

Social organization of cooperatively breeding long-tailed tits: kinship and spatial dynamics

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Summary

1. Long-tailed tits *Aegithalos caudatus* L. are cooperative breeders in which breeders that have failed in their own breeding attempt become helpers at the nest of relatives. We investigated the effects of kinship on the spatial dynamics of non-breeding flocks of long-tailed tits in order to determine the information available on the kinship of other members of the population from their use of home ranges.
2. A novel method of home range analysis was devised based on ‘convex hull peeling’. This method takes into account the dispersion of all fixes within a home range and permits the quantitative analysis of home range use. In addition, the method allows the extent of overlap between adjacent home ranges to be determined and the use of those areas to be investigated.
3. Non-breeding flocks of long-tailed tits were composed mainly of relatives, but also included unrelated immigrants. Flock ranges were large and there was extensive overlap between adjacent flocks.
4. The degree of range overlap was significantly affected by the relatedness of flocks. If two flocks contained close relatives they were more likely to overlap than two flocks containing non-relatives. Moreover, the amount of overlap was significantly greater for two adjacent related flocks than for two adjacent unrelated flocks.
5. The use of overlapping areas of non-breeding ranges of long-tailed tit flocks was also influenced significantly by relatedness. Overlapping flocks that were unrelated to each other usually avoided areas of overlap, while related flocks did not generally show such avoidance behaviour.
6. Kinship has significant effects on the spatial dynamics of non-breeding flocks of long-tailed tits and therefore flock behaviour can provide information on the relatedness of other members of the population that might be important for helping decisions in this cooperatively breeding species.

Key-words: *Aegithalos caudatus*, cooperative breeding, home range, kin selection, minimum convex polygon, convex hull peeling.

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Introduction

Cooperative breeding systems typically comprise family groups that live together on permanent stable territories; offspring that have delayed dispersal

become helpers-at-the-nest of subsequent broods on their natal territory (Brown 1987). The evolution of such breeding systems is usually viewed as a two-step process: (i) the decision of grown offspring to delay dispersal and independent breeding by staying at home; and (ii) the decision of those individuals who have stayed at home to become helpers (Emlen 1982). The first step in this model is usually attributed to the existence of constraints on independent breeding (Emlen 1982; Arnold & Owens 1998, 1999; Hatchwell

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& Komdeur 2000). The second step of the model envisages that individuals that have delayed dispersal gain a net fitness benefit by helping. Helpers may accrue direct fitness benefits, e.g. through shared reproduction or inheritance of a territory, and/or indirect fitness benefits through the increased survival and productivity of their relatives (for reviews, see Brown 1987; Emlen 1991; Cockburn 1998). These indirect or kin-selected benefits are widely regarded as being of fundamental importance in the evolution of avian cooperative breeding systems (Emlen 1997), but such benefits can be accrued only if helpers assist their relatives. This means that there must be a mechanism enabling the effective discrimination of relatives from non-relatives.

There is some evidence for kin recognition through self-referent phenotype matching in birds (Bateson 1982; Petrie, Krupa & Burke 1999), but this is probably not widespread (Komdeur & Hatchwell 1999). Instead, the stable territorial system of most cooperative breeders suggests that indirect 'rules of thumb' based on spatial distributions and/or familiarity could provide reliable cues to kinship. Current evidence points to the use of learning of phenotypic traits of family members as the most likely mechanism for recognition and discrimination (e.g. Curry 1988; Price 1998, 1999; Komdeur & Hatchwell 1999; Hatchwell *et al.* 2001).

Any recognition system is susceptible to errors, the error rate depending on the ecology of the species in question, and particularly on the overlap between the distributions of recognized traits in desirable and undesirable recipients (Reeve 1989; Sherman, Reeve & Pfennig 1997). If kin recognition is achieved through discrimination between familiar and unfamiliar individuals, the potential for errors may be slight when the defence of stable, exclusive territories results in a clear dichotomy between familiar individuals on the same territory and less familiar individuals on neighbouring or more distant territories. Since relatedness should vary in a predictable manner among these categories, a rule of thumb based on familiarity will provide a good approximation to kinship, assuming that extra-group paternity and brood parasitism are infrequent and that breeder turnover is either rare or accounted for within the recognition system.

However, not all cooperatively breeding birds have exclusive territories. Colonial species, such as members of the *Meropidae*, have no clear spatial boundaries that define the distribution of relatives (Emlen 1990; Lessells 1990). In some other cooperative species, kin groups are augmented by non-kin and occupy ranges that overlap with other groups containing non-kin (Nakamura 1969; Dow & Whitmore 1990; Marzluff & Balda 1990). In these circumstances the reliability of a rule of thumb based on home ranges might be prone to kin recognition errors. Therefore, it is important to understand the quality of information on kinship available to individuals from their spatial distribution.

Analysing the home range of an animal from a set of observations may present difficulties when attempting

to remove outlying fixes objectively (Wray *et al.* 1992). Objective analysis of the overlap between two home ranges may present even more difficulties. We have devised a powerful novel technique that is both simple and tractable. The method is based upon 'convex hull peeling' (Green 1981; Worton 1995; Anderson 1998) and is a simple iterated extension of calculating the minimum convex polygon (MCP), as described below (see Methods). Its power lies in the fact that it does not simply use extreme data (as in the MCP) but uses all of the data and effectively takes into account the dispersion of data within the range.

Here, we use this method to investigate the effect of kinship on the spatial dynamics of non-breeding flocks of cooperatively breeding long-tailed tits *Aegithalos caudatus* L. Long-tailed tits have a loose familial structure and they are ideal for this study because, unlike the great majority of cooperative species, they occupy large ranges with extensive overlap between flocks. All birds breed independently in each year and they only become helpers following breeding failure (Glen & Perrins 1988). Observations and experiments have shown: (i) that helpers prefer to help at the nests of close relatives despite the frequent presence of non-relatives in close proximity (Russell & Hatchwell 2001); and (ii) that recognition is based on association rather than relatedness *per se* (Hatchwell *et al.* 2001).

The primary objective of this study was to determine whether relatedness influenced the spatial dynamics of non-breeding flocks of long-tailed tits. We analysed home ranges to assess the extent and use of areas of range overlap with the ultimate aim of determining the nature of the information available to individuals on the kinship of other members of the population from spatial organization. We show that relatedness among flocks influences both the extent and use of range overlap.

Methods

STUDY SPECIES

Long-tailed tits spend the non-breeding season in flocks that occupy large, non-exclusive ranges. Flocks break up in early spring; males occupy part of the flock range for breeding, and females either disperse to other ranges to find a partner or remain within the flock range and pair with a male from that flock. All birds start each season breeding independently in pairs, occupying non-exclusive breeding ranges that are substantially smaller than non-breeding ranges (Nakamura 1969, 1972; Gaston 1973). Nest failure is very frequent (Hatchwell *et al.* 1999), and if a pair fails after early May then, instead of re-nesting, breeders may become helpers by feeding the nestlings and fledglings of another pair (Glen & Perrins 1988). About 50% of broods in our study site have helpers (range 1–3). Helpers allow parents to reduce their provisioning rate (Hatchwell & Russell 1996; Hatchwell 1999) and they also increase the condition and subsequent recruitment

of helped offspring (Glen & Perrins 1988; Russell 1999; B.J. Hatchwell, unpublished).

STUDY POPULATION

We studied the non-breeding social organization of a colour-ringed population of long-tailed tits from 1996 to 1999 in the Rivelin Valley, Sheffield, UK. The study site of approximately 3 km² includes areas of mature oak *Quercus robur* L. and beech *Fagus sylvatica* L. woodland, birch *Betula* and hawthorn *Crataegus* scrub and farmland. The boundary of most of the study site was delimited either by areas inhospitable to long-tailed tits (e.g. moorland), or by narrow bottlenecks of habitat. In our analyses we excluded any flock that was observed to spend time outside the study area. For the present study we monitored the breeding activity of 37–41 pairs throughout the breeding seasons (March–June) of 1996–98. We uniquely colour-ringed most breeders (1996: 90%, $n = 82$ 1997: 91%, $n = 74$ 1998: 85%, $n = 80$) and fledglings (1996: 92%, $n = 77$ young from 12 broods 1997: 100%, $n = 56$ young from 7 broods 1998: 93%, $n = 92$ young from 14 broods) in each year. The presence of helpers at the nest was determined in hour-long observations of each nest on alternate days during the nestling phase.

OBSERVATIONS OF NON-BREEDING HOME RANGES

We studied long-tailed tit ranges in the non-breeding seasons of 1996–97, 1997–98 and 1998–99. Observations started in June (1997 and 1998) or October (1996) and continued until flocks broke up in February of the following year. No observations were conducted during August or September. On fine days (colour rings are difficult to read in poor light conditions) we located and followed flocks for periods from 15 min to 4 h, i.e. until contact was lost or until poor light/weather intervened. We attempted to obtain similar intensities of observations for each flock by initiating our searches in different areas of the study site on successive observation days. While following a flock we recorded the identity of as many birds as possible; we were rarely able to record the identity of all birds in a flock on a single observation day, but we assumed that sighting of three or more individuals of known flock membership was a reliable indicator of flock identity. In fact, given the small number of flocks present in the study site in each year, flock identification presented no difficulty.

Flock size and composition is presented only for those flocks with a minimum of 65 fixes because we reasoned that observation time may have influenced the number of individuals seen as well as where they were seen (see below). Flock size was the number of ringed individuals seen in a flock; it was not possible to quantify precisely the small number of unringed birds that dispersed into our study flocks, so this is a minimum estimate. The kinship of individuals within flocks was

determined from pedigrees. Pedigrees offer a reliable estimation of true kinship in long-tailed tits because extra-pair paternity (2.4–6.9% of nestlings) is low and intraspecific brood parasitism (< 0.5%) is negligible (B.J. Hatchwell *et al.*, unpublished). For each flock we determined which individuals were known to be related with a coefficient of relatedness of $r \geq 0.25$, termed kin hereafter. Others are described as non-kin. We assumed that immigrants had no close kin in the population, including among other immigrants; this assumption may not be valid in all cases because close relatives sometimes disperse together between flocks within the study population, so our estimation of relatedness is a minimum estimate. The description of some relatives as non-relatives is unlikely to have produced spurious results because the error will be conservative in the sense that it would weaken any differences in relation to kinship.

Flock movements are erratic; periods of steady movement are interspersed with occasional long flights and with stationary periods lasting up to 15 min. We recorded movements by registering flock location on large-scale maps of the study area (scale 1 cm: 50 m) at approximately 2-min intervals. Thus, our mapping gave us information on the time spent in different parts of the range as well as the size of that range. Map registrations were later converted to map coordinates with a resolution of 10 m.

The number of flocks present in each non-breeding season varied according to reproductive success in the preceding breeding season. We pooled data across years because although a few individuals would have been observed in successive non-breeding seasons, long-tailed tit mortality is high (Hatchwell 1999) and a substantial proportion of flocks is made up of juveniles from the previous breeding season. Even within a season, flock composition is not fixed because two or more flocks may coalesce during the non-breeding period if initial brood size is small or as mortality and emigration reduce initial flock size (Russell 1999; this study). In 1996–97, four flocks were observed from October to February during which time they all retained their separate status. In 1997–98, flocks were observed from June to February; of nine initial flocks, two coalesced shortly after fledging and were treated as a single flock, resulting in observations of eight flocks that retained separate status until the end of July. From October 1997, there were four flocks that remained distinct until the following February. In 1998–99, observations ran from June to February, starting with 12 separate flocks. Two flocks coalesced in early June giving 11 flocks up to late July; from October to January these 11 flocks retained their separate identities. Given the merger of some flocks in late summer, data on flock ranges were split into two categories: ‘early’ (June–July) and ‘late’ (October–February); within these two periods each flock remained distinct and the total number of flocks remained the same. We also used a ‘whole season’ data set which amalgamates observations for each flock

over the whole non-breeding period but only for those flocks that retained their separate identity throughout that period. For example, a flock that remained distinct throughout the non-breeding period would appear in the 'early' data set (June–July), the 'late' data set (October–February) and the 'whole season' data set (June–February); while if two flocks were separate in June–July, but had merged to form a single flock in October–February, they would appear as separate flocks in the 'early' data set, a single flock in the 'late' data set, but would not appear in the 'whole season' data set.

It was necessary to combine observations across months because of the effect of sample size (number of fixes) on the measured range area. The measured range of a flock increased as the number of fixes increased, before levelling off [analysis on the central 50% of fixes (= core area, see following section) of 91 monthly data sets with total sample sizes ranging from $n = 6$ to $n = 693$: quadratic regression $F_{2,88} = 28.25$, $P < 0.001$]. To remove this sample size effect, small data sets were progressively excluded from this analysis until there was no significant relationship between sample size and core range size. The significant effect of sample size on range area persisted to a minimum sample of 60 fixes (quadratic regression $F_{2,37} = 3.83$, $P = 0.03$), but disappeared with a minimum of 65 fixes (quadratic regression $F_{2,34} = 2.59$, $P = 0.09$). Therefore, it was determined that 65 fixes are required to obtain a robust measure of a flock's core range, so this was the minimum sample for inclusion in analyses.

ANALYSIS OF HOME RANGES

The simplest and most frequently used technique used to analyse home ranges is the minimum convex polygon (MCP), a polygon joining the extreme points of a set of 'fixes' (White & Garrott 1990). However, this technique is highly sensitive to outliers which can dramatically increase the area of the polygon, so other techniques (parametric and non-parametric) have been devised (White & Garrott 1990). Here, we studied home ranges using a simple yet powerful technique based on 'convex hull peeling' (Green 1981; Worton 1995; Anderson 1998). The MCP of the data set is formed and its area and the number of points forming the polygon are calculated. These points are then removed from the data set; in a sense we peel off the outer set of points, termed a 'convex peel' (Green 1981). This process, forming the MCP and then peeling off the data, is then iterated on the reduced data set until the final convex peel is reached in which each datum is a vertex. By convention, the outermost peel is denoted peel 1, the next peel 2, etc. (Fig. 1; Table 1).

Analysis of dispersion of fixes within home range

The set of peels can be used in a variety of ways. First, the '50% peel', i.e. the peel that contains the central

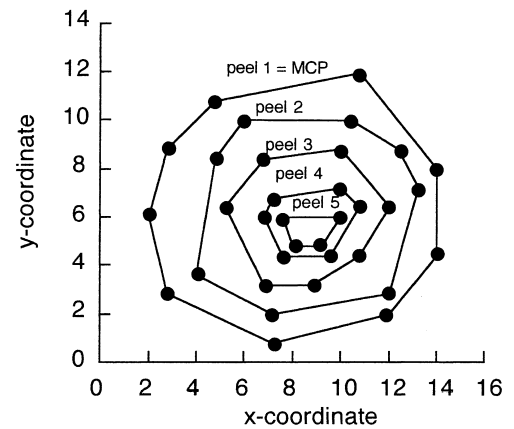


Fig. 1. Convex hull peeling: minimum convex polygons are removed from the total set of hypothetical fixes in a series of iterated peels, enabling range area to be measured in relation to the proportion of fixes remaining (see Table 1 and Methods).

Table 1. Convex hull peeling: analysis of hypothetical data set of home range fixes (see Fig. 1 for graphical representation). The data form a set of five peels, the minimum convex polygon (MCP, i.e. peel 1) being 98.00 arbitrary units. The MCP is 3.84 times larger than the core area (50% of fixes). The lower section of the table shows range estimates for defined levels obtained by linear interpolation (see Methods). Range estimates could not be computed for the 0.1 level because there was no lower bounding peel

Peel	No. of fixes	Proportion of fixes	Area	Area/MCP	Area/50% core area
1	9	1.00	98.00	1.000	3.843
2	8	0.73	56.50	0.577	2.216
3	7	0.50	25.50	0.260	1.000
4	6	0.29	9.00	0.092	0.353
5	4	0.12	2.50	0.026	0.098
100%		1.00	98.00	1.000	3.843
90%		0.90	82.32	0.840	3.228
80%		0.80	66.64	0.680	2.613
75%		0.75	58.81	0.600	2.306
70%		0.70	51.85	0.529	2.033
60%		0.60	38.68	0.395	1.517
50%		0.50	25.50	0.260	1.000
40%		0.40	17.49	0.178	0.686
30%		0.30	9.47	0.097	0.371
25%		0.25	7.38	0.075	0.289
20%		0.20	5.53	0.056	0.217

50% of all the observations, is a robust measure of core area that is insensitive to outliers (Worton 1995). Hereafter, we call the 50% peel the flock's 'core area'. This non-parametric technique effectively weights the shape of the peels by the density of points. An area with a high density of points will tend to retain an apex and polygon edges within that region for several successive peels, so the rate at which the edge of the polygon moves towards the central fixes during successive peels is roughly inversely proportional to density of fixes in that region.

Second, the dispersion of points within a home range can be analysed. For instance, central-place

foragers will have relatively few fixes at home range boundaries, while animals behaving territorially will have a relatively large proportion of fixes at the edges of their home range. Our analysis plots the cumulative proportion of points contained within each peel (i.e. all the fixes that lie on or within the polygon; x -axis) against the area of each peel divided by the size of the 50% peel (core area; y -axis). Dividing the areas of the peels by the core area scales for the absolute area of the individual peels, thus enabling comparisons of area utilization between different data sets to be made, based on a robust measure – the central 50% of fixes.

The curve has a number of useful properties.

1. The shape indicates where the group is spending its time. A group that uses its home range randomly (i.e. fixes are randomly distributed across the range) will have a curve that is a straight line from the origin to $x = 1, y = 2$ (Fig. 2a). [By definition, all curves must pass through both the origin and the point (0.5, 1)]. However, a group that avoids boundary regions will have a curve that passes above the line $y = 2x$ when x is greater than 0.5 (Fig. 2b). Conversely, a group that spends a larger than expected amount of time at the boundaries, e.g. during territorial or pseudo-territorial behaviour (Stewart, Anderson & Macdonald 1997) will have a curve of the opposite form (Fig. 2c).

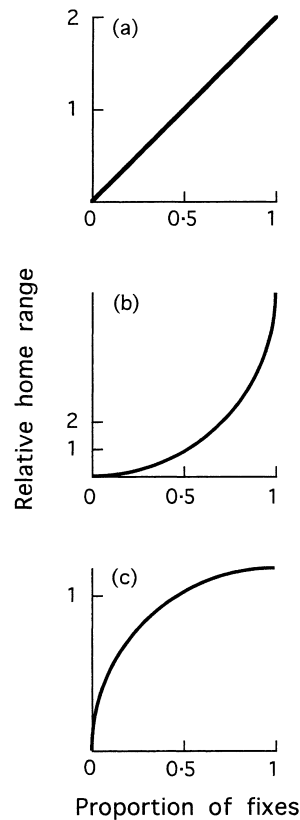


Fig. 2. Simulated relationships between relative home range area and peel level for groups that: (a) occupy their range uniformly, (b) avoid peripheral areas or prefer core areas, and (c) behave territorially or pseudo-territorially. Note differences in scale of y -axis.

2. The loss of a distinct cluster of fixes from a subsequent peel will appear as a kink in the curve, because loss of the cluster causes a large decrease in peel area but a small decrease in the number of remaining fixes.

Analysis of overlapping ranges

If two neighbouring home ranges overlap, then the set of peels for the two groups can be used to analyse how the home ranges overlap, e.g. to gauge interaction between the two groups such as territorial or avoidance behaviour. For a particular proportion of the data set under consideration – hereafter ‘level’, e.g. the ‘80% level’ is the central 80% of points for each home range – we can estimate the area, A , used by each group. These areas are denoted A_{1i} and A_{2i} (where subscripts 1 and 2 represent the two data sets and subscript i the level). We can also estimate the area of overlap at that focal level (denoted O_i). The curves O_i/A_{1i} and O_i/A_{2i} against i indicate whether the two groups tend to avoid the area of overlap, prefer areas of overlap, or use the range uniformly (Fig. 3 and below).

The areas for each level will usually have to be estimated because the set of levels produced by performing the convex hull peeling on a single data set depend on the particular dispersion of the points themselves. For instance, convex hull peeling on one set may produce 100, 73, 50, 29 and 12% (as in Fig. 1, Table 1) but analysis of another data set may produce 100, 79 and 58%, and so on. Thus, when analysing the overlap it is necessary to choose the levels of interest. We chose the following levels: 100, 90, 80, 75, 70, 60, 50, 40, 30, 25, 20 and 10%. A_{1i} and A_{2i} can be estimated by linear interpolation from the two peels bounding level i (Table 1). The area of overlap, O_i , however, is found using planar interpolation. Full details of this procedure will be published elsewhere (C. Anderson & P.G. Blackwell, unpublished) and only a brief description is given here. For a particular level, we take each of the two bounding peels from one flock’s data set and find the exact area of intersection with each of the bounding peels for the other flock.

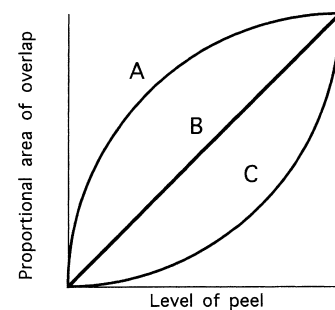


Fig. 3. Simulated relationships between proportional area of overlap (O_i/A_i) and level of peel (i) for pairs of flocks that occupy areas of overlap either uniformly with respect to the rest of their range, or in preference to the rest of their range (A), or avoid areas of overlap with neighbouring flocks (B and C).

Table 2. The composition of flocks of long-tailed tits during the early (June–July) and late (October–January) periods of the non-breeding season

	Early (<i>n</i> = 8)	Late (<i>n</i> = 13)	Mann–Whitney tests	
			<i>U</i>	<i>P</i>
Flock size ¹	17.0 ± 7.4	13.5 ± 5.6	36.5	0.26
% seen in other flocks ²	32.8 ± 23.2	30.0 ± 25.0	46	0.88
No. with close kin per flock ³	12.1 ± 7.5	8.1 ± 4.3	31	0.13
% with close kin per flock	68.6 ± 23.5	63.2 ± 24.7	48	0.77
No. of families per flock ⁴	2.50 ± 1.4	2.00 ± 1.5	37.5	0.26
No. of juveniles per flock ⁵	7.90 ± 5.2	4.85 ± 3.4	34	0.19
% juveniles per flock	45.0 ± 19.3	38.6 ± 32.8	42.5	0.49

¹Mean (± SD) number of ringed birds per flock.

²Proportion of ringed individuals seen in another flock.

³Number of ringed birds with close kin ($r \geq 0.25$) in the same flock.

⁴Number of families with two or more members in the same flock.

⁵Number of juveniles (i.e. birds < 1 year old) in a flock.

Working in three dimensions, if the level for the first flock is the variable on the *x*-axis, the level for flock two is the variable on the *y*-axis, and the exact amount of intersection is the variable on the *z*-axis, then we have four points which form two intersecting triangular planes (intersecting along one of the two diagonals). By default the higher of the two diagonals is chosen as the line of intersection. Using these two subplanes, we can calculate the height of the plane (the amount of overlap) at the level of interest (i.e. at $x = y = \text{focal level}$). This procedure, finding the four exact intersection areas using bounding peels, forming the two subplanes, and then calculating the height at the focal level, is performed separately for each chosen level of interest.

If overlap areas are used uniformly then A_{1i} against i and A_{2i} against i will both be linear, meaning that the proportional area of intersection (O_i/A_{1i} and O_i/A_{2i}) will be concave (Fig. 3). A similar relationship will result if flocks prefer the overlap area. If flocks avoid the boundaries of their home ranges (i.e. there is a greater density of fixes towards the core area) then the curves for area (A_{1i} and A_{2i}) against i will be non-linear but the proportional intersection area will be either linear or convex, i.e. concave-up, depending on the strength of the avoidance (Fig. 3).

Results

FLOCK COMPOSITION AND RANGE SIZE

There were no significant differences in flock size or composition between the early and late periods of the non-breeding season (Table 2). About a third of individuals were seen in more than one flock within each period (Table 2), but flock composition was fairly stable because most observations of flock-switches were made on a single occasion. Approximately two-thirds of flock members had at least one close relative ($r \geq 0.25$) in the same flock, with about two separate families represented per flock on average (Table 2).

Table 3. Home range size (hectares) for non-breeding flocks of long-tailed tits. Range sizes are given for the total range (100% of fixes) and core range (central 50% of fixes) for the early, late and whole season data sets

Period	Total range size (ha) mean ± SD (range)	Core range size (ha) mean ± SD (range)
Early (<i>n</i> = 8)	31.9 ± 23.2 (6–71)	15.7 ± 15.8 (1–47)
Late (<i>n</i> = 13)	40.9 ± 12.2 (24–59)	11.3 ± 6.2 (6–28)
Whole (<i>n</i> = 8)	59.2 ± 26.4 (27–108)	17.0 ± 10.6 (7–38)

Juveniles constituted around 40% of flocks (Table 2), but there was considerable variation among flocks, particularly during the late period (range: 0–100% juveniles).

Non-breeding flocks of long-tailed tits occupied large home ranges (Table 3). Total range sizes measured across the whole non-breeding season tended to be larger than early and late season ranges (Kruskal–Wallis test $H = 5.68$, d.f. = 2, $P = 0.06$), but there was no significant difference in core area (Kruskal–Wallis test $H = 2.24$, d.f. = 2, $P = 0.33$). The larger total range measured across the whole season was not a consequence of a larger number of fixes because there was no significant effect of fix number on total range size within any of the data sets (Spearman correlations: early $r_s = 0.64$, $n = 8$, $P = 0.09$; late $r_s = 0.39$, $n = 13$, $P = 0.18$; whole season $r_s = 0.43$, $n = 8$, $P = 0.26$).

Long-tailed tits appeared to change the manner in which they occupied their ranges across the non-breeding season. In the early period there was a linear relationship between home range size and peel level (Fig. 4a), indicating uniform use of the home range. However, for the late and whole season data sets the relationship was non-linear (Fig. 4a), with the concave curves indicating preferential use of a core area with less frequent use of more peripheral areas. This seasonal difference in the pattern of range use was also apparent in analyses of relative range size (Fig. 4b).

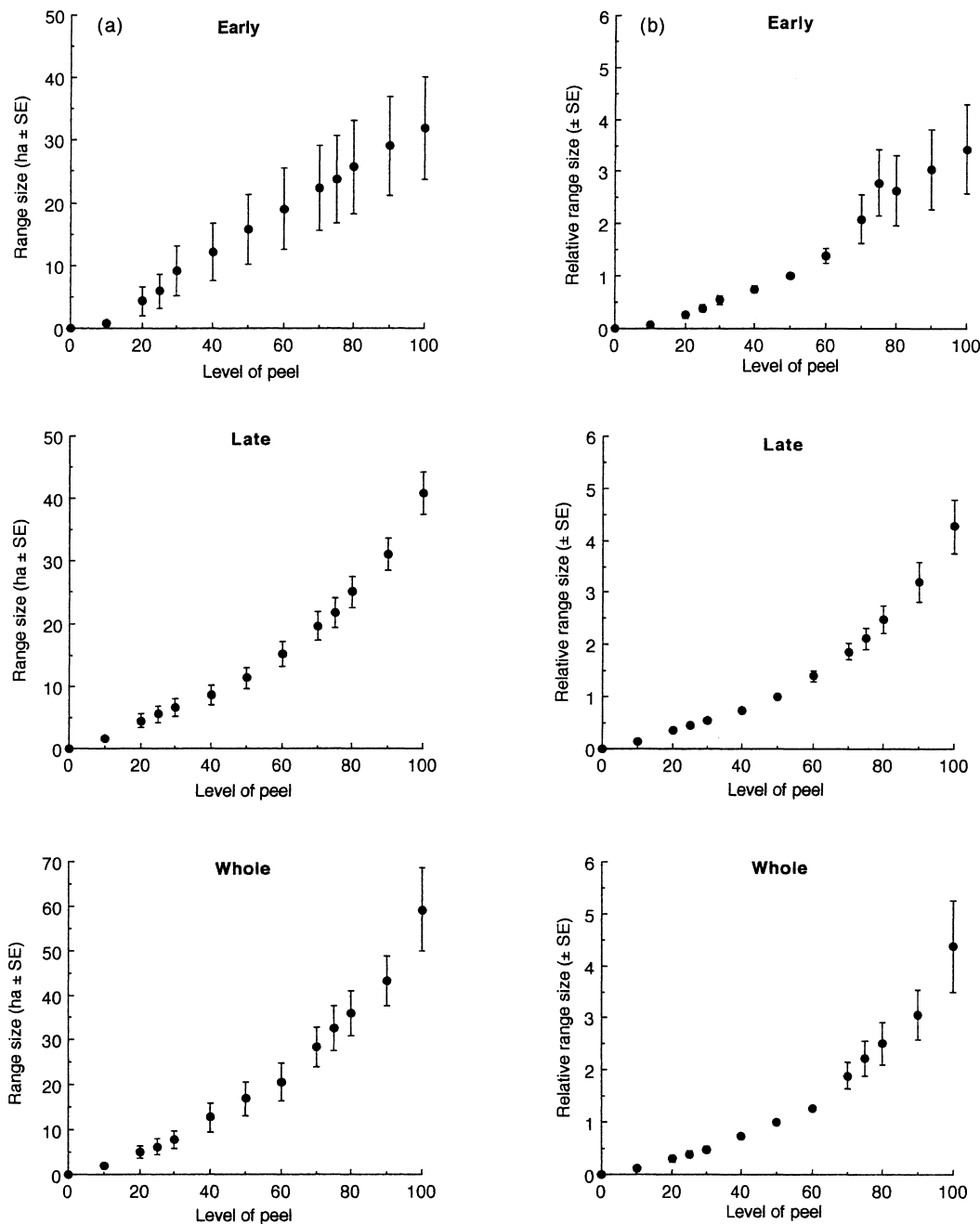


Fig. 4. Relationship between range area and peel level for: (a) absolute home range size during early, late and whole season periods; and (b) relative home range size during early, late and whole season periods. In comparisons of quadratic and linear regressions, the early season data sets were fitted best by linear models (absolute $F_{1,93} = 0.04$, $P > 0.50$; relative $F_{1,93} = 1.07$, $P > 0.50$), while late and whole season data sets were best fitted by quadratic models (late season: absolute $F_{1,153} = 21.75$, $P < 0.001$; relative $F_{1,153} = 31.36$, $P < 0.001$; whole season: absolute $F_{1,93} = 9.04$, $P < 0.01$; relative $F_{1,93} = 14.43$, $P < 0.001$).

DOES KINSHIP INFLUENCE WHETHER FLOCK RANGES OVERLAP?

As a consequence of dispersal, close relatives often spent the non-breeding season in different flocks. We used pedigrees in a similar manner to that used to describe flock composition to determine whether two flocks contained close relatives (hereafter ‘related flocks’) or did not contain close relatives (hereafter ‘unrelated flocks’). Two flocks contained close relatives

in 19% of 52 possible pair-wise comparisons; the most frequent relationships were parent-offspring and siblings. Among related flocks the mean number of birds with a relative in the other flock was 6.7 ± 3.7 ($n = 10$).

We determined whether related flocks were more likely than unrelated flocks to overlap at two levels: 100% (all fixes) and central 50% (core area) of a flock range. Our observations enabled us to make 52 pair-wise comparisons from the early and late non-breeding

Table 4. Occurrence of range overlap between related and unrelated non-breeding flocks of long-tailed tits during the non-breeding season. Comparisons were conducted at the 100% level and the 50% levels. Data include pair-wise interactions between flocks from the early and late non-breeding periods, but each pair of flocks is included once only (the period with the largest number of fixes was used)

Level	No. of flock ranges overlapping (%)		<i>P</i> ¹
	Related flocks	Unrelated flocks	
100% level	10/10 (100%)	19/42 (45%)	0.001
50% level	5/10 (50%)	9/42 (21%)	0.08

¹Fisher exact test.

periods. There was some range overlap in 56% of pair-wise comparisons at the 100% level and in 27% of pair-wise comparisons at the 50% level. The probability of two ranges overlapping was positively associated with flock relatedness, although the association was significant only at the 100% level (Table 4). This association is unsurprising because of male philopatry: the probability of two neighbouring (hence overlapping) flocks being related is high, and the probability of two distant (hence non-overlapping) flocks being related is low. It is more interesting to ask whether the extent of overlap between adjacent overlapping flocks varied with relatedness, and whether use of overlap areas by flocks varied with relatedness. We next consider these two questions.

Table 5. Effect of kinship on the extent of range overlap between flocks of long-tailed tits during early, late and combined non-breeding periods. The amount of overlap (proportion of the total area of each overlapping range) was compared for related and unrelated flocks, at levels from 50% to 100% using two-way ANOVA. (a) Includes data from all adjacent ranges with any overlap. (b) Includes only those overlapping ranges with overlap at all levels from 50% to 100%. The combined data sets includes pairs of overlapping flocks from both early and late periods, but each pair of flocks is included once only (the period with the largest number of fixes was used)

Time period	Factor	<i>F</i>	d.f.	<i>P</i>
(a) All overlapping ranges				
Early season	Kinship	9.54	1,46	0.003
	Level	0.05	6,46	1.00
	Kinship × Level	0.04	6,46	1.00
Late season	Kinship	17.44	1,254	< 0.001
	Level	0.18	6,254	0.98
	Kinship × Level	0.30	6,254	0.94
Combined	Kinship	10.54	1,292	< 0.001
	Level	0.18	6,292	0.98
	Kinship × Level	0.14	6,292	0.99
(b) Ranges overlapping at all levels from 50% to 100%				
Early season	Kinship	12.78	1,28	< 0.001
	Level	0.15	6,28	0.99
	Kinship × Level	0.09	6,28	1.00
Late season	Kinship	43.40	1,154	< 0.001
	Level	3.37	6,154	0.004
	Kinship × Level	0.31	6,154	0.93
Combined	Kinship	32.88	1,182	< 0.001
	Level	3.52	6,182	0.003
	Kinship × Level	0.39	6,182	0.89

DOES KINSHIP INFLUENCE THE AMOUNT OF OVERLAP BETWEEN FLOCK RANGES?

Early and late season data sets were used to determine whether the amount of overlap between overlapping flocks varied according to whether those flocks were related or unrelated. For each period there was a significant effect of kinship on the amount of overlap at levels between 50% and 100% (Table 5a), related flocks having more overlap than unrelated flocks. There was no significant effect of level on the area of overlap; this appears counter-intuitive because overlap should be greater at the 100% level than at the 50% level. In fact, the absence of a level effect is simply a consequence of the progressive inclusion of additional pairs of ranges with small amounts of overlap as the level was increased from 50% to 100%. When only those pairs of flocks whose ranges overlapped at all levels from 50% to 100% were included in the analysis, the significant effect of kinship on the extent of overlap remained and the level of peel was also significant for the late season and combined data sets (Table 5b; Fig. 5). Thus, the amount of overlap was greater when two overlapping ranges belonged to relatives.

DOES KINSHIP INFLUENCE THE USE OF OVERLAP BETWEEN RANGES?

Finally, we address the question of whether the use of areas of range overlap by flocks differed in relation to their relatedness. We determined the relationship

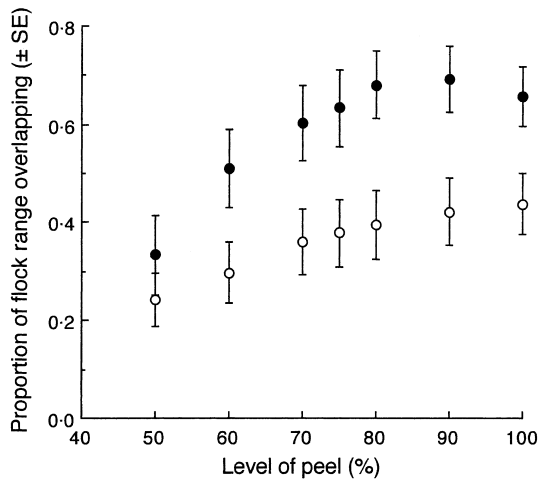


Fig. 5. The relationship between area of overlap between adjacent flocks of long-tailed tits and the level of peel. Results are shown for related (closed circles, $n = 10$) and unrelated flocks (open circles, $n = 18$) that overlapped at the core level (i.e. 50% level). Overlap area is expressed as a proportion of total range area at each level (\pm SE). For statistics see Table 5.

Table 6. Effect of kinship on the use of range overlap between flocks of long-tailed tits during the late and combined non-breeding periods. Uniform or preferential use of overlap areas was indicated by a significant concave quadratic regression between overlap area as a proportion of total area and level. Avoidance of overlap areas was indicated by a significant linear or convex quadratic regression between the same variables. Only those ranges with overlap at a minimum of five levels (i.e. 70% to 100%) were included, and just one range was excluded from the late and combined data sets because regressions were non-significant. The combined data set includes pairs of overlapping flocks from both early and late periods, but each pair of flocks is included once only (the period with the largest number of fixes was used)

Use of overlap	Related flocks	Unrelated flocks
Late season		
Uniform/preferred	11 (92%)	4 (36%)
Avoided	1 (8%)	7 (64%)
	Fisher exact test: $P = 0.008$	
Combined data		
Uniform/preferred	14 (78%)	4 (27%)
Avoided	4 (22%)	11 (73%)
	$\chi^2 = 6.68$, d.f. = 1, $P = 0.01$	

between overlap area and peel level for both flock ranges in each pairwise interaction. Data from both flocks in an interaction were used because although the overlap area is common to both flocks, it is expressed as a proportion of the total range of each flock. If flocks preferred overlap areas or used their range uniformly, a concave relationship between overlap area as a proportion of total range and level would result. Conversely, if groups avoided overlap areas, the relationship between overlap area and level would be either linear or convex (see Methods). Therefore, we examined the relationship between overlap area and level for each overlapping range to determine whether the regression model

that best described the data was concave quadratic, linear or convex quadratic (Zar 1996).

The use of areas of range overlap differed significantly according to whether interacting flocks were related or unrelated (Table 6). For the late and combined non-breeding period, unrelated flocks were most likely to use areas of overlap in a manner indicating avoidance, while related flocks used areas of overlap at least in proportion to the relative area of overlap, i.e. uniform or preferred use of overlap areas. There were too few data for analysis of the early non-breeding period. These analyses were not confounded by variation in the number of levels available for regression analyses (mean number of levels for: related overlaps: 6.56 ± 0.71 , $n = 18$; unrelated overlaps: 6.23 ± 0.93 , $n = 13$; t -test: $t = 1.11$, d.f. = 29, $P = 0.28$).

Discussion

Non-breeding flocks of long-tailed tits are composed largely of relatives, although they also include unrelated immigrants. Application of a novel analytical technique to home range data revealed that related flocks were more likely to overlap than unrelated flocks, that the amount of overlap between adjacent overlapping flocks was greater for related than for unrelated flocks, and that unrelated flocks tended to avoid areas of range overlap while related flocks did not exhibit avoidance.

The modified convex hull-peeling technique (Anderson 1998; C. Anderson & P.G. Blackwell unpublished) has wide applicability in the quantitative analysis of home ranges. In particular, the ability of this technique to take account of the density of fixes in calculating range size offers a potentially important tool for range analysis of animals that have multi-nuclei within their range, e.g. song-posts. The data must have a temporal component for the relative use of different parts of the range to be determined, but in practice this is the usual procedure, especially in automated radio-tracking studies (Kenward 2000). In this paper, the density of fixes in different parts of the home range is assumed to reflect the time spent in those areas, and the application of this method has enabled investigations of flock association that would have been intractable otherwise.

Previous studies have found that non-breeding flocks of long-tailed tits are composed primarily of relatives (Nakamura 1969; Gaston 1973; Ezaki, Miyazawa & Sakikawa 1991; Russell 1999). However, our results differed from most earlier studies in terms of range exclusivity and size. Gaston (1973) reported mean flock ranges of 25 ha, compared to 41 ha at the same time of year in this study. Across the whole non-breeding period, Glen (1985) and Nakamura (1969) recorded ranges of 17–25 ha, compared to our mean of 59 ha. The relatively large ranges in our population may reflect ecological differences between study sites, or may be a function of the number of fixes obtained in different studies (see Methods); sample sizes are not reported in most previous studies.

The other striking difference between this study and those of Nakamura (1969), Gaston (1973), Glen (1985) and Ezaki *et al.* (1991) is that we found extensive overlap of flock ranges, whereas previous studies have usually referred to ranges as 'discrete', 'defended' territories. This description is clearly not applicable in our population, as evidenced by the extensive range overlap and the absence of avoidance behaviour in many overlap areas. Furthermore, the pattern of range use is inconsistent with territorial behaviour (Fig. 4). This difference could result from sampling differences, but we regard this as unlikely given the extent of range overlap. It is more likely that the relatively large ranges in our study site are a consequence of harsher conditions during the non-breeding season making invertebrate prey relatively sparse compared to Japan and southern Britain where previous studies were conducted. Such large ranges may not be economically defensible (Brown 1964). Under more extreme winter conditions, e.g. in northern Europe and Asia, long-tailed tits are either migratory or show eruptive behaviour (Ehrenroth 1976; Harrap & Quinn 1996).

In the context of cooperative breeding, the key features of long-tailed tit non-breeding social organization are that: (i) flocks are composed largely, but not exclusively, of relatives; (ii) there may also be relatives in adjacent flocks; (iii) the nature of interactions between adjacent overlapping flocks varies according to their relatedness. The spatial organization of groups in cooperative breeders has important implications for kin discrimination. The occupation of stable, exclusive ranges by nuclear families is the norm (Brown 1987; Emlen 1991), and in such territorial systems, discrimination based on spatial cues or familiarity may pose few problems (Komdeur & Hatchwell 1999). In a more labile social system, as described here, such cues may be less reliable, especially when there are multiple breeding attempts by members of large groups of variable kinship (e.g. Brown & Brown 1990; Dow & Whitmore 1990).

It is known that kin discrimination in long-tailed tits is based on familiarity rather than kinship *per se* (Hatchwell *et al.* 2001). However, it is not known when the crucial period for kin recognition through association is, nor whether recognition cues are family-specific, flock-specific or individual-specific. The social organization and spatial dynamics described in this study allow us to speculate on both questions. First, a sensitive period for the acquisition/learning of a kin recognition label must precede the breakdown of discrete family units during the non-breeding period to be effective in kin recognition. There was considerable mixing of families even during the early period of the non-breeding season (Table 2), suggesting that the putative kin-learning period must be during the nestling or fledgling phases. Second, the fact that interactions between related flocks differ from those between unrelated flocks indicates that recognition is not based simply on flock-membership. This view is substantiated

by the observations that although flocks include non-relatives, long-tailed tits are able to discriminate between the calls of kin and non-kin and prefer to help their kin even when the discrimination or preference involves individuals from the same social unit (Hatchwell *et al.* 2001; Russell & Hatchwell 2001). In addition, our results suggest that cooperation need not be restricted to members of the same social group and that, potentially, kin-directed helping could occur across flock boundaries.

Our results do not allow us to conclude whether recognition is individual- or family specific, nor do they permit us to investigate the frequency of recognition errors. A key determinant of the error rate in a kin recognition system is the relative importance of direct and indirect fitness benefits. If direct fitness benefits are substantial and kin-selected benefits are relatively unimportant for the evolution of cooperation (Cockburn 1998), a recognition system may be generous in the sense that there is a relatively high rate of acceptance errors (i.e. treating non-kin as kin). However, if indirect fitness benefits are of primary importance and the cost of errors is high, a stringent recognition system in which acceptance errors are minimized is likely to operate (Reeve 1989). Kin selection is important in the cooperative system of long-tailed tits (Russell & Hatchwell 2001), so a low rate of recognition errors would be expected despite the labile social system. In fact, although experiments suggest that potential helpers become helpers only when kin are available, pedigrees and genetic analyses show that some helpers do assist non-kin (Russell & Hatchwell 2001). Whether such non-kin-directed helping is adaptive or is a consequence of recognition errors remains to be determined.

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