



Reduction of bias when estimating bird abundance within small habitat fragments

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Abstract: We used the distance detection function from five-minute point counts entirely within large woody vegetation patches to derive a method of truncating counts of birds detected close to the observer to estimate their relative abundance in small habitat patches. Our method trades off loss of information by truncation of bird sightings at successively larger distances from the observer to reduce sampling bias. Truncation of counts to include detections within 10 m of the observer gave similar absolute density as distance methods for the six most abundant native and six introduced species. Distance analysis showed that introduced species were in general more conspicuous than New Zealand native species. Use of counts very close to the observer reduces detectability biases for species and habitat comparisons to give more robust measures of community structure, allows inclusion of very small habitat fragments into the analysis, and provides a density measure for infrequently encountered species. However, the counts are still best treated as relative indices rather than absolute density estimates. Much of the international literature using counts and distance sampling estimation methods to claim increased bird diversity and abundance in larger habitat patches may be unreliable because these include directional biased estimation of abundance in small patches.

Keywords: distance analysis; farmland bird; five-minute point count; sampling bias

Introduction

Point counts are frequently used to generate bird abundance estimates. A key drawback to this methodology is that it often does not account for detection bias, which may vary greatly according to a number of factors such as observer, individual species behaviour, habitat type, vegetation density and season (Norvell et al. 2003; dos Anjos 2007; Johnson 2008). Increasingly, distance sampling theory and analysis (Buckland et al. 2001, 2004) are used to eliminate detection bias by describing a detection function for each species and habitat type or landscape. The detection function describes the probability of detecting a bird present at successively larger distances from the observer. If detection differs by habitat types (e.g. because of effects of vegetation thickness on detectability), the measure of differential detectability is incorporated to convert the number of detections to an unbiased estimate of absolute density (birds ha⁻¹).

The basic assumptions behind distance sampling are that (1) all animals at zero distance from the observer are detected, (2) detectability declines monotonically with distance, (3) animals do not move in response to the observer before they are detected, and (4) measurements of distance from the observer to the animal are accurate (Buckland et al. 1993, 2001, 2004). We encountered a fifth and usually unstated assumption when

we counted birds in woody habitat patches on New Zealand sheep & beef farmland, such as forest remnants and farm shelterbelts; that is, that sufficient habitat is present around the observer for counts at successive distances to decay away fully and thereby reliably reveal the detection function. In many cases the woody vegetation patches on sheep & beef farms are each so small that the habitat itself runs out well before the probability of detecting a bird at increasing distance from the observer is extinguished. A standard distance sampling analysis approach will therefore seriously distort density calculations. Our main objective was to identify associations between species richness and habitat metrics, such as patch size and patch shape complexity within continuous vegetation, so that we can advise farmers on how to monitor bird abundance and diversity. To accomplish this we needed a method to describe community composition with minimal detection and sampling bias between different patches and habitat types, some of which were very small. Our study goals therefore precipitated a major conceptual problem about how to estimate a detection function from counts pooled from several small, medium and large patch sizes, rather than the typical circumstance of pooling all bird detections in a global landscape study.

This paper first describes the conceptual problem in more detail, then proposes a range of potential solutions. A modified estimation methodology is described that uses short radial

truncation distances to simultaneously mitigate sampling and detection biases so that relatively unbiased comparisons of relative abundance and diversity in different habitats and patch sizes can follow. The performance of the new method is investigated by comparing density estimates with classical distance estimates for six native and six introduced bird species in mixed native and exotic forest patches on South Island sheep & beef farms. We end by discussing the limits and utility of the modified method for other studies.

Methods

Study questions and data collection

Bird surveys were conducted within woody habitat patches on 12 sheep & beef farms on the South Island of New Zealand over the course of eight field circuits from 2007 to 2009 (Meadows 2011). Five-minute point counts were conducted according to the general methods of Dawson and Bull (1975), but incorporated distance sampling field methods by measuring the radial distance and angle from the observer to each recorded bird. On each farm, five-minute-count locations were generated using Hawth's Analysis Tools for ArcMap v.9.2 (Beyer 2004; ESRI 2006), which generated 15 random sample points within vector polygons representing shelterbelts and woody patches of each farm's boundary for every survey circuit. Although points were generated at random within individual patches, an area term was used to account for spatial representation of varying patch sizes across the landscape. The end result was that points were generated such that more counts occurred within large vegetation patches than small patches. All survey points were at least 100 m apart to avoid double-counting.

In accordance with prior related research (Blackwell et al. 2005), observers waited for 2 min upon reaching each sample point before starting the five-minute count in order to ensure that any species that might have been disturbed would have returned to the site and recommenced movement or singing. The following data were recorded for all birds detected within a 5-min period: species, individual or group, number of individuals (cluster/flock size), detection cue (seen, heard or both), behaviour and location (distance and angle to observer using a range finder (Bushnell Yardage Pro®, Bushnell Performance Optics, Overland Park, KS, USA). We avoided the peak calling periods at dawn and dusk, when conspicuousness and detectability can change rapidly (Dawson & Bull 1975).

Each habitat polygon was assigned to one of seven habitat types: mixed native trees, mixed native and exotic trees, mānuka/kānuka trees, exotic conifer trees, shrubland, exotic conifer shelterbelt, mixed-tree shelterbelt. As our fundamental ecological question centred on species' presence within woody vegetation, a habitat boundary truncation rule was applied. First, radial distance and angle information were used to generate a GIS map of bird sightings across the landscape for all farms; all sightings located outside of vegetation patches (usually open paddock) were eliminated. Second, to ensure sightings within polygons were representative of bird presence within a given habitat, and not error around coordinate estimation by GPS units, observer-reported habitat was compared to habitat type information for each polygon. Recorded habitat information tightly corresponded to that of ArcMap, and only a few points were eliminated based on disparities between habitat data.

Generating a detection function using distance theory

When using distance sampling in conjunction with point counts, observers record the distance from a randomly placed point to an animal detected within a conceptual truncation radius w (Fig. 1). Not all animals within distance w will be detected, but a fundamental assumption is that all animals at zero distance are detected, or failing that, the proportion of detections at zero distance is known. The distribution of the observed distances is used to estimate a detection function $g(r)$ that describes the probability of detecting a bird at radial distance r , where $g(0) = 1$ (Buckland et al. 1993, 2001, 2004). If the assumptions hold, this function allows the estimation of the average probability P of detecting a bird given that it is within radius w around the point. Density can then be estimated as $D = n/(P*a)$, where n is the number of animals detected and a is the size of the region covered (the total number of survey points multiplied by πw^2). A related and useful metric associated with distance analysis is the 'effective strip width' (ESW; for counts along transects), or 'effective detection radius' (EDR; for point counts like those employed in this study). The EDR is the distance beyond which as many extra birds are actually detected as were present but not detected inside the radius (Fig. 1). The area of a circle with a radius of EDR is therefore equivalent to the area where all birds have been censused (i.e. probability of detection is 1).

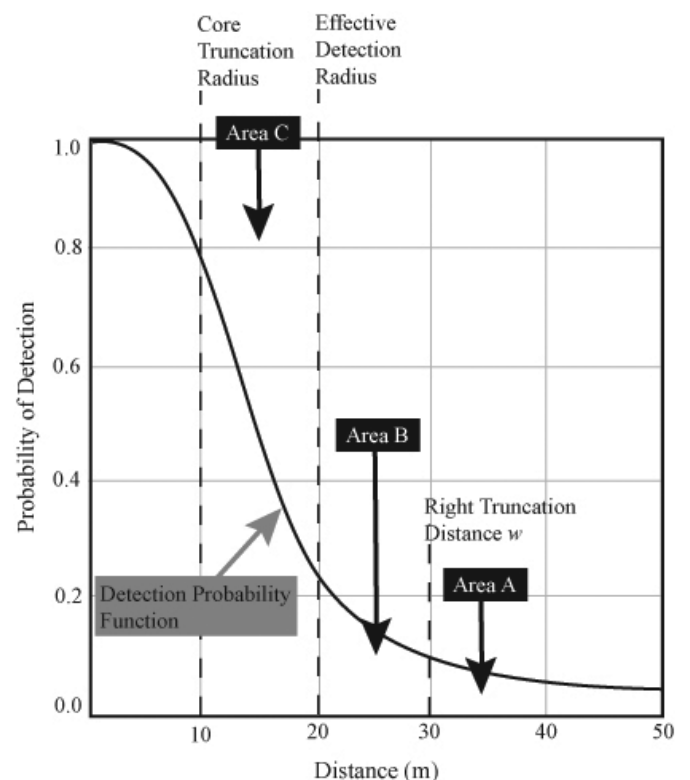


Figure 1. Underlying model behind distance estimation. All data in Area A are eliminated to help model the detection function within radius w . The 'effective detection radius' (EDR) is estimated so that the same number of birds are missed within the EDR as are detected outside it; i.e. Area B (below the detection function line and between 20 and 30 m) and Area C (above the detection function but within the EDR) will therefore have the same size. This study proposes the instigation of a 'core-truncation-radius' at 10 m within which nearly all the birds will be detected.

It is recommended that in order to reliably estimate a detection function and density, a minimum total of 60–80 sightings from 10–20 replicate transects is needed within a study area (Buckland et al. 2001; Mazerolle et al. 2007). To maximise model fit for point count data, it is further recommended (Buckland et al. 2001) that data are ‘right truncated’ beyond the radial distance (‘right-truncation distance’) w at which the probability of detection in the initial model is less than 0.10 (Fig. 1).

Limitations of distance sampling for estimates in small habitat patches

Distance density estimates are mostly used to estimate species’ densities at a landscape scale, with little focus on delineating differences in size and type of discrete habitat patches within the land matrix. While habitat may be included as a covariate in fitting a detection function, there is no clear established methodology for looking at patch-level differences in density estimates. A fundamental and usually unstated assumption of distance modelling is that a continuous sampling domain is available, with birds present all the way out and well beyond the right-truncation distance. If so, the rate of fall of the detection probability function at increasing distance from the observer is driven entirely by the conspicuousness of the birds and the observer’s ability to detect the birds in such a habitat type. However, if the radius of some of the patches sampled for distance estimation is less than the right-truncation distance, part of the decrease in the number of birds detected is also driven by the distribution of patch sizes in the landscape. Any density estimates generated using a common detection function from all bird counts pooled from several patches will therefore be distorted, with the degree of distortion depending on the proportion of the overall habitat sampled that is made up of small patches with a radius less than the EDR. Most seriously, the abundance and diversity of birds in very small habitat patches would be underestimated compared with that in larger patches where the radius of the patch is greater than distance w .

Potential solutions to unbiased estimation at the individual-patch level

There appear to be at least three interrelated ways to obtain unbiased estimates of patch-level bird abundance and diversity using distance analysis. One approach would be to treat each individual patch as a separate study area and generate patch-by-patch detection probability functions and then density estimates for each focal species. Alternatively, a global detection function could be generated based only on data from relatively large patches (where the radius of the patch exceeds the right-truncation distance) of a given habitat type, and excluding sample points close to the habitat patch edges. Normally, the habitat type influence on the detection probability function would be calculated by ‘post-stratification’ within Program Distance software (Buckland et al. 1993, 2001, 2004). If it can be reliably assumed that the detection probability function applies equally well to small and large patch sizes of a given habitat type, patch-level density estimates could instead be obtained in two ways. First, the total number of birds detected in each count could be divided by a modified and aggregated estimate of the probability of detection for the patch as a whole. This ‘patch probability of detection’ will depend on patch size and could be found by integrating the area under the distance probability detection function for

successively larger patch radii (r) and dividing it by the area of a circle of radius r . Second, the data could be truncated to only admit detections very close to the observer into the analysis. For example, if a ‘core-truncation-radius’ of 10 m was used (Fig. 1), birds more than 10 m from the observer would be eliminated from consideration. The global detection function generated from large continuous habitat patches approximates 1 at these short truncation distances, so it could be assumed that nearly all of the birds present in the inner circle (10 m radius) around the observer would be detected. There would also be virtually no scope for detection bias from habitat-type or patch-size effects at such short distances from the observer. Nevertheless data from very small habitat patches that have a radius less than the left-truncation distance would need to be further delineated and treated separately, i.e. such patches should be either eliminated from the analysis altogether or their combined physical area calculated and divided into the total count to estimate absolute abundance for the patch.

Approach followed in our study

The current study recorded a total of 33 different species. There were very few patches for which distance sampling recommendations regarding sightings and replicate transects could be sufficiently met. Even when pooling across patches of similar habitat types, there were still insufficient sightings in one or more habitats to meet the recommendations for generating global detection functions. This precluded the generation of patch-by-patch detection functions, making calculations of global detection functions from data pooled only from the relatively large patches (i.e. where the radius of the patch was greater than w) the only valid approach. Within this, the ‘patch probability of detection’ approach was also impractical because (1) integration of global detection functions for individual species (each including upper and lower confidence intervals to account for uncertainty) would have been too complex, and (2) patches were irregular shapes, hence assuming they were circular could have introduced several errors. As a result, the ‘truncation’ approach for generating patch-level estimates of bird abundance and community composition was employed.

Eliminating all data beyond the core-truncation-radius removes detection bias from raw counts. However, such severe truncation also results in a loss of potentially valuable ecological information. If severe, this loss could undermine statistical power for hypothesis testing. Our initial line of inquiry therefore focused on the optimum choice of the core-truncation-radius to trade off reduction in potential bias against loss of sampling information (i.e. setting the truncation distance too far out introduces potential habitat and patch-size biases, while setting it too close to the observer forces elimination of more data than necessary in order to make unbiased comparisons).

Results

Point counts

Altogether, 9050 birds were detected at 1086 points distributed between 246 habitat patches over the 2-year study. There were sufficient data to generate unbiased distance sampling estimates for six native species (bellbird *Anthornis melanura*, fantail *Rhipidura rhipidura*, grey warbler *Gerygone igata*, rifleman *Acanthisitta chloris*, silveryeye *Zosterops lateralis*, tomtit *Petroica macrocephala*) and six introduced species

(blackbird *Turdus merula*, chaffinch *Fringilla fringilla*, goldfinch *Carduelis carduelis*, redpoll *C. flammea*, starling *Sturnus vulgaris*, yellowhammer *Emberiza citrinella*). These were also chosen as candidate indicator species for the main study (Meadows 2011).

Distance analysis within large patches

Detection functions were based on data only from patches with an average radius greater than 30 m. A global detection function was generated for each species then post-stratified by habitat type. Cursory preliminary distance analysis using a truncation probability of detection of 0.10 pointed to a right-truncation distance of 30 m. This corresponds very well to right-truncation distances selected by MacLeod et al. (2012) and Weller et al. (2012) for farm-landscape-level distance models. All subsequent distance analyses and associated detection probability functions and EDRs were therefore generated from a pooled sample of counts taken only from patches with continuous habitat of radius ≥ 30 m (assuming the area of the patch was a circle). After the removal of patches with radii < 30 m a number of smaller habitats, such as mixed-tree stands and plantation conifer blocks, contained insufficient sightings for reliable habitat-level estimates. Hence, detection functions could only be described for two prominent habitat types that were present on the majority of study farms (mixed native and exotic trees, and mixed native trees). Best fits were found using half-normal and hazard-function cosine relationships after right truncation at 20–30 m where the detection probability reached 0.10 (Table 1). Whether a species was first seen or heard, observer, and season were covariates that were of greatest utility in fitting detection functions (Table 1).

Detection function shape varied considerably between species. Starlings were the most detectable (conspicuous) and fantails the least, whereas bellbird is an example of a species with medium detectability (Fig. 2; Table 1). Introduced species were generally more conspicuous than native species; i.e. their EDRs were much higher and detection probability only started to inflect downwards c. 10 m or more from the

observer, whereas average detection probability had already fallen to 0.3–0.7 for native species at this distance (Fig. 2b,c; Meadows 2011).

Core truncation to create an unbiased index of abundance

Although truncation at a core radius of 10 m resulted in retention of only c. 20% of the original bird detections, only 48 (20%) of the habitat patches were excluded from analysis. However, since shelterbelts are generally smaller than bush and scrub patches, counts at 13 (42%) of the 31 shelterbelts were excluded. Choosing a truncation distance of more than 10 m from the observer would have started to seriously impair overall average detectability, particularly of the native species (Table 1; Fig. 2). The higher the proportion of birds missed, the more scope there is for habitat and observer influences on detectability. Therefore the truncation distance was fixed at 10 m for all point counts as a practical compromise and reasonable trade-off between the overall loss of information (birds detected > 10 m from the observer), retaining the ability to sample small woody vegetation patches, and minimising bias by keeping detection probability close to 1.

Comparison of absolute density from distance sampling and point counts

To test the expectation that counts truncated at 10 m would not be seriously biased, their density estimates (birds detected within a circle of 10 m radius) were compared with those generated for large patches in each of the two main habitat types. Distance estimates for each species were calculated by dividing the number of birds detected out to the right-truncation distance (20–30 m depending on species) by a circle with the EDR estimated for that species as its radius (Table 1). As detection probability within the 10 m inner core around the observer is expected to be close to 1, the densities estimated by dividing the truncated counts by an area of a circle of radius 10 m (314 m²) should be similar to those generated from EDRs.

There was a reasonably close correspondence between average absolute densities estimated from truncated counts and

Table 1. Model selection for each of 12 candidate species for two predominant habitat types, including detection function, truncation distance and covariates for the best-fit mode. A maximum of two covariates were selected.

Species	Detection function (expansion): cosine relationships	Right truncation (m)	Covariates	EDR mixed native & exotic (m)	EDR mixed native (m)	Probability of detection at 10 m
Native						
Bellbird	Half-normal	30	None	14.06	15.43	0.6
Fantail	Half-normal	20	None	9.26	9.63	0.3
Grey Warbler	Half-normal	30	Observer	16.3	16.3	0.75
Rifleman	Half-normal	20	None	11.94	11.94	0.55
Silvereye	Hazard-rate	30	Seen/heard	16.09	16.45	0.9
Tomtit	Hazard-rate	20	Seen/heard, Season	11.42	11.42	0.5
Introduced						
Blackbird	Hazard-rate	30	Observer	17.34	17.54	0.8
Chaffinch	Hazard-rate	25	None	17.19	17.19	1
Goldfinch	Hazard-rate	30	Seen/heard	19.06	19.06	1
Redpoll	Hazard-rate	25	Seen/heard	17.47	17.47	1
Starling	Half-normal	30	Seen/heard	18.77	19.21	1
Yellowhammer	Hazard-rate	30	Seen/heard	17.69	17.86	0.9

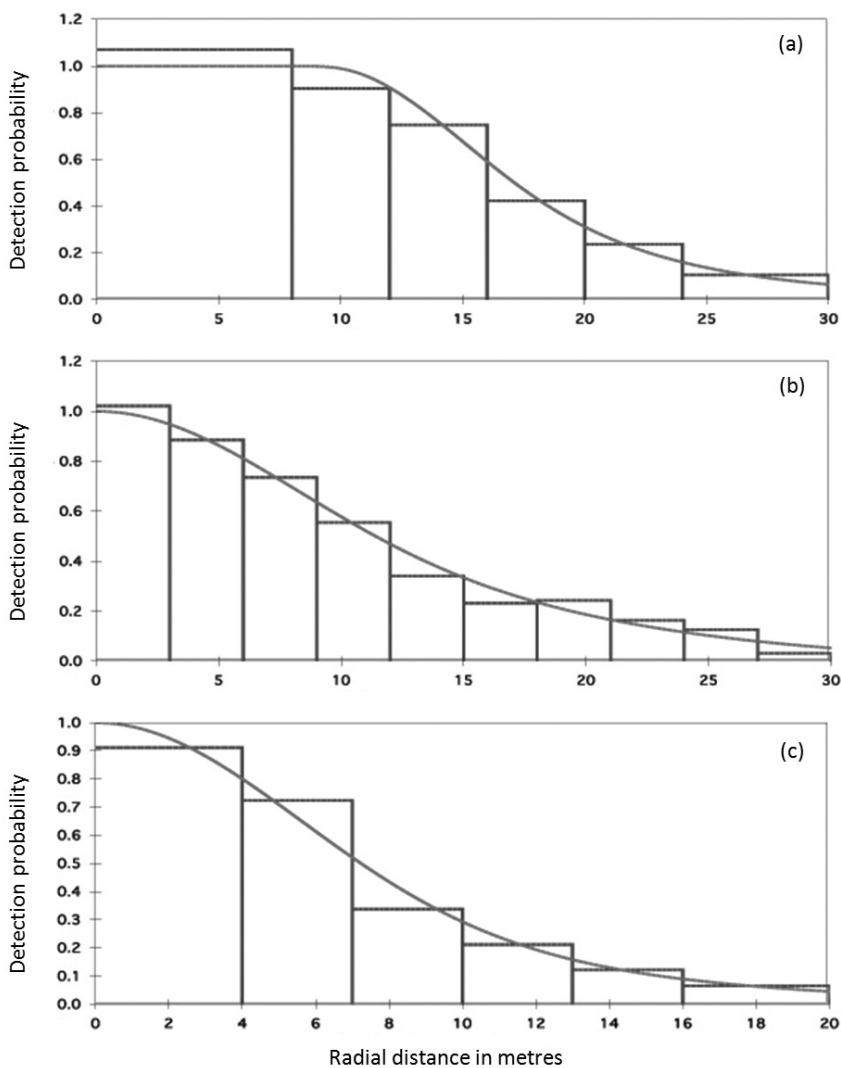


Figure 2. Estimated detection function pooled over the two main habitat types for (a) starling, (b) bellbird, and (c) fantail. The histogram shows the number of detections in three bands out from the observer and the line is fitted by program Distance from data pooled from large (radius ≥ 30 m) patches using a 20–30 m right-truncation-distance (as in Table 1).

those estimated from distance sampling using EDRs (Fig. 3). The largest discrepancy was for the fantail, the species with lowest conspicuousness. Otherwise, most of the estimates fell on or just above the line of parity (only silveryeye estimates lie to the right), as would be expected with probability of detection beginning to dip before 10 m distance from the observer is passed. Some scatter around the line of parity is expected because of stochastic variation in the number of birds in any patch that occur within the inner 10 m core around the observer during the five-minute count, compared with how many occur in the wider zone out to the right-truncation distance. With such a short period of observation, and continuous movement of the birds, it is to be expected that the proportion of the birds in the two zones will fluctuate between 5 min monitoring periods. As the inner core (10 m radius) is generally a third the size of the area censused by distance models (a circle of radius EDR, c. 20–30 m; Table 1), the variance of the 10-metre count is likely to be higher than that of the distance estimate for the same point. Also, disturbance by the observer may trigger a net movement out of the 10 m radius inner core, leading to more birds being detected using the wider EDR method from Distance (Table 1).

Discussion

Distance model building

In accordance with our results, MacLeod et al. (2012) and Weller et al. (2012) similarly found, for much larger datasets, that a 20–30 m right truncation was most appropriate, and that whether a bird was first seen or heard often improved model fit (Table 1). However, in the current study, application of our ‘truncation’ method meant that detection functions could only be fitted for 12 species within two key habitats, in order to meet recommendations for detection and replication of the modelling. This emphasises the limitations of distance sampling in describing bird community composition in fragmented habitat mosaics, especially when the key ecological processes to be researched require unbiased estimates or indices of bird abundance at the individual-patch level, as opposed to the landscape level.

A second issue with estimating density within habitat patches arises from ‘edge sampling’ bias. Estimation by distance analysis will underestimate density when many sampling points fall near the edge of habitat patches. A segment of the standard detection circle (out to the right-truncation distance

w) that lies outside the patch cannot easily be excluded from the detection function without reducing the sampling area by the proportion of a full circle that falls outside the patch. When sampling points are randomly assigned, as in the present study, the probability of a point falling near the edge of a small patch is very much greater in small patches than for large patches. This will result in serious underestimation of bird density when using distance methods in smaller patches. Using counts with a very short truncation distance therefore also helps the robustness of the bird abundance estimation by being relatively unaffected by this edge sampling bias compared with much greater distortions likely from distance estimation. While methods exist to account for the presence of excluded or uncovered portions in the surveyed area (Buckland et al. 2001), they are computationally difficult and normally would require the use of an accurate GIS map. The strength of this edge bias has generally not been quantified in other studies using distance analysis. This study therefore asserts that near-truncation counts are likely to be relatively unbiased compared with full distance sampling estimates in fragmented habitat mosaics.

Choice of core-truncation-radius

We chose a single truncation distance of 10 m for all species. As a result, the correspondence of our counts with distance estimates varied between species (e.g. starlings vs fantail; Fig. 3). Other studies, particularly those focussing on a few species, may benefit from species-specific truncation distances. However, using a single distance keeps the method simple, facilitates field recording, and allows direct comparisons between measures of bird density and habitat quality (all of which can be conducted within the same 10 m radius of the observation point). Also, keeping the truncation distance as long as possible maximises the information gathered and might minimise the disturbance effects of the observer; there are several examples in the distance estimation literature where attraction or repulsion of the birds from the immediate vicinity of the observer can distort density estimation (Gutzwiller & Marcum 1997; Buckland et al. 2001, 2004; Diefenbach et al. 2003).

The traditional five-minute bird count method normally excludes all birds detected more than 200 m from the observer (Dawson & Bull 1975). Our study using distance methods underscores how such as large truncation distance has the potential to seriously bias five-minute bird counts for interspecies comparisons. Similarly, we would expect strong biases between five-minute bird counts in open habitats, compared with relatively closed ones like bush and scrub where line of sight is rapidly occluded by woody vegetation. Indeed, the main conclusion of our study is that the truncation distance must be very short (in the order of 10 m) to minimise bias when using raw counts to compare the abundance of different species, or of the same species in different habitats.

Truncation does not remove bias altogether

Counts truncated at 10 m still failed to detect some birds (Figs 2 & 3), so they are best used as a relative index of abundance rather than for calculating absolute abundance (birds ha^{-1}). Native species density will be particularly underestimated by the core count method, at least when a core truncation radius of 10 m is used. However, by minimising area C in Fig. 1, little scope remains for differential bias between very different habitat types and species, so diversity indices and relative abundance can be investigated with less risk of detectability having confounded conclusions.

A large gain for our study was realised by being able to estimate relative abundance from core counts even for the infrequently encountered species. Data constraints made it impossible to estimate density by distance methods for 65% of the 17 native species and 31% of the 16 introduced species recorded, whereas relative indices were available for all of them, and also from small habitat patches provided we assume that the detection functions of all the species are very similar close in to the observer. However, it is important to note that we only compared the two methods at the exact same locations within a very restricted set of conditions (only two habitat types and only in large patches ≥ 30 m). Although the EDRs for the two types of forest were remarkably similar (Table 1), application of the method to much smaller habitat patches or different habitat types might introduce more error from the

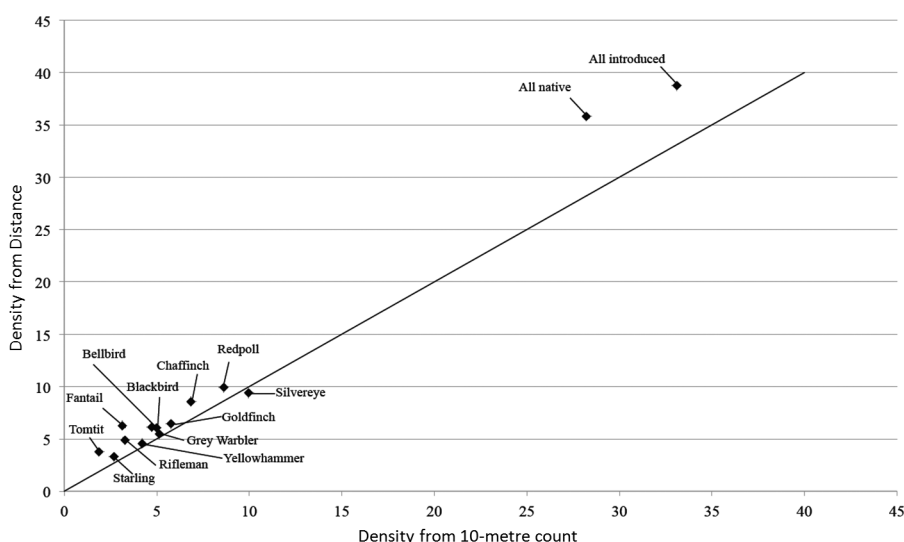


Figure 3. Comparison of the average density calculated from 10-metre truncated bird counts (x-axis) and the predicted density from distance methodology (y-axis). The line shows parity (i.e. equivalent density estimates from the two methods). The combined density estimates of all six native species and all six introduced species are shown at the top right.

10-metre-truncation counts as estimates of absolute density. For example, if smaller habitat patches have more undergrowth because of increased light penetration, detectability functions estimated within large patches of the same broad habitat type will no longer be accurate. Similarly, detectability of birds in close scrubby habitats may be so different from that in the mature tree habitats used here for calibrating and cross-checking the truncated count technique that even a severe truncation distance of 10 m may lead to some birds in scrub not being detected.

Until a larger sample of sightings in alternative habitats can be gathered to build comparative distance samples that actually measure the detectability differences in these very different types of habitat, we recommend that the 10-metre truncated counts are treated only as relative indices of abundance. For now they should only be used for cautious comparisons of relative abundance between different habitat types. Truncation will have reduced potential bias, albeit not totally eliminated it. A logical next step in testing the efficacy of the method will be to conduct power analyses to examine how truncation affects counts for low density species across multiple habitat types.

Extending the duration of counts

Severe truncation of bird observations to include only those close to the observer minimises bias, but it also causes loss of data. For some agendas, such as calculating species diversity indices, the many zero core counts would make statistical analysis difficult (Meadows 2011). We recommend further study to test the utility of extending the count duration well beyond the 5 min protocol commonly used in New Zealand. However, while this may increase the diversity of species detections, it might also introduce new problems of double-counting of the same individual birds.

Bias in previous studies

Much of the international literature using counts and distance sampling estimation methods concludes that bird diversity and abundance increase in larger habitat patches (Uezu et al. 2005; Davis et al. 2006; Marsden et al. 2006; Mitchell et al. 2006). If so, ecological restoration should prioritise creation of fewer but larger patches over many small ones for a given diversion of land use from production to conservation goals (Diamond 1976; Brotons et al. 2003; Donald & Evans 2006). We are concerned that some of these conclusions may be unreliable because of underestimation of bird abundance and diversity in small habitat patches. In general, we urge more critical evaluation of the influence of scale of habitat patches on density estimation, no matter which method is deployed. The traditional use of five-minute bird counts in habitat fragments in New Zealand will potentially have been very misleading.

Conclusion

Though a somewhat rudimentary approach, the truncation of sightings to such a close distance to the observer ensures that nearly all present species and individuals are recorded, and thus serves as a relatively unbiased and locally comprehensive index. Further, it provides abundance indices for all present species in the majority of sampled habitat patches and allows a more comprehensive description of community composition than is possible with distance sampling. Loss of data from exclusion of detections greater than a core-truncation-radius could undermine statistical power for testing hypotheses about habitat and farming effects on avian diversity and abundance,

but at least any differences detected can now be more reliably interpreted as being real ecological patterns rather than artefacts of differential detectability.

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