0.007
Tarsus (whole length)	20.50	0.22	9	20.58	0.18	6	-0.27	0.792
Bill length from nostril (BN)	8.28	0.08	15	8.47	0.09	11	-1.42	0.168
Bill length from skull (BS)	12.20	0.14	15	12.09	0.08	11	0.69	0.496
Bill depth	4.52	0.05	15	4.31	0.03	11	3.62	0.001
Bill width	4.33	0.08	15	4.21	0.11	11	0.88	0.389
Weight	13.76	0.25	15	13.56	0.19	11	0.59	0.559
Bill depth/BS	0.371	0.005	15	0.356	0.003	11	2.13	0.044
Bill depth/BN	0.547	0.009	15	0.509	0.006	11	3.3	0.003

3.2 Range mapping

In order to obtain some idea about ranging and territory-size, an area of about 12 ha was mapped by plotting the location of 96 numbered trees on graph paper using a compass and measuring tape. This formed my base map. While following focal birds I mapped out the areas they used by recording their locations during 15 min follows. Each location was plotted by taking a bearing to the bird using a compass, and estimating its distance, both from the closest numbered tree. The locations then were transferred onto the base map using these measurements.

3.3 Time-budgets

Behavioural data were obtained by following focal individuals for as long as possible and recording the following parameters at one minute intervals (determined by using a using a digital watch): time, identity, activity, foraging habitat, number of conspecifics in a radius of 20 m, and identity of nearest conspecific neighbour. Activities included foraging, maintenance (preening and bathing), sitting, singing, and aggression. Foraging was initially classified as either searching or handling, but these categories were clubbed for analysis. Foraging habitat included whether the bird was on the ground, or in vegetation. If on a plant, the species of plant was recorded, as well as its height (0-2, 2-5, 5-10, 10-20, or 20-30 m). For plants taller than 2 m, the position of the focal bird in the plant (top, middle or bottom) was noted, as was the substrate (trunk, branch: > 1 cm in diameter, or twig: < 1 cm in diameter). The number of conspecifics within a radius of 20 m was taken as a measure of group size. This measure is not ideal. Two individuals separated by less than 20 m were sometimes not foraging in concordance, and conversely, a pair was sometimes separated by more than 20m. These situations did not occur frequently, though, and I retain this criterion for a rough measure of group size.

Studies on social organization/flocking often count the number of individuals in a flock, and then calculate average flock size. However, the average group size may not be the same as the number of individuals an average animal finds itself with (see Jarman 1982 for an example). Here, by counting the number of conspecifics within 20 m of the focal bird, I focused on sociality from the point of view of the individual (level 1. of Matthysen 1990, pg. 242).

All point observations were recorded in the field by speaking into a dictaphone, and the data were subsequently transcribed. Most data were obtained from the ten or twelve individuals which occupied the 12 ha main study area. In all, 400 sequences of five points (i.e. five minutes) or longer were obtained. The mean length of a sequence was 10.1 minutes, with a range of 5 to 61 minutes. Thus, the distribution is highly skewed towards a predominance of shorter observations.

3.4 Analysis

Since the interval between two successive point observations was only one minute, they cannot reasonably be assumed to be independent of each other. In order to overcome this difficulty, I took each *sequence* of observations to be an independent data point (there was usually a gap of 10 min between successive sequences on the same bird). For each sequence with five or more successive observations, I calculated proportions of observations where the focal bird was performing the activity of interest.

Since most focal individuals were colour-banded, I was able to avoid the problems of data-pooling (Leger and Didrichsons 1994) by calculating a mean score for each individual. The advantage of this is that I avoided violating statistical assumptions of independence of points, since different data points collected on the same individual (even if widely distributed in space or time) are, strictly, not independent of each other. A disadvantage of this procedure is that, since I was able to follow only five males and five females intensively, a large data set collapsed into what were essentially very few independent points, and consequently sample sizes are low.

While comparing between sexes or between months, average proportions were computed for all individuals represented by three or more sequences. These averages were then used as independent points in Mann-Whitney-Wilcoxon tests (between sexes) or Kruskal-Wallis one-way ANOVAs (between months)(Zar 1984). Sample sizes for all tests between sexes, or across months, are as given in Table 5 unless otherwise mentioned. Sample sizes in all cases correspond to number of individuals. For comparing data with Gibb (1954), only the first points in sequences of any length were used to calculate proportions, since this is most similar to the methodology he followed. Likewise, first points were used to calculate the proportion of time spent with different numbers of conspecifics within a 20 m radius. Statistical tests were carried out using the SPSS/PC+ program. All significance figures represent 2-tailed p-values unless otherwise specified. For testing directional hypotheses, one-tailed P-values were calculated by halving the two-tailed values obtained. Home ranges were calculated using the Minimum Convex Polygon (Mohr 1947) option in the program CALHOME.

4. RESULTS

4.1 Social organization

Grey tits in Naina Devi do not move around in conspecific flocks during the non-breeding season. Focal birds rarely had more than a single conspecific within a radius of 20 metres between December and February (Fig 2), and this was clearer in March-April, as birds paired up (Fig 3). When present, a conspecific was most likely to be of the opposite sex (Table 2). Of the six males which were seen regularly, two were always in the company of a particular female; these birds were probably paired when I started field work in end November. Although other females were often seen with the other males, they settled down with one particular bird only later (Table 3). I took the date of pairing to be the date from which the birds were seen together regularly. The dates of this 'pairing-up' were thus quite different for each of these males (and, of course, for their respective mates), but I could not determine whether this was related to the age or former breeding status of males. Of the two pairs always seen together (Table 3), both males, and one female were definitely adults (i.e. > 1 year), since they carried rings from a study the previous winter. Certainly, all the males were resident in their respective areas (see 'Ranging' below). The earlier birds paired, the earlier they bred (Table 3).

Thus tits were most often seen either alone or in pairs, and only rarely in larger aggregations. The exception was a trio consisting of one male and two females (Y♀ and R♀). After these two females were banded (on 3/12/94 and 9/12/94 respectively), they were almost always seen in the company of one specific male (Pi♂). However, on 31/1/95, a neighbouring male (P♂) was observed foraging with the trio, and the next time (2/2/95) these females were seen, Pi♂ had disappeared and P♂ had taken his place. P♂ eventually mated with one of the females, R♀, while Y♀ paired up and bred with another male.

Table 2 : Sex of nearest conspecific in relation to the sex of the focal bird

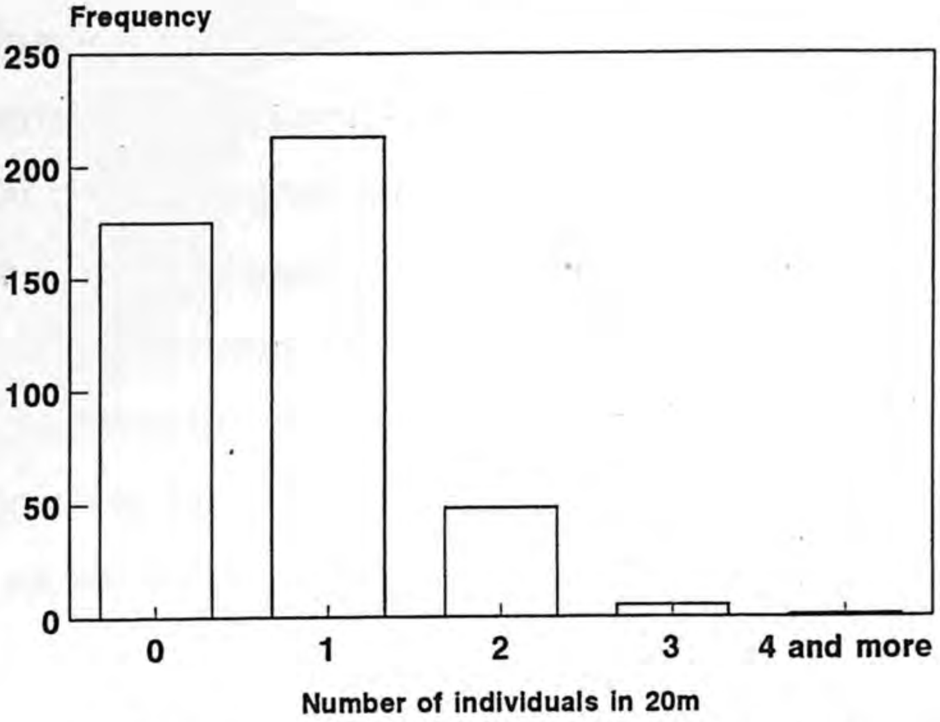
Sex of neighbour	Sex of focal individual							
	December		January		February		March	
	Male	Female	Male	Female	Male	Female	Male	Female
Male	6	11	1	37	6	51	6	51
Female	8	0	41	9	54	3	54	3

Table 3: Breeding date as related to pairing date.

PAIR	DATE OF PAIRING	DATE OF BREEDING (EGG-LAYING)
DGL♂˙, PiL♀˙	before January	not known
LB♂˙, DB♀	before 19th December	c. 12th April
P♂,R♀	c. 1st February	c. 15th April
RL♂, LG♀	c. first week of March	last week of April
O♂, Y♀	c. first week of March	last week of April

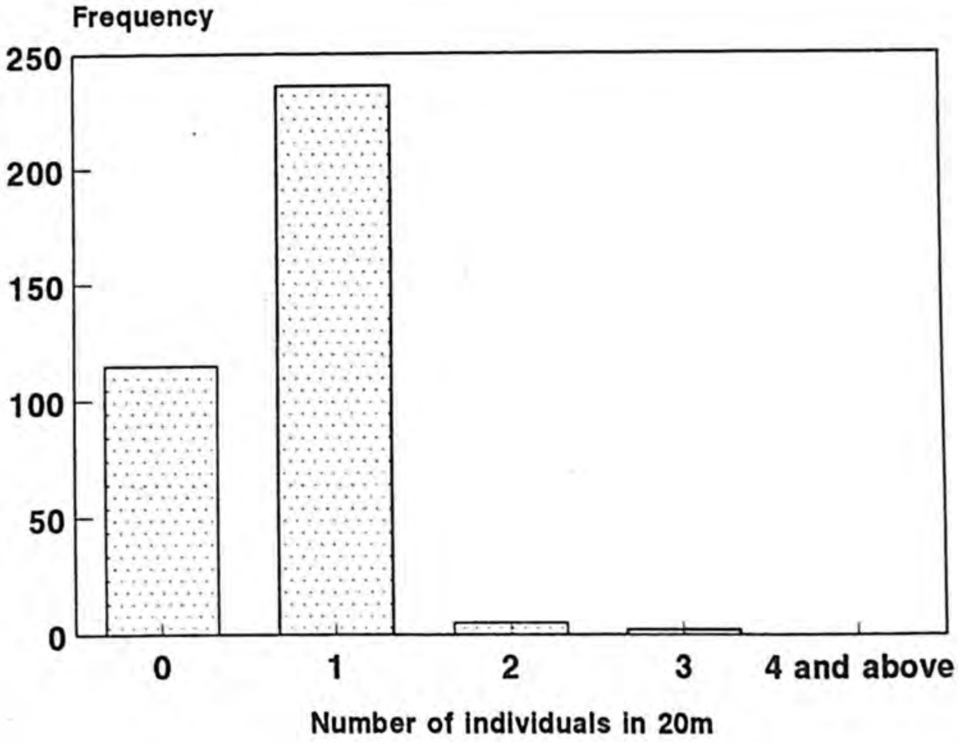
Note: Date of pairing is actually the date from when the two individuals were regularly seen together. Individuals marked with an ˙ are adults (> 1 yr).

Figure 2 : Sociality in the months
December to February



The number of conspecifics within a radius of 20 m; only first points in sequences considered.
Sexes pooled, n= 553 observations.

Figure 3 : Sociality in the months
March and April



As above.
n= 457 observations

Although unpaired birds were often seen together with another individual in the winter, these 'pairs' were unstable, and tended to last for a few weeks at most, with the two birds accompanying each other for only a few hours at a time. In no cases did these pairs consist of individuals of the same sex (contra Löhrl's 1950 caution for marsh tits *Parus palustris*). When two males were seen together (Table 2), this was usually during an agonistic encounter, especially in March.

Grey tits did not seem to spend much time in heterospecific flocks, although this was not formally quantified. Such flocks consisted largely of winter migrants like the grey-headed flycatcher-warbler *Seicercus xanthoschistos*, yellow-rumped leaf-warbler *Phylloscopus proregulus* and yellow-bellied fantail *Rhipidura hypoxantha*, and some resident species like the chestnut-bellied nuthatch *Sitta castanea*. The flocks disbanded towards the beginning of March, when the migrants left. Tits were occasionally seen in these flocks, but never appeared to stay in them for long.

4.2 Ranging

The general pattern of ranging over the winter involved sedentary males with fairly well-defined home ranges, while females were more catholic in their choice of area. Ninety-five percent minimum convex polygons for January and February, calculated for four males were as given in Table 4. These must be taken as minimum areas, since I could not determine whether my sampling was adequately reflected true home-range.

Table 4: Home-ranges of individual males during January and February, 1995; calculated by the minimum convex polygon method.

Individual	RL♂	LB♂	O♂	P♂
95% MCP (ha)	5.79	4.38	3.2	4.5

Females were less faithful to a particular area, and two females' home ranges overlapped with those of two males (although ranging data for females were not analyzed). These females (W♀ and LG♀) foraged in the vicinity of different males at different times. This did not hold for the females of the permanent pairs (DB♀ of LB♂ and DB♀; and PiL♀ of PiL♀ and DGL♂), who remained exclusively within their mate's range. Breeding territories largely corresponded with the core areas of winter ranges, except in the case of O♂, who shifted to the periphery of his former range as breeding started.

4.3 Time budgets

Time-activity budgets are presented for males and females during two seasons in Table 5. A large proportion of time was spent in feeding (searching for, and handling food) both in the winter and spring. However, it is seldom possible to estimate the absolute time spent in any particular activity, since time-budget studies are very sensitive to the procedures used to sample behaviour and analytical methods, as well as the inherent (and mostly unknown) biases in both sampling procedure and analysis (Morrison 1984, Bradley 1985). Therefore my main aim in this section will be to investigate differences between males and females, as well as across seasons.

Males and females showed some differences in time budgets within months. Males tended to spend less time foraging than females in January (Mann-Whitney U=7, p=0.0750), though not in February (M-W U=9.0, p=0.8057), but this pattern again appeared in March (M-W U=4.0, p=0.0190)(Fig 4). Males, tended to spent more time than females in aggression in February (M-W U=5.0, p=0.0910) and March (M-W U=9.5, p=0.0931), and, unsurprisingly, spent more time singing in March (M-W U=0.0, p=0.0026). Overall, levels of aggression were low in the winter, and I saw less than five supplanting events involving grey tits until February.

Comparing time budgets within sex across months, males spent a significantly lower proportion of time foraging in March and April than they did in January and February (K-W one-way ANOVA χ^2= 8.33, p=0.0395). An increase in aggression over the season was not significant

Table 5 : Monthly time budgets for males and females. All figures are in percentages. Figures in parentheses are standard errors.

MONTH	Aggression	Foraging	Resting and maintenance	Song and Forage-song	Other	n
MALES						
Jan	0.37(±0.35)	88.84(±2.68)	9.86(±2.67)	0 (0)	0.92(±0.7)	6
Feb	0.98(±0.51)	89.53(±4.27)	9.48(±3.92)	0 (0)	0(0)	4
March	2.03(±0.68)	75.54(±4.47)	10.12(±2.11)	11.87(±3.49)	0.44(±0.21)	8
April	3.22(±1.49)	60.56(±9.71)	12.10(±3.92)	23.09(±11.38)	1.02(±0.83)	3
FEMALES						
Jan	0(0)	93.92(±3.39)	5.22(±3.53)	0(0)	0.86(±0.71)	6
Feb	0(0)	87.66(±4.22)	12.04(±4.27)	0(0)	0.3(±0.27)	5
March	0.24(±0.21)	91.02(±2.90)	6.94(±2.23)	0(0)	1.81(±0.79)	5

Note : Figures for December (males), and December and April (females) are not presented because of low sample size.

(K-W χ^2= 4.6720, p=0.1975). Males started to sing in early February, but at first only rarely, and song did not occur during my observations until March. The time budgets of females did not change significantly between January and March; these were the only months for which I could sample female's use of time since from April onwards, females were either nest-building or incubating, and it was not possible to obtain estimates comparable with the previous months.

4.4 Foraging

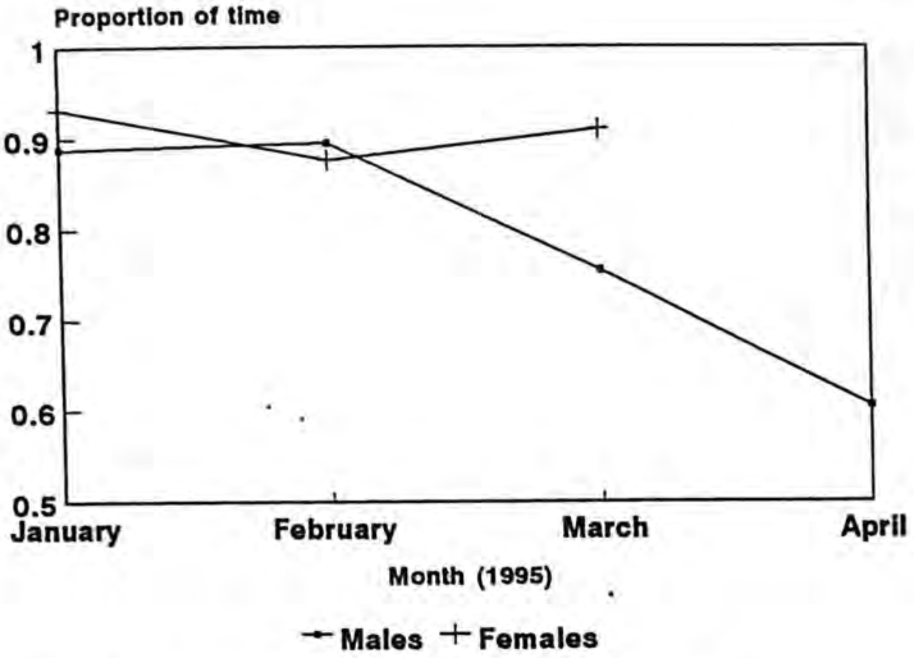
Since it was difficult to objectively quantify *what* the birds were eating, it is not possible to assign a proportion to the different foods consumed. From observation, though, it was quite obvious that an overwhelming part of the grey tit's diet consisted of arthropods. The only exception to this was *Acacia catechu* pods, which tits prised open with their beaks to get at the inside. They would then hammer open the seed. Even here, though, they might have been eating insect larvae from inside the seeds, although I could not establish this. Towards the beginning of my study (in end November), I noticed tits foraging on the berries of the exotic shrub *Lantana camara*, but, whether they were actually eating the fruit, or only picking out insect larvae from infested berries is unclear.

Tits use a wide variety of foraging stations. Figure 5 shows the proportion of time the birds spend on trees of different heights, and on the ground, averaged over all months. Since tits spend most of their time in trees 5-20 metres high, I analyzed whether they were found more at certain heights (top, middle or bottom) within these trees. The results are summarized in Table 6. Within trees, grey tits tend to forage in the upper or middle canopy.

The ground is an important foraging substrate in February (Table 7; Figure 6), when tits spend a large part of their time searching for caterpillars that have fallen to the ground to pupate, but not at other times. In March, a significant proportion of foraging is on the flowers and leaves of the exotic herb *Ageratum conyzoides*, from which grey tits (as well as flocks of *Prinia hodgsonii*) pick out insects.

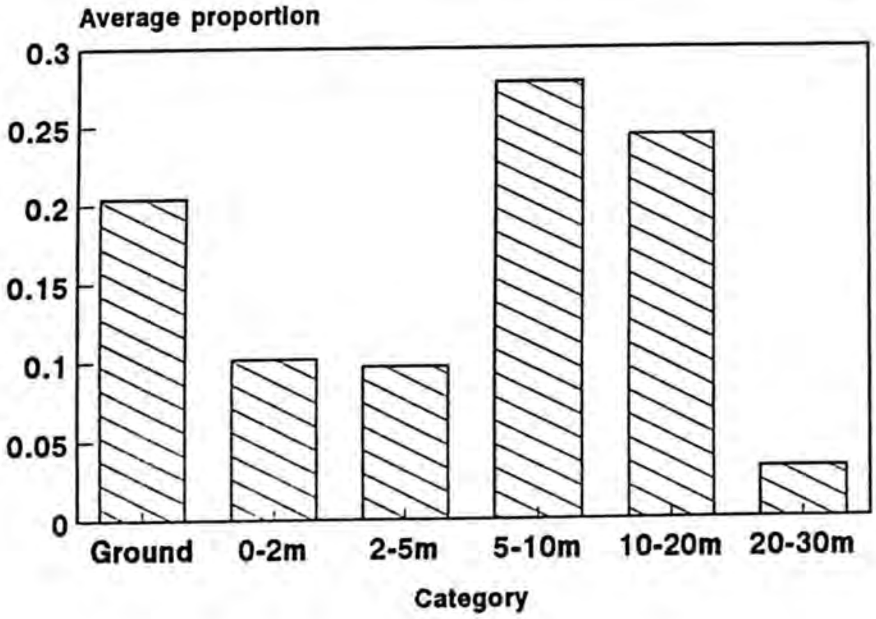
There is a clear seasonal pattern in the use of different foraging sites. Table 7 shows the change in time spent foraging in *Dalbergia sissoo*, *Acacia catechu*, and on the ground. The use of each of these three sites reaches a maximum at different times. *Acacia catechu* is used intensively during December and January (K-W ANOVA sexes pooled χ^2= 11.732 p=0.0195), when tits forage mostly on the pods. Later, in February, as Acacia leaves and pods start dropping, tits forage largely on the ground (K-W ANOVA χ^2=12.0474, p=0.0170), from where I saw them take only large, hairy caterpillars, which presumably had fallen down from the *Acacia* to pupate. These caterpillars were occasionally up to 4 cm in length, and would take up to 20 minutes to prepare and consume. *Dalbergia sissoo* assumes most importance in March (K-W ANOVA χ^2= 15.8286, p=0.0033), when the (formerly leafless) twigs start budding fresh leaves. Tits would probe into the leaf buds of this

Figure 4 : Changes in the time spent foraging - males and females



Proportions calculated by first averaging within, and then among, individuals. Sample sizes are as in Table 5

Figure 5 : Time spent on the ground and in trees of different height classes



averaged over all months and individual

Table 6 : Kruskal-Wallis ANOVAs (sexes combined) on the proportion of time spent at different heights (top, middle, bottom) within trees (as a proportion of total time spent within a tree of that height-class).

Tree height	5 to 10m			10 to 20 m		
	χ^2	$n_1=n_2=n_3$	p	χ^2	$n_1=n_2=n_3$	p
January	15.35	12	0.0005	7.77	11	0.0205
February	7.15	9	0.0279	1.99	9	0.3688
March	8.86	12	0.0118	24.46	12	0.0000
April	8.76	4	0.0125	4.89	4	0.0866

Note : Results are presented separately for two tree height-classes. In all cases where there is a significant difference ($p < 0.05$), **top** is not different from **middle**, and both are used more than **bottom**.

tree for small arthropods, often breaking the whole bud off in the process. The importance of these two trees, and the ground is indicated by the fact that these three foraging substrates together account for a fairly constant 60-70% of time spent foraging in all months (Fig 6). (All ANOVAs in this previous paragraph include December and April even though sample sizes for these months are low. Results are however not altered if these months are excluded.)

Thus, through the season, the time spent on these three substrates varied with respect to each other. Even though all three together formed a more or less constant proportion of total foraging time, their relative importance was different at different times. Comparing between *Acacia*, *Dalbergia*, and the ground, one or the other of these was dominant in all months except April: December and January - *Acacia* (K-W χ^2=6.5434, p=0.0379 and χ^2=10.311, p=0.0066); February - Ground (K-W χ^2=8.9292, p=0.0115); March - *Dalbergia* (K-W χ^2=12.1520, p=0.0023) (sample sizes for these tests can be obtained by adding the samples for both sexes in Table 5).

4.4.1 Ecomorphology:

In the end of January, while looking at morphological measurements of the birds I had caught so far, I noticed that males differed from females in the shape of their beaks. The beak depth/beak width ratio was significantly different between males and females ($t=2.13$ $p=0.044$; see Table 1). Great tits with a higher beak depth/beak length ratio are more efficient at handling beech seeds (Gosler 1987; see section 1.4.2). They show a similar sexual dimorphism in beak shape in the winter, with males foraging more on beech seeds than females. In Naina Devi, the only hard material a tit was observed to handle were *Acacia* pods, and I tested the hypothesis that males foraged more on *Acacia* than females using data from December to February (after which use of *Acacia* declined: see above). Males do tend to forage more on *Acacia* than females, although the difference is only marginally significant (Mann-Whitney $U= 5.0$, $n_1=n_2=5$, p(one-tailed) = 0.058).

Table 7 : Proportion of time spent foraging on different substrates. All figures are percentages of total time. Standard errors are given in parentheses.

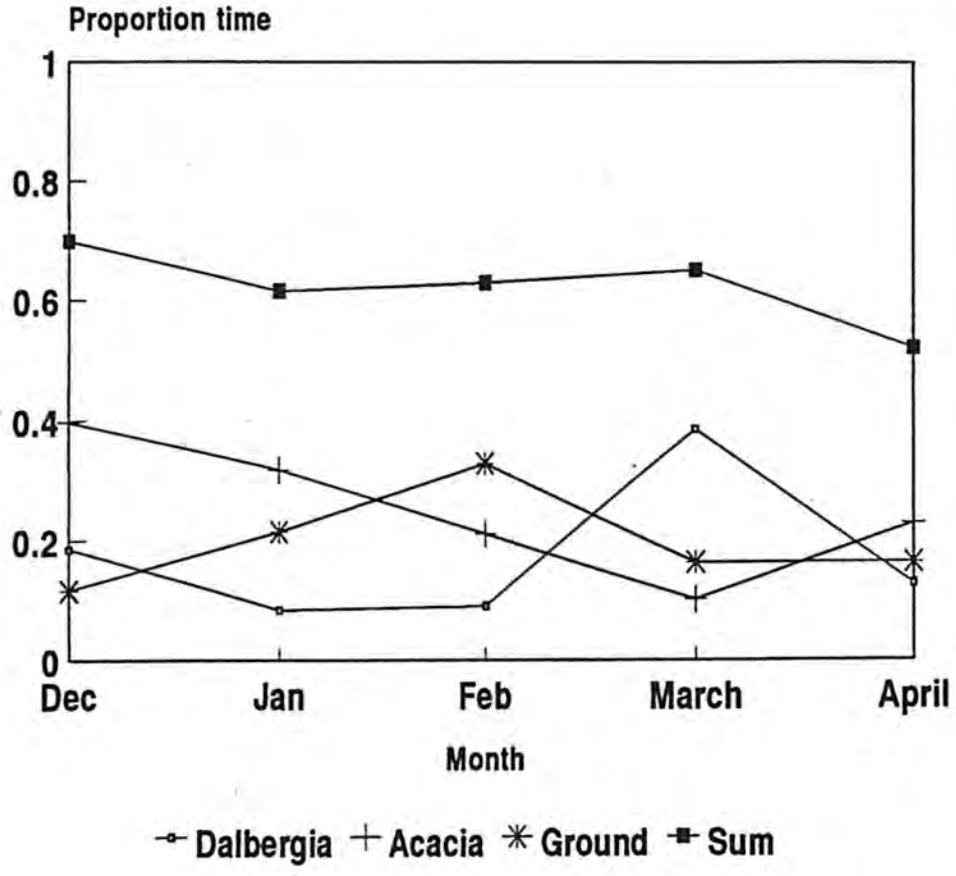
	Dalbergia (a)	Acacia (b)	Ground (c)	Sum of a,b,& c	Total time foraging	n
December	15.48(±2.69)	33.12(±3.76)	9.72(±2.93)	58.32	83.48(±3.34)	3
January	7.59(±2.85)	28.98(±5.57)	19.55(±1.74)	56.13	91.25(±2.29)	12
February	7.95(±2.74)	18.64(±5.91)	29.02(±5.65)	55.62	88.49(±3.032	9
March	32.65(±5.35)	8.58(±2.18)	13.87(±2.13)	55.11	84.79(±2.83)	12
April	8.94(±2.37)	15.99(±3.62)	11.45(±1.31)	36.38	69.91(±7.68)	4

Table 8 : A comparison with Gibb (1954): foraging and time spent on ground.

Activity	December	January	February	March
Foraging	87.2 (81)	87.2 (71)	87.4 (65)	71 (59.5)
Ground	7.0 (26)	22.3 (50)	30.5 (57)	16 (73)

Note : Percentage of individuals seen foraging or on the ground (for foraging, percentage of total, and for the ground. percentage of feeding observations). Figures in parenthesis are the equivalent percentages from Gibb (1954).

Figure 6: Time spent foraging on three substrates



All proportions out of total time spent foraging.
'Sum' is the sum of proportions for the three substrates

5. DISCUSSION

Some interesting possibilities arise from what has been described. In this section, I shall attempt to place what I have found in the context of behavioural theory in general and studies on the great tit in particular.

5.1 Social organization

Most studies on social organization outside the breeding season have focused on questions like foraging efficiency or predation avoidance (Krebs *et al.* 1972, Caraco *et al.* 1980). The strategies birds follow in this regard are likely to be dictated by short-term needs (Matthysen 1993), and in fact, many workers chose the non-breeding season for such studies because they assume that long-term considerations do not operate, and birds simply try and maximise survival during this time (e.g Caraco 1979). By short- and long-term benefits, I mean benefits accruing immediately, and only in subsequent seasons, respectively (Matthysen 1993). For example, the 'long-term' defence of fruit resources in the winter by mistle thrush (*Turdus viscivorous*) described by Snow and Snow (1984) does not translate into direct benefits in the breeding season, but represents a strategy for surviving the period of food shortage. Similarly, the pair-territoriality of migratory stonechats in the winter (Gwinner *et al.* 1994) is a short-term strategy, since this behaviour does not translate into benefits in the breeding season. Recent work on long-term functions suggests that non-breeding strategies can be related to future breeding benefits. For example, there is evidence that prior occupancy of an area results directly in a higher dominance position with respect to non-occupants (great tit, Sandell and Smith 1991; willow tit *Parus montanus*, Koivula *et al.* 1993). The fact that even small differences in time of occupancy made a large difference to dominance in these experiments, suggests that there is strong selective pressure to remain resident on future breeding grounds.

Both males and females benefit from site-fidelity, by continued occupancy of a high-quality territory and by dominance resulting from the prior residency effect (Krebs 1981, Sandell and Smith 1991, Koivula *et al.*, 1993). Site-fidelity by both members of a pair would predict prolonged pair bonds and correspondence of winter territories with former (or future) breeding territories. This may be also be a form of 'prospective resource defence' (Stamps and Tollestrup 1984). A general prediction is that pair territoriality in the nonbreeding season should exist wherever possible, even when breeding is seasonal. Matthysen's (1993) findings, that this is indeed the case in environments with little seasonality, are consistent with this prediction.

Given the considerable advantages of remaining territorial throughout the non-reproductive period, why does the social organization of great tits at this time vary so much, with flocking populations in more northern latitudes, and non-flocking birds in India ? Intraspecific differences in social organization are not unknown among *Parus*. Matthysen (1990) describes examples for the varied *P. varius*, willow and marsh tits (p.227), with flocking and pair-living occurring in the same species. Flocking may occur for a variety of reasons; for example, predator detection and avoidance, and increased foraging success. Flocking has been shown to decrease the time spent scanning for predators (and hence increase the time available for foraging: Kenward 1978, Bertram 1980). Also, Krebs *et al.* (1972) showed that great tits increased their foraging success by feeding in the vicinity of conspecifics by imitating the foraging habits of other birds. Additionally, sharing of information among individuals may not only increase average foraging success, but may also decrease its variance (Matthysen 1990). Complementing these studies is the common observation that great tits show a greater tendency to forage in flocks when food is scarce (Morse 1978, Grubb 1987, Székely *et al.* 1989). However, while the provision of extra food in an area decreases the number of great tits that join mixed flocks, it has no effect on the size of conspecific flocks (Grubb 1987), regardless of the perceived level of predation (Székely *et al.* 1989). Weather may also influence flocking. Saitou (1978) saw an increase in flock size in colder weather, and this has been seen in other tits as well (Matthysen 1990, p. 232).

Looking at the problem from the point of view of territoriality, Brown (1964) predicted that territorial defence would be beneficial only in the middle ranges of food availability, since costs would outweigh benefits if food was either very scarce, or superabundant. Work on nectarivores has supports this (Gill and Wolf 1975). Davies (1976) showed that pied wagtails *Motacilla alba* defend feeding territories in the winter when the food supply is replenished regularly, but abandon their territories to feed in flocks when there is a temporary local superabundance of food. This brings us to patchiness. If food resources are patchy on a large scale, this would both decrease the advantage of maintaining a territory, and increase the benefit of information sharing within a species (Clark and Mangel 1984). Crops of beechmast and hazelnuts while extremely important to great tits in some areas, are very variable (Perrins 1979, Gosler 1987, Grubb 1987). With this in mind, Matthysen (1990) suggests great tits may live in large non-exclusive home ranges during the winter due to the unpredictable and uneven distribution of their food supplies.

In Naina Devi, there is little indication of any single source of food that is important enough and patchy enough to warrant such a strategy. Coupled with this are the generally higher winter temperatures (except higher up in the Himalaya), which may reduce the energetic demands on individuals. Higher temperatures, along with winter rain may mean that invertebrate stock undergoes a continual (if low level of) renewal; such a renewal in resources may be essential for the maintenance of territoriality. In Israel, most adult great tits may remain territorial throughout the winter (Yavin 1987 in Gosler 1993).

The findings of this study are consistent with the hypothesis that species in milder or less seasonal climates are less likely to join nonbreeding flocks, and may instead show some form of territoriality on their future breeding grounds. The abundance of food during the winter is difficult to estimate, as is the amount of seasonality. The study area had a low density of trees (Appendix A.). A degree of seasonality in food abundance does, however, certainly exist. In Delhi, 300 km South of Naina Devi, Gaston (1981) found a marked annual fluctuation in resources, with insect abundance reaching a peak in August and September, during the monsoon. Seasonality in food abundance (which in India is likely to be governed more by the pattern of rainfall than by temperature) in Indian habitats needs to be investigated in further detail.

5.2 Pairing and laying

What is the significance of the relationship between pairing date and laying date ?. It is often assumed that permanent pair bonds are adaptive, because they facilitate breeding as early as possible (Matthysen 1993, Rowley 1983). In the Kittiwake gull *Rissa tridactyla*, pairs which have mated in previous years breed earlier than those (of the same age) which breed together for the first time (Coulson, 1966). In many birds (including the great tit: Perrins 1965), individuals which breed early within the breeding season have a higher reproductive success than those which breed later (Perrins 1970). This is possibly because birds try and produce young when resources are most abundant, but are constrained in doing so by the nutrition available to the females to form eggs (for a more detailed discussion, see Perrins 1970). Dhondt *et al.* (1984) showing that Belgian great tits breed earliest in urban habitats, suggested that this was due to the availability of artificial food. In addition, food quality over the season may also decline. An increase in tannin concentration as oak leaves mature, may adversely affect hatchlings when they are fed caterpillars from these trees (Perrins 1976). Another reason for the higher survival of juveniles which fledge early is that these birds are dominant over later fledged young, due to their being larger (Garnett 1981), or just because they have been around (resident) longer (Sandell and Smith 1991, Koivula *et al.* 1993). In a laboratory experiment, Sandell and Smith (1991) showed that, within juvenile *Parus major*, early established individuals were dominant to later birds. Similarly, in the marsh tit, establishment by juveniles in a winter flock depends on dominance and survival both of which are correlated with early breeding (Nilsson and Smith 1988). In a field experiment which involved inducing repeat clutches, there was a strong reduction in post-fledging recruitment among the juveniles from these later clutches (Verhulst and Tinbergen 1991).

It is important to bear in mind that all of the studies cited above were carried out in temperate regions. Whether similar patterns of juvenile survival hold true in less extreme, more tropical climates is unknown. In less seasonal climates, food resources might build up gradually, and since the extent to which females are constrained in date of laying is likely to depend on how sharply food resources increase to a peak, it is possible that all females are able to lay at the optimal time with respect to food availability for young. However, in species where social dominance among juveniles is an important factor in determining access to resources, early laying (or more accurately, early hatching) would still be selected for. Dispersing juvenile male great tits acquire local dominance during late summer and early autumn in areas where they will later establish breeding territories (Dhondt 1971, Drent 1983), and early establishment in an area is important in determining later dominance positions (q.v. Nilsson and Smith 1988). Clearly, it is necessary to know more about the dispersal and establishment of juveniles grey tits in order to reach a conclusion. In birds which are facultatively double-brooded, the advantage of a second brood would be an additional incentive to lay early.

Retaining the same mate for successive breeding seasons may result in earlier breeding and/or higher reproductive output. This could be due to shared experience in courtship or breeding (e.g. Chardine 1987 in Matthysen 1990). However this has not been demonstrated in passerines, in which the possibility of remating is rather small since there is typically a high mortality between years (approximately 50% in the great tit: Bulmer and Perrins 1973). It is difficult to assess whether individuals that I followed had bred together earlier, partly because of difficulties in ageing the birds, which has not been worked out for this subspecies. Of the two pairs which seemed to be paired before I started work, however, both individuals of one pair were definitely adults, as was the male of the other pair (section 4.1). Nevertheless, even if a previous mate is not present, it may be advantageous to secure a mate long before the breeding season (blue tit *Parus caeruleus*: Nilsson and Smith 1988).

This study demonstrates an association between early pairing and early breeding. Correlation, though, does not necessarily imply causation, and it is not possible to conclude that early pairing *per se* is advantageous because it results in early breeding (assuming that early breeding *is* beneficial for grey tits). It might well be that it is the adults who are paired, and the juveniles (1st-year birds) which are not. Since adults tend to breed earlier in the season than juveniles (Perrins 1965), age alone could explain the observed pattern. Similarly, if females in better condition tend to pair up early, this alone (i.e. good body condition) may be the reason that they breed earlier.

Causally, if females are limited by the amount of food available to them, perhaps being paired allows them to survive the winter with greater nutrient reserves (e.g. for migratory waterfowl: Bluhm 1988). This might occur if their mates undertook some form of mate care, like access to preferred feeding sites (willow tit: Lens and Dhondt 1993), increased vigilance, direct provisioning (c.f. 'courtship feeding': Royama 1966), or protection from aggression by conspecifics (Hogstad 1992).

5.3 Time budgets and foraging

Both Gibb (1954) and Felix (1958 in Gibb 1960) report that the proportion of time great tits spend feeding during the winter is around 75 to 80%. In contrast, this study indicates that the figure for grey tits is around 85 to 90%. Given the longer winter day-lengths and higher temperatures in Naina Devi, it is perhaps surprising that grey tits here spend a larger proportion of their time foraging over the winter than their European counterparts. If this difference is real, it could mean one of three things: **a.** resources are less abundant in Naina Devi over the winter than at, say, Oxford. **b.** the available food is of lower quality in Naina Devi. **c.** grey tits in Naina Devi forage at a lower *intensity* than great tits in England. Again, while the proportion of tits observed feeding by Gibb (1954) decreased markedly from December to March (Table 8), in Naina Devi, grey tits spent similar proportions of time foraging from December to February, and it was only in March that this showed a decrease (Table 5). A possible interpretation is that since grey tits are not in flocks, they spend less time in aggression than Gibb (1954) noticed for great tits, and consequently are able to spend more time foraging. Another possibility is that food resources did not vary markedly over the winter. This may result in scenario **c**. A low intensity of foraging may permit birds to perform other essential activities like scanning for predators (although *Accipiter* hawks were seen only rarely during winter).

The wide foraging niche of the grey tit in Naina Devi is possibly due to the absence of competing congeners. In Europe, great tits use foraging habitat different from their congeners (Gibb 1954, Lack 1971, Suhonen *et al.* 1994). They forage closer to the ground, and when on trees, closer to the boles, than other Parids, and this separation seems to be most pronounced when resources are scarce (Gibb 1954). Among possible competitors of the grey tit in Naina Devi, white eyes *Zosterops palpebrosa* and ioras *Aegithina tiphia* have similar modes of foraging. Closer to the ground, flocks of Franklin's wren-warblers *Prinia hodgsonii* may feed on similar items as the grey tit, but aggression between the species was seen only once. In February, Prinias were seen foraging on the ground for caterpillars alongside grey tits. Minivets *Pericrocotus* spp. are leaf gleaners in the upper canopy, and these, along with *A. tiphia* are the only arboreal gleaning insectivores comparable in size with tits, the other species being markedly smaller.

The data I collected suggest that a pattern of foraging specialization exists *within* the species, and this is similar to that found in England (Gosler 1987). The details are different, with male grey tits foraging on *Acacia* pods rather than on the ground as in England, but the seed/insect dichotomy between males and females is common to the two systems. This suggests that the processes underlying this pattern (possibly intersexual competition: Gosler 1987) may be similar. While Gosler demonstrated that bill shape is very labile, changing considerably between seasons and years, it is also conceivable that a part of the variation observed is heritable. However, further research needs to confirm the existence of such a pattern of foraging specialization, since the data are not conclusive. A complication is that use of *Acacia* may not translate directly into use of pods, since insects are also taken from this tree. Thus, these results would be invalidated if females foraged more on pods when on *Acacia*, while males foraged more on insects. This seems unlikely, but must be taken into account when designing future studies of this phenomenon.

CONCLUSION

More research needs to be done on the behavioural strategies of animals under tropical regimes. Much of our knowledge on aspects like timing of reproduction, clutch size, juvenile survival, inter- and intraspecific competition and general life-history theory comes from studies in highly seasonal climates. The comparative approach may be useful in sorting out the different mechanisms which are involved in the evolution of divergent social systems and life-history strategies. This study indicates that tits in less seasonal climates may show a strikingly different social system from those in temperate areas, while certain patterns of intersexual ecomorphology may be similar across large distances.

One problem with the approach outlined in this thesis is the possible difficulty in removing the effects of historical legacy: a null model might argue that social organization diverged early in the evolution of the *cinereus* group of *Parus major*, and that the different patterns are non-adaptive phylogenetic artefacts. Here, the mountains of the Himalaya provide a unique opportunity to study the effects of different climate regimes over a small geographic scale. In the context of this work, one would predict that grey tits show a gradient in winter social organization with altitude, the occurrence and size of flocks increasing as one goes higher. A lower site-fidelity is likely at higher, colder altitudes, as is the likelihood that birds remain resident year-round. Indeed Ali and Ripley (1983) mention that grey tits from the Himalaya spread out onto the plains in the winter. It seems likely that these are birds from higher up, which leap-frog over the resident populations of the Himalayan foothills; this would predict another gradient in area-fidelity, from complete residency to complete migration, with partially migratory populations at intermediate elevations.

This work is one of the surprisingly few studies done in India on birds using colour-bands for individual identification. Due to the large differences in climate types within the country, investigating the effects of climate and seasonality are made easier. The Himalaya, as mentioned above, provide one such opportunity to study the influence of these effects on various aspects of bird behaviour and ecology.

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Note : references marked with an *have not been seen in original.

APPENDIX A:

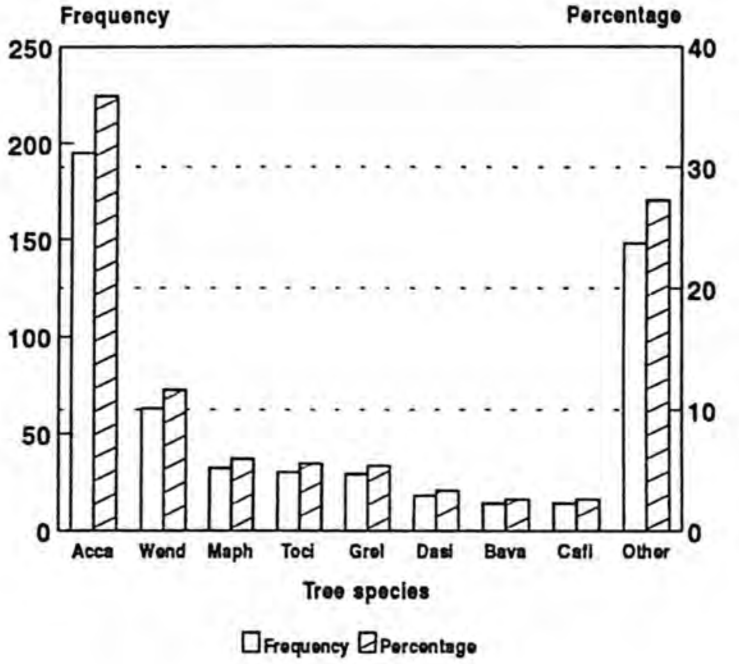
VEGETATION SAMPLING

I attempted to describe habitat parameters by quantifying vegetation parameters in circular plots of fixed radius. I took advantage of the base map that I had already prepared on graph paper in order to locate plots randomly. Random numbers were generated using a calculator; these were taken as X-Y coordinates on the base map. In this way, the centres of 30 plots were determined. The plots were located in the field by taking compass bearings and distances (as determined from the base map) from the closest numbered trees. Tree species, their number, girth at breast height, and estimated height (in the same height classes as given above) was recorded within a circle of 10m radius. The species, and number, of shrubs (< 2m in height) was recorded in a circle of 5m radius. Table A.1. and Figures A.1. and A.2. summarize some of the information collected in this way.

Table A.1: Vegetation characteristics. Figures in parentheses are standard errors. *n* in all cases is 30.

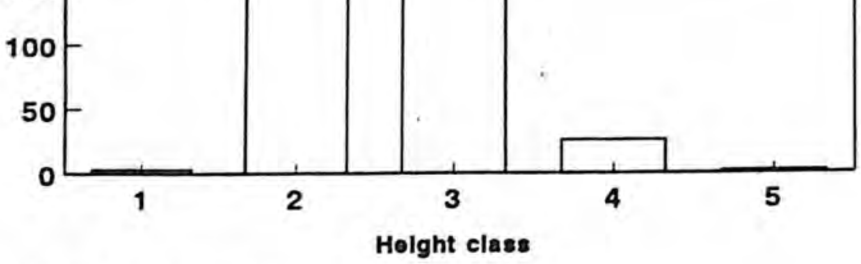
	Mean (per plot: 314m^2)
All trees > 2 m in height	18.10 (±1.29)
Trees > 19 cm GBH	10.56 (±1.25)
All Acacia > 2 m in height	6.50 (±1.34)

Figure A.1 Frequency distribution of tree species



Acca - Acacia catechu
Wend - Wendlandia sp.
Maph - Mallotus philippensis
Toci - Toona ciliata
Grel - Greweia elaśtica
Dasi - Dalbergia sissoo
Bava - Bauhinia variegata
Cafi - Cassia fistula

Figure A.2 : Frequency distribution of height classes of all tree species



based on thirty 10 m radius plots

APPENDIX B:

COLOUR CODES USED FOR INDIVIDUAL BIRDS

MALES

P♂	Purple (on right leg)
RL♂	Red on left leg
LB♂	Light Blue (on right leg)
DGL♂	Dark Green on left leg
O♂	Orange on (right leg)
YL♂	Yellow on left
Pi♂	Pink (on right)

FEMALES

W♀	White (on right)
Y♀	Yellow (on right)
R♀	Red (on right)
LG♀	Light Green (on right)
DB♀	Dark Blue (on right)
PiL♀	Pink (on left)