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The ranging behaviour of some granivorous passerines in winter on farmland: Report for the second season Winter 2003/04

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EXCECUTIVE SUMMARY

1. This report describes a second season of fieldwork (in 2003/04) to investigate the ranging behaviour of seed-eating finches and buntings (granivorous passerines) on farmland in winter and follows from a pilot study carried out in 2002/03.

2. Knowledge of the ranging behaviour of granivorous passerines on farmland in winter would permit targeted conservation measures to be delivered in a cost-effective way by identifying what is the optimal scale and also timing at which to provide winter food sources for birds.

3. Systematic mark-recapture ringing was undertaken in two 25 km^2 study areas, one in West Fife (the site for the pilot study) and the other in East Lothian. 16 Yellowhammers and 16 Chaffinches were radio-tracked in West Fife. Systematic survey work monitored bird abundance through the winter in the two study areas.

4. A total of 795 capture events of granivorous passerines were made in West Fife and 714 in East Lothian during the winter 2003/04. Data gathered on movements from mark-recapture was sparse and it was only possible to model the movements for one species (Yellowhammer) in one study area (West Fife) where they ranged between sites 3 – 5 km distant. 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.

5. For the two species radio-tagged (Yellowhammer and Chaffinch), both tended to range greater distances in the early half of the winter (November – December) than in the late half (January-February). For Yellowhammers, the difference was statistically significant (mean distance between systematically determined radio fixes at 3 day intervals: 1.11 km (SE = 0.19) and 0.57 km (±0.11)). There were no significant differences between the two study years for either Yellowhammer or Chaffinch. Some radio-tagged Chaffinches may have left the study area in the first half of the winter.

6. Including data from both study years for three radio-tagged species: Tree Sparrows tended to range the greatest distances (mean distance between systematically determined radio fixes at 3 - 4 day intervals of 1.30 km (±0.47)); Yellowhammers were intermediate (0.75 km (±0.09)) and Chaffinches ranged the least distance (0.65 km (±0.08)).

7. The above ranking by species is the same as that determined by mark-recapture ringing in West Fife in 2002/03. The number of captures, and also abundance in the West Fife study area as determined from field surveys tended to be lower for most species (including Chaffinch and Tree Sparrow) in 2003/04 than in 2002/03. In contrast, House Sparrow and Yellowhammer were more abundant with a correspondingly greater number of captures.

8. Radio-tracking and field surveys of Yellowhammers and Chaffinches highlighted the importance of scrub and some stubbles in West Fife. Field surveys in East Lothian did not identify any habitat preferences, which may have been a result of intensive and continuous feeding (baiting) at the ringing sites; the surveys in East Lothian were less frequent than in

West Fife, however, with an associated reduced power to detect differences in habitat selection.

9. All roost sites of radio-tagged birds were within the individual's normal diurnal 'home range'.

10. Further knowledge on the winter ranging behaviour of granivorous passerines will be best delivered by radio-tracking studies with intensive and systematic monitoring of tagged individuals. Ringing can provide broader information on regional, within season and between season movements provided sufficiently large numbers are marked and there is and adequate spread and intensity of capture effort.

1. INTRODUCTION

1.1 Background

The deleterious effects of agricultural intensification on the abundance and diversity of birds on farmland are now generally accepted (Fuller *et al.* 1995, Donald *et al.* 2001, Benton *et al.* 2003). Reversing the declines of key bird species in agricultural environments is now a high priority as recognised by the strategy proposed by the Scottish Biodiversity Forum for the Scottish Executive, by Defra's adoption as one of its Public Service Agreement targets to reverse some of these declines by 2020 and by the inclusion of a numbers of farmland birds as species prioritised by the UK Government's Biodiversity Action Plan. The exact mechanisms by which changes in farming practice have impacted on bird populations is widely debated (Benton *et al.* 2003) but the availability of seed through the winter has certainly influenced a number of granivorous species (Siriwardena *et al.* 1998, 1999), a number of which are listed in the targets and priorities above. General links have been shown between the availability of seeds in winter and the use of areas by birds (Wilson et al. 1996), and also between annual survival rates and population trends for granivorous species (Siriwardena *et al.* 1999). Reduced seed availability on farmland in the winter is likely to be contributing to, or even driving, the population declines of some species. A recent extensive survey found that half of the total count of farmland birds in winter in Scotland were found on just 1.4% of the total area surveyed (Hancock & Wilson 2003).

A range of measures have been introduced to improve the winter feeding conditions for a number of declining seed-eating birds on farmland: for example, within the Rural Stewardship Scheme, the prescriptions for the 'Introduction or Retention of Extensive Cropping' (Prescription 24) and for 'Unharvested Crops' (Prescription 26) (SEERAD 2004). These incentives will only be successful if they (i) provide an adequate food source for the birds through the winter and, (ii) are appropriately distributed in order for the target species to be able to move between them (and locations for their other requirements) without adversely affecting their survival chances. Very little is known about the ranging behaviour of granivorous passerines in winter. Accordingly, knowledge of how the spatial distributions of winter food sources influence their availability to birds is largely absent and guidance on the spatial planning of mitigating measures is currently lacking.

1.2 The pilot study in 2002/03

During the winter 2002/03, BTO Scotland, in partnership with the Tay Ringing Group, undertook a pilot study to determine the efficacy of field and analytical methods for investigating the ranging behaviour of granivorous passerines on farmland (Calladine *et al.* 2003). Four field methods were assessed in a 25 km^2 study area in West Fife, Scotland: (i) mark-recapture ringing of birds at multiple sites, (ii) radio-telemetry, (iii) colour-ringing followed by searches to find marked birds, and (iv) plumage dying followed by searches to find marked birds. Mark-recapture ringing and radio-telemetry were the most successful of these techniques in that quantitative data suitable for subsequent analyses were collected. The two colour marking methods, although providing qualitative and supportive data were less successful in that reliable observation of marks in the field proved to be problematic.

By adapting the use of multi-strata survival models and the program MARK (Hestbeck *et al.* 1991, White 2002) the likelihoods of movements between pairs of sites were quantified for Yellowhammer *Emberiza citrinella*, Chaffinch *Fringilla coelebs* and Tree Sparrow *Passer montanus* using data gained from mark-recapture and radio-telemetry. A significant caveat to these was that they are from just one study area (in West Fife) and from one winter (2002-03). Of the three study species, Tree Sparrows tended to range the furthest (5-20% likelihood of movements between sites 3-5 km distant), Yellowhammers were intermediate (9-40% likelihood of movements between 2-4 km) and Chaffinches ranged the least (17% likelihood of a 2 km movement). There were also parallels between ranging likelihoods and levels of habitat selectivity. Chaffinches were the most generalist in terms of their use of the range of habitats available. Tree Sparrows had the finest habitat requirements, while Yellowhammers were intermediate.

1.3 Aims of the second study season (2003-04)

This report describes a second season's work at the original study site in West Fife (mark-recapture ringing and radio-telemetry) and that at an additional site in East Lothian (mark-recapture ringing only). Principal aims were:

1. To repeat the mark-recapture and radio-telemetry protocols within the same study area in West Fife as part of an ongoing objective to measure between-year variation in winter ranging behaviour by granivorous passerines.
2. To repeat the field surveys within the same study area in West Fife to determine between-year variations in the abundance, distribution of granivorous passerines and their within-season changes, against which movements measured by the above methods could be placed in context.
3. Assess habitat use by granivorous passerines from field surveys and radio-telemetry in West Fife and, again, make between-year comparisons.
4. To undertake comparable work in a second study area (in East Lothian) to initially assess any differences in ranging behaviour between sites and to assess the practicalities of using volunteer bird ringers and field surveyors alone to undertake such research work.

For winter 2003/04, Tree Sparrows were not radio-tagged, principally because of limitations associated with the signal strength and duration of the small tags required (Calladine *et al.* 2003)

2. METHODS

2.1 Study areas

Fieldwork was undertaken in two 25 km^2 study areas (5 km by 5 km). One study area in West Fife, centred on 56° 05′ N, 3° 31′ W, immediately west of Dunfermline (Figure 1), was the same as used for the pilot study in 2002/03. The second site was in East Lothian, centred on 55° 54′ N, 2° 46′ W, around Gifford (Figure 1). Both areas included mixed arable and pasture farmland, woodlands and built-up areas (Table 1). Thirty-eight percent of arable ground in the West Fife study area was under stubbles in late October 2003, but this proportion had reduced to 23% by late December. This compares to 42% that remained under stubbles through the whole winter 2002/03. Habitat and crop types were only recorded in January 2004 for the East Lothian study area when 10% of the arable ground retained stubbles.

2.2 Mark-recapture ringing

2.2.1 *Trapping protocol*

Birds were caught using mist nets (Redfern & Clark 2001) at four sites within the West Fife study area (Figure 2) and at three sites in the East Lothian study area (Figure 3). Distances between the West Fife catching sites varied from 2.1 to 4.9 km and those in East Lothian from 2.2 to 3.2 km. All sites were sampled at least once during each of 6 four-week periods (Table 2). Sampling involved the erection of 50 – 100 metres of four-shelved mist nets, immediately prior to first light in the morning, and continued until catches were infrequent or ceased, usually within 2 – 5 hours. Each bird caught was marked with a standard BTO ring (uniquely numbered) on one leg or, if 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 nearest 0.1 g) and fat score (using the ESF/Kaiser system) were recorded following Redfern & Clark (2001).

All sites were baited with grain in order to concentrate birds at netting sites; the baiting regime differed between the two study areas however. In West Fife, the baiting regime varied, with three periods of ‘intensive baiting’ interspersed with periods of light baiting. Intensive baiting periods were:

1) 20 October – 4 November
2) 20 December – 4 January
3) 27 February – 14 March

Bait was placed in feeders, of which there were typically six to ten per site. Intensive 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. This variable baiting regime was followed for the West Fife Study area in the winter 2002/03. In East Lothian, the three catching sites were baited continuously through the winter by dumping copious amounts of grain on the ground. In comparison with west Fife, the East Lothian sites were effectively intensively baited throughout the study period.

2.2.2 *Analytical methods to estimate ranging behaviour*

Multi strata models within the program MARK (Hestbeck *et al.* 1991, White 2002) was used to estimate the likelihoods of birds moving between catching sites (Calladine *et al.* 2003). The strata in each model represented ringing sites where a species had been caught within either study area. For West Fife, up to four strata were included in each model and in East Lothian, up to three. Where a species was never caught at a site, then that site was excluded from the relevant models for that species. The first encounter for each bird was its capture for ringing and subsequent encounters for that individual constituted recaptures at one or more of the ringing sites. A matrix of encounter histories is produced that includes a bird's capture as a positive event, or as a 'zero' if a bird is not caught, for each sampling period. The basic model allows the varying probability of recapture to be accounted for in the estimation of survival rates. In the multi-strata models used here, each encounter is attributed to one of the ringing sites, and the non-capture of an individual during each ringing period is attributed a zero. In addition to producing survival and recapture rate estimates, these models estimate the probabilities of transfer between strata; in this study, these are the likelihoods of birds moving between ringing sites within either study area. 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 (Table 2).

This group of models (Hestbeck *et al.* 1991) necessarily assume that survival is constant across sites and, given sample size limitations, we also here assume constant survival through the winter period and between sexes and age classes of birds. Our most general models included site-specific recapture probabilities and different transfer probabilities between strata and between the two directions of transfer between each stratum pair. Subsequent simplified models include (i) common recapture probabilities across sites, (ii) common transfer probabilities for the two directions between strata pairs, and (iii) a common transfer probability between all strata pairs. A general model, and three reductions were run and compared for each species as follows:

General model{ScPsTs}
Survival constant; Recapture probability site-specific; Transfer probability site and direction specific.
First reduction {ScPcTs}
Survival constant; Recapture probability constant; Transfer probability site and direction specific.
Second reduction {ScPcTp}
Survival constant; Recapture probability constant; Transfer probability specific between pairs of sites.
Third reduction {ScPcTc}
Survival constant; Recapture probability constant; Transfer probability constant.

The Akaike information criterion (AIC), the lowest value of which suggests the most parsimonious model for the data set, was used to investigate which model best described the data for each species (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.

2.3 Radio-telemetry

2.3.1 *Protocol*

In the winter 2003/04, 16 Yellowhammers and 16 Chaffinches were radio-tagged in the West Fife study area (Table 3). Birds were tagged in two cohorts, with eight of both species monitored during November and December ('early period') and another eight of both species monitored from January to early March ('late period'). Yellowhammers were fitted with 0.8 g tags and Chaffinches 0.5 g (PIP transmitters from Biotrack Ltd, Wareham, UK) and were tail-mounted, attached to the two central tail feathers with super glue and additionally tied with fine nylon chord. Radio-tagged individuals were tracked using hand-held three-element Yagi antennae. To overcome problems with restricted transmission distances, a systematic search protocol was used, whereby scans for all active frequencies were made in all directions from 59 points within the 25 km^2 study area (Figure 4). Scanning points were selected to achieve as complete a coverage of the area as was practical based on topography, accessibility and known concentrations of birds, and were the same as those used during the winter of 2002/03 (Calladine *et al.* 2003). The locations of tagged birds were determined through triangulation, based on the strength and direction of the 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. In addition, signals were occasionally followed (1-3 individuals per week) to confirm their determined locations. In all instances, individuals were at or close (within 20 m) to their expected positions. In most instances, the necessary close approach disturbed the birds, however, causing them to relocate. The sample of birds thus checked was low in order to reduce the influence of the radio tracking procedure on their movements.

At least two complete 'systematic searches' were made each week while radios were active. The order in which search points were checked was varied to exclude any biases through checking certain points at the same time of day. A number of additional casual searches were made with radio receivers within the study area, including some at night to locate roosting birds. Each radio location was plotted onto a digitised map of the study area, prepared using the Arc View Geographic Information System (ESRI), which included the distribution of habitat and crop types listed in Table 1.

2.3.2 *Estimating ranging behaviour*

'Traditional' analyses of radio-telemetry rely on a relatively large number of determined locations, for example a minimum number of 50 per individual to determine home ranges (Kenward 1987). A sufficiently large number of fixes from the necessarily small and relatively short-lived radios used would only be obtained with very short sampling intervals, giving rise to autocorrelation between points, or by replacing tags several times on the same individual. The latter was deemed to be too intrusive (the level of disturbance to an individual was likely to influence its behaviour) for this study. Data collected during the winter 2002/03 were analysed in the same way as for the mark-recapture ringing (see Section 2.1.3) where the strata were defined by aggregations of bird locations determined by radio-telemetry (Calladine *et al.* 2003). Data from birds tagged during winter 2003/04 did not readily fall into such aggregations, thus the adaptation of multi-strata survival modelling was not appropriate. An alternative approach was adopted based on the distances between determined locations on consecutive systematic searches. Data from winter 2002/03 were similarly reanalysed to permit direct comparison.

The distances between subsequent locations determined from the systematic searches were measured for each tagged individual from the GIS. If an individual was located more than once in any one day, only the first location was used. Each distance measurement was weighted according to the number of days between subsequent fixes. All distances were weighted according to the formula:

Weighting = (Maximum period + 1) – Actual period

where the 'Actual period' is the number of days elapsed between a pair of fixes and the 'Maximum period' is the greatest number of days elapsed between systematically determined fixes for each species within a season. Thus a weighting of 1 was given to the distance measurement following the greatest period of time between subsequent systematic radio fixes and greater weighting was given to measurements with lesser intervening times. This gives the greatest weighting to measurements taken between subsequent systematic searches with proportionally decreased weight given to measurements where individuals were not located during increasing numbers of sequential systematic searches. For each individual, the mean distance between locations was thus determined. As this approach does not account for additive movements whereby an individual moves progressively from further from the original location with time, an alternative analysis considered the unweighted mean of the distances between all possible pairs of systematically determined radio-locations for each individual.

ANOVAs, with the mean distance moved per individual as the dependent variable, examined the effects of species (n=3), year (n=2; 2002-03 and 2003-04) and period (n=2; early = November – December, late = January – March) and their two-way interactions. The mean distances were further weighted by the sample size contributing to that mean (i.e. the number of systematic radio fixes). As only two species were tagged in winter 2003-04 and only one period (late) was monitored in 2002-03, three separate models were used:

1. Species, Year and their two-way interactions for Chaffinch and Yellowhammers during the late period only.
2. Species, Period and their two-way interactions for Chaffinch and Yellowhammer only (corrected for year effect when required).
3. Species for Chaffinch, Yellowhammer and Tree Sparrow for the late period only (corrected for year effect when required).

All independent variables were categorical. The Tukey test was used to make pair-wise comparisons to identify the sources of any significant differences. The mean duration between locating radio tagged birds through systematic searching was 4 days for all three species in winter 2002/03 and 3 days for the two species monitored in winter 2003/04.

2.3.3 *Estimating the time spent at baited catching sites*

A concurrent study reported separately (McClymont 2004). The two baited ringing sites where birds were tagged (Craigluscar and West Camps in West Fife) were scanned for all active radiotag frequencies at 30 minute intervals through daylight hours of one day per week at each site. Birds were recorded as present if they were detected as being within 100 m of the baited areas. The proportion of scans in which individual was present was used to estimate the proportion of time they spent at, or close, to the sites. Data was truncated according to the recorded presence of each individual in the wider 25 km^2 study area (Section 2.2.1).

2.4 Habitat use

Habitat use by those species for which winter ranging behaviour was modelled was investigated by two approaches:

1. From the locations of individual radio-tagged birds (for the West Fife study area only), and;

2. From repeated systematic surveys of bird distribution and abundance throughout both study areas.

2.4.1 *Radio-telemetry*

Habitat use by radio-tagged birds was investigated by comparison of the habitat composition found within a 30 m radius of each point where an individual bird was located with that available within the minimum convex polygon (MCP) drawn around the plotted fixes for that individual. A 30 m radius was considered to have been representative of the actual habitats being utilised and also allowed for the estimated error in determining a bird's location through triangulation (see Section 2.2.1). 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 with a repeated measures procedure. The log ratios were the repeated measures identified by the individual tagged bird. 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); 2) stubbles (cereals and lupins); 3) pasture; 4) scrub; 5) woodland; and 6) 'other' (including urban and other 'human sites'). The area of stubbles in the West Fife Study area (the only area where radio-telemetry studies were undertaken) declined through the study period as these were ploughed and replaced with bare till or early-sown ('autumn sown') cereals (Table 1). 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 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. As the MCPs determined from radio-telemetry are produced from a relatively small number of fixes, it is expected that they will underestimate the true home range of individuals, thus the analyses are likely to produce conservative estimates of habitat preferences.

2.4.2 *Field surveys*

The number of birds seen during weekly field surveys (see Section 2.4) in each habitat was used as an indication of habitat use. Compositional analysis was used to compare proportional habitat use with availability. 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. For West Fife, where changes in habitat (typically the ploughing in of stubbles) were recorded throughout, this referred to that available on the day of the survey. In East Lothian, the single habitat measures taken in January were used for all survey dates.

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. In the West Fife study area, a 37-km transect was cycled fortnightly between 18 October 2003 and 3 March 2004, and all finches and buntings encountered were recorded (Fig 2). In East Lothian, a 24 km cycle route was surveyed once per month between October and March inclusive (Fig 3). Routes were 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 maps of the study area that included habitat and crop types.

ANOVAs with the bird abundance, expressed as birds per km (log-transformed), as the dependant variable examined the effects of species (n=8), study area (n=2), year (n=2; 2002/03 and 2003/04) and period (n=2; early = October – December, late = January – March) and their two-way interactions. As counts from only one study area were available for both seasons and there were insufficient counts from East Lothian for a meaningful assessment of the effects of period within the winter season, two separate models were used:

1. Species, Period and Study Area and their two-way interactions for data from winter 2003/04 only.
2. Species, Period and Year and their two-way interactions for data from West Fife only.

All independent variables were categorical and the Tukey test was used to make pair-wise comparisons to identify the sources of any significant differences.

3. RESULTS

3.1 Abundance of birds

Eight species of granivorous passerine were counted during cycle transects at both study areas during winter 2003/04 (Table 4). The only significant differences in apparent abundance between the two study areas were for House Sparrow and Tree Sparrow (with over 6 and over 5 times as many, respectively, recorded per km in West Fife than in East Lothian) and for Greenfinch (with over 3 times as many recorded per km in East Lothian) (Tables 5 & 6).

In the West Fife study area, both House Sparrow (62% more registrations) and Yellowhammer (41% more registrations) were recorded in significantly greater numbers during 2003-04 than during 2002/03 (Tables 5 & 6). Although the general trend for most other species was for lower abundance in 2003/04, the differences were not statistically significant (Tables 5 & 6). There was little difference in relative abundance between early and late winter in the West Fife study area, with the exceptions of Greenfinch and Reed Bunting that were both more abundant during the early half of the season (Tables 5 & 6).

3.2 Estimating ranging behaviour

3.2.1 *By Mark-recapture ringing*

A total of 795 capture events were achieved in West Fife and 714 in East Lothian for 8 species of granivorous passerines during systematic ringing sessions in winter 2003/04 (Table 2). In West Fife, only three species (Yellowhammer, Chaffinch and Tree Sparrow) were recaptured within a 4-week sampling period subsequent to that in which they were originally caught (Table 2). These between-period recaptures constituted 7.5% of all capture events in West Fife. A similar proportion (7.7%) of capture events in East Lothian were of between-period recaptures, however these constituted a broader suite of species (7 out of 8, Table 2). Between-site recaptures were made of just two species, Yellowhammer (n=10 in West Fife, n=1 in East Lothian) and Chaffinch (n=2 in both West Fife and East Lothian) (Table 2). Multi-strata models to estimate movement likelihoods were run in MARK for these two species.

In West Fife, the likelihood of retrapping ringed Yellowhammers between any of the four-week sampling periods was estimated at 14% (SE ± 5%) (Table 8). Movements by ringed Yellowhammers were recorded between 4 out of the 6 possible pairings of sites, where the likelihoods of movements between each four-week sampling period were estimated at between 6 – 21% (Table 8). There was no apparent relationship between distance between ringing sites and the likelihood of a movement between them. In East Lothian, there was a lesser likelihood (7%, SE ±3%) of retrapping Yellowhammers between the sampling periods (Table 8), though that difference was not statistically significant. The single between site movement recorded by a ringed Yellowhammer in East Lothian produce an estimated transfer probability of 1% (± 1%) (Table 8). The MARK models with more parameters (in this instance, the General, First and Second reduced models) failed to converge, probably due to the sparseness of data (Table 7).

The probability of retrapping Chaffinches between sampling periods was lower than for Yellowhammers, 4% (SE ± 2%) at West Fife and 3% (SE ± 2%) at East Lothian, though the differences were not significant (Table 8). Again, the more complex models failed to converge (Table 7). Although estimates of transfer probabilities are presented (see Table 8), these have large associated standard errors suggesting such estimates generated from sparse data are not reliable (Table 8).

For Yellowhammers in West Fife, the species and area with most between-site recaptures, the lowest AIC suggested that the second and third model reductions were equally the most parsimonious, though the Likelihood ratio test between the two models suggested a close to significant difference, potentially giving cause to reject the simplest model (Table 7).

3.2.2 *By Radio-telemetry*

Sequential movements between the systematically determined radio-locations of individuals did not appear to be additive (ie no directional movement was implied) as there were no significant differences between the distance measurements derived from subsequent fixes and those derived from measures between all possible pairs of fixes (t_{116} = 1.59, P = 0.11 for all species combined, and P > 0.16 for the three species considered separately). Significant differences in the mean distances moved between subsequent systematically determined fixes were detected between species and between the early and late winter periods (Table 9). Although the measured distance between subsequent fixes tended to be greater in 2003-04 than in 2002-03 for both Yellowhammers and Chaffinches, the differences were not significant (Tables 9 & 10). Amongst the three species monitored over the two winters, Tree Sparrows tended to move the greatest distances (mean 1259 m between systematic fixes), Yellowhammers were intermediate (mean 601 m) and Chaffinches moved the least distance (557 m). The difference between distances moved by Chaffinches and Tree Sparrows was significant (Table 10). Of the two species monitored in both early and late winter periods, Chaffinch and Yellowhammer, both tended to move greater distances during the early winter; the difference was only significant for Yellowhammers, however, for which distances were on average 90% greater during the early part of the winter (Table 10). Radio tagged Chaffinches were detected within the West Fife Study area for an average of nine days longer during late winter than during the early period (Table 3b) suggesting that those caught and tagged in November 2003 tended to leave the study area before their tags stopped transmitting. However, the tags used in the two winter periods were manufactured separately, and so a difference in their capability cannot be totally eliminated. As the tags used between periods were of an identical specification, and there was no significant difference in the duration of Yellowhammer tags between periods (Table 3b) or between Chaffinches tagged in the late period in 2002/03 and 2003/04 (t_{16} = 1.11, P = 0.28), this is, perhaps, unlikely.

3.3 Habitat use

3.3.1 *Assessed by Radio-telemetry*

Only individuals with over five radio fixes (systematic and casual observations combined) were considered. Within this reduced sample, some 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 in West Fife, based on that within the immediate vicinity of radio fixes, differed significantly from random, based on habitat availability within individual home-ranges (for Yellowhammer, $F_{4,69} = 4.41$, $P < 0.003$; for Chaffinch, $F_{4,44} = 5.67$, $P < 0.001$). The simplified habitat rankings in order of preference for Yellowhammers were (significant differences ($P < 0.05$) from paired t-tests are indicated by triple symbols):

Scrub >>> Stubble >>> Pasture > Autumn sown crops > Other >>> Woodland (Table 11)

Simplified habitat rankings in order of preference for Chaffinch were (significant differences ($P < 0.05$) from paired t-tests are indicated by triple symbols):

Scrub >>> Stubble = Woodland >>> Other > Pasture > Autumn sown crops (Table 11)

3.3.2 *Assessed by field survey*

Habitat use by the two species for which winter movements were modelled, was also determined from the counts of birds in each habitat as proportions of all individuals of that species seen within the study area. For Yellowhammers, these differed significantly from random based on that available throughout the whole West Fife study area though not at the East Lothian study area (for West Fife, $F_{4,50} = 6.59$, $P < 0.001$; for East Lothian, $F_{4,25} = 2.23$ $P = 0.09$). The simplified habitat rankings in order of preference for Yellowhammer at West Fife were:

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

For Chaffinch, habitat selection differed significantly from random in the West Fife study area ($F_{4,50} = 42.5$, $P < 0.001$), though, as for Yellowhammers, did not at the East Lothian study area ($F_{4,25} = 1.95$, $P = 0.13$). Simplified habitat rankings for Yellowhammer in West Fife were:

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

3.3.3 *Proportion of birds at baited ringing sites*

In the West Fife study area, 57% of all Yellowhammer (n = 1120) and 34% of all Chaffinch (n = 2282) registrations during the field surveys in winter 2003/04 were within 100 m of the four periodically baited ringing sites. In East Lothian, similar proportions (63% of Yellowhammer (n = 500) and 40% of Chaffinch (n = 766) registrations) were within 100 m of the three baited ringing sites.

Monitoring for the presence of radio-tagged individuals at the two sites in west Fife where they were caught and tagged suggested that individual Yellowhammers spent an average of 16% (SE = 6%) of daylight time within 100 m of the baited ringing sites and Chaffinches 3% (±1%) (McClymont 2004).

3.3.4 *Roost sites*

The roosting sites of seven individual radio-tagged Yellowhammers (a combined total of 17 fixes at night) and eight Chaffinches (a combined total of 11 fixes at night) were located. In all cases, these were within the MCPs determined for the individual from systematic radio-tracking and in scrub or hedges. In no instance was more than one tagged individual located at the same site.

4. DISCUSSION

4.1 Estimates of winter ranging behaviour

Both radio-telemetry and mark-recapture ringing produced information on the ranging behaviour of granivorous passerines during winter 2003/04. Despite the expansion of the mark-recapture ringing to cover two study areas for this second field season, the data on between-site movements were sparse; out of 8 species of granivorous passerines ringed in both study areas, estimates of the likelihood of movements were produced only for Yellowhammers in the West Fife study area. Radio-telemetry proved more successful in terms of measuring ranging behaviour: this was undertaken in West Fife only and an alternative analytical approach to that used for 2002/03 was necessary (Section 2.2.2). This alternative analysis assumes that the distances moved between radio-telemetrically determined locations, in this instance at 3 – 4 day intervals, are in direct proportion to the distances ranged by the birds within that period. Reanalysis of the radio-telemetry data from 2002/03 showed general agreement with the results of the original analyses that treated the data as mark-recapture in that Tree Sparrows moved the greatest distances, Chaffinches the least and Yellowhammers were intermediate, though the relatively small difference between Chaffinches and Yellowhammers was not statistically significant (Table 14). Habitat preferences in winter suggest that Tree Sparrows had the finest requirements of the three species (Calladine *et al.* 2003); the greater distances ranged by Tree Sparrows probably reflects the need to travel between more restricted feeding areas.

The mean distances moved between radio-telemetrically determined locations in 2003/04 tended to be greater for both Chaffinch and Yellowhammer during the first half of the winter than during the second. For Yellowhammers, that difference was statistically significant with the distances in the early period being just less than twice that measured in the late period. In the early part of the winter there could be a degree of 'settling' behaviour before the birds locate the most reliable feeding areas, or alternatively, some more dispersed resources may become depleted or prove less worthwhile visiting in the latter part of the winter. Some, or most of the Chaffinches radio-tagged in the early part of the winter (in early November) probably left the study area before their transmitters failed. Although a difference between the longevity of the radios used on Chaffinches between periods cannot be totally eliminated, it is unlikely (Section 3.2.2). Therefore, the distances moved by the Chaffinches tagged in November 2003 are probably greater than our measurements suggest, however such movements could actually be of dispersal, or even migration (i.e. between season), rather than within-season ranging. Combining data from both seasons, where this was possible, and for all three species that were tagged over the two seasons, Tree Sparrows tended to range the greatest distances and Chaffinches the least. Yellowhammers were intermediate, though the measurements (mean distance moved between fixes at 3–4 day intervals) did not differ significantly from the other two species. The comparison between the three species is for the latter half of the winter only.

Mark-recapture ringing proved to be of limited success in determining estimates for ranging behaviour by granivorous passerines during winter 2003/04. Of the two species for which movements were detected by being caught at more than one ringing site within the season, only Yellowhammers in one study area (West Fife) produced sufficient data for movements of known distances to be modelled. For Yellowhammers in East Lothian and Chaffinches at both study sites, the data were too sparse to estimate movement rates between pairs of sites. This is comparable with the findings from winter 2002/03 for West Fife, the only site where fieldwork was carried out in that winter (Table 13). In contrast with the previous winter, no movements by ringed Tree Sparrows were recorded in 2003-04, however fewer were caught than in 2002/03 (50 capture events in 2003/04 compared to 114 in 2002/03). With a similar recapture rate as in 2002/03, it could have been expected to record 5 – 6 recaptures for Tree Sparrow in West Fife in 2003/04. Although transect counts suggest that Tree Sparrows were less abundant in the West Fife study area in 2003/04 than in 2002/03 (also supported by the lesser numbers caught for ringing) the difference was not statistically significant and there was no difference in abundance between the early and late halves of the season that might imply net movements into or out of the study area during the winter (Table 6). Yellowhammers that were significantly more abundant in 2003/04 than in 2002/03 (Table 6) were caught more frequently (349 capture events in 2003/04 compared to 193 in 2002/03) with a proportionally greater number of recaptures. Although Chaffinches were caught in the greatest numbers in both study areas, comparison of estimates of movement likelihoods derived from mark-recapture ringing and from radio-telemetry in 2002/03 did question how representative was mist-netting in sampling the habitats used by that species (Calladine *et al.* 2003). In addition, the radio-tracking of Chaffinches suggested that a high proportion of individuals caught in the early half of the winter may be transients through the West Fife study area and thus recaptures, particularly of early caught birds, might be expected to be few. However, seven out of the 21 Chaffinch recaptures in West Fife during winter 2003/04 were of individuals initially caught in October or November and subsequently recaptured in January to March. In addition, there is no suggestion of gross changes in the number of Chaffinches from field surveys within the study area between early and late winter (Table 6). If most Chaffinches caught during October and November were transients, it might be expected that this proportion would be lower. Reasons for this apparent contradiction, other than an unlikely difference in radio longevity remain unclear.

4.2 Habitat preferences

Habitat preferences in West Fife, determined from both field survey and radio-telemetry in 2003/04 highlighted the importance of scrub and stubbles for Yellowhammers and Chaffinches. Woodland was avoided by Yellowhammers but selected by radio-tagged Chaffinches. The contradictory low preference ranking for woodland by chaffinches from field surveys is likely to be a result of the survey methodology. The cycle transects principally aimed to record birds in fields and their margins and are unlikely to have reliably recorded birds in the more enclosed habitats such as woodland. These preferences are broadly similar to those found in 2002/03.

In East Lothian, no habitat preferences by either Yellowhammer or Chaffinch were apparent from the field surveys undertaken. With less data, as fewer counts were undertaken, there would have been less power to detect differences; power analyses suggest there would have been a 26% probability of detecting a significant difference in habitat use from data collected in East Lothian, compared to a 92% probability from West Fife. Alternatively, the different baiting regimes between the two study areas may have influenced habitat use with birds in East Lothian more persistently present at the continuously baited sites. A similar proportion of registrations from the field surveys were close to the baited ringing sites in both study areas (in West Fife and East Lothian respectively, 57% and 63% of Yellowhammer and 34% and 40% of Chaffinch registrations were within 100 m of the baited ringing sites), suggesting that distribution of birds were not necessarily influenced by the differing baiting regime between the two study areas. Although high proportions of birds were recorded near to the baited sites, the determination of any influence of baiting on the distribution of birds is confounded by the fact that they were selected initially because of existing concentrations of finches and buntings. Monitoring for radio-tagged birds at two baited sites in West Fife suggests individuals spent relatively little time at them (averages of 16% for Yellowhammers and 3% for Chaffinches; McClymont 2004). In West Fife, at least, it appears that although a high proportion of birds within the area use the baited sites, most individuals are only present for relatively short periods.

4.3 Efficacy of methods used and their further application

Knowledge of the ranging behaviour of granivorous passerines on farmland in winter has direct applications in the advocacy, planning and implementation of conservation prescriptions that aim to halt the declines in their populations. Such information would ensure mitigating measures deliver their conservation targets in a cost-effective way by identifying what is the optimal scale and also timing at which to provide winter food sources for birds. Over two winters we have tried a number of techniques to determine which would be suitable for quantifying ranging behaviour in a way that would permit comparison between species, across regions and seasons and to guide applied conservation work and also measure its effectiveness. Ringing is a widely used technique for studying bird movements (Marchant 2002), though has been little used for short-distance movements or ranging behaviour. Although data from the retrapping of ringed birds was sufficient to model some movements by some species, even where this was possible, the estimates of likelihoods of movements were too imprecise for most comparisons. For some species, in our experience the Chaffinch, ringing may not representatively sample the habitats used and thus their movements. Increased effort in systematic ringing is unlikely to increase that precision greatly, and in practice, with the vagaries of winter weather, there may be little scope for increased effort in any case. The general ringing of granivorous passerines remains valuable in monitoring general movements and the collection of biometric data to potentially inform geographic origins and physiological condition.

Provisioning bait or some other manipulation of food sources to concentrate birds is normally required to catch sufficient numbers in order to reasonably expect to recapture them elsewhere and generate data on movements. Although intensive monitoring of radio-tagged birds at the baited sites in West Fife, suggested that individuals spent relatively little time at them, baiting, or other food manipulation is still likely to influence movements. However, this is unlikely to any different to the conservation measures currently advocated that aim to create or maintain concentrated sources of available seed or grain.

Radio-telemetry provided quantitative information on ranging behaviour that is of sufficient precision to permit statistical comparison. With current available technology, effective transmission distances of the radios and their longevity, the species that can be effectively monitored is perhaps restricted. During winter 2002/03, the data collected from radio-tagged Tree Sparrows was severely limited both by the short active life span of the radios and the restricted distances from which they could be reliably detected (mean 11 days duration and reliably detected at < 150 m; Calladine *et al.* 2003). Experience from radio-tracking Chaffinches during the early part of winter 2003/04 suggests that some birds may disperse too far to be effectively monitored and that this may vary through a season. Yellowhammers appeared to be species that were effectively and consistently monitored by radio-telemetry both through the season and between seasons.

Colour marking, as a technique to monitor ranging behaviour, was tried only in 2002/03. Plumage dying proved unreliable, at least the use of temporary dyes used for domestic animals, and the resighting of colour rings in the field through the winter proved difficult (Calladine *et al.* 2003). Alternative marking techniques, for example other plumage dyes, or small tags attached to nape or mantle feathers may prove more successful. The preparation of sites from which to search for colour-ringed birds (maintaining feeding sites with short vegetation and observing from hides) may also improve detection rates.

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TABLES

Table 1. The extent of crop types and other broad habitats within the West Fife and East Lothian study areas in winter 2003-04.

CROP or HABITAT	% COMPIOSITION (of 25 km^2)		
	WEST FIFE		EAST LOTHIAN
	October 03	January 04	January 04
Autumn sown cereal	15	22	28
Autumn sown rape	5	5	3
Pasture	31	30	16
Set aside	1	1	<1
Scrub	1	1	1
Stubble	16	10	5
Till	6	8	12
Built-up	7	7	3
Open water	<1	<1	0
Woodland	9	9	25
Other	7	7	7

Table 2. The frequency of sampling and capture events for granivorous passerines within the West Fife and East Lothian study areas, winter 2003-04.

SAMPLING PERIOD	Number of sampling events at each ringing site				Number of capture events							
					Y.	CH	TS	GR	RB	GO	HS	BL
WEST FIFE	CL	CA	WC	CR								
1/10 – 28/10	2	1	2	3	0	26	3	21	0	0	0	0
29/10 – 25/11	2	2	2	4	11	76	27	43	2	4	2	1
26/11 – 24/12	2	2	1	3	89	77	5	11	3	1	1	0
25/12 – 20/1	2	2	2	1	142	68	5	3	2	0	0	0
21/1 – 17/2	1	2	1	1	57	36	4	2	0	0	0	1
18/2 – 16/3	2	2	2	1	50	7	6	1	7	0	1	0
TOTAL NUMBER OF CAPTURE EVENTS					349	290	50	81	14	5	4	2
Number of same-site recaptures					29	18	1	0	0	0	0	0
Number of between-site recaptures					10	2	0	0	0	0	0	0
EAST LOTHIAN	GF	EG	MB									
29/10 – 25/11	1	1	1		13	21	4	19	2	0	1	0
26/11 – 24/12	2	1	2		7	66	3	9	1	0	0	2
25/12 – 20/1	1	1	1		59	35	3	5	4	0	5	0
21/1 – 17/2	1	1	1		49	22	1	1	2	1	11	0
18/2 – 16/3	2	1	1		134	80	2	6	15	14	7	2
17/3 – 14/4	2	1	1		37	46	0	0	13	4	8	0
TOTAL NUMBER OF CAPTURE EVENTS					299	270	13	40	37	19	32	4
Number of same-site recaptures					24	13	1	1	4	1	8	0
Number of between-site recaptures					1	2	0	0	0	0	0	0

Notes:

1) Ringing sites: CL – Craigluscar; CA – Cairneyhill; WC – West Camps; CR – Crossford; GF – Gifford; EG – Eaglescairney; MB – Morham Bank.
2) Birds: Y. – Yellowhammer; CH – Chaffinch; TS – Tree Sparrow; GR – Greenfinch; RB – Reed Bunting; GO – Goldfinch; HS – House Sparrow; BL – Brambling.
3) Capture events refer to an individual being caught within one of the 4-week sampling periods. A bird caught more than once within any one period remains a single capture event.

Table 3a. Radio-tracking periods for Yellowhammers and Chaffinches tagged in the West Fife study area, winter 2003-04.

SPECIES	Age[+]	Sex[*]	Site tagged	Date tagged	Date of last radiolocation
CHAFFINCH					
	3	F	West Camps	25/11/03	20/12/03
	3	F	West Camps	25/11/03	15/12/03
	3	F	West Camps	25/11/03	15/12/03
	3	M	West Camps	25/11/03	02/12/03
	3	F	Craigluscar	26/11/03	02/12/03
	4	F	Craigluscar	26/11/03	04/12/03
	4	M	Craigluscar	26/11/03	02/12/03
	3	F	Craigluscar	26/11/03	04/12/03
	5	F	Craigluscar	29/01/04	13/02/04
	5	F	Craigluscar	29/01/04	19/02/04
	6	F	Craigluscar	29/01/04	19/02/04
	6	F	Craigluscar	29/01/04	26/02/04
	6	F	Craigluscar	29/01/04	18/02/04
	6	M	Craigluscar	29/01/04	13/02/04
	5	M	Craigluscar	29/01/04	29/02/04
	6	M	Craigluscar	29/01/04	18/02/04
YELLOWHAMMER					
	4	F	West Camps	25/11/03	15/12/03
	3	M	West Camps	25/11/03	24/12/03
	3	M	West Camps	25/11/03	24/12/03
	3	M	West Camps	25/11/03	20/12/03
	3	M	Craigluscar	26/11/03	20/12/03
	3	F	Craigluscar	26/11/03	20/12/03
	3	F	Craigluscar	26/11/03	24/12/03
	4	F	Craigluscar	26/11/03	20/12/03
	5	F	West Camps	28/01/04	28/01/04
	5	F	West Camps	28/01/04	07/03/04
	5	M	West Camps	28/01/04	07/03/04
	5	M	West Camps	28/01/04	04/03/04
	5	F	West Camps	28/01/04	18/02/04
	5	M	West Camps	28/01/04	19/02/04
	5	F	West Camps	28/01/04	24/02/04
	5	M	West Camps	28/01/04	07/03/04

[+] M – Male, F – Female.
[*] Age is at the time of tagging using EURING codes (Redfern & Clark 2001) where:
3 – hatched during current calendar year
4 - hatched before current calendar year
5 – hatched within the previous calendar year
6 – hatched within the calendar year two years previous

Table 3b. A comparison between early winter (November – December) and late winter (January – February) of the duration for which Chaffinches and Yellowhammers were radio-tracked in West Fife in winter 2003/04.

SPECIES	Early Winter		Late Winter		Comparison
	Mean (days)	SE	Mean (days)	SE	
Chaffinch	13.4	7.9	22.4	5.6	t_{14}=2.63, P = 0.02
Yellowhammer	27.6	4.4	33.4	8.8	t_{13}=1.65, P = 0.12

Table 4. Counts of granivorous passerines seen during transect surveys in West Fife and East Lothian during winter 2003 – 04.

DATE	Y.	CH	TS	GR	RB	HS	GO	LN	BL
WEST FIFE (37 km transect)									
18 October	77	250	30	33	22	65	0	24	0
31 October	59	214	54	66	29	82	0	0	5
15 November	65	208	42	16	15	120	0	232	0
28 November	97	333	74	34	15	167	12	90	0
14 December	132	143	40	12	2	155	30	30	0
24 December	84	129	11	12	9	80	5	10	0
7 January	101	179	24	4	7	90	0	140	0
21 January	134	195	45	18	7	125	6	0	0
4 February	152	178	15	6	6	70	25	60	0
17 February	140	286	33	28	6	162	0	150	0
3 March	79	152	10	9	2	160	0	70	0
EAST LOTHIAN (24 km transect)									
23 October	6	80	0	8	0	11	8	40	0
20 November	53	74	1	22	0	18	4	0	0
18 December	92	138	10	72	0	5	10	30	3
24 January	95	197	8	94	0	6	19	0	0
21 February	190	184	4	73	0	18	32	50	0
25 March	64	97	0	20	11	10	3	0	0

Table 5. Results of ANOVAs examining the influence of Species, Study area, Year, Period within the winter season and their interactions on systematic counts of granivorous passerines in the West Fife and East Lothian study areas in winter 2003-04.

Source of variation		**Model 1**			**Model 2**	
	df	F-value	*P*	df	F-value	*P*
Model	24	13.39	<0.001	23	14.39	<0.001
Species	7	35.92	<0.001	7	39.5	<0.001
Study area	1	2.32	0.13	not applicable		
Year	not applicable			1	3.82	0.05
Period	1	4.41	0.04	1	1.36	0.26
Species*Study area	7	4.41	<0.001	not applicable		
Species*Period	7	1.06	0.39	7	1.48	0.18
Species*Year	not applicable			6	3.73	0.002
Study area*Period	1	5.38	0.05	not applicable		
Year*Period	not applicable			1	1.59	0.21
Error	111			162		

Note:

Model 1 includes the categorical variables Species, Study area, Period within the winter and their two-way interactions. This is for counts during the winter 2003-04 only.

Model 2 includes the categorical variables Species, Year, Period within the winter and their two-way interactions. This is for counts at the West Fife study area only.

Table 6. Pair-wise comparison using Tukey tests following the ANOVAs shown in Table 5. Significant differences ($P < 0.05$) are shown in bold.

	MEAN COUNT (birds per km) ± SE		**Comparison (*P*)**
Species between study areas (winter 2003-04 only)			
	West Fife (n=11)	**East Lothian** (n=6)	
Chaffinch	5.57 (± 0.51)	5.35 (± 0.91)	0.82
Goldfinch	0.19 (± 0.09)	0.53 (± 0.19)	0.08
Greenfinch	**0.58 (± 0.15)**	**2.01 (± 0.61)**	**0.01**
House Sparrow	**3.14 (± 0.33)**	**0.47 (± 0.10)**	**<0.001**
Linnet	1.98 (± 0.60)	0.83 (± 0.39)	0.21
Reed Bunting	0.29 (± 0.07)	0.08 (± 0.07)	0.07
Tree Sparrow	**0.93 (± 0.16)**	**0.16 (± 0.07)**	**0.004**
Yellowhammer	2.75 (± 0.27)	3.47 (± 1.04)	0.40
Species between seasons (West Fife only)			
	2002-03 (n=14)	**2003-04** (n=11)	
Chaffinch	7.41 (± 0.83)	5.57 (± 0.51)	0.09
Goldfinch	0.14 (± 0.07)	0.19 (± 0.09)	0.66
Greenfinch	1.27 (± 0.36)	0.58 (± 0.15)	0.12
House Sparrow	**1.94 (± 0.44)**	**3.14 (± 0.33)**	**0.04**
Linnet	3.59 (± 0.73)	1.98 (± 0.60)	0.11
Reed Bunting	0.44 (± 0.11)	0.29 (± 0.07)	0.32
Tree Sparrow	1.57 (± 0.36)	0.93 (± 0.16)	0.15
Yellowhammer	**1.95 (± 0.22)**	**2.75 (± 0.27)**	**0.03**
Species between periods (West Fife only)			
	Early season (n=12)	Late season (n=13)	*P*
Chaffinch	7.19 (± 0.90)	6.05 (± 0.61)	0.30
Goldfinch	0.24 (± 0.09)	0.36 (± 0.17)	0.46
Greenfinch	**1.58 (± 0.38)**	**0.41 (± 0.11)**	**0.006**
House Sparrow	2.41 (± 0.52)	2.51 (± 0.0.36)	0.88
Linnet	2.63 (± 0.83)	3.11 (± 0.62)	0.64
Reed Bunting	**0.53 (± 0.12)**	**0.24 (± 0.06)**	**0.04**
Tree Sparrow	1.49 (± 0.33)	1.10 (± 0.29)	0.38
Yellowhammer	1.95 (± 0.22)	2.63 (± 0.26)	0.06

Note Bramblings were only recorded on one occasion in each study area (Table 4) and have thus been excluded from the above analyses.

Table 7. A comparison of the models for mark-recapture estimates of movement probabilities using the program MARK on ringing data.

SPECIES **(Study area)**	**Parameters**[1]	**AIC**	**Likelihood ratio tests**[2] χ^2	**df**	***P***
YELLOWHAMMER					
(West Fife)					
General model	{ScPsTs}	340			
First reduced model	{ScPcTs}	337	4.28	3	0.23
Second reduced model	{ScPcTp}	330	5.98	6	0.43
Third reduced model	{ScPcTc}	330	10.94	5	0.05
(East Lothian)					
Third reduced model	{ScPcTc}	193			
CHAFFINCH					
(West Fife)					
First reduced model	{ScPcTs}				
Second reduced model	{ScPcTp}	212	1.58	6	0.95
Third reduced model	{ScPcTc}	208	7.04	5	0.22
(East Lothian)					
Third reduced model	{ScPcTc}	160			

Notes:
1. Model parameters:
   - Sc: Survival constant across all sites.
   - Pc: Recapture probability is site dependent.
   - Pc: Recapture probability is constant across all sites.
   - Ts: Transfer probability is both pair and direction dependent.
   - Tp: Transfer probability is pair dependent but the same for either direction of movement.
   - Tc: Transfer probability is constant between all pairs.
2. Likelihood ratio tests compare each reduced model with its immediate predecessor.
3. Models not listed in the table failed to converge, probably due to sparseness of data.

Table 8. Model parameter estimates of movement probabilities using the program MARK on mark-recapture ringing data.

SPECIES (Study area)	PARAMETER Estimate	Standard Error	DISTANCE (km)
YELLOWHAMMER			
(West Fife)			
Survival probability	0.65	0.13	
Probability of retrapping	0.14	0.05	
Second reduced model			
Transfer probability A↔B	0.06	0.04	4.9
Transfer probability B↔D	0	-	3.9
Transfer probability C↔D	0.10	0.10	3.8
Transfer probability A↔D	0.21	0.09	3.6
Transfer probability A↔C	0.07	0.05	3.0
Transfer probability B↔C	0	-	2.1
Third reduced model			
Transfer probability	0.07	0.02	
(East Lothian)			
Third reduced model			
Survival probability	0.82	0.18	
Probability of retrapping	0.07	0.03	
Transfer probability	0.01	0.01	
CHAFFINCH			
(West Fife)			
Third reduced model			
Survival probability	0.80	0.17	
Probability of retrapping	0.04	0.02	
Transfer probability	0.02	0.01	
(East Lothian)			
Third reduced model			
Survival probability	0.96	0.20	
Probability of retrapping at A	0.03	0.02	
Transfer probability	0.03	0.02	

Notes:

1) Parameter estimates are presented for models selected by having the lowest AIC and not being rejected by likelihood ratio tests (Table 7)
2) The survival probability is a product of the bird surviving and likelihood of remaining within the immediate vicinity of ringing sites.

Table 9a. Results of ANOVAs examining the influence of Species, Year, Period within the winter season and their interactions on mean distances moved between subsequent systematically determined fixes by radio-tagged Yellowhammers, Chaffinches and Tree Sparrows in the West Fife during winters 2002-03 and 2003-04.

Source of variation	**Model 1**			**Model 2**			**Model 3**		
	df	F-value	*P*	df	F-value	*P*	df	F-value	*P*
Model	3	0.56	0.64	3	3.27	0.04	2	3.39	0.04
Species	1	0.41	0.52	1	0.02	0.90	2	3.39	0.04
Year	1	0.22	0.64	not applicable			not applicable		
Period	not applicable			1	7.54	0.01	not applicable		
Species*Period	not applicable			1	0.25	0.62	not applicable		
Species*Year	1	1.44	0.24	not applicable			not applicable		
Error	31			30			40		

Note:

Model 1 includes the categorical variables Species (Chaffinch and Yellowhammer only), Year and their interaction. This is for data from the late periods only.
Model 2 includes the categorical variables Species (Chaffinch and Yellowhammer only), Period within the winter and their interactions. This is for data from winter 2003-04 only.
Model 3 includes all three species (Chaffinch, Yellowhammer and Tree Sparrow) as categorical variables and is for data collected during the late periods of both winters.

Table 9b. Results of ANOVAs examining the influence of Species, Year, Period within the winter season and their interactions on mean distances between all possible pairs of systematically determined fixes of radio-tagged Yellowhammers, Chaffinches and Tree Sparrows in the West Fife during winters 2002-03 and 2003-04.

Source of variation	**Model 1**			**Model 2**			**Model 3**		
	df	F-value	*P*	df	F-value	*P*	df	F-value	*P*
Model	3	0.82	0.49	3	2.45	0.08	2	4.20	0.02
Species	1	0.59	0.45	1	0.05	0.83	2	4.20	0.02
Year	1	0.13	0.72	not applicable			not applicable		
Period	not applicable			1	7.02	0.01	not applicable		
Species*Period	not applicable			1	0.34	0.56	not applicable		
Species*Year	1	1.43	0.24	not applicable			not applicable		
Error	31			30			40		

Note:

Model 1 includes the categorical variables Species (Chaffinch and Yellowhammer only), Year and their interaction. This is for data from the late periods only.
Model 2 includes the categorical variables Species (Chaffinch and Yellowhammer only), Period within the winter and their interactions. This is for data from winter 2003-04 only.
Model 3 includes all three species (Chaffinch, Yellowhammer and Tree Sparrow) as categorical variables and is for data collected during the late periods of both winters.

Table 10a. Pair-wise comparison of mean distances between systematic radio-telemetry fixes using Tukey tests following the ANOVAs shown in Table 9a. Significant differences (*P* < 0.05) are shown in bold.

	MEAN DISTANCE (metres) ± SE		Comparison (*P*)	
Model 1: Species between years (late period only)				
	2002-03 (n=10)	**2003-04** (n=8)		
Chaffinch	445 (± 91)	632 (± 107)	0.44	
Yellowhammer	652 (± 128)	570 (± 106)	0.18	
Model 2: Species between periods (winter 2003-04 only)				
	Early period (n = 8)	**Late period** (n = 8)		
Chaffinch	1002 (± 225)	632 (± 107)	0.19	
Yellowhammer	**1106 (±191)**	**570 (± 106)**	**0.03**	
Model 3: Between all three species (late period only)				
Chaffinch (n = 18)	557 (± 71)		Chaffinch vs Yellowhammer	0.60
Yellowhammer (n = 17)	601 (± 79)		**Chaffinch vs Tree Sparrow**	**0.04**
Tree Sparrow (n = 8)	1259 (± 471)		Yellowhammer vs Tree Sparrow	0.07

Table 10b. Pair-wise comparison of mean distances between systematic radio-telemetry fixes using Tukey tests following the ANOVAs shown in Table 9a. Significant differences (*P* < 0.05) are shown in bold.

	MEAN DISTANCE (metres) ± SE		**Comparison (*P*)**	
Model 1: Species between years (late period only)				
	2002-03 (n=10)	**2003-04** (n=8)		
Chaffinch	619 (± 187)	784 (± 131)	0.54	
Yellowhammer	1031 (± 203)	660 (± 115)	0.30	
Model 2: Species between periods (winter 2003-04 only)				
	Early period (n = 8)	**Late period** (n = 8)		
Chaffinch	1230 (± 290)	784 (± 131)	0.20	
Yellowhammer	**1275 (±209)**	**660 (± 115)**	**0.02**	
Model 3: Between all three species (late period only)				
Chaffinch (n = 18)	719 (± 110)		Chaffinch vs Yellowhammer	0.34
Yellowhammer (n = 17)	801 (± 118)		**Chaffinch vs Tree Sparrow**	**0.02**
Tree Sparrow (n = 8)	1875 (± 613)		Yellowhammer vs Tree Sparrow	0.06

Table 11. Ranking matrices for Yellowhammer and Chaffinch in West Fife during winter 2003-04 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	+		+++	---	+++	+++	4
PA	+	---		---	+++	+++	3
SC	+++	+++	+++		+++	+++	5
WD	-	---	---	---		---	0
OT	-	---	---	---	+++		1

Scrub >>> Stubble >>> Pasture > Autumn sown crops > Other >>> Woodland

b) **Chaffinch**

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

Scrub >>> Stubble = Woodland >>> Other > Pasture > Autumn sown crops

Note: A '+' indicates that birds were recorded in the numerator habitat more than the denominator habitat with respect to the proportions that were available. Triple symbols indicate a statistically significant ($P < 0.05$) difference.

Table 12. Ranking matrices for Yellowhammer and Chaffinch in West Fife during winter 2003-04 based on the counts of each species as a proportion of the total count in a particular habitat with the proportion of each habitat in the study area.

a) **Yellowhammer in West Fife**

Numerator / Denominator

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

Scrub >>> Stubble > Pasture >>> Other >>> Autumn sown crops = Woodland

x) **Chaffinch in west Fife**

Numerator / Denominator

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

Scrub >>> Pasture . Stubble > autumn sown crops >>> Other > Woodland

Note: A '+' indicates that birds were recorded in the numerator habitat more than the denominator habitat with respect to the proportions that were available. Triple symbols indicate a statistically significant ($P < 0.05$) difference.

Table 13. A comparison of parameter estimates of movement probabilities from mark-recapture ringing in West Fife between the two winters 2002/03 and 2003/04.

SPECIES	**PARAMETER**			
	2002/03		**2003/04**	
	Estimate	**Standard Error**	**Estimate**	**Standard Error**
YELLOWHAMMER				
Survival probability	0.73	0.22	0.65	0.13
Probability of retrapping	0.09	0.05	0.14	0.05
Transfer probability	0.08	0.03	0.07	0.02
CHAFFINCH				
Survival probability	0.56	0.18	0.80	0.17
Probability of retrapping	0.04	0.02	0.04	0.02
Transfer probability	0	0	0.02	0.01
TREE SPARROW				
Survival probability	0.85	0.19	0.61	0.25
Probability of retrapping	0.11	0.05	0.02	0.02
Transfer probability	0.07	0.03	0	0

Table 14. A comparison of two analytical approaches to radio-telemetry data ((i) as mark-recapture, and (ii) by measuring distances between sequential fixes) from west Fife in late winter 2002/03.

	Likelihood of moving X km from mark-recapture analyses*		Mean distance between sequential fixes[+]
Tree Sparrow	16-20%	3.7-4.8km	1.26 km
Yellowhammer	5-28%	1.9-2.8km	0.60 km
Chaffinch	17%	2km	0.56 km

***** From Calladine *et al.* (2003).
[+] From Table 10.

FIGURES

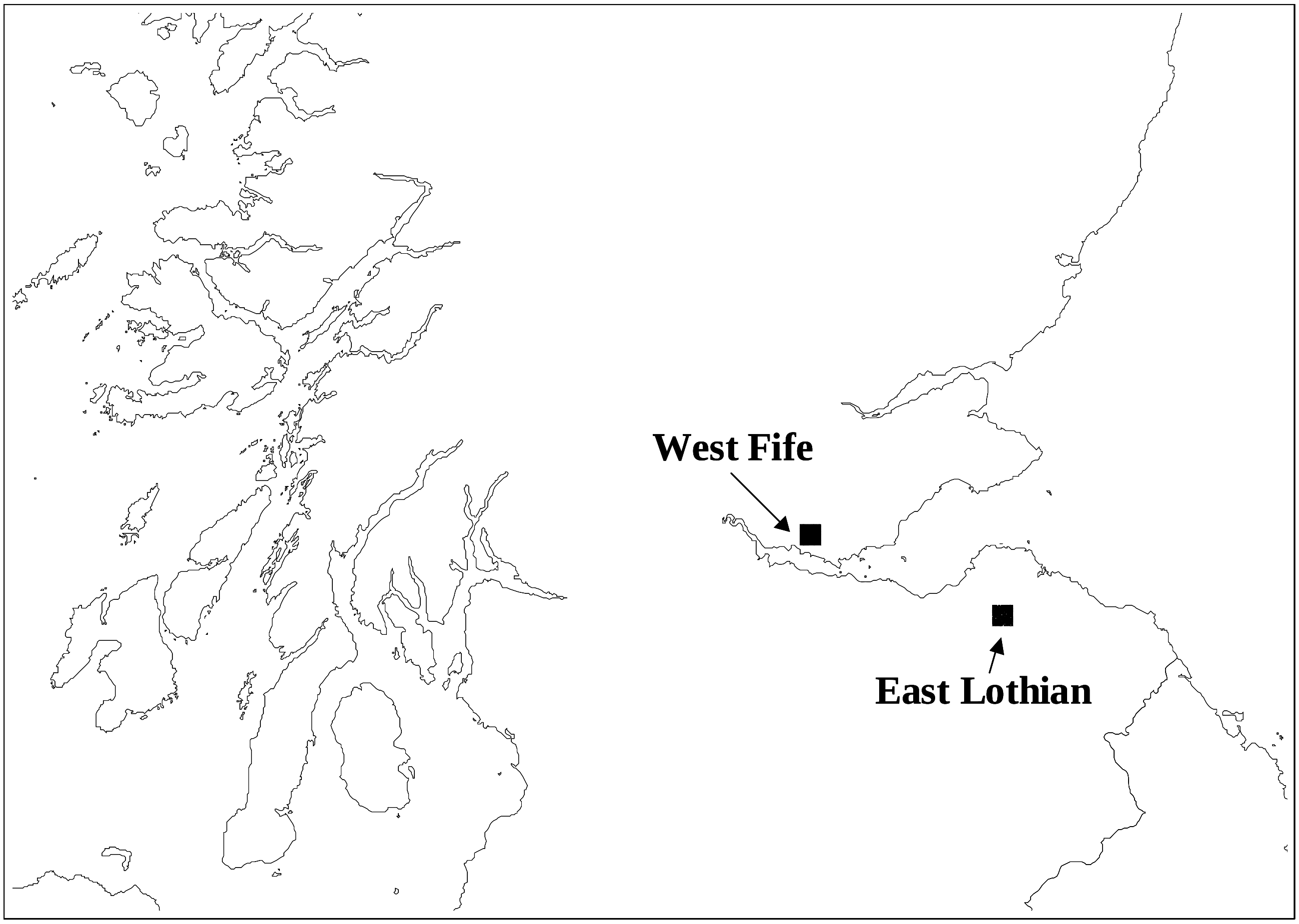

Figure 1. Location of the two study areas.

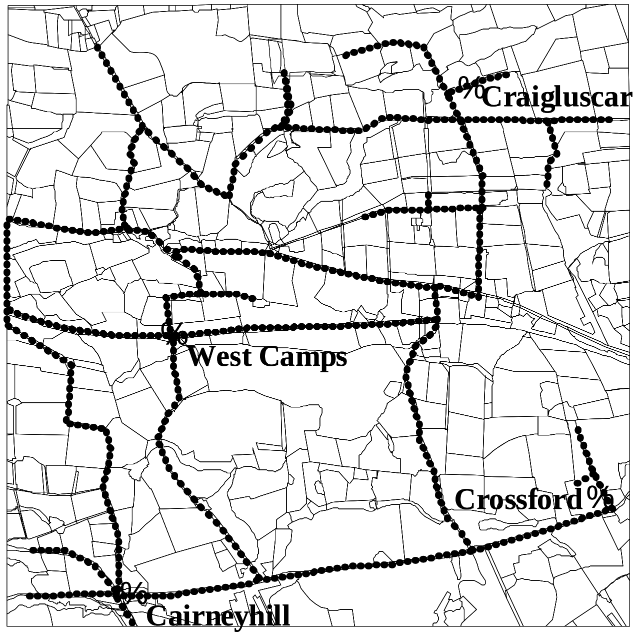

Figure 2. Map of West Fife study area (5 km by 5 km) showing the location of the four ringing sites and the cycle transect route for monitoring bird abundance.

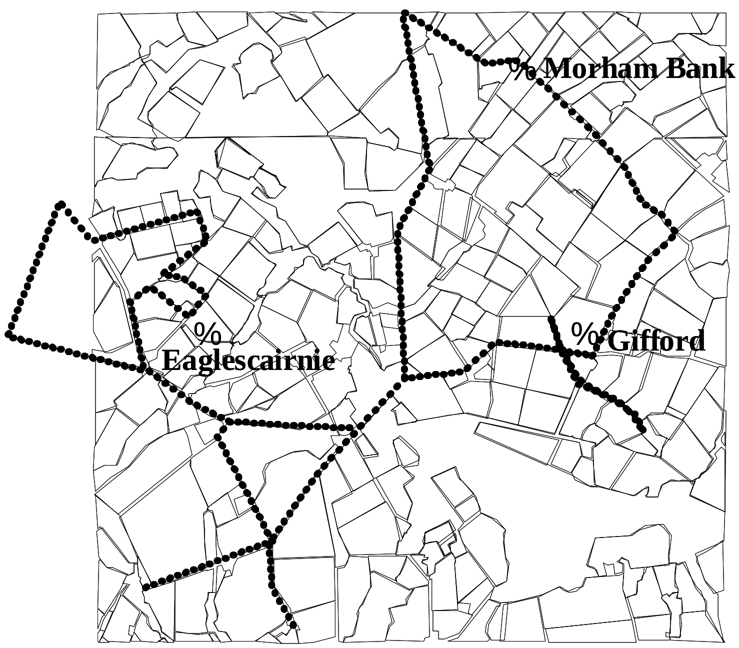

Figure 3. Map of East Lothian study area (5 km by 5 km) showing the location of the three ringing sites and the cycle transect route for monitoring bird abundance.

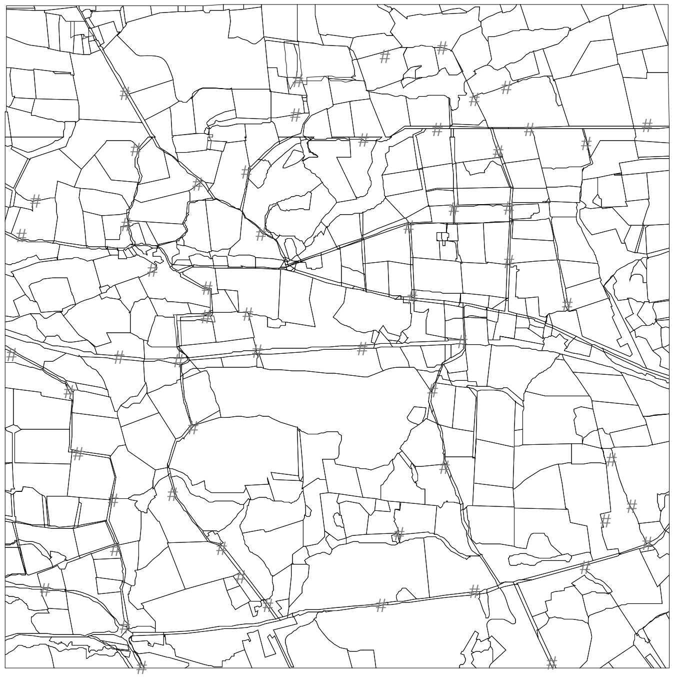

Figure 4. The 59 scanning points used in systematic radio-telemetry in the West Fife study area.