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POINT TRANSECT SURVEYS FOR SONGBIRDS: ROBUST METHODOLOGIES

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ABSTRACT. – Point transect sampling is widely used for monitoring trends in abundance of songbirds. It is conceptualized as a snapshot method in which birds are 'frozen' at a single location. For conventional methods, an observer records birds detected from a point for several minutes, during which birds may move around. This generates upward bias in the density estimate. We compare this conventional approach with two other approaches: a method in which the observer records locations of detected birds at a snapshot moment; and a method which records distances to detected cues (songbursts), rather than birds. We implement all three approaches together with line transect sampling and territory mapping in a survey of four bird species. The conventional method gave a biased estimate of density for one species. The snapshot method was found to be the most efficient of the point sampling methods. Line transect sampling proved more efficient than the point sampling methods for all four species. This is likely to be generally true, provided the terrain and habitat allow easy use of a design with random transect lines. We conclude that the snapshot method is more appropriate than the conventional timed count method for surveying songbirds. Although precision for the cue-based method was rather poor (partly because too few resources were devoted to cue rate estimation), it might be particularly useful for some single-species surveys. In addition, it is the only valid method for estimating abundance from surveys in which acoustic equipment is used to detect the birds.

The importance of bird monitoring programs has been highlighted by the outcome of the 2002 World Summit on Sustainable Development at Johannesburg. Political leaders agreed to strive for 'a significant reduction in the current rate of loss of biological diversity' by the year 2010. This has forced scientists to review methods for monitoring population trends, and relating those trends to changes in biodiversity. Point sampling, either point counts or point transect sampling, are especially popular tools for monitoring songbirds, and this paper seeks to provide better methods for such monitoring programs.

Point counts are widely used to assess relative abundance of songbirds. An observer goes to each of a series of points, and counts the number of birds he or she can detect, either using 'counts to infinity' or by counting within a fixed radius of the point. The methodology is simple, and untrained volunteer observers can gather the data, provided they can correctly identify the species. However, point counts provide data of limited value, because the size of the count depends on detectability of the birds as well as on their abundance. Thus comparisons of counts across species are invalid, because different species have different detectabilities, and comparisons within a species across different habitats are invalid, because different habitats result in different detectabilities. Even comparisons over time in counts made at the same locations are compromised if habitat succession affects detectability, or if an observer's hearing ability changes over time, or if observers change, or, in the case of surveys near roads, if traffic noise increases over time. Norvell et al. (2003) found that detectabilities of birds recorded on point counts varied three to five fold, and concluded that population trends based on point count data were unstable, and did not allow reliable inference.

Bibby and Buckland (1987) found that detectability changed appreciably as restocked conifer plantations grew. They used point transect sampling theory to estimate the detection function (probability of detection as a function of distance from the point) for several species. Averaging across species, they estimated that 50% of birds were detectable at 57 m when the trees were just two years old, but by the time they were 11 years old, this distance was 30 m. Thus point counts to infinity would overestimate abundance in two-year-old plantation almost four-fold relative to 11-year-old plantations. For some species, results are more extreme; the corresponding distances for Willow Warblers (*Phylloscopus trochilus*) were 81 m and 28 m, indicating that they are more than eight times ($(81/28)^2$) as detectable in two-year-old plantation as in 11-year-old plantation! Even when Willow Warbler counts were truncated at 30 m from the point, they were still found to be twice as detectable in two-year-old plantation as in 11-year-old-plantation, leading to 100% overestimation of relative abundance in the former habitat compared with the latter.

For the above reasons, we do not consider that point counts provide a useful measure of abundance, whether absolute or relative. Corrections of counts for detectability are required (Pollock et al. 2002). The most common way to achieve this is through use of distance sampling, which comprises a set of methods in which distances of detected birds from a line or point are recorded (Buckland et al. 2001). Extension of point count methods to distance sampling is termed point transect sampling or variable circular plots.

Point transect surveys of breeding songbirds are subject to several difficulties that may lead to substantial bias in estimates of density: singing birds are often much more detectable than non-singing birds, so that if detections of both are pooled, models for the detection function may yield biased estimates (Burnham et al. 2004:392); in closed habitats, most detections are aural, so that it is difficult to estimate distances to detected birds; measurement errors generate substantially more bias in density estimates than do errors of similar magnitude in line transect sampling (Buckland et al. 2001:195); for species that do not sing frequently, birds very close to the point may be missed, especially in closed habitats, which violates the assumption that all birds at or near the point are detected; any movement of birds during the count period generates substantial bias in density estimates, even if the movement is independent of the observer (Buckland et al. 2001:173); surveys are often multi-species, and it is difficult to devise simple field procedures that will give low bias across a wide range of species.

We consider different methods for conducting point transect surveys. The first method is the standard approach of recording any birds detected, together with estimated distances from the point, within a fixed count period. The second method is closely similar to the first, but is the ‘snapshot’ method of Buckland et al. (2001:173), in which the observer attempts to record the locations of detected birds at a ‘snapshot’ moment, with time spent before this moment to determine what is around, and after this moment to confirm locations of birds. The third method is based on recording distances to detected cues for a pre-determined length of time at each point (Burnham et al. 2004:356-9). A cue is defined to be a single burst of song (or the start of a songburst, if it lasts for a significant length of time). The theory of cue counting applies to such data. As a comparison, we also consider a line transect survey, conducted using standard protocol.

This paper was prompted by a belief that the standard implementation of point transect sampling sometimes yields estimates of density with substantial bias. In addition, some authors justify using point counts without adjustment for detectability, noting deficiencies, real and imagined, in point transect sampling methods, while ignoring the greater deficiencies of point counts. An example is Hutto and Young (2002); see Ellingson and Lukacs (2003) and Hutto and Young (2003) for ensuing discussion. Diefenbach et al. (2003) give an excellent account of the consequences of failure to adjust for detectability in the case of strip transect sampling, and Norvell et al. (2003) do the same for point counts.

METHODS

FIELD STUDY

The study area was an area of woodland and parkland at Montrave Estate near Leven in Fife, Scotland. The target species identified for testing the methods were Common Chaffinch (*Fringilla coelebs* L.), Winter Wren (*Troglodytes troglodytes* L.), Great Tit (*Parus major* L.) and European Robin (*Erithacus rubecula* L.). For the point sampling methods, data were recorded at the 32 points shown in Fig. 1, while for the line transect survey, the transects shown by the diagonal lines were walked. Each point was surveyed twice by each method, and the detections from the two visits pooled, as recommended by Buckland et al. (2001:294). Similarly, each line was surveyed twice in the line transect survey, and data pooled. Total time in the field under each method was recorded. Detection distances were estimated with the aid of a laser rangefinder.

For all methods, females were not recorded, because they are much less detectable than males, so that combining data for both results in a detection function that is problematic to model (Burnham et al. 2004:343). At the season (28 March to 11 April 2004) and time of day (approximately 0600 to 1100 hrs GMT) that the surveys were conducted, most males of all four species could be expected to sing during the time the observer was at a given point. Rarely, males were detected visually that did not sing. For Common Chaffinch and Great Tit, these were identifiable from their plumage; for Winter Wren and European Robin, they were sometimes identified from behavior towards a mate, and sometimes because they were heard to sing as the observer approached or departed from the point. Such birds were included in the data for the conventional and snapshot point transect methods; for the cue-based method, they were recorded for estimating cue rate (see below), but were recorded as giving no cues in the recording period. Any bird that was seen but could not be sexed was not recorded under any of the methods.

Method 1: conventional point transect survey. – In method 1, the observer visited each point of the design. A minute was allowed for the birds to resume normal behavior, then birds were recorded for five minutes, as suggested by Bibby et al. (2000:97). The location of the bird was estimated, based on its location when first detected. The observer remained at the point for the full five minutes, but was allowed to locate birds more accurately after the end of the five-minute period, to obtain improved estimates of distance for birds that could not be seen, and whose location was not obvious from their song.

Given an appropriately randomized survey design, the important assumptions for method 1 are (Buckland et al. 2001:29-37):

1. Birds at the point are detected with certainty.

2. Birds are detected at their initial location.
3. Measurements of bird-to-observer distances are exact.

The length of the recording period at each point (five minutes here) is a compromise between the requirements of assumptions 1 and 2. If the time period is too short, then a significant proportion of target birds may fail to sing during the count period, especially at times of day when activity is reduced. If the habitat is closed so that such birds may pass undetected even at the point, or if such (male) birds cannot be identified visually even if they are seen, this leads to downward bias in density estimates. By contrast, failures of assumption 2 lead to upward bias, which increases as time spent at the point increases. Point transect sampling is a 'snapshot' method, in that it attempts to estimate the number of birds in a sample plot at a single instant of time. If birds are moving around, the longer the count period, the greater the number of birds that will use the plot at some point during the count period. The observer therefore detects and records birds that were not on the plot at the start of the count period, leading to upward bias in density estimates. The problem is made worse because, even if a bird is moving around within the confines of the plot, it is more likely to be detected when it is closer to the point, so that detection distances tend to be too small, generating further upward bias. Assumption 2 also implies that birds do not move prior to detection (either away from the point, generating negative bias, or towards it, generating positive bias) in response to the observer.

Bias in distance measurements generates greater bias in point transect estimates of density than in line transect estimates. For example, if all distances are underestimated by 10%, this generates 11% upward bias in line transect estimates of density, but 23% upward bias in point transect estimates (Buckland et al. 2001:176). However, even if estimates are unbiased on average, random error in distance estimates generates bias in density estimates, and again, the bias is greater for point transects than for line transects. This is because the number of birds available for detection increases with distance from the point; we expect twice as many birds at 20 m as at 10 m. If we estimate these distances, then a majority of the birds recorded as being at say 10 m will in fact have been at a distance greater than 10 m, simply because there were more birds there to be recorded. The extent of this bias is explored for the closely-related cue-counting method by Buckland et al. (2001:195).

To minimize problems with assumption 3, a laser rangefinder was used. Even for cues that are purely aural, a rangefinder reduces measurement error significantly, as it is usually possible to identify the bush or tree in which the bird is hidden if the observer has the flexibility to move away from the point, either during the count or after. The distance from the point to the bush or tree can then be measured.

Method 2: snapshot survey. – In method 2, the 'snapshot' moment was defined to be precisely three minutes after arrival at the point. The observer did not move during the pre-snapshot period, and concentrated on identifying the locations of target birds. After the snapshot moment, the observer was allowed to move around, and to take whatever time was needed, to verify suspected locations corresponding to the snapshot moment. If the location of a previously-detected bird could not be confirmed, or had changed appreciably so that distance from the point at the snapshot moment could not be determined with reasonable precision, it was treated as undetected.

Assumptions are the same as for method 1. Use of a snapshot moment ensures that assumption 2 is met, provided birds have not moved in response to the observer by the snapshot moment. The time spent before and after the snapshot moment is to try to ensure that assumption 1 is met. Again, a laser rangefinder was used to minimize failures of assumption 3.

Method 3: cue-count survey. – Cue counting (Hiby 1985, Buckland et al. 2001:191-7) was designed to estimate whale abundance. Observers travel on a ship or in an aircraft along a line transect, recording cues (usually whale blows) within a sector ahead of the platform, along with distances of those cues from the platform. The methodology estimates the number of cues produced per unit time per unit area. Hence, effort is measured as the time spent observing, not the distance travelled. Thus the method is equally applicable to point transect surveys, in which the observer does not move at all while on effort. This also allows the sector angle to be taken as 360 degrees; that is, all detections are recorded, irrespective of angle. To convert the number of cues per unit time per unit area to an estimate of animal density, an estimate of cue rate (average number of cues per unit time per animal) is required.

In implementing method 3, the same points were used as for methods 1 and 2. As with method 1, the observer waited one minute for birds to settle, then recorded for five minutes at each point. During this period, every detected songburst of the target species was recorded, along with an estimate of its distance from the point. Movement of the observer away from the point up to approximately 10 m was allowed, so that positions of singing birds could be more accurately located.

A note was made of those birds for which the observer was confident that all songbursts during the five-minute count had been recorded. This included birds that did not sing during the count, provided they could be identified as male from plumage or behavior, or they were heard to sing outside the count period.

The important assumptions for method 3 are:

1. Songbursts at the point are detected with certainty.
2. The locations of songbursts are unaffected by the presence of the observer.
3. Measurements of songburst-to-observer distances are exact.
4. The recorded cue rate (songbursts per unit time per bird) is an unbiased estimate of the cue rate of the male birds present during the survey.

This method thus solves both of the more problematic assumptions of methods 1 and 2. If a bird is immediately above the observer, it may remain undetected. However, if it sings, its song almost certainly will be heard. Further, movement of birds that is independent of the observer does not bias the method; we record the location of the songburst, which is well-defined, rather than the location of the bird, which may vary appreciably through the count period. When cues rather than birds are recorded, assumption 3 may be rather more difficult to satisfy, as more distance measurements must be made, and an observer may easily become 'swamped' in multi-species surveys, with too much information to record. However, the distances are now better defined, so that method 3 is likely to give estimates of density with lower bias if the number of species being surveyed is small. Assumption 4 should not be problematic provided cue rate is estimated as an integrated part of the survey protocol as here. Bias might be substantial if for example fieldwork was conducted in the morning, and cue rates estimated in the afternoon. Cue rates should be recorded at a representative set of times and locations, synchronously with the point transect survey.

Method 4: line transect survey. – For comparison, line transect surveys were conducted along the diagonal lines of Fig. 1. As with all other methods, a laser rangefinder was used to measure distances. Because the survey area was small, sampling along each line was extended into a buffer zone, as recommended by Strindberg et al. (2004:200), to reduce edge effects.

Given a randomized design, the key assumptions of method 4 are:

1. Birds on the line are detected with certainty.
2. Birds are detected at their initial location.
3. Measurements of perpendicular distances of birds from the line are exact.

Movement of birds that is independent of the observer is less problematic for line transect sampling than for point transect sampling. Provided average speed of the birds is under around half the speed of the observer, bias is small (Buckland et al. 2001:131). For most songbird species, if only the singing birds are recorded, this is likely to be the case. Measurement error also generates less bias in line transect estimates than in point transect estimates. The implications of assumption 1 are similar to those for point transect methods 1 and 2, except that the observer will have less time to ensure that a bird on the line is detected.

Method 5: territory mapping. – To provide a benchmark for assessing the methods, an attempt was made at mapping the territories for each of the four species, using recording methods similar to those recommended by Bibby et al. (2000). Locations of detected birds during each of the eight visits (two for each of the four distance sampling methods) were recorded, and a ninth visit was used exclusively for territory mapping, in conjunction with the locations recorded in earlier visits. Because the study area was small, this was achievable, and the resulting estimates are likely to have better precision than the other methods, and with low bias. However, it is not possible to quantify precision and bias of the territory mapping method. Further, the method is not practical for surveying larger areas, and care must be taken in dealing with territories that extend beyond the study area. In this study, if more than 50% of a territory was judged to be outside the study area, it was excluded.

Data analyses. – The distance data were analysed using Distance 4.1 Release 2 (Thomas et al. 2003). For most analyses under methods 1, 2 and 4, the model with the smallest AIC value, selected from the hazard-rate model, Fourier series model, Hermite polynomial model and half-normal model with cosine adjustments, was chosen. However, models with similar AIC values were also examined, and if histograms of the data, taken together with goodness-of-fit tests, suggested that another model should be preferred, it was selected. For method 3, model selection was done in a more subjective way, using at most two parameters to fit the detection function, due to the tendency to overfit cue-count data, which exhibit overdispersion (see below).

SIMULATION STUDY

For practical reasons, the methods were tested in a small study area (approximately 33 ha). As a consequence, points were only 100 m apart, so that many birds were detected from more than one point. Additionally, some bias due to edge effects might be anticipated.

The first assumption failure we explore is that of independent detections, which is violated when birds are detected from more than one point, a common occurrence when the study area is small. We thus seek to assess the statement in Buckland et al. (2001:176) that this violation is of little practical consequence. The second assumption we examine is that birds are distributed independently with respect to the point locations. Under this assumption, the number of birds at distance 20 m from the point should be around double the number at distance 10 m, because the area of an annulus of radius 20 m is twice that of an annulus of radius 10 m. This assumption is generally achieved by placing a grid of points randomly over the survey area, but for small survey areas, edge effects can become problematic. This may be overcome by use of buffer zones (Strindberg et al. 2004:193), in which the grid of points is extended beyond the survey region. However, for very small survey regions, this can add substantial survey effort with a relatively modest increase in detections. Hence for our point-based methods, we did not sample in the buffer zone, and instead we explore the bias arising from the resulting edge effect. In our simulations, we assume that no birds occur outside the study area; if they do, bias can be reduced by recording distances to birds detected beyond the boundary. This policy was adopted in the real survey.

Three populations were simulated. In the first, 10,000 bird locations were randomly generated from a uniform distribution through a square study area of size 10 km by 10 km. The area was divided into a grid of 100 squares, each of size 1 km by 1 km, and a point was located at the centre of each grid square. Detections from each point were generated from an untruncated half-normal detection function, $g(r) = \exp\left(-r^2/2\sigma^2\right)$, where r is distance from the point and $\sigma = 75$ m. Under this model, half of the birds at 88 m are detected, as are 10% of birds at 161 m. Thus in this case, points are sufficiently separated that the same bird (which is assumed to have a fixed location) is highly unlikely to be detected from more than one point, and no point is less than 500 m from the edge of the study area, so that edge effects can be ignored. The data were analysed assuming a half-normal detection function, so that all assumptions hold, and estimation should be reliable.

In our second population, the study area was again square, but with side 1.5 km. Density was as before, so that 225 birds were present, randomly distributed through the study area. Sampling was restricted to a central square of side 1 km, giving a belt of width 250 m all around, so that there would be no edge effects. Density in the central 1 km square was estimated by conducting a point transect sample survey, again comprising 100 points. The 1 km square was divided into a grid of squares each of size 1 ha, and a point was located at the centre of each square. The same half-normal detection function was used to simulate detections as for the first population. Thus most birds within the central 1 km square will be detected from at least two points, so that the assumption of independent detection distances is badly violated.

In the third population, we used the Montrave site as the study area, with 32 points located as for the real survey. A randomly-distributed population was simulated with true density equal to one bird per hectare. Detections were generated from the half-normal model with $\sigma = 50$ m, which corresponds to an effective detection radius of about 71 m, comparable with the species in the real survey. Thus many birds will be detected from more than one point, and there is a strong edge effect, so that number of birds available for detection at distance r increases more slowly than linearly with distance from the point.

RESULTS

FIELD STUDY

The data are summarized in Table 1, and density estimates in Table 2. For 10 of the 12 analyses under methods 1, 2 and 4, the model with the smallest AIC value was selected. However, Common Chaffinch and Winter Wren showed some evidence of observer avoidance. For two of the 12 data sets, this resulted in a fitted hazard-rate detection function with certain detection out to 60 m or so, with an implausibly rapid fall-off beyond 70 m. In these two analyses, a model with a slightly higher AIC value and a more plausible fit to the detection function was selected.

All methods yield 95% confidence intervals for each species that include the territory mapping density estimate, with one exception: method 1 gave an estimate of density (0.58 territories ha^{-1}) for Great Tits that was significantly higher than the territory mapping estimate of 0.21 territories ha^{-1}. Great Tits at this site seemed to have large territories, and moved around fairly rapidly within them. This frequently resulted in the detection of a bird close to a point during the five-minute recording period that had not been in detectability range at the outset of the count. Three Great Tit territories had been excluded from the territory mapping estimate because they were judged to be mostly outside the study region. Even if all three had been included, the resulting territory mapping estimate of 0.30 territories ha^{-1} would still have been well below the lower confidence limit of 0.36 territories ha^{-1} using conventional point transect sampling methods.

Of the other estimates of Table 2, there is weak evidence that method 1 overestimated Common Chaffinch density (perhaps for the same reason as Great Tit), and that method 2 underestimated Winter Wren density (perhaps due to observer avoidance); in both cases, the 95% confidence interval for density only just includes the value obtained from territory mapping.

Table 3 shows fairly consistent estimates of effective detection radius for methods 1-3. The estimates of effective strip half-width for method 4 are surprisingly close to the estimates of effective radius; *a priori*, smaller values were expected, because the number of birds potentially available for detection increases linearly with distance from a point, but is uniformly distributed with distance from a line.

Table 4 shows that line transect sampling required least time in the field, followed by the snapshot method. The two methods that required five minutes' recording time at each point took the longest. Taking account of precision of estimates, line transect sampling was estimated to be the most efficient method for all four species. Amongst the point transect methods, there was no clear winner: the snapshot method was most efficient for European Robin and Winter Wren, and the conventional method for Common Chaffinch and Great Tit. The cue-count method tended to have poor precision. Although increased numbers of detections led to higher precision in estimates of effective radius (Table 3), there was large overdispersion in the counts, and hence the variance in encounter rate across points was high. Further variance was introduced by having to estimate the cue rate. Averaging across the four species, 9% of the variance in the cue-count density estimates was due to estimating the effective radius, 41% to estimating encounter rate, and 50% to estimating cue rate. This is a clear indication that more resources should have been devoted to estimating the cue rate.

SIMULATION STUDY

Results of the simulations are summarized in Table 5. For population 1, the assumptions of the method all hold, except for the fact that variance estimation assumes that the points randomly sample the region, whereas we used a systematic grid of points. For animals that have patchy distributions, with areas of high and low density, Strindberg et al. (2004:195-6) noted that this strategy, coupled with random placement of the grid, tends to yield smaller variation among different realizations of the design than does simple random sampling. The results of Table 5 show that the mean of the estimated standard errors of estimated density, calculated assuming simple random sampling, is 0.0754 birds ha^{-1}, whereas the actual standard error, estimated by the standard deviation of estimated densities in 1000 simulations, is 0.0706 birds ha^{-1}. This suggests that the conventional variance estimator is slightly conservative.

For population 2, there was severe overlap between plots, so that most birds in the study area were detected more than once. On average there were 356 detections from a population of 225 birds, of which only 100 birds were within the central 1 km square that was surveyed. Nevertheless, there was almost no bias in estimated bird density: true density was one bird ha^{-1} and the mean of the 1000 estimated densities was 1.0056 birds ha^{-1} (SE 0.0026). There was also only mild underestimation of the standard error: true standard error (estimated by the standard deviation of the 1000 population size estimates) was 0.0815 while the mean of the 1000 analytic standard errors was 0.0750.

Population 3 was designed to match closely the real populations of the previous section. Using the untruncated half-normal model, there was downward bias in estimated density (true density one bird ha^{-1}, estimated density 0.9509 birds ha^{-1} with standard error 0.0061). This arises because the model for the detection function attempts to fit the combined effects of declining detectability with distance and the reduced availability of birds for detection at greater distances. This composite function is no longer half-normal in shape, and so the use of a half-normal model introduces bias. If we use the more flexible models of Distance (as was the case in the previous section), this bias is substantially reduced. Even though there is large bias in our estimates of detectability by distance, this bias is absent at zero distance where detection is certain. Thus if we model the composite function well, we estimate average density at the points with low bias. If those points are representative of the whole study area (as they are by design), then average bird density in the study area is well estimated. In fact, even if we retain the inflexible half-normal model, but truncate the distances at 80 m, bias is negligible (estimated density 0.9961 birds ha^{-1}), although precision is reduced.

DISCUSSION

Typically, field tests of distance sampling methods are conducted on small study sites, as here. Fewer resources are required (an important consideration when testing out several methods), and it is often feasible to estimate the total population with high precision, as was done here using a mapping census. The great value of distance sampling however is that it can provide estimates of abundance over very large areas with only modest resources. Survey design issues are addressed by Buckland et al. (2001, 2004).

For methods based on songbursts or cues rather than birds, multiple songbursts from the same bird will often be recorded. This violates the assumption of independence. Distance sampling estimation methods are very robust to such violations, but one aspect of the analysis is not: goodness-of-fit testing and model selection (Buckland et al. 2001:171). Hence greater care is needed in judging which model provides the best fit, with a tendency to overfit the data if standard model selection criteria are used.

Point transect methods based on cues avoid the major biases that often affect estimated densities from standard point transect sampling. Cue-based methods remain valid even if birds are moving large distances during the count, and the assumption that a song is detected with certainty when the bird is at the point is more plausible than the assumption that the bird is detected with certainty, whether it sings or not. The methods work best when cues are short and well-defined, especially for single-species surveys, or surveys of a small number of species. Cue definition should be carefully considered. For species that typically have long songbursts, the start of a songburst might be defined as the cue. For a species that gives a wide variety of songs and calls, only those easily detectable and associated with territory-holding birds might be considered a cue. Cue rate estimation can be problematic. In some studies (including studies of other bird groups such as calling gamebirds), it may be possible to estimate cue rate from a sample of radio-tagged birds.

Multi-species surveys are problematic for the cue count method. If the observer must record all songbursts heard while on effort, swamping may easily occur, resulting in poor data quality. A possible solution suggested by the associate editor is to divide the species of interest into two or more groups. At each point, the observer records species from the first group. Having completed recording for this group, he or she immediately starts recording species in the second group, and so on. If there are multiple observers, each group could be assigned to one observer, with simultaneous recording.

It may prove impossible to estimate cue rate simultaneously with detection of cues, so that additional time will need to be spent at each point, or a subset of points, to estimate cue rates for each species. An additional difficulty is that, unless the cue rate survey work is conducted with great care, there will be a tendency to bias the sample towards more detectable individuals, which typically will have higher cue rates than less detectable individuals – a form of size-biased sampling. A strategy that addresses these difficulties is to use two observers. One conducts the distance sampling survey, while the other simultaneously estimates cue rates. This second observer is given a set of plots to survey, where each plot is sufficiently small that all males of the relevant species can be detected with near certainty. The cue rate of each detected male is monitored for a fixed period of time; if none is detected in the plot, the observer proceeds to the next plot. This strategy would also resolve the problem of high variance in the cue rate estimates encountered in this study.

Acoustic systems are now available that record songbursts, and allow estimation of the distance of a songburst from a point. When these are used for surveys, typically the recording time at each point is long. Thus conventional point transect methods should not be used to analyse these data, because of the upward bias arising from bird movement. Conventional methods also require that different songbursts from a single bird are identified as coming from one bird. By contrast, the cue-count method is unaffected by bird movement, and the recording unit is the individual songburst, not the bird. Hence the method is ideally suited to analysis of acoustic data – provided cue rate can be estimated reliably.

Because different species can show markedly different behaviors, a single method is unlikely to work well across all species. In multi-species surveys, a possible solution to this problem is to have observers working in teams. One or two of each team might operate a cue-based approach for a subset of species, while another observer uses a method based on bird detections for the remaining species. As a check, for one or two species that should be well-surveyed by either approach, data might be collected using both approaches. Comparative analyses can then be conducted, to determine whether the two estimates differ significantly, and which method yields the better precision. If the two estimates do not differ significantly, they might be averaged, with weights proportional to the reciprocals of the variances, to yield a more precise estimate.

This study shows that the snapshot method (Buckland et al. 2001:173) is practical to implement. Like the cue-based method, it does not assume that birds are frozen at a single location during the recording period, and so avoids the potential for marked upward bias of conventional methods with a fixed count period at each point. We implemented the conventional method using five-minute counts. Many groups use ten-minute counts or even longer, so that bias arising from bird movement can be expected to be substantially greater than seen here.

In practice, the snapshot method will be a compromise between the ideal of recording bird locations at an instant in time and the need to spend some time at a point to be able to detect and identify birds. A convenient way to define the snapshot moment is to set a watch to beep. Every effort should be made to monitor locations of birds near the point as the snapshot moment approaches, and the first priority after the snapshot moment should be to record the distances of these birds from the point. For birds further away, if their distance from the point at the snapshot moment can be estimated with reasonable confidence, they should be recorded. If they could not be located after the snapshot moment, or they were found to have moved from their previous location so that distance at the snapshot moment is not known with any certainty, they should not be recorded.

Line transect sampling proved the most efficient method of those assessed. This is likely to be the case generally in relatively open habitat where a straight line can be walked without large deviations. However, in more difficult habitats and terrains, line transect sampling may be impractical, or only workable by cutting transect lines, in which case they may prove less efficient than point transect methods.

The majority of detections in this study were purely aural. Nevertheless, the survey rangefinder was invaluable for estimating distances. It was often possible to identify the exact bush or tree that a detected bird occupied, and then to measure the distance to it accurately. Where more guesswork was involved, distances were often confirmed using the rangefinder when walking out from the point. This allowed frequent feedback on the accuracy of estimated distances, as well as accurate measurement of more problematic detections. Beyond about 70 m, less care was taken to ensure accuracy, for two reasons: first, it is time-consuming to measure longer distances accurately if the location of the bird cannot be accurately determined from the point (and many of those distances may be truncated at the analysis stage); and second, provided there is no bias in shorter distances, bias in these long distances does not bias density estimates. Such bias generates bias in the estimated detection function, but if flexible models are used for the detection function, this does not generate bias in the resulting density estimate, for much the same reason that edge effects do not bias density (see simulation study).

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Table 1. Summary of the data. Method 1 is conventional point transect sampling with five minutes per point; method 2 is the snapshot method; method 3 is the cue-count method; method 4 is line transect sampling; and method 5 is territory mapping. Detections beyond distance *w* were deleted before analysis (termed truncation, Buckland et al. 2001:15-17).

Species	Common Chaffinch	Great Tit	European Robin	Winter Wren
Method 1 (*w*=110 m)				
No. of detections	74	44	57	132
Method 2 (*w*=110 m)				
No. of detections	63	18	50	117
Method 3 (*w*=92.5 m)				
No. of cues detected	627	177	785	765
Cue rate				
Sample size	33	12	26	43
Mean	7.94	8.17	17.92	7.28
Std error	1.19	3.72	2.43	1.21
Range	0-23	0-41	0-43	0-29
Method 4 (*w*=95 m)				
No. of detections	73	32	80	155
Method 5				
No. of territories	25	7	28	43

Table 2. Estimated number of territories per hectare ($\hat{D}$) for each species under each survey method. 95% confidence limits are shown in parentheses; measures of precision are not estimable for method 5.

Species	Common Chaffinch	Great Tit	European Robin	Winter Wren
Method				
1	1.03	0.58	0.52	1.29
	(0.74,1.43)	(0.36,0.94)	(0.26,1.06)	(0.80,2.11)
2	0.90	0.22	0.60	1.02
	(0.62,1.29)	(0.12,0.39)	(0.38,0.94)	(0.80,1.32)
3	0.71	0.26	0.82	1.21
	(0.44,1.14)	(0.08,0.79)	(0.51,1.32)	(0.81,1.80)
4	0.64	0.26	0.68	1.07
	(0.46,0.89)	(0.16,0.43)	(0.47,1.00)	(0.86,1.36)
5	0.75	0.21	0.84	1.30

Table 3. Estimated effective detection radii (m) by species and method. For method 4 (line transect sampling), the effective strip half-width (m) is shown. 95% confidence limits are shown in parentheses.

Species	Common Chaffinch	Great Tit	European Robin	Winter Wren
Method				
1	67	62	74	71
	(58,78)	(51,74)	(52,104)	(57,90)
2	67	64	65	75
	(57,78)	(54,75)	(54,77)	(69,83)
3	74	65	51	66
	(70,79)	(58,71)	(47,57)	(63,69)
4	59	63	60	75
	(48,72)	(47,84)	(44,83)	(65,86)

Table 4. Coefficients of variation (%) for estimated density (cv), hours of fieldwork (hrs), and estimated number of hours of fieldwork to achieve a coefficient of variation of 10% (hrs_{10}), by species and method. These estimates are obtained by assuming that the standard error of an estimate is proportional to the reciprocal of the square root of sample size.

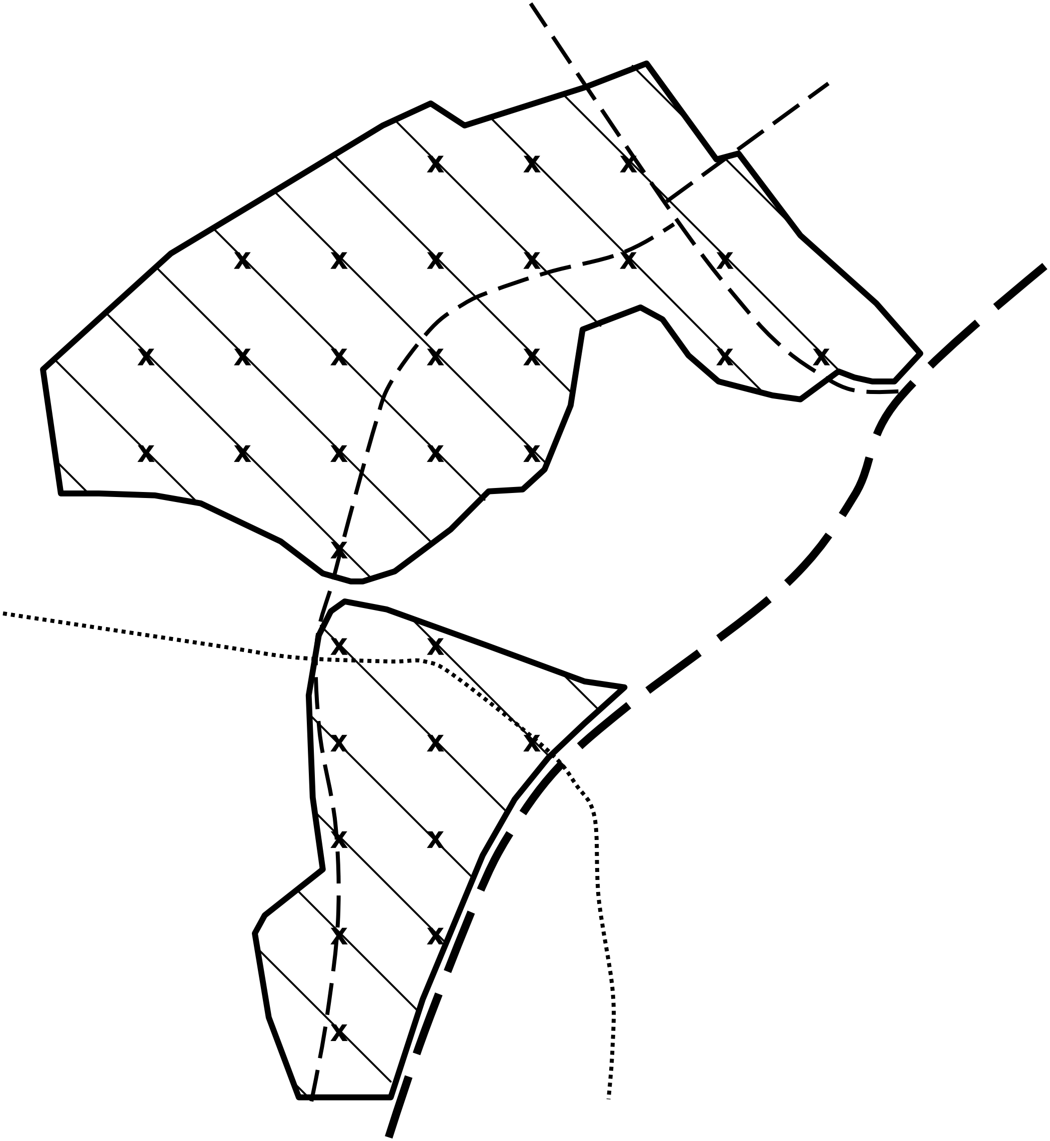
Method	Species	Common Chaffinch	Great Tit	European Robin	Winter Wren
1	cv	16.9	24.7	36.7	25.1
	hrs	9.75	9.75	9.75	9.75
	hrs_{10}	27.8	59.5	131.3	61.4
2	cv	18.6	28.9	22.9	12.8
	hrs	8.38	8.38	8.38	8.38
	hrs_{10}	29.0	70.0	43.9	13.7
3	cv	23.6	59.3	23.9	20.0
	hrs	10.00	10.00	10.00	10.00
	hrs_{10}	55.7	351.6	57.1	40.0
4	cv	16.5	25.0	19.3	12.0
	hrs	7.88	7.88	7.88	7.88
	hrs_{10}	21.5	49.2	29.4	11.3

Table 5. Summary of simulation results. All assumptions were satisfied for population 1. For population 2, plots overlapped so that most birds were detected from more than one point. For population 3, an edge effect was present. The half-normal detection function without truncation was fitted for all three populations; truncation at 80 m was also implemented for population 3. True density was $D = 1$ bird ha^{-1}. For all populations, 1000 realizations were generated. Tabulated are the mean number of detections ($\bar{n}$), the mean of the resultant estimates of density (mean($\hat{D}$), birds ha^{-1}), the corresponding standard deviation of these estimates (sd($\hat{D}$), birds ha^{-1}), the standard error of the mean of the estimates (se(mean($\hat{D}$))=sd($\hat{D}$)/√1000, birds ha^{-1}), and the mean of the estimated standard errors of $\hat{D}$ (mean(se($\hat{D}$)), birds ha^{-1}).

	Popn 1	Popn 2	Popn 3	Popn 3, $w = 80\,\mathrm{m}$
$\bar{n}$	353	354	41	32
mean($\hat{D}$)	1.0029	1.0056	0.9509	0.9961
sd($\hat{D}$)	0.0706	0.0815	0.1924	0.3160
se(mean($\hat{D}$))	0.0022	0.0026	0.0061	0.0100
mean(se($\hat{D}$))	0.0754	0.0750	0.2099	0.3557

Caption to fig

Fig. 1. The study site at Montrave in Fife, Scotland. The dotted line is a small stream, the thin dashed lines are tracks, and the thick dashed line a main road. The 32 points, which comprise the design for methods 1-3, are shown by crosses, and are laid out on a systematic grid with 100 m separation. The diagonal lines are the transects used for method 4.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