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The movements of some granivorous passerines in winter on farmland: a pilot study

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EXCECUTIVE SUMMARY

1. This report describes some novel pilot work to investigate the ranging behaviour of seed-eating finches and buntings (granivorous passerines) on farmland in winter.

2. Other, demographic studies have shown that reductions in the annual survival rates of some granivorous passerines have probably contributed to marked declines in their populations over recent decades. A reduction in the food available to them during winter is likely to be a principal cause of these changes in some species. Knowledge of the ranging behaviour of key species will permit the implementation of mitigation measures (management to maintain seed availability through the winter) at an appropriate scale appropriate for the normal ranging abilities of target bird species, for example through agri-environmental incentives.

3. Three approaches to assessing winter ranging behaviour by granivorous passerines were undertaken within a 25 km^2 study area in West Fife, Scotland: (i) Ringing and retrapping of birds at multiple sites; (ii) Radio-tracking; (iii) Colour-marking, followed by searches to find marked birds. Assessments of bird abundance, its variation through the winter, and habitat use by key species were used to put any measured ranging behaviour into context.

4. The three principal study species were Yellowhammer, Chaffinch and Tree Sparrow. They were selected with the aim of including species with contrasting population trends and those expected to have different ranging behaviours.

5. A total of 1,123 captures of finches and buntings were made during winter 2002-03 within the study area. These included 232 captures of Yellowhammers, 522 of Chaffinch and 117 of Tree Sparrow. The rates at which ringed birds were recaptured were used to estimate their likelihood of moving between four key ringing sites. These analyses used a multi-strata modelling approach within the program MARK and generated estimates of the probability of individuals moving between pairs of sites, with associated measures of the error attached to the estimates.

6. Ten Yellowhammers, ten Chaffinches and eight Tree Sparrows were radio-tracked in January and February 2003. To overcome problems associated with restricted detection ranges and active life span for the small radios attached, a systematic-search approach was adopted. Analyses treated the radio-tracking fixes as mark-recapture data and also used a multi-strata modelling approach within the program MARK. As for the analysis of the ringing data, this gave probability estimates for movements between sites.

7. Both systematic ringing and radio-tracking, the two quantitative methods, produced comparable measures for the ranging behaviour of the three study species. Tree Sparrows tended to range the greatest distance (individuals moved between pairs of sites 3.6 – 4.9 km apart), Yellowhammers were intermediate (individuals moved between pairs of sites 1.9 – 3.6 km apart) and Chaffinches tended to be the least mobile (the only detected movement was between a pair of sites 2.0 km apart). Relationships between the probability of movement and distances between sites were complex, however, in that probabilities did not necessarily decline with increasing distance. This suggests that movements are influenced by a knowledge, or retained memory, of preferred sites.

8. The efficacy of colour-marking (colour-rings and plumage dyes) was assessed for Yellowhammers and Chaffinches. Both provided qualitative support for the ranging behaviour measured by ringing and radio-tracking. The colour-ringing of Yellowhammers could be usefully developed to provide more quantitative measures, but the resighting of colour-rings on Chaffinches proved problematic and of low potential value. The use of plumage dyes was confounded by variable rates of fading.

9. Chaffinches were the most generalist in terms of their use of the range of habitats available, including woodland and human sites. Tree Sparrows had the finest habitat requirements, with the most marked preferences for stubbles compared with the other habitats available. Yellowhammers

were intermediate and used all but the most enclosed habitats. All three species showed a preference for stubbles.

10. Although we acknowledge the limitations of this study, undertaken in a single season and within one study area, there are interesting suggested relationships between ranging behaviour, habitat preferences and population trends. Of the three study species, the most widely ranging, and potentially most habitat-specialist, the Tree Sparrow, has undergone the most dramatic decline in breeding numbers, while populations of the apparently generalist, and seemingly less mobile, Chaffinch have remained stable or even increased. Both the measured ranging behaviour and habitat selectivity of Yellowhammers were intermediate between the two other species and their recent population trend has also been intermediate, with their decline starting later and being less marked than for Tree Sparrow.

11. Using the field and analytical techniques tested and developed in this study, we now recommend a full-scale study that involves replicate study areas and the collection of data over a number of years in order to assess variation in winter ranging behaviour within and between species. The acquisition of this knowledge has important practical implications for the advocacy and implementation of conservation prescriptions. The distribution of seed food resources, such as those that are likely to be created through agri-environment schemes, needs to be on a scale appropriate for the normal ranging abilities of the target bird species. This would ensure cost effective provision of such resources for birds.

12. The techniques developed are appropriate for further extension of such a project to address over-winter survival of granivorous passerines, and its influences and interactions between resident and immigrant wintering birds.

1. INTRODUCTION

1.1 Background

Many species of birds associated with farmed habitats in Britain have undergone marked population declines since the 1970s, with associated contractions in their distribution (Fuller *et al.* 1995, Siriwardena *et al.* 1998a, Baillie *et al.* 2001). Environmental changes driven by the policies that determine agricultural practices (Brouwer & Van Berum 1996) are generally regarded as major causal factors for many of these declines. Such changes include the loss of food resources through increased use of agrochemicals and their increased effectiveness, the simplification of crop rotations, the polarisation of land-use into either pasture or arable at a landscape level reducing habitat diversity, the loss or degradation of non-cropped habitats such as hedgerows, and changes in the densities of grazing livestock and the intensification of pastoral management (Fuller *et al.* 1995, Wilson *et al.* 1999, Perkins *et al.* 2000, Thompson *et al.* 1995, Gillings & Fuller 1998, Robinson *et al.* 2001, Robinson & Sutherland 2002,).

Most autecological studies of birds on farmland have concentrated on breeding biology and summer ecology with some intensive studies having shown agricultural change as the driving force behind declines. For example, the Grey Partridge *Perdix perdix* has suffered from the indirect effect of herbicides, reducing the availability of invertebrate food for chicks (Potts 1986), and changes in the timing of mechanical operations have lead to the decline of the Corncrake *Crex crex* (Stowe *et al.* 1993). A reduction in the seasonal availability of seeds is likely to have reduced the number of breeding attempts made by Turtle Doves *Streptopelia turtur* in any one year and thus have contributed to their recent decline (Calladine *et* al 1997, Browne & Aebischer 2001). Broader investigations of bird demography have identified other stages during the life of birds during which environmental, including agricultural change, will have had an impact. Changes in annual survival rates appear to have contributed to some population changes, for example those of Goldfinch *Cardeulis cardeulis*, House Sparrow *Passer domesticus*, Reed Bunting *Emberiza shoeniclus* and Song Thrush *Turdus philomelos* (Thomson *et al.* 1997, Peach *et al.* 1999, Siriwardena *et al.* 1998a, 1998b, 1999). These broader demographic studies based on national data sets include only species for which some population trends are reliably known and of which large numbers have been individually marked, notably as part of the BTO ringing scheme (Clark & Wernham 2002). Changes in the survival rates of full-grown birds are very likely to have contributed to the changing status of other bird species on farmland but insufficient numbers of individuals have been marked for many trends and relationships to be determined.

The availability of food through the winter is likely to be an important determinant of passerine survival rates in Britain, and for many farmland birds, this constitutes seed present within cultivated land (Fuller *et al.* 1995). On agricultural land, the availability of seeds to granivorous birds has declined in recent decades as a result of the loss of winter foddering sites for livestock, improved harvesting efficiency and less spillage, the loss of winter stubbles, and improved herbicides that reduce the abundance of weeds, and hence their seeds, within crops and stubbles (Lack 1992). A number of studies give direct evidence of the importance to granivorous passerines of seed availability through the winter on farmland; near Oxford, stubbles that retained spilt crop product and a variety of seed bearing weeds generally supported higher numbers of birds, with greater species diversity, relative to other field types (Wilson *et al.* 1996); the winter distribution of Yellowhammers *Emberiza citrinella* and Skylarks *Alauda arvensis* on farmland in Norfolk was related to the density of seeds present within fields (Robinson & Sutherland 1999); and a range of farmland passerines were attracted to specially planted seed-bearing crops in County Durham (Stoate *et al.* 2003).

In an attempt to reverse the declines of granivorous farmland birds, incentives are now available to farmers and other land managers to increase and maintain the availability of seeds to birds through the winter. These have taken the form of agri-environment schemes offering payments to maintain over-winter stubble, extensive cropping practices, the leaving of some unharvested crops through the winter and the specific planting of other seed bearing crops (*e.g*. DEFRA 2003, SEERAD 2003). Of note, the restoration of some Cirl Bunting *Emberiza cirlus* populations in Devon has been at least partly attributed to the provision of weed-rich, and therefore seed-rich, winter stubbles, principally using agri-environment schemes as the incentive to deliver those features (Peach *et al.* 2001). In addition, set-aside arable land can provide opportunities to enhance seed availability to birds (Evans *et al.* 1998, Buckingham 1999). Although there is a need to develop further some of the prescriptions associated with these incentives to improve their effectiveness as tools for conservation (*e.g.* Stoate *et al.* 2003, Potts 2003), the basic principal of maintaining seed availability through the winter is accepted. There is currently no guidance as to the scale at which these prescriptions need to be implemented, however, in order to effectively conserve granivorous bird populations on farmland. Very little is known about the winter ranging behaviour of granivorous passerines. Accordingly, knowledge on just how dispersed winter food sources need to be in order to be both accessible to sustain populations of birds through the winter, and also offer value for money and effort to those implementing and funding, is currently absent. Research on the local movements of birds, including those that are resource-related, and the development of techniques to quantify such movements have been identified amongst the highest of priorities for applied bird conservation science (Wernham & Baillie 2002).

1.2 Aims of the study

This report describes some novel pilot work to investigate the ranging behaviour of granivorous passerines on farmland during the winter of 2002-03. This includes:

1. Ringing and retrapping of birds at multiple sites on or immediately adjacent to farmland within a defined study area;
2. Radio-tracking of Yellowhammers, Chaffinches and Tree Sparrows;
3. Colour-marking of Yellowhammers and Chaffinches using colour-rings and plumage dyes;
4. Systematic counts to assess the relative abundance of granivorous passerines within the study area through the winter, to quantify any changes and habitat use against which the movements measured by the above methods could be placed in context.

The trial methods used are described and their efficacy compared. Some of the first quantified measures of winter ranging distances for Yellowhammers, Chaffinches *Fringilla coelebs* and Tree Sparrows *Passer montanus* are presented. Recommendations are made for a full-scale study that will further elucidate the factors that are of direct importance in the advocacy and implementation of conservation prescriptions for granivorous birds.

1.3 Study area

This research was undertaken within a 25 km^2 (5 km by 5 km) study area immediately west of Dunfermline, in West Fife, Scotland (centered on 56° 05’ N, 3° 31’ W) (Fig 1). Within this area, there has been a targeted effort by the Tay Ringing Group to mark granivorous passerines since 1995. The area includes mixed arable and pasture farmland, a number of woodlands, areas of open water and villages (Table 1). The area is generally undulating and the altitude ranges from 35 m above mean sea level in the south to 220 m in the north.

1.4 Study species

The three principal study species were Yellowhammer, Chaffinch and Tree Sparrow. Their selection was based on three criteria, (i) the Tay Ringing Group’s success in catching these species in the study area in previous winters, (ii) to include species that based on general ringing recoveries are thought to have differing winter ranging strategies, and (iii) to include species that have contrasting population trends at the UK level.

1.4.1 *Yellowhammer* Emberiza citrinella

Although a very small number of Yellowhammers of Scandinavian origin are believed to pass through Britain (*e.g.* Thom 1986), Yellowhammers are generally thought to be sedentary in the UK, with over 95% of ringing records from Britain and Ireland within 25 km of where they were ringed (Balmer 2002). Numbers of breeding Yellowhammers began to decline in the UK as a whole in the 1980s, somewhat later than the declines observed for many other species on farmland. In Scotland, two ornithological atlases show a 17% reduction in the number of 10-km squares occupied by breeding Yellowhammers between periods centered on 1970 and 1990 (Gibbons *et al.* 1993), however, the Breeding Bird Survey (BBS – a national monitoring scheme organised by the BTO) suggests stability in breeding populations between 1994 and 2000 (Baillie et al. 2001). There is some evidence that annual survival rates have decreased since the 1980s (Siriwardena 1998b). The Yellowhammer is now on the 'red list' as a species of high conservation concern based on its rapid (>50%) decline in UK breeding abundance over the last 25 years (Gregory *et al.* 2002).

1.4.2 *Chaffinch* Fringilla coelebs

Chaffinches breeding in Britain and Ireland are thought to be largely sedentary, however, birds of Fenno-Scandinavian origin augment their numbers in winter. 32% of ring recoveries from the northern half of Britain indicate movements in excess of 20 km (Norman 2002) implying that the species might be somewhat more mobile than Yellowhammers; division into the geographic origins of these birds were not known however. Recent surveys suggest a shallow increase in breeding numbers at both the UK and Scottish scales (Gibbons *et al.* 1993, Baillie *et al.* 2001).

1.4.3 *Tree Sparrow* Passer montanus

Again, Tree Sparrows are generally considered as rather sedentary residents in the UK, although 23% of ringing recoveries were over 20 km away from the site of ringing (Netherwood & Summers-Smith 2002). Tree Sparrow numbers in the UK has crashed between the late 1970s and mid-1980s. The species is inadequately monitored in Scotland to allow a country-specific trend to be determined currently, however there was a 30% reduction in the number of 10-km squares occupied by breeding Tree Sparrows in the twenty years between two ornithological atlases undertaken around 1970 and 1990 (Gibbons *et al.* 1993). It is likely that changing survival rates have powered much of the decline, although too few have been ringed to provide direct evidence (Siriwardena *et al.* 1998b, Baillie *et al.* 2001). The Tree Sparrow is 'red listed' as a species of high conservation concern based on its rapid (>50%) decline in the UK breeding population over the last 25 years (Gregory *et al.* 2002).

2. METHODS

2.1 Ringing and retrapping

2.1.1 Trapping protocol

Birds were caught using mist nets (Redfern & Clark 2001) at four ‘key sites’ within the study area: Craigluscar, West Camps, Cairneyhill and Crossford (Fig 1). Additional sites at Bandrum, Langfaulds, Cowstrandburn and Easter Clunes are either outside of the main study area and form part of ongoing ringing studies by the Tay Ringing Group or were used irregularly as trial sites for potential future use. Only data collected from the key sites are used in the formal analyses to quantify ranging behaviour, however data from other sites have been used to add qualitative support to some findings. All ringing sites were selected on the basis of the occurrence of granivorous passerines in winter and their practicality for catching birds using mist nets. All sites were baited, principally with grain (principally oats), in order to concentrate the birds at netting sites. The baiting regime varied, with periods of ‘heavy baiting’ for three weeks interspersed with periods of ‘light baiting’. Heavy baiting periods were:

1. 15 October 2002 – 3 November 2002
2. 17 December 2002 – 5 January 2003
3. 17 February 2003 – 9 March 2003

Bait was placed in feeders, of which there were typically six to ten per site. ‘Heavy baiting’ comprised the twice-weekly filling of feeders with additional grain scattered on the ground with the aim of maximising catches. ‘Light baiting’ maintained some food in one or two feeders at each site, although this was permitted to run out for periods of one to three days at a time each week. The light baiting aimed to continually attract birds to the specific netting areas but was considered insufficient to meet all of their food requirements, thereby ensuring that they had to forage for other resources away from the immediate netting area.

A total of 65 ringing sessions were completed between 2 October 2002 and 13 March 2003 (Table 2). A typical ringing session comprised the erection of 50 – 100 metres of four-shelved mist nets, immediately prior to first light in the morning, and continued until catching rates were slow or catching ceased, usually within 2 – 5 hours. Each bird caught was marked with a standard BTO ring (uniquely numbered) on one leg or, if it had been previously ringed, the number was recorded (a ‘recapture’). At each capture, the birds were aged and sexed following Svensson (1992), and the wing length (maximum chord), weight (to the nearest 0.1 g) and fat score (using the ESF/Keiser system) were recorded following Redfern & Clark (2001).

2.1.2 Analytical methods to estimate dispersal rates

The rates at which ringed birds were recaptured were used to estimate their likelihood of dispersal using a multi-strata modelling approach (Hestebeck *et al.* 1991) within the program MARK (White 2002). Up to four ‘strata’ were included in each model representing the four key ringing sites. Where a species was never caught at a site, then that site was excluded from the relevant models for that species. MARK is principally a program to estimate survival rates of animals based on the encounter histories of marked individuals. The first encounter was the capture and ringing of a bird. Subsequent encounters for that individual were its recapture at one of the key ringing sites. A matrix of encounter histories is produced that includes a bird’s capture either as a positive event or as a ‘zero’ for each ringing session. As such, the varying probability of a bird’s recapture can be accounted for in the estimation of its survival rate. In a multi-strata model, each encounter is attributed to one of the key ringing sites, and the non-capture of an individual during each ringing session is attributed a zero. The models estimate the transfer probabilities between strata; in this study, these are the likelihood of birds moving between key ringing sites.

The winter season was divided into six four-week periods, the sampling interval entered into the models, and each ringing session was attributed to one of these periods. Each sampling interval used a combination of one or more ringing sessions. The periodicity of ringing sessions permitted all sites to be sampled at least once during each four-week period, but sites where more birds were present and 'catchable' were used the most frequently. For this pilot study, maximising the marked sample of birds was considered of greatest importance; any introduced biases could be checked for within the models developed.

The models assume that survival was constant across sites. Although this assumption has often been considered difficult to accept for birds (White 2002), in this study the proximity and similarity of the different strata (ringing sites) lead us to believe that this assumption was not likely to be badly invalidated. The initial models to be run included site-specific recapture probabilities and different transfer probabilities between strata and between the two directions of transfer between strata pairs. Subsequent simplified models included common recapture probabilities across sites and common transfer probabilities for the two directions between strata pairs, that is the probability of a bird moving from A to B was the same as that for movement from B to A (ie no sources or sinks of birds within the measured period). The Akaike information criterion (AIC), the lowest value of which suggests the model that describes the data most parsimoniously, was used to investigate which model best described the data (Lebreton *et al.* 1992). Likelihood ratio tests compared pairs of nested models and the simpler one was rejected in each case if a significant difference ($P < 0.05$) was detected.

2.2 Colour-marking

Between 11 January and 8 March 2003, 83 Yellowhammers and 61 Chaffinches were colour-ringed (Table 3). Each was marked with two colour-rings (Darvic and sealed with PVC cement); one was site specific, identifying the place of capture, the other was season specific (*i.e.* winter 2002-03). Within the same period, 46 Yellowhammers and 52 Chaffinches were plumage-dyed (Table 3). Coloured dye (non-toxic sheep dye) was applied to the flanks and sides of the breast, with different colours used for different sites of capture. All plumage-dyed birds were also colour-ringed. All birds seen during weekly surveys of abundance and distribution (see Section 2.5) were systematically checked for colour-marks and birds were opportunistically checked for colour-rings and plumage-dyes during other fieldwork. In order to give some quantification of the proportion of marked birds within samples searched, we attempted to count the number of individuals where either the legs or flanks were thought to have been reliably checked for colour-marks. For this pilot work, birds were not individually marked and the colour-marking was only expected to provide qualifying evidence for the dispersal distances measured by other methods. The main aim here was to assess potential of the techniques for more quantitative approaches in future.

2.3 Radio-telemetry

2.3.1 Protocol

Ten Yellowhammers, ten Chaffinches and eight Tree Sparrows were fitted with tail mounted radio transmitters in January and February 2003 (Table 4). Yellowhammers were fitted with 0.8 g tags, Chaffinches 0.5 g and Tree Sparrows 0.35 g; all tags were commercially available 'Biotrack' PIP or Micro-PIPs (www.biotrack.co.uk). Radio-tagged individuals were tracked using hand-held three-element Yagi antennae. As the detection of tagged birds was frequently restricted to less than 200 m, a systematic search protocol was used. Fifty-nine points within the 25 km^2 study area were selected based on topography, accessibility and known occurrences and concentrations of birds (the latter determined from surveys of bird distribution within the study area - see Section 2.5) and to aim for as thorough a coverage of the area as was practical (Fig 2).

A scan for all frequencies, in all directions, was made at each point and the bearing of any signal recorded. Locations were determined through triangulation based on the strength and direction of signals received. Where necessary, signals were ‘followed’ in order to ascertain a reliable location for a bird or to confirm that a bird was still alive and its radio attached. Complete coverage of all search points within the study area required between 7 – 9 hours, that is all daylight hours of a day in winter. Two complete searches were made each week while radios were active. The order in which the search points were checked was varied in order to exclude any biases introduced through checking certain points at the same time of day. A number of additional casual searches with radio-receivers were made within the study area and also at some sites with concentrations of granivorous passerines outside of the main study area.

Each radio location was plotted onto a digitised map of the study area, prepared using the ArcView Geographic Information System (ESRI), which included the distribution of the habitat and crop types listed in Table 1. Home ranges were evaluated using minimum convex polygons (MCPs) drawn around the plotted fixes for each individual bird (Kenward 1987).

2.3.2 Estimating rates of movement

The time required for conducting the systematic-search approach (necessitated through the restricted range for detection of tagged birds see Section 2.3.1) inevitably resulted in a relatively low encounter frequency of those birds. Similarly, the evaluated home ranges of individuals were minima in that no systemic searches were conducted outside of the arbitrarily defined study area. Because of these potential caveats, further analyses of the radio-tracking data were undertaken treating them as mark-recapture data (as for the ringing and retrapping analyses). All radio locations for each species were plotted in order to visually identify aggregations. Each aggregation was then defined as a ‘site’ or stratum for subsequent analysis, using a multi-strata modelling approach and the program MARK (as described in Section 2.1.2). Although all locations of tagged birds were used to identify aggregations, only those from systematic searches where included in subsequent analytical models. The sampling interval entered into the models was one week, each a combination of two complete systematic searches. For each species, survival was assumed constant across sites and time. As for the ringing and retrapping analyses, the initial models included site-specific ‘recapture’ (*i.e* detection) probabilities and different transfer probabilities for each stratum (*i.e.* across sites) and between the two directions of transfer between strata. Subsequent simplified models included common recapture probabilities across sites and common transfer probabilities for the two directions between strata pairs (see Section 2.1.2 for model selection and comparison). Note that survival estimates obtained from these models are composites of both bird survival and the longevity of the radio-tag, the recapture probabilities are a measure of the detection ability of the radios within the study area using the systematic-search approach and the transfer probabilities, the principal parameters of interest, are a measure of the likelihood of birds moving between pairs of sites.

2.4 Habitat use

Habitat use was investigated by two approaches:

1) From the locations of radio-tagged birds that could be followed as individuals, and;
2) From repeated systematic surveys of bird distribution and abundance throughout the study area.

2.4.1 Radio-telemetry

Habitat use by radio-tagged birds was investigated by comparison of the habitats found within a 30 m radius of each point where an individual bird was located with that available within its MCP home range (see Section 2.3.1). A 30 m radius is considered to have been representative of the actual habitats being utilised. Compositional analysis was used to compare proportional habitat utilisation (that around radio fixes) with the proportions of habitats available within an individual's home range (Aitchison 1986, Aebischer *et al.* 1993). As proportional data are not independent (their sum is unity), habitat proportions were transformed to log-ratios (the ratio of each habitat proportion divided by that of another, the denominator being arbitrarily chosen but of the same habitat type throughout, and that ratio then log-transformed). Zero proportions were replaced by 0.01% following Aebischer *et al.* (1993). Each log-ratio was weighted according to the number of 'fixes' (individual birds were detected at some favoured localities on multiple occasions) and the differences between the log-ratios for habitat use and availability were compared by multivariate analysis of variance and the test statistic 'Wilk's Λ'. A significant difference ($P < 0.05$) suggested that some habitat types were used preferentially, rather than simply at random based on availability. In order to avoid habitat comparisons containing large numbers of unused habitat types, the number of habitat types was reduced to the following six broad types: 1) autumn sown crops (cereals and rape, including bare till and potatoes); 2) stubbles (cereals and lupins); 3) pasture; 4) scrub; 5) woodland; and 6) 'other' (urban and other 'human sites'). Habitat availability in our study area remained constant throughout the study period. Where habitat use differed significantly from random, habitat types were ranked according to relative use from a matrix created by each possible pair of habitats and forming log-ratios of use and availability. Paired *t*-tests between these latter log-ratios indicated the pairs that differed significantly. The one of a pair of habitats that was shown to be preferred by birds was assigned a positive value, and the sum of all positives in each row of the matrix gave the ranking of that habitat.

2.4.2 Field surveys

The number of birds seen during weekly field surveys (see Section 2.5) in each habitat was used as an indication of habitat use. Compositional analysis was used to compared proportional habitat use with availability (see Section 2.4.2). For these count data, proportional use was expressed as the number of birds of a particular species in a given habitat relative to the count total on that day. Availability was expressed as the proportion of each habitat type within the study area relative to the total area. Habitat availability remained constant through the study period.

2.5 Field survey of distribution and abundance

To put any observed ranging behaviour and preferential habitat uses into context, the abundance and distribution of granivorous passerines within the study area were monitored throughout the study period. A 37-km transect was cycled weekly between 25 November 2002 and 26 February 2003, and all finches and buntings encountered were recorded (Fig 2). The same observer undertook all counts to reduce any observer bias and the route was undertaken from different starting points (selected at random) and in different directions to exclude any biases associated with time of day. All observations were plotted onto the digitised map of the study area that included habitat and crop types. Counts were compared by month to assess any variation in the abundance of the three main study species through the winter season using generalised linear modelling of the count data, assuming a Poisson error distribution and using a logarithmic link function.

3. RESULTS

3.1 Abundance of birds

Counts of the three main study species varied by month within the study period (for Yellowhammer $F_{3,13} = 14.6$, $P < 0.01$, for Chaffinch $F_{3,13} = 110.5$, $P < 0.01$, and for Tree Sparrow $F_{3,13} = 50.3$, $P < 0.01$). However, apart from low counts for Yellowhammer in November and for both Chaffinch and Tree Sparrow in February, there was little variation through the rest of the season (Fig 3).

3.2 Ringing and retrapping

3.2.1 *Captures*

A total of 1,123 captures of finches and buntings were made at all ringing sites (Table 5). 8% of Chaffinch captures were of individuals previously caught within the same winter (same-season retraps), and 0.2% were recaptures at sites different to their original or previous site of capture. For Tree Sparrows, 20.5% of all captures were of same-season retraps (3.2% between-site), for Yellowhammer 9.1% (2.6% between-site) and for Greenfinch 10.6% (none between-site). Of the species caught in relatively low numbers, 15% of Lesser Redpoll and 10% of Reed Bunting captures were same-season retraps, of which none were between-sites. There were no retraps for Brambling, Goldfinch or House Sparrow (Table 5). Additional reports of same-winter recoveries of ringed birds of which we were aware at the time of writing are: A Yellowhammer ringed at Crossford and recaught at Menstrie (24 km to the west); two Greenfinches originally ringed at Langfaulds, one recaught at Torry Bay (7 km to the south) and the other at Crossford (10 km to the south-east); two Greenfinches ringed at Craigluscar, one found dead in Dunfermline (5 km east) the other recaught in Dunblane (29 km west); and a Chaffinch ringed at West Camps was found dead in Cairneyhill village (2 km south).

3.2.2 *Estimates of movement rates using MARK*

Of the granivorous species caught, only Yellowhammer and Tree Sparrow produced between-site recaptures within the key ringing sites. For Yellowhammers, the model included four strata and for Tree Sparrows, three. Six sampling occasions (each a four-week period) were included for both species. The lowest AIC was for the simplest models for both species, in which the probability of relocation (P) was constant across all sites and the transfer probabilities (T) between pairs of sites were the same for both directions of movement. In all cases, likelihood ratio tests comparing more complex nested models found no significant differences (Table 6). In the absence of any significant justification for either rejecting or accepting any particular model, the standard convention was adopted to accept that with the lowest AIC.

Within a four-week sampling period, the program MARK estimated probabilities of 37% (SE ±17%) and 9% (±7%) for movement by Yellowhammers between pairs of sites 3.0 km and 3.6 km distant respectively (Table 7). Four other potential transfers, with between–pair distances of 2.1 – 4.9 km produced negligible transfer probabilities (Table 7). Tree Sparrows were caught at three of the key ringing sites. The likelihood of movement within a four-week sampling period between a pair of sites 3.6 km distant was estimated as 15% (±8%), and 4.9 km distant as 5% (±5%) (Table 7). The estimated probability of transfer between the remaining potential pairing (3.9 km distant) was negligible (Table 7). The two between-site movements of Chaffinches detected through ringing were both between Craigluscar and Bandrum (2.6 km), the latter not one of the key ringing sites and thus ringing and retrapping did not produce data appropriate for multi-strata modelling using the Program MARK

3.3 Colour-marking

Sightings of colour-marked birds on the same day of capture and marking are not considered. Otherwise, there were 21 sightings of colour-marked Yellowhammers and 12 of colour-marked

Chaffinches. Amongst the Yellowhammer sightings, both colour-rings and plumage dyes were visible on four occasions, only plumage dyes on seven occasions and colour-rings only on birds that were also plumage dyed but for which no dye was apparent on five occasions. The remaining five sightings of colour-marked Yellowhammers are of plumage-dyed birds for which no effort was recorded in checking for colour-rings. Amongst the Chaffinch sightings, there were ten instances when only plumage dyes were seen, and two when both plumage dyes and colour-rings were seen. In all cases, effort was made to look for both types of marks. Attempts to count the number of legs and flanks checked for colour-markings, in order to give some quantification of search effort, proved impractical because of the nature and frequency of bird movements within flocks and the restricted visibility of most areas where they occurred.

Seven sightings of colour-marked Yellowhammers were away from their original site of capture and marking:

2 individuals from Cairneyhill to Craigluscar (4.9 km)
1 sighting from Craigluscar to West Camps (3.0 km)
1 sighting from Cairneyhill to West Camps (2.1 km)
1 sighting from Cowstrandburn to Bandrum (1.0 km)
2 sightings from Craigluscar to Cowstrandburn (2.8 km)

Single colour-marked Chaffinches from Craigluscar were seen at Kinnedar (2.5 km) and Loanhead (1.0 km). All other sightings of both colour-marked species were at or close (within 300 m) to the area where they were marked.

3.4 Radio-telemetry

3.4.1 *Home ranges*

The mean active duration of the radio-tags attached to Yellowhammers was 28 days, for those attached to Chaffinches, 19 days, and, for Tree Sparrows, 11 days. Within those periods, the mean recorded home range (MCPs) for Yellowhammers was 149 ha (range <1 ha - 380 ha). Chaffinches ranged less widely with a mean home range size of 51 ha (range < 1 ha – 165 ha). The mean home range of 20 ha recorded for Tree Sparrows was probably unrepresentative because relatively few fixes were obtained and, for three individuals, these included single fixes 4.5 km from their others (Table 8).

3.4.2 *Estimates of movement using radio-telemetry as mark-recapture data*

All radio fixes for Chaffinch and Tree Sparrow lay within three discrete aggregations for each species (Fig 3). These aggregations were classed as different sites or ‘strata’ for modelling ranging behaviour. Although three sites could also be justified for Yellowhammers, three locations for one individual (all the locations determined for that bird) and a single location for another lay outside those three discrete areas. For simplicity, these locations were excluded from subsequent analyses.

The number of potential encounter occasions (each one representing a week) was 7 for Chaffinch and 8 for both Yellowhammer and Tree Sparrow, but note that birds were introduced into the model (*i.e.* tagged and released) within different weeks. For all three species, the lowest AIC was for the simplest model, in which the probability of relocation (P) was constant across all sites and the transfer probabilities (T) between pairs of sites were the same for both directions of movement. The survival probability (S) was assumed to be constant for each species across all sites. In all cases, likelihood ratio tests comparing more complex nested nested models found no significant differences (Table 9).

Within a one-week sampling period, the estimated transfer probabilities were 30% (SE ±9%) and 8% (±6%) for Yellowhammers between pairs of sites with centres 2.9 km and 1.9 km distant respectively (Table 8). The estimated probability of movement between the remaining potential between-pair transfer, with a centre-to-centre distance of 4.5 km, was negligible (Table 8). The locations of radio-tagged Yellowhammers outside of the 'sites' derived from aggregations of fixes conformed qualitatively to these results; a bird tagged at Cowstrandburn was detected 1.2 km distant, while another from West Camps was detected at 1.9 km distant.

The likelihood of movement by radio-tagged Chaffinches between the two areas (2 km from centre to centre) was estimated as 17% (± 8%) within the one-week sampling period. Probabilities of movement involving the third site (between-pair distances of 4.0 km and 1.9 km) were estimated as less than 0.01% (Table 10).

For radio-tagged Tree Sparrows, the probability of movement between a pair of sites 4.8 km distant was estimated at 20% (± 13%) and that with a between-pair distance of 3.7 km at 16% (± 14%). A negligible transfer probability was estimated for the remaining pairing (distance 3.6 km) (Table 10)

3.5 Habitat use

3.5.1 *Assessed by radio-telemetry*

To reduce the risk of biases arising from analyses of the smallest sample sizes, only individuals with over five radio fixes (systematic and casual observations combined) were considered. Within this reduced sample, some home range MCPs were linear, or nearly so, being based on overlying points or close clusters at just two separate points; these were inappropriate for subsequent analyses. Habitat use by Yellowhammers and Chaffinches, based on that within the immediate vicinity of radio fixes, differed significantly from random, based on habitat availability within individual home-ranges (for Yellowhammer, $\Lambda = 0.19$, $P < 0.001$; for Chaffinch, $\Lambda = 0.21$, $P < 0.001$). Insufficient data remained to assess relative habitat use by radio-tagged Tree Sparrows. The simplified habitat rankings in order of preference for Yellowhammers were:

Scrub > Pasture > Stubbles > Autumn sown crops > Woodland and 'Other' (Table 11)

No between-pair differences were apparent within the four most favoured habitats, but both Woodland and Other were used significantly less frequently than all the other broad habitat types.

Simplified habitat rankings in order of preference for Chaffinch were:

Scrub, Stubbles and Woodland > Pasture > Autumn sown crops > 'Other' (Table 11)

Significant differences, from paired t-tests, in the apparent use of pairs of habitats indicated a preference for both Stubbles and Woodland over Pasture, while Scrub was used significantly more than 'Other'.

3.5.2 *Assessed by field survey*

Habitat use by the three study species, determined from the counts of birds in each habitat as proportions of all individuals of that species seen within the study area, differed significantly from random based on that available throughout the whole study area (for Yellowhammer $\Lambda = 0.22$, $P < 0.001$; for Chaffinch $\Lambda = 0.21$, $P < 0.001$; for Tree Sparrow $\Lambda = 0.13$, $P < 0.001$). The simplified habitat rankings in order of preference for Yellowhammer were:

Stubbles > Pasture > Autumn sown crops > Scrub > Other > Woodland (Table 12)

Although Scrub was ranked lower, in terms of its relative use, compared to information collected by radio-telemetry, the only significant between-pair difference showed it to be used less frequently than Stubbles. Yellowhammers were also seen significantly less frequently in Autumn sown crops than in either Stubbles or Pasture. As with radio-telemetry data, there appeared to be an avoidance of both Woodland and ‘Other’.

Simplified habitat rankings in order of preference for Chaffinch were:

Stubbles > Pasture > Other > Autumn sown crops > Scrub > Woodland (Table 12)

In strong contrast to information collected by radio-telemetry, relatively few Chaffinches were seen in Woodland; the field survey was designed to determine relative abundances of birds in open farmland, however, and will not have sampled woodland as effectively.

Simplified habitat rankings in order of preference for Tree Sparrow were:

Stubbles > Pasture and Autumn sown crops > Scrub and Woodland and Other (Table 12)

Tree Sparrows were seen in Stubbles significantly more frequently than in any other habitat type.

4. DISCUSSION

4.1 Estimates of winter ranging behaviour

Both radio-telemetry and ringing-recapture produced quantified estimates of ranging behaviour in winter for the three main study species. Within the season and area of study, Yellowhammers tended to have more extensive home ranges as determined by radio-telemetry and showed a greater probability of moving between areas of the study site compared to Chaffinches, as determined by both radio-telemetry and ringing. The models developed suggest that movements between sites less than 3 km distant for Yellowhammer and less than 2 km distant for Chaffinch were readily undertaken within the sampling periods considered. Movements between sites separated by greater distances were estimated by the modelling approach as having a very low or negligible likelihood of occurrence. Colour-marking provided qualitative support for these ranges but, along with additional non-systematic recoveries of ringed birds, also demonstrated that longer distance movements by Yellowhammers at least, do indeed occur. Movements by Tree Sparrows were also modelled from data collected by both techniques but the home ranges recorded by radio-telemetry were probably serious underestimates based on their apparent readiness to disperse distances in excess of 4 km.

There was consistency in the relative likelihood of movements between comparable pairs of sites, as estimated using the program MARK, between data derived from both radio-telemetry and ringing. A direct comparison of the estimates derived from the two methods is confounded, however, by the different sampling periods (1-week for radio-telemetry and 4-weeks for ringing with recaptures) and by the assumptions involved in the modelling approach. The models assume the potential for just a single movement within the sampling period and also that the birds have no memory of the sites visited. Both these assumptions are unlikely to be met in reality. Radio-telemetry demonstrated that return movements between pairs of sites within a four-week sampling period (that used in the ringing and recapture model) do occur for all three species monitored. A direct conversion of a 30% likelihood of a Yellowhammer moving the 3 km between Craigluscar and West Camps in a one-week sampling period (as estimated from radio-telemetry) converts to a 49% likelihood of it having moved, and not returned, after four weeks, assuming that there is an equal probability of a bird returning to the original site in each subsequent week. This compares to the estimated 37% probability of detecting a movement with a four-week sampling period from ringing and retrapping, though it lies within the 95% confidence interval associated with that estimate. In all instances where comparisons of similar movements can be made, conversion of the estimate from radio-telemetry to a four-week sampling period gave a greater likelihood of movement than that estimated by ringing and retrapping but was always contained within the precision of that estimate. If birds retained no memory of sites visited and the direction of dispersal were random, then a negative relationship between distance and movement probabilities would be expected. Within the relatively limited samples of movements by individuals within this study, this was not the case, with estimated dispersal probabilities being greater for movements between apparently favoured pairs of sites than between other pairs with similar or lesser separating distances. Other multi-strata modelling studies have demonstrated the importance of sites preferred by individuals, and a retained memory of their whereabouts, in determining their movements (Hestbeck *et al.* 1991, Brownie *et al.* 1993). For granivorous passerines in winter, a favoured site is presumably one that has seed resources readily available to foraging birds.

The multi-strata models available in the program MARK assume that the sum of the survival probabilities across all strata is the same as that for the animal in question. This constraint has the effect that if a marked animal moves outside of the sampled strata, then it is assumed not to have survived, thereby biasing the survival estimate (White 2002). Using the ringing and retrapping data, the apparent survival estimate is effectively a product of actual survival and the probability that the birds remain within the discrete areas of the key ringing sites. Within the four-week sampling periods, actual survival probabilities are expected to be relatively high, and thus the apparent survival estimates will be largely determined by the probability of remaining within the immediate vicinity of the key ringing sites. Amongst the three species for which movements are modelled from retrapping ringed birds, Tree Sparrow has the greatest apparent survival rate, then Yellowhammer, and Chaffinch has the lowest estimate. Although estimates from only three species are considered here, it is perhaps surprising that these values, measures of a species' tenacity to specific sites, are negatively related to their apparent tendencies to range. The possibility of Chaffinches having a low tenacity to the study area through the winter is refuted by the high rates of relocating radio-tagged birds (see below) and also by the relatively little variation in abundance recorded through the season. The low apparent tenacity for Chaffinch may actually be a product of their trap-shyness (an awareness and ability to avoid mist nets once caught) or perhaps their selection for habitats not readily being sampled by ringing (see Section 4.2); the probability of retrapping Chaffinches (4% between the 4-week sampling periods) compared to 9% for Yellowhammer and 11% for Tree Sparrow.

Within the MARK models run for data collected from radio-tagged birds, the apparent survival estimates are a product of actual survival of the bird, radio longevity and fidelity to the study area. Within a one-week sampling period, actual survival rates are likely to be high. Relocation rates were high within each sampling period for each species (81% for Yellowhammer and 100% for both Chaffinch and Tree Sparrow), indicating the effectiveness of the searching strategy adopted. Therefore, radio longevity will have overwhelmingly determined the apparent survival estimates and thus the values will have little biological meaning.

4.2 Habitat preferences

Habitat preferences, determined from both field survey and radio-telemetry, highlighted an importance of stubbles for the three main study species through the winter. However, stubbles were not used to the exclusion of other habitats, suggesting the importance of a mosaic of habitats. Indeed, from radio-telemetry, both scrub and pasture were ranked higher than stubbles in terms of relative use by Yellowhammers, although the difference was not significant. Differences in relative habitat use as determined by the two methods were also apparent, however, with Chaffinches detected in woodland more frequently by radio-tracking individual birds than suggested by the number of birds actually seen during field surveys. Similarly, both Yellowhammer and Chaffinch were detected in scrub more frequently by radio-telemetry than was suggested by field surveys. Although the field survey was designed to measure the relative abundance of birds using open farmland, quantification of the detection efficiency for birds in the range of habitats encountered (for example, by further validation against radio-telemetry results for each species) would be needed to draw firmer conclusions on the relative importance of habitats and habitat patches from field surveys alone.

Measures of movements within the winter suggest that, of the three species studied, Tree Sparrows have the tendency to range most widely, followed by Yellowhammers and Chaffinches the least. Chaffinches were the more generalist in terms of their use of the habitats available than were Yellowhammers. The latter showed a preference for scrub, stubbles and pasture, presumably as a result of the available seed food resources found within those habitats (Robinson & Sutherland 1999); hence Yellowhammers perhaps need to range more widely in search of food through the winter. Chaffinches, with an apparent ability to find sufficient resources within a broader mosaic of habitats available within a given area, perhaps have less need to range. By analogy, Tree Sparrows would be expected to have finer habitat requirements than the other two species and have to disperse over greater distances to find sufficient resources. Although habitat use by Tree Sparrows was only effectively assessed by field survey, with its potential biases (see above), a greater preference for stubbles over all other habitat types was the most apparent in that species.

Continuing this comparison of the three study species, the more dispersive and potentially most habitat-specialist Tree Sparrow has undergone the most dramatic decline in breeding numbers, while the populations of the apparently generalist and least dispersive Chaffinch have remained stable or even increased (Baillie *et al.* 2001). Both the measured ranging behaviour and habitat selectivity of Yellowhammers were intermediate between those of the two other species and the recent population trend has also been intermediate for Yellowhammers, with their decline starting later and occurring at a slower rate than that of the Tree Sparrow (Baillie *et al.* 2001).

4.3 Efficacy of methods used

4.3.1 Radio-telemetry

For this pilot work, quantified estimates of winter ranging behaviour were obtained from a relatively small sample of radio-tagged individuals (10 Yellowhammer, 10 Chaffinch and 8 Tree Sparrow) that were monitored for relatively short periods of time (means of 28, 19 and 11 days respectively). In any such future work, the sample of radio-tagged birds will not only be limited by the number of tags available but also by the manpower available to follow them and the ability to find the tagged birds. The restricted transmission ranges and longevity of the small radios necessarily used on small birds, birds feeding on the ground reducing transmission range even further, and undulating topography potentially creating 'blind' areas, all combined to reduce the detection ability for all three species. It is generally recommended that a minimum of 50 radio fixes are required for each animal tagged in order to undertake meaningful analyses of home ranges using standard techniques and software (Kenward 1987). To obtain a similar number of fixes for an individual granivorous passerine would require considerable manpower, and could even then still be compromised by the difficulties of detection, and also by the longevity of the radios. The latter could also compromise the independence of each data point collected, in that many fixes would have to be taken within a short time period giving rise to autocorrelation problems. We believe that the approach taken in this pilot study was a workable compromise, whereby the systematic searching for up to 20 tagged individuals at anyone time by one fieldworker covering a 25 km^2 study area provided data that, when analysed appropriately (using a 'mark-recapture' approach) gave satisfactory measures of winter ranging behaviour for the study species followed. An increased sample size would be essential in order to give increased precision to the estimates derived from a study site and to give increased statistical power to allow further testing of some of the key modelling assumptions. A staggered approach to tagging whereby in the order of 20 active radios were on birds at any one time throughout the winter period November to February inclusive would permit the following of 60 individual birds per fieldworker per study site. This pilot work was undertaken in just a single study area but replicate study areas and several winters of data would be essential to assess variations in ranging behaviour that could result from regional differences in habitat composition, bird population densities and the influence of weather.

4.3.2 Ringing

Estimates of ranging behaviour were generated from 42 within-season retraps of ringed Yellowhammers, 21 of Chaffinches and 24 of Tree Sparrows. As with the radio-tracking data, the simplest models were selected as the most parsimonious based on AIC values. For Tree Sparrow, however, and to a lesser degree for Yellowhammer, the likelihood ratio tests between these and more complex models, one with site-specific recapture probabilities (the most general model) and the other with common recapture probabilities across all sites (a reduced model) indicated only marginally non-significant differences (Table 6). Although individual characteristics of the key ringing sites, such as shrub height and exposure, will influence capture likelihoods, the trapping protocol will also exert an influence. For this pilot study, ringing effort was related to bird abundance within a protocol that ensured that all key sites were sampled at least once within each sampling period (Section 2.1.2). The influence of a more rigid trapping protocol on the precision of the estimates of ranging behaviour is worthy of further investigation.

In order to generate the retraps of granivorous passerines needed to begin to model their ranging behaviour in this study, the total number of Yellowhammers caught during the winter 2002-03 within the study area exceeded 10% of the typical annual totals ringed in Britain and Ireland in recent years. For Tree Sparrows, that total was over 5% of typical recent annual totals and for Chaffinch less than 2%. To complete the 65 ringing sessions that achieved these totals required in the order of 400 man-hours from trained and qualified bird ringers, including a large input by volunteers. Such an effort is probably as intensive as could realistically have been achieved especially considering the vagaries of winter weather (2002-03 was a relatively benign winter). Therefore, the precision of ranging estimates from ringing and retrapping is unlikely to be improved upon within a single study area. As with radio-telemetry, however, replicate study areas and winters of data are needed to assess the potential variation in ranging behaviour before these can be used for applied purposes.

4.3.3 Colour-marking

Yellowhammers and Chaffinches were colour-marked by cohort (site of capture and season) rather than individually. As such, only qualified measures of ranging behaviour could be obtained in support of the two quantitative methods used. An important assessment of the colour-marking methods for further use was possible for the two species, however. Colour-rings could be seen and their colours determined on Yellowhammers, especially with the use of a tripod-mounted telescope. On the other hand, colour-rings proved very difficult to see on Chaffinches, even when other marks indicated that a bird had been colour-ringed, without even trying to determine individual combinations. Our experience within the study area was that Chaffinches tended to feed on the ground or rest in dense cover where, in both instances, their legs were obscured. Yellowhammers were more obliging and tended to perch in exposed positions on trees and shrubs giving clear views of their legs. Individually colour-ringing Yellowhammers, and subsequently searching for them, is likely to generate useful information on ranging behaviour and potentially also on the breeding origins of those birds using the winter feeding areas. For Chaffinches, the technique may have very limited use.

Plumage dyes were readily seen on both Yellowhammers and Chaffinches, and indeed proved a useful marker with which to test the efficacy of colour-ringing. However, the dyes faded within a couple of weeks and the rate of fading varied between individuals. This technique is therefore probably not suitable for a quantitative approach and is limited to providing supporting evidence to measures of ranging behaviour obtained by other techniques.

4.3.4 The study site

Selection of the study site was based on its proven history of providing catches of granivorous passerines by an active local team of voluntary bird ringers. Its size and boundaries were largely arbitrary but aimed to include an adequate number of key ringing sites at varying distance from each other but also be of an appropriate size for a single fieldworker to ‘cover’ in a single day. For the three chosen study species, and in the winter considered, the study area proved highly suitable for this pilot work to assess the possibility of quantifying the winter ranging behaviour of some granivorous passerines. However, how typical the area is would need to be tested across space and time. Replicate sites in other parts of Scotland, or wider at the UK level, with work carried out over a number of winters is required. During the pilot study, sufficient data were obtained for the three main study species within the 25 km^2 study area. However, although 160 Greenfinches were caught during the season, which generated at least three within-season recoveries at sites other than where ringed, none were within the study area. This suggests that the area covered *may* not have been sufficiently extensive to effectively measure ranging behaviour by that species at least.

Bait, mostly grain, was used at all ringing sites to concentrate birds for catching. The baiting regime ensured that birds were not totally reliant on such provisioning, however (Section 2.1.1). Bait will certainly have influenced the distribution and therefore movements of birds. Within the study area, some sites have been baited in winter, to some degree, for at least five years. Accordingly, movements could have become entrained in local bird populations from year to year as older individuals use these sites, and attract other birds in the process. The selection of ringing sites, and therefore sites to bait, was initially based on the presence of granivorous passerines without baiting and so the influences of ‘naturally’ occurring food and of bait are confounded. In reality, provisioning with supplementary food, in this study to facilitate the capture of birds, effectively mimics the creation of food sources through other deliberate (*e.g.* game bird-feeding or unharvested cropping as part of an agri-environment package) and non-deliberate (*e.g.* grain spillage or within fodder for livestock) provisioning, all of which are spatially isolated and, to varying extents, tend to be recurrent from year to year. Accordingly, we are confident that the ranging behaviour by birds observed amongst baited ringing sites will be representative of that between other food sources within a modern agricultural environment, where a significant proportion of the seed food resource is provided as part of deliberate actions by the farming managers.

4.4 Potential applications

Knowledge of the ranging behaviour of granivorous passerines on farmland has clear implications for the advocacy and implementation of conservation prescriptions. To maintain viable populations of granivorous birds through the winter, land management should ensure adequate and available seed resources (*e.g.* amongst stubbles, in weedy patches or through crops specifically grown for that purpose) that remains available through the winter season. The distribution of such seed resources should be on a scale appropriate to the usual ranging abilities of the target bird species. Suitable seed resources should perhaps not be too localised in order to maintain connectivity between populations. In practice, the provision of areas of winter feeding can be resource expensive in terms of the actual costs of creation, for example through agri-environment schemes or set-aside options, or through profits forgone by not putting all land to its most intensive agricultural use. As such, knowledge of the scale at which such areas should be created or maintained can offer value for money in terms of conservation benefit against cost.

Although we acknowledge the limitations of this single winter of pilot study, our initial findings suggest that Yellowhammers could respond to the maintenance of seed supplies in open habitats (stubbles and lightly grazed pasture) and within semi-enclosed habitats such as scrub (though not woodland), provided there is sufficient seed available through the winter and that the resources are located within 3 km of each other. Tree Sparrows perhaps have more specific requirements in that seed resources potentially need to be in more open habitats (*e.g.* within stubbles) but not necessarily in quite such close proximity. These are examples only; further work is required for the confident advocacy of such prescriptions for conservation. For example, it may be that Tree Sparrows, use excessive energetic resources by ranging widely, and comprising their overall fecundity, hence their more marked decline at the UK level.

4.5 Future work

The needs for a broader study with replicate study areas and to collect data over a number of winters in order to assess the variation in ranging behaviour have already been discussed (Section 4.3). The ranging behaviour of some other species could also be included within a broader study, although issues of appropriate study area size and the intensity of fieldwork required to collect sufficient data need to be considered (Section 4.3.4).

Further developments of the models for quantifying ranging behaviour could make fuller use of the data that can be collected. The relationships between probabilities of movement and distances between sites were complex for all three study species, implying that some sites are preferred and that movements can be conditional upon a knowledge of the whereabouts of those sites. With a greater number of birds marked and recaptured or relocated, analyses that include conditional likelihoods of transfers between sites based on individuals' previous occurrences at a site (*i.e.* a retained memory of favoured sites), could provide more realistic estimates of movement probabilities. A comparable approach has been adopted for modelling movements by Canada Geese between widely dispersed wintering areas (Hestebeck *et al.* 1991, Brownie *et al.* 1993). Calibration of the different quantifying methods, in this study, radio-tracking and ringing, could permit the incorporation of data derived from different sources into the same models, potentially increasing the precision of transfer probability estimates. Similarly, a more powerful approach with the sparse data (that is perhaps inevitable with such a study) might be to include inter-site distance as a continuous covariate rather than looking at the different transfers as separate levels of a factor (as in the reported analyses).

Knowledge of what makes a site preferred by individuals of any particular species has clear practical applications. To sustain a population of birds through a winter requires that sufficient 'preferred sites' remain within an acceptable ranging distance. For granivorous passerines, this will depend on seed resources at different sites, their availability and how they vary through the winter. It will be of little use if there is ample food in November and December but none available within a radius appropriate for the target species in January and February. A measure of the carrying capacity of patches managed or retained for conservation purposes, and the periodicity of that carrying capacity, could be incorporated into spatial models. Comparable approaches have been developed for wildfowl with similarly restricted winter foraging areas (Goss-Custard *et al.* 2003). Further investigation of this would usefully include the experimental manipulation of bait to mimic the depletion of seed resources at certain sites and their provision at others through the winter period.

Some wider issues that could be addressed in a broader study include the determination of over-winter survival rates, and influencing factors, for granivorous passerines. Over-winter survival has been identified as a potential key demographic rate driving the declines of several granivorous passerine species (Section 1.1), yet almost nothing is known about the individual physiological condition or external environmental factors driving inter-annual variation. With an enhanced knowledge on ranging behaviour, and therefore the likelihood of emigration from particular areas, estimates of over-winter survival should be obtainable from mark-recapture data (from ringing or colour-ringed individuals) over a number of years. The biometric data collected whilst handling birds for ringing (Section 2.1.1) could also inform the influence of individual physiological condition. Similarly, the biometric data could also identify the geographic origins of some populations with the potential to investigate how resident and immigrant populations of the same species interact in winter. The biometric data already collected will be hopefully analysed separately by volunteers.

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Table 1 The extent of crop types and other broad habitats within the West Fife study area in winter 2002-03.

CROP or HABITAT	AREA (ha)	% Composition
Autumn sown cereal	406	16
Autumn sown rape	97	4
Lupins	36	1
Pasture	788	31
Till	42	1.5
Potatoes	19	<1
Set aside	19	<1
Scrub	60	2.5
Stubble	367	15
Urban	195	8
Open water	20	<1
Woodland	212	8.5
Other	234	9

Table 2 The number of ringing sessions undertaken at the four key catching sites, and others combined, in each month, October 2002 – March 2003.

SITE	MONTH					
	Oct	Nov	Dec	Jan	Feb	Mar
Craigluscar	1	3	5	4	2	1
West Camps	0	1	2	3	2	1
Cairneyhill	0	1	2	2	3	1
Crossford	1	3	2	3	1	2
Other	0	4	7	2	5	2
TOTAL	2	12	18	14	13	7

Other sites include Easter Clunes and Cowstrandburn within the main study area (Fig 1) plus two additional areas, Bandrum (NT0391) 1 km to the north and Langfaulds (NT0093) 3.5 km to the north-west.

Table 3 The number of birds colour-marked at sites in the West Fife study area, 11/1/2003 – 8/3/2003.

	YELLOWHAMMER		CHAFFINCH	
SITE	Colour-ringed	Plumage-dyed	Colour-ringed	Plumage-dyed
Craigluscar	23	19	43	42
Cairneyhill	24	0	4	3
West Camps	14	10	10	6
Crossford	17	17	3	3
Cowstrandburn	5	0	1	1

Note: 1) All plumage-dyed birds were also colour-ringed.
2) All radio-tagged birds (Table 3) were also colour-ringed but not plumage-dyed.

Table 4 The locations and dates of radio-tagging granivorous passerines in West Fife, winter 2002-2003.

SPECIES	Radio frequency	Site tagged	Date tagged	Age*	Sex+
Chaffinch	196	West Camps	08/02/2003	6	F
Chaffinch	344	Cairneyhill	19/01/2003	6	F
Chaffinch	697	Glassiebarns	09/02/2003	5	M
Chaffinch	708	West Camps	19/01/2003	5	M
Chaffinch	722	Craigluscar	18/01/2003	5	M
Chaffinch	731	Craigluscar	18/01/2003	5	M
Chaffinch	740	Glassiebarns	09/02/2003	5	F
Chaffinch	751	West Camps	19/01/2003	5	F
Chaffinch	760	West Camps	08/02/2003	5	M
Chaffinch	773	Glassiebarns	09/02/2003	5	F
Tree Sparrow	782	Craigluscar	18/01/2003	4	
Tree Sparrow	815	Craigluscar	18/01/2003	4	
Tree Sparrow	173	Cairneyhill	18/02/2003	4	
Tree Sparrow	823	Cairneyhill	18/02/2003	4	
Tree Sparrow	870	Cairneyhill	18/02/2003	4	
Tree Sparrow	854	Cairneyhill	18/02/2003	4	
Tree Sparrow	791	Cairneyhill	18/02/2003	4	
Tree Sparrow	848	Cairneyhill	18/02/2003	4	
Yellowhammer	208	Cowstrandburn	09/02/2003	5	M
Yellowhammer	229	Cairneyhill	13/02/2003	5	M
Yellowhammer	240	West Camps	08/02/2003	6	F
Yellowhammer	253	Craigluscar	18/01/2003	5	F
Yellowhammer	270	Craigluscar	18/01/2003	5	M
Yellowhammer	287	West Camps	08/02/2003	5	F
Yellowhammer	298	West Camps	08/02/2003	5	F
Yellowhammer	309	Craigluscar	18/01/2003	5	M
Yellowhammer	324	West Camps	18/01/2003	6	F
Yellowhammer	338	Craigluscar	18/01/2003	5	F

* Age using EURING codes (Redfern & Clark 2001) where:

4 - hatched before current calendar year.
5 - hatched within the previous calendar year.
6 - hatched within the calendar year two years previous.

+ M – Male, F – Female. Tree Sparrows can not be reliably sexed.

Table 5 The frequency of captures of granivorous passerines within the West Fife study area, winter 2002 – 03.

SPECIES	Number of all Captures	Recaptures Same-site	Between-site
Chaffinch	522	41	1
Brambling	5	0	0
Greenfinch	160	17	0
Goldfinch	14	0	0
Lesser Redpoll	20	3	0
House Sparrow	3	0	0
Tree Sparrow	117	20	4
Reed Bunting	40	4	0
Yellowhammer	232	15	6

Note: A recapture is a bird caught for at least the second time. A between-site recapture refers one that was caught at a site different to its previous encounter.

Table 6 A comparison of the models for mark-recapture estimates of movement probabilities using the program MARK on ringing and retrapping data.

	General model	AIC	Reduced model	AIC	Likelihood ratio test X^2	df	*P*
YELLOWHAMMER							
	{ScPsTs}	184	{ScPcTs}	183	5.6	3	0.13
	{ScPcTs}	183	{ScPcTp}	169	1.0	6	0.98
TREE SPARROW							
	{ScPsTs}	156	{ScPcTs}	154	4.7	2	0.09
	{ScPcTs}	154	{ScPcTp}	152	5.6	3	0.13

Model parameters:

Sc: Survival constant across all sites.
Ps: Recapture probability is site dependant.
Pc: Recapture probability constant across all sites.
Ts: Transfer probability is both pair and direction dependant.
Tp: Transfer probability is pair dependant but the same for either direction of movement.

Table 7 Model parameters for mark-recapture estimates of movement probabilities using the program MARK on ringing and retrapping data.

YELLOWHAMMER	**Parameter Estimate**	**Standard Error**	**Distance (km)**
Survival probability	0.73	0.22	
Probability of retrapping	0.09	0.05	
Transfer probability A↔B	<0.0001	<0.0001	4.9
Transfer probability A↔C	0.37	0.17	3.0
Transfer probability A↔D	0.09	0.07	3.6
Transfer probability B↔C	<0.0001	<0.0001	2.1
Transfer probability B↔D	<0.0001	<0.0001	3.9
Transfer probability C↔D	<0.0001	<0.0001	3.8
CHAFFINCH			
Survival probability	0.56	0.18	
Probability of retrapping	0.04	0.02	
Transfer probability A↔B	-	-	4.9
Transfer probability A↔C	-	-	3.0
Transfer probability A↔D	-	-	3.6
Transfer probability B↔C	-	-	2.1
Transfer probability B↔D	-	-	3.9
Transfer probability C↔D	-	-	3.8
TREE SPARROW			
Survival probability	0.85	0.19	
Probability of retrapping	0.11	0.05	
Transfer probability A↔B	0.05	0.05	4.9
Transfer probability A↔D	0.15	0.08	3.6
Transfer probability B↔D	<0.0001	<0.0001	3.9

Notes:

1) The survival probability is a product of the bird's survival and its likelihood of remaining within the immediate vicinity of ringing sites.

2) There were no between-site movements for Chaffinch within the key ringing sites.

Table 8 Descriptive parameters for the home ranges of Yellowhammer, Chaffinch and Tree Sparrow determined by radio-tracking in West Fife, winter 2003.

YELLOWHAMMER

Radio frequency	MCP home range (ha)	Max. internal distance of home range (km)	No. of fixes	Duration (days)
208	1.7	1.4	5	23
229	29.9	1.2	9	42
240	104.8	2.3	9	17
253	312.7	2.9	15	37
270	2.9	0.8	5	25
287	0.2	0.1	13	20
298	380.3	3.6	9	20
309	183.0	3.4	8	20
324	200.5	4.0	7	33
338	275.0	3.8	20	38
Mean	149.1	2.3	10	27.5
Standard error	47.3	0.4	1.5	2.9

CHAFFINCH

Radio Frequency	MCP home range (ha)	Max. internal distance of home range (km)	No. of fixes	Duration (days)
196	26.8	1.1	3	10
344	16.9	1.1	23	31
697	7.3	0.9	4	13
708	18.5	3.1	10	22
722	160.3	3.0	13	30
731	165.1	3.4	8	25
740	58.2	1.6	6	17
751	0.1	0.1	5	16
760	11.9	1.3	3	10
773	42.5	1.7	7	13
Mean	50.7	1.7	8.2	18.7
Standard error	20.5	0.3	1.9	2.5

TREE SPARROW

Radio Frequency	MCP home range (ha)	Max. internal distance of home range (km)	No. of fixes	Duration (days)
782	2.9	0.9	3	5
791	36.4	4.3	5	11
815	31.0	1.4	3	14
823	42.0	4.5	8	11
834	39.5	4.0	10	18
848	0.8	0.4	6	9
854	5.3	0.4	10	11
870	3.0	0.5	6	9
Mean	20.1	2.0	6.4	11
Standard error	7.0	0.7	1.0	1.4

Table 9 A comparison of the models for mark-recapture estimates of movement probabilities using the program MARK on radio-tracking data.

	General model	AIC	Reduced model	AIC	Likelihood ratio test X^2	df	*P*
YELLOWHAMMER							
	{ScPsTs}	138	{ScPcTs}	133	1.6	2	0.46
	{ScPcTs}	133	{ScPcTp}	127	2.1	3	0.54
CHAFFINCH							
	{ScPsTs}	90	{ScPcTs}	83	0	2	1.00
	{ScPcTs}	83	{ScPcTp}	75	0	3	1.00
TREE SPARROW							
	{ScPsTs}	70	{ScPcTs}	57	0	2	0.99
	{ScPcTs}	57	{ScPcTp}	53	1.6	1	0.20

Model parameters:

Sc: Survival constant across all sites.
Ps: Recapture probability is site dependant.
Pc: Recapture probability constant across all sites.
Ts: Transfer probability is both pair and direction dependant.
Tp: Transfer probability is pair dependant but the same for either direction of movement.

Table 10 Model parameters for mark-recapture estimates of movement probabilities using the program MARK on radio-tracking data.

YELLOWHAMMER	Parameter Estimate	Standard Error	Distance (km)
Survival probability	0.91	0.06	
Probability of relocation	0.81	0.07	
Transfer probability D↔E	0.30	0.09	2.9
Transfer probability D↔F	<0.0001	0	4.5
Transfer probability E↔F	0.08	0.06	1.9
CHAFFINCH			
Survival probability	0.76	0.07	
Probability of relocation	1.00	0	
Transfer probability A↔B	0.17	0.08	2.0
Transfer probability A↔C	<0.0001	0	4.0
Transfer probability B↔C	<0.0001	0	1.9
TREE SPARROW			
Survival probability	0.59	0.12	
Probability of relocation	1.00	<0.0001	
Transfer probability G↔H	0.20	0.13	4.8
Transfer probability G↔I	<0.0001	0	3.6
Transfer probability H↔I	0.16	0.14	3.7

Note: Survival probability is a combination of that of the bird and that of the radio.

Table 11 Ranking matrices for Yellowhammer, Chaffinch and Tree Sparrow based on comparing proportional habitat use within 30-m radii of radio locations with the proportion of each habitat within the individual's MCP range.

a) **Yellowhammer**

Numerator Denominator

	AC	ST	PA	SC	WD	OT	Rank
AC		-	-	-	+++	+++	2
ST	+		-	-	+++	+++	3
PA	+	+		-	+++	+++	4
SC	+	+	+		+++	+++	5
WD	---	---	---	---			0
OT	---	---	---	---			0

SC>PA>ST>AC>(WD=OT)

b) **Chaffinch**

Numerator Denominator

	AC	ST	PA	SC	WD	OT	Rank
AC		-	-	-	-	+	1
ST	+		+++	-	+	+	4
PA	+	---		-	---	+	2
SC	+	+	+		-	+++	4
WD	+	-	+++	+		+	3
OT	-	-	-	---	-		0

(ST=SC) > WD > PA > AC > OT

Notes:

1) AC – Autumn sown crop; ST – Stubbles: PA – Pasture; SC – Scrub; WD – Woodland; OT – Other.
2) '+' Indicate more frequent use by the numerator of the pairs of habitat types.
3) '+++' Indicate a significant difference (paired t-test) between use of the pairs of habitats.

Table 12 Ranking matrices for Yellowhammer, Chaffinch and Tree Sparrow based on comparing the counts of each species as a proportion of a total count in a particular habitat with the proportion of each habitat within the study area.

a) **Yellowhammer**

Numerator				Denominator			
	AC	ST	PA	SC	WD	OT	Rank
AC		---	---	+	+	+	3
ST	+++		+	+++	+++	+++	5
PA	+++	-		+	+++	+++	4
SC	-	---	-		+++	+++	2
WD	-	---	---	---		-	0
OT	-	---	---	---	+		1

ST > PA > AC > SC > OT > WD

b) **Chaffinch**

Numerator				Denominator			
	AC	ST	PA	SC	WD	OT	Rank
AC		---	---	+	+++	-	2
ST	+++		+	+++	+++	+++	5
PA	+++	-		+++	+++	+++	4
SC	-	---	---		+	-	1
WD	---	---	---	-		-	0
OT	+	---	---	+	+		3

ST > PA > OT > AC > SC > WD

c) **Tree Sparrow**

Numerator				Denominator			
	AC	ST	PA	SC	WD	OT	Rank
AC		---	-	+++	+++	+++	3
ST	+++		+++	+++	+++	+++	5
PA	+	---		+++	+++	+++	3
SC	---	---	---		+	-	1
WD	---	---	---	-		+	1
OT	---	---	---	+	-		1

ST > (PA = AC) > (SC = OT = WD)

Notes:

1) AC – Autumn sown crop; ST – Stubbles: PA – Pasture; SC – Scrub; WD – Woodland; OT – Other.
2) '+' Indicate more frequent use by the numerator of the pairs of habitat types.
3) '+++' Indicate a significant difference (paired t-test) between use of the pairs of habitats.

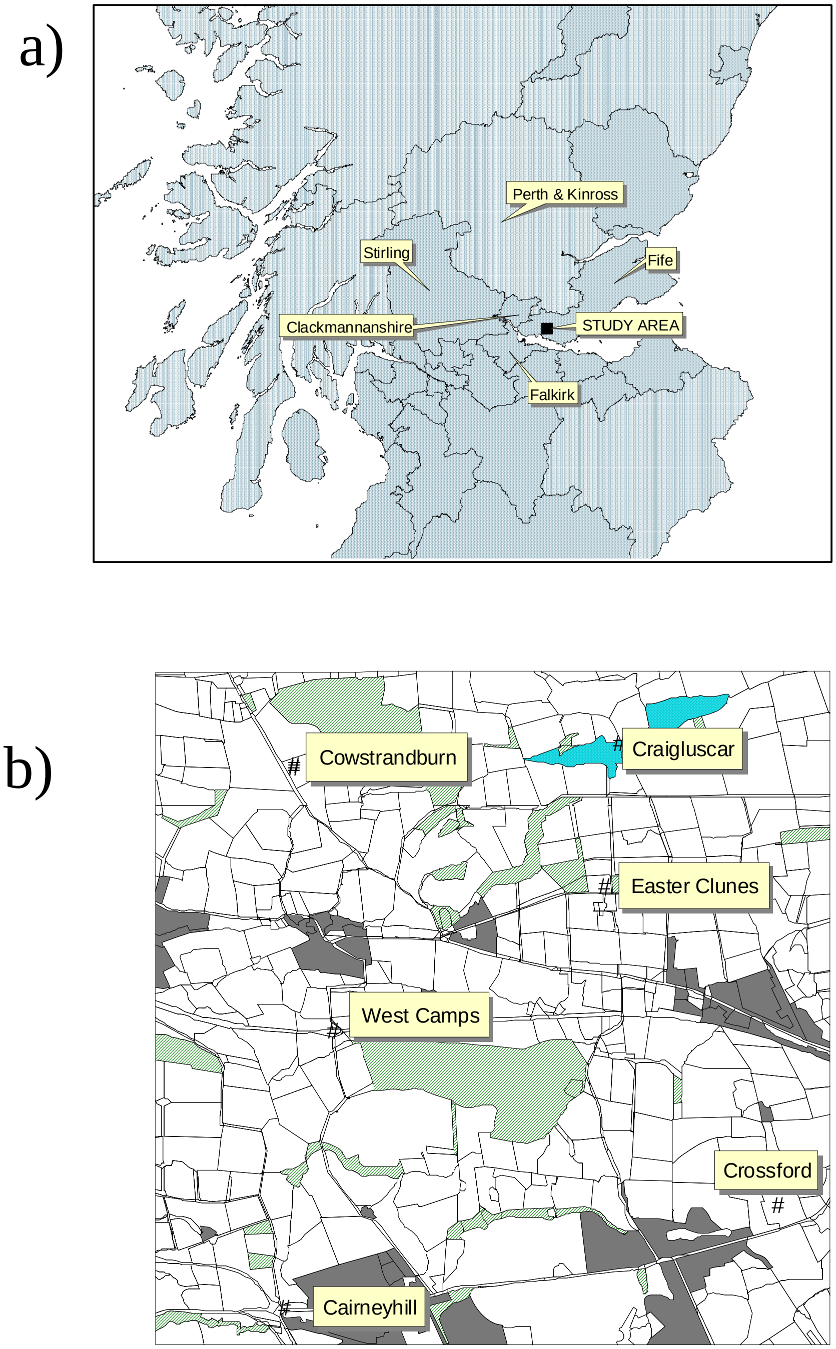


Figure 1 The location of (a) the study area in West Fife, and (b) the ringing sites within the study area. The study area is 5 km by 5 km, centred on 56° 05' N, 3° 31' W.

Figure 2 The survey route (thick dark lines) to assess the abundance and distribution of granivorous passerines and the systematic scanning points (circles) for radio-tracking. The area included in the figure is a 5 km x 5 km square, 56° 05’ N, 3° 31’ W.

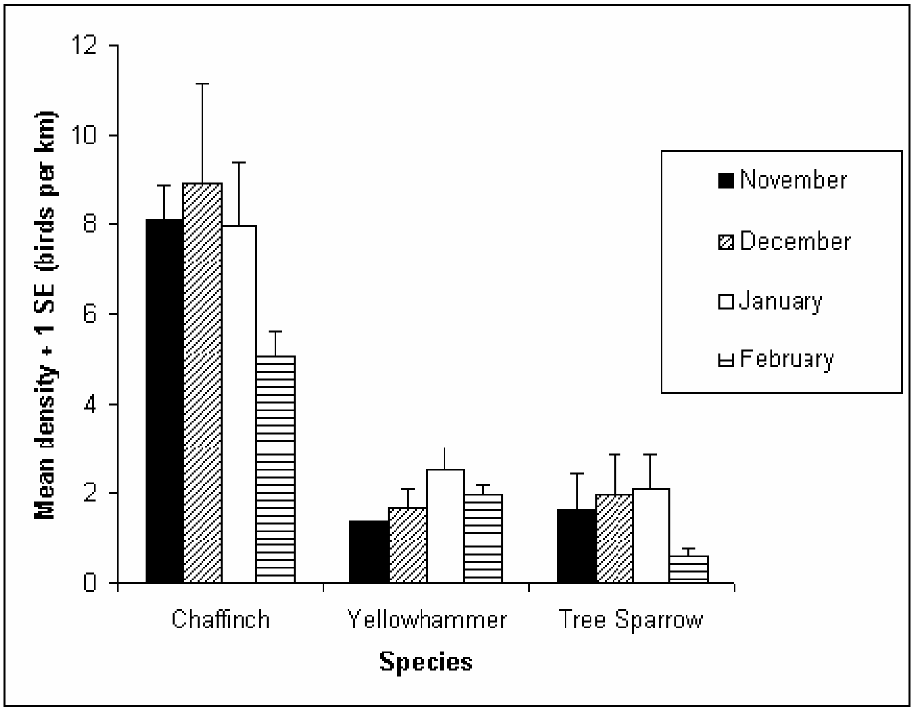


Figure 3 Mean monthly counts of Chaffinch, Yellowhammer and Tree Sparrow in the West Fife study area, November 2002 – February 2003.

Figure 4a The aggregated sites derived from radio-tracking fixes of Chaffinch used in the MARK analysis to estimate ranging behaviour.

Figure 4b The aggregated sites derived from radio-tracking fixes of Tree Sparrow used in the MARK analysis to estimate ranging behaviour.

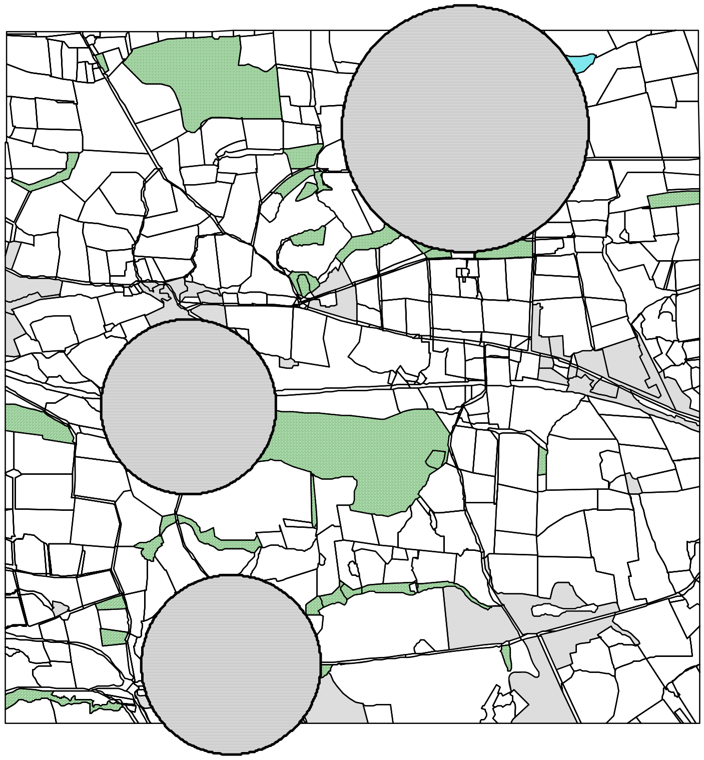
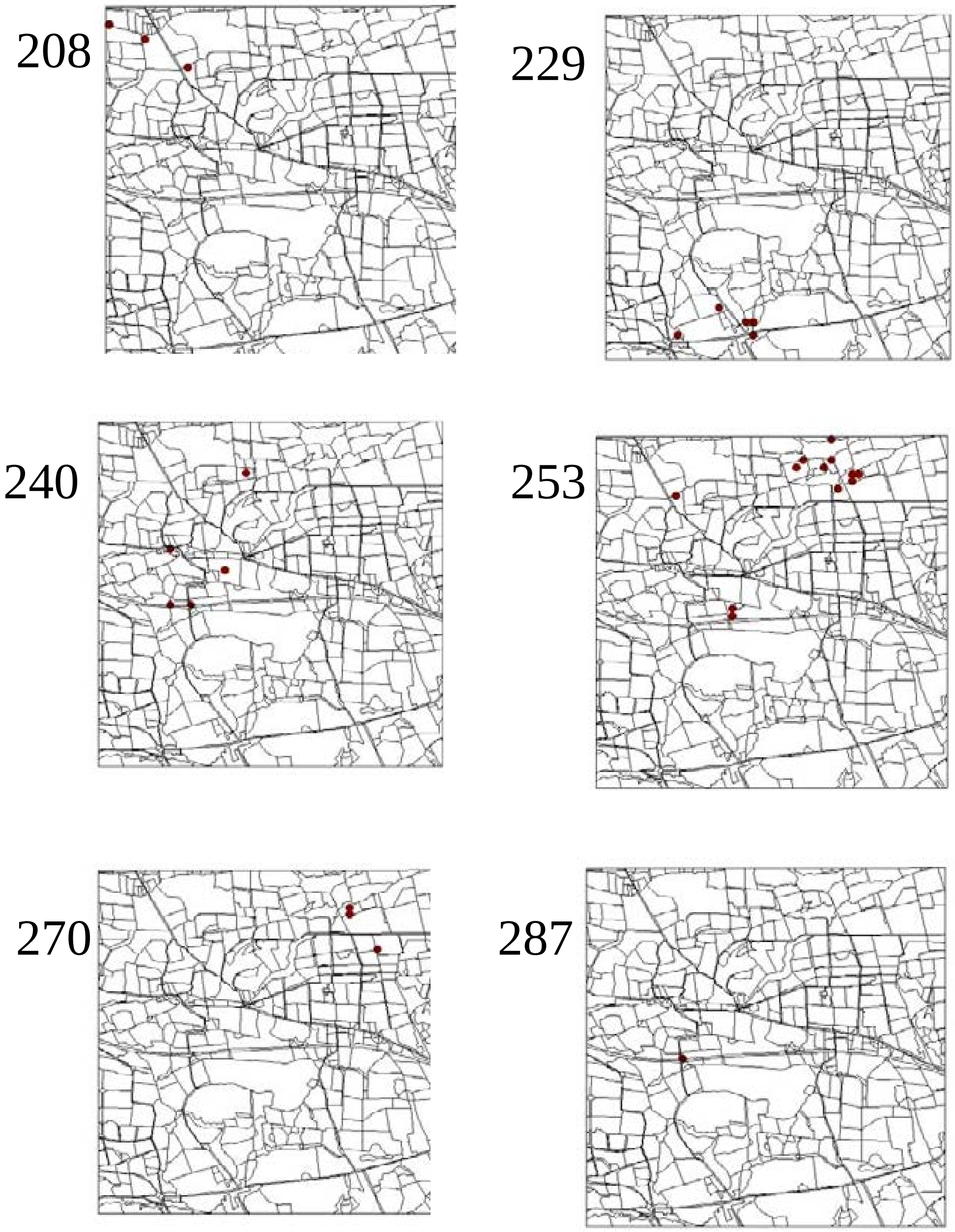
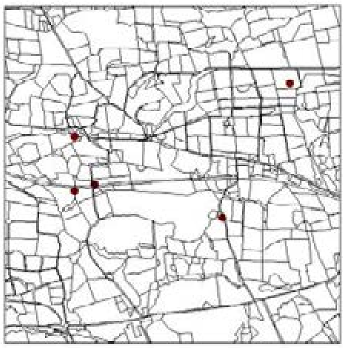


Figure 4c The aggregated sites derived from radio-tracking fixes of Yellowhammer used in the MARK analysis to estimate ranging behaviour.

Appendix 1 Radio locations for individually tagged Yellowhammers. Note that some points are superimposed – the number of fixes obtained for each individual is given in Table 8.



298



309

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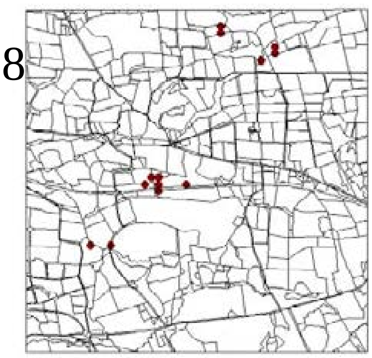
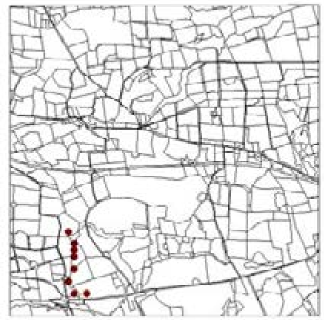
338



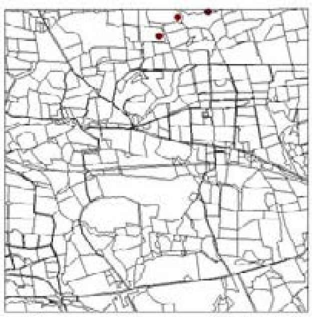
Appendix 2 Radio locations for individually tagged Chaffinches. Note that some points are superimposed – the number of fixes obtained for each individual is given in Table 8.

196

344



697



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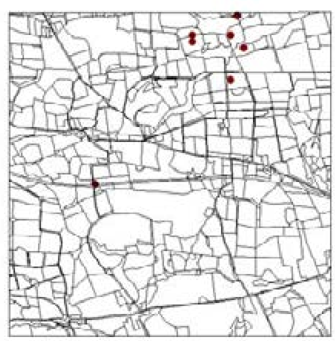

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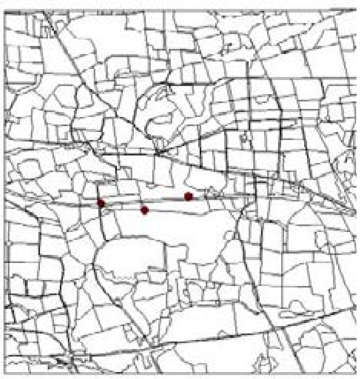


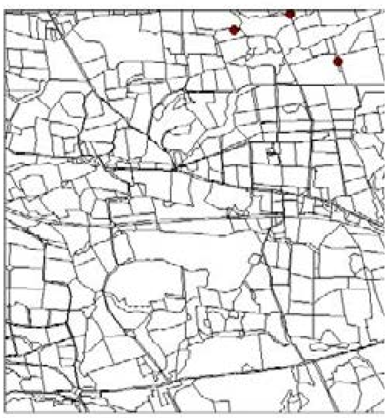
773

Appendix 3 Radio locations for individually tagged Tree Sparrows. Note that some points are superimposed – the number of fixes obtained for each individual is given in Table 8.

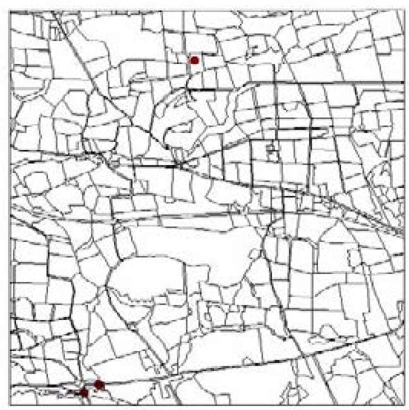
782

791

815



823



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