

A comparative evaluation of transect, point count and two-hectare search methods for bird abundance estimates in dry sclerophyll forest and rainforest

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Received: 23 October 2013

Birds were counted with transect, point count and two-hectare search methods at one dry sclerophyll forest site and one subtropical rainforest site in northern New South Wales. Five population density estimators and one reporting rate index were evaluated. True densities were unknown and comparisons focused on variation between methods. Distance sampling line transect and point transect estimates averaged 2.24 and 5.12 times greater than unadjusted strip transect and circular plot densities respectively. Point transects were likely affected by bird movements and densities averaged 2.62 times greater than line transects. Two-hectare search densities were comparable to line transects in dry sclerophyll forest and to strip transects in rainforest. Relative density estimates were more consistent, with strong correlations ($r = 0.71-0.95$) between all five estimators. Two-hectare search reporting rates correlated strongly with density, although the relationship was curvilinear. Reporting rates confound abundance and occupancy and should be interpreted cautiously. Pilot studies are recommended to test assumptions and expose the strengths and weaknesses of different bird survey methods. Transects were more efficient than point counts and two-hectare searches for estimating relative densities in this study.

INTRODUCTION

Estimates of abundance are useful for studies of the ecology of bird populations and their conservation (Bibby *et al.* 2000). Three measurement scales have commonly been used: nominal (presence/absence, e.g. species lists), ratio (relative, e.g. unadjusted counts) and absolute (e.g. intensive territory mapping with colour banding and nest searching) (Verner 1985). An index of abundance is some measurement that correlates strongly with absolute abundance (Sinclair *et al.* 2006).

Unadjusted counts often give biased estimates of abundance because some individuals are not seen or heard, birds move into and out of the search area and some individuals may be counted multiple times (Bibby *et al.* 2000). This problem is typically formulated as $c = pN$ where c is the count, N is the true number present and p is the proportion counted (Johnson 2008). The proportion counted varies with observer performance, physical and behavioural attributes of the birds, weather, topography, vegetation and over time (Rosenstock *et al.* 2002). Index counts have been criticised for assuming that p is constant, meaning that changes in counts are directly proportional to changes in true population size (e.g. Anderson 2001; Rosenstock *et al.* 2002).

Distance sampling methods have been heavily promoted for adjusting bird counts (e.g. Bibby *et al.* 2000; Buckland *et al.* 2008; Rosenstock *et al.* 2002). Distance sampling data are usually acquired with transects (termed 'line transects') or point counts (termed 'point transects'). Modelling of the decline in detection frequency versus distance produces an estimate of the proportion counted. For species that may be detected in groups (termed 'clusters'), distance sampling estimates cluster density which is then multiplied by average cluster size.

Very few evaluations of distance sampling for Australian birds have been published. Bell and Ferrier (1985) compared transect densities for seven eucalypt woodland bird species with known population sizes obtained through intensive observations of colour-banded, resident birds. They reported an average bias of -15 percent (range -43 to +37) for line transect estimates, which was a satisfactory result considering they did not account for seasonal variation in detectability. Given the improved methods since the 1980s (e.g. Buckland *et al.* 2001; Buckland *et al.* 2008), modern evaluations of distance sampling for Australian birds are required.

Species lists have been a popular bird survey method in Australia (Recher 1988). Reporting rate (also called frequency or incidence rate) is the number of lists in which a species was recorded divided by the total number of lists (Verner 1985). Presence/absence can be measured more easily than counts, but false negatives (failure to record a species when it is in fact present) will negatively bias reporting rates (Tyre *et al.* 2003).

The ongoing Atlas of Australian Birds (<http://www.birddata.com.au>) recommends a 20-minute, two-hectare search method for collection of species lists. Szabo *et al.* (2012) extended the two-hectare search for population size estimation by counting species inside the two-hectare plot, but acknowledged their estimates for woodland birds in South Australia may be negatively biased because reporting rates and counts were not adjusted for detectability. The Atlas of Australian Birds is the largest Australian bird survey database and further evaluations of two-hectare search reporting rates and densities are required.

Craig and Roberts (2001) reported that a 30-minute, one-hectare search method gave 'reliable' bird population density estimates in Western Australian eucalypt forests. Their small

radio-tracking study for Western Yellow Robin *Eopsaltria griseogularis* suggested that movements of birds into the plot compensated for under-counting. This reasoning should not be assumed for multi-species surveys however, where birds differ in mobility and behaviour.

Two preceding papers have evaluated bird survey methods for species inventory in dry sclerophyll forest (DSF) (Totterman 2012) and in subtropical rainforest (Totterman 2014). This paper examines abundance data from those two studies. Results illustrate the wide variation in densities possible from different methods and a curvilinear relationship between reporting rate and density. Transects were most efficient and improvements for the two-hectare search are recommended.

METHODS

Study sites

The DSF study site was Carwong State Forest (SF), New South Wales (29°03'S, 152°57'E, area 570 ha, elevation 50–90 m asl). The subtropical rainforest site was Acacia Plateau, within Koreelah National Park, New South Wales (28°19'S, 152°25'E, area c. 80 ha, elevation 900–1070 m asl). Carwong SF was surveyed in winter 2010 and Acacia Plateau in summer 2011–2012.

Survey methods

Random, patch-scale sampling was applied to both sites. For line transects and point transects in DSF, birds were counted in two distance categories: 0–25 metres and 25–75 metres. Three categories were used in rainforest: 0–15 metres, 15–50 metres and beyond 50 metres. Line transects were 400 metres long at both sites. Transect durations were nominally 20 minutes in DSF and 25 minutes in rainforest. Point count durations at both sites were five minutes, preceded by 'settling down' period of three minutes. Birds that moved away when approaching a point were added to the count. Two-hectare search dimensions were 200 by 100 metres and count durations were 20 minutes (Barrett *et al.* 2003). Study sites and methods are described in further detail in the two preceding papers (Totterman 2012, 2014).

Abundance estimation

All birds were counted: breeders and non-breeders, adults and juveniles, males and females, singing and non-singing individuals. Detectability is reduced in windy conditions (Bibby *et al.* 2000) and a few samples were removed before estimating abundances. To strengthen the concordance between densities and reporting rates, observations of overflying birds were removed before estimating abundances (Szabo *et al.* 2012). For each survey method, abundance was estimated for species seen or heard at least 10 times.

Strip transect densities were computed for the 150-metre wide strip in DSF and 100-metre wide strip in rainforest. Line transect and point transect densities were estimated with Distance version 6.0 release 2 (Thomas *et al.* 2009). Rainforest counts beyond 50 metres were truncated, because counts within an unbounded category are difficult to interpret (Buckland *et al.* 2001). With only two distance categories, there was insufficient data for model selection, adjustment and goodness of fit evaluation. A half-normal detection function was assumed, as recommended for count data in two distance categories (Buckland *et al.* 2001). Distance sampling models expect detectability to decline with distance from the observer.

Results associated with 'reverse' detection profiles (i.e. most detections in the outer distance band) were ignored. For species that frequently occurred in pairs or flocks, mean cluster sizes were estimated from visual contacts.

Statistical analyses

Statistical computations were performed with R version 3.0.1 (R Development Core Team 2013). Following Distance version 6.0, coefficients of variation were computed as standard error divided by mean (not standard deviation divided by mean). Reporting rate standard errors were estimated using the Wilson score interval method for binomial proportions (Wilson 1927, evaluated by Brown *et al.* 2001). Relationships between methods were examined using Standardised Major Axis (SMA) linear regression (Warton *et al.* 2006). These were computed using the R package smatr3 (Warton *et al.* 2012). Correlations were measured with Pearson's linear correlation or Spearman's rank correlation coefficients.

RESULTS

Sample sizes in DSF were 23 transects, 106 points and 27 two-hectare searches. Sample sizes in rainforest were 14 transects, 72 points and 18 two-hectare searches. Abundance was estimated for a total of nine species in DSF (21 per cent of total 42 species richness) and 15 species in rainforest (42 per cent of total 36 species richness) (Table 1).

Scatterplots showed systematic differences between density estimators (Fig. 1). Eight of ten SMA regression slopes were significantly different from unity (Table 2). Distance sampling estimates averaged 2.24 and 5.12 times greater than unadjusted strip transect and circular plot densities (Figs. 1a, 1b). Point transect densities averaged 2.62 times greater than line transects (Fig. 1c). Unadjusted circular plot densities agreed closely with strip transects (Fig. 1d; $\beta = 1.19$, 95 per cent c.i. = [0.92, 1.53]). Differences in line transect and point transect densities were therefore mainly driven by differences in detection probability estimates (Fig. 1e).

Two-hectare search densities agreed with line transects in DSF (Fig. 1f). In rainforest, two-hectare search densities were lower than line transects for most species. A SMA regression for the rainforest data alone returned a slope significantly less than unity ($\beta = 0.54$, 95 per cent c.i. = [0.38, 0.77]).

With large variation between methods, median densities (computed from line transect, point transect and two-hectare search estimates) were assumed to provide more reliable measures of density than any single method. Two-hectare search reporting rates correlated strongly with median densities ($r_s = 0.88$, $n = 15$, $P < 0.001$) although the relationship was curvilinear (Fig. 2).

An efficient survey method will deliver precise abundance estimates (i.e. small standard errors) quickly. Total surveying time includes site preparation and marking, waiting, counting and intervals between consecutive counts. Sampling was with rotation between methods and total surveying time for each could not be recorded. Instead, comparisons of precision are made on the basis that total counting time was equal (Totterman 2012, 2014). Reporting rates were most precise (mean c.v. = 0.15), followed by strip transects, two-hectare search densities and circular plots (mean c.v. = 0.21–0.22). Line transects were substantially less precise (mean c.v. = 0.33) and point transects were least precise (mean c.v. = 0.44).

Table 1

Abundance estimates (mean ± s.e.) for birds at the dry sclerophyll forest and rainforest sites. Abundance not estimated for species with < 10 detections. 'Reverse' detection profiles (R) do not satisfy the distance sampling shape criterion. Dry sclerophyll forest reporting rates are different to previously published in Totterman (2012) because one sample with bad weather was excluded and observations of overflying birds were removed before estimating abundances.

Species	Strip transect		Line tr.	Circular Plot		Point tr.	Two-hectare search		
	Number of detections	Density (birds/ha)	Density (birds/ha)	Number of detections	Density (birds/ha)	Density (birds/ha)	Number of detections	Density (birds/ha)	Reporting Rate
Dry Sclerophyll Forest									
Little Lorikeet <i>Glossopsitta pusilla</i>	39	0.5 ± 0.1	1.2 ± 0.3	37	0.4 ± 0.1	3.1 ± 0.7	24	1.0 ± 0.2	0.56 ± 0.09
Brown Treecreeper <i>Climacteris picumnus</i>	26	0.2 ± 0.04	0.3 ± 0.1	17	0.1 ± 0.02	R	7		
Superb Fairy-wren <i>Malurus cyaneus</i>	3			14	0.2 ± 0.1	0.6 ± 0.3	11	0.6 ± 0.2	0.37 ± 0.09
Red-backed Fairy-wren <i>Malurus melanocephalus</i>	26	0.8 ± 0.2	R	39	0.6 ± 0.1	2.1 ± 0.7	22	1.3 ± 0.2	0.59 ± 0.09
Fuscous Honeyeater <i>Lichenostomus fuscus</i>	273	2.6 ± 0.2	5.0 ± 0.5	398	2.7 ± 0.2	10.7 ± 1.0	211	5.4 ± 0.4	1.00 ± 0.03
Scarlet Honeyeater <i>Myzomela sanguinolenta</i>	3			12	0.1 ± 0.02	R	3		
Noisy Friarbird <i>Philemon corniculatus</i>	3			12	0.1 ± 0.02	R	3		
Grey Shrike-thrush <i>Colluricincla harmonica</i>	7			14	0.1 ± 0.02	0.4 ± 0.2	8		
Willie Wagtail <i>Rhipidura leucophrys</i>	7			13	0.1 ± 0.02	R	8		
Rainforest									
Brown Cuckoo-Dove <i>Macropygia amboinensis</i>	9			10	0.2 ± 0.1	R	7		
White-throated Treecreeper <i>Cormobates leucophaea</i>	12	0.2 ± 0.1	0.5 ± 0.2	22	0.4 ± 0.1	0.6 ± 0.4	9		
Yellow-throated Scrubwren <i>Sericornis citreogularis</i>	49	1.1 ± 0.2	3.7 ± 0.8	34	0.7 ± 0.1	9.6 ± 2.2	33	1.2 ± 0.2	0.89 ± 0.08
White-browed Scrubwren <i>Sericornis frontalis</i>	22	0.7 ± 0.1	2.2 ± 0.7	28	1.1 ± 0.2	9.2 ± 2.6	17	0.8 ± 0.2	0.72 ± 0.10
Large-billed Scrubwren <i>Sericornis magnirostra</i>	38	1.4 ± 0.2	3.1 ± 0.9	28	1.0 ± 0.2	4.9 ± 1.8	22	1.3 ± 0.3	0.72 ± 0.10
Brown Gerygone <i>Gerygone mouki</i>	61	1.6 ± 0.2	3.5 ± 0.8	85	2.6 ± 0.2	10.0 ± 2.4	55	2.8 ± 0.3	1.00 ± 0.04
Brown Thornbill <i>Acanthiza pusilla</i>	16	0.4 ± 0.1	0.9 ± 0.4	21	0.6 ± 0.1	4.8 ± 1.7	22	1.1 ± 0.2	0.72 ± 0.10
Lewin's Honeyeater <i>Meliphaga lewinii</i>	26	0.5 ± 0.1	R	45	0.8 ± 0.1	0.8 ± 0.4	15	0.4 ± 0.1	0.67 ± 0.10
Australian Logrunner <i>Orthonyx temminckii</i>	35	0.9 ± 0.1	2.0 ± 0.5	21	0.5 ± 0.1	2.5 ± 0.9	21	0.8 ± 0.1	0.83 ± 0.09
Eastern Whipbird <i>Psophodes olivaceus</i>	15	0.3 ± 0.1	0.3 ± 0.2	13	0.3 ± 0.1	0.4 ± 0.3	12	0.4 ± 0.2	0.39 ± 0.10
Golden Whistler <i>Pachycephala pectoralis</i>	22	0.4 ± 0.1	0.4 ± 0.2	19	0.3 ± 0.1	R	13	0.4 ± 0.1	0.39 ± 0.10
Grey Shrike-thrush <i>Colluricincla harmonica</i>	6			10	0.2 ± 0.1	0.4 ± 0.3	3		
Rufous Fantail <i>Rhipidura rufifrons</i>	10	0.2 ± 0.04	0.5 ± 0.2	7			4		
Black-faced Monarch <i>Monarcha melanopsis</i>	15	0.3 ± 0.1	R	17	0.3 ± 0.1	0.4 ± 0.3	15	0.4 ± 0.1	0.56 ± 0.11
Eastern Yellow Robin <i>Eopsaltria australis</i>	16	0.3 ± 0.1	0.5 ± 0.2	18	0.4 ± 0.1	0.4 ± 0.3	10	0.3 ± 0.1	0.50 ± 0.11

Table 2

Standardised major axis linear regression and Pearson's linear correlation results for five population density estimators. All correlations were highly significant ($P < 0.01$). All slopes (β) were significantly different than unity ($P < 0.01$) except for circular plot versus strip transect ($P = 0.18$) and two-hectare search versus line transect ($P = 0.79$). All intercepts (α) were indistinguishable from zero ($P < 0.05$).

		Circular plot (CP)	Line transect (LT)	Point transect (PT)	Two-hectare search (TH)
Strip transect (ST)	Model	CP=1.19ST-0.09	LT=2.24ST+0.02	PT=6.01ST-0.65	TH=2.07ST-0.46
	β [c.i.]	1.19 [0.92, 1.53]	2.24 [1.82, 2.75]	6.01 [4.07, 8.88]	2.07 [1.69, 2.54]
	α [c.i.]	-0.09 [-0.39, 0.21]	0.02 [-0.45, 0.49]	-0.65 [-3.20, 1.90]	-0.46 [-0.90, 0.01]
	r	0.89	0.94	0.77	0.95
Circular plot (CP)	Model		LT=1.87CP+0.23	PT=5.12CP-0.28	TH=1.69CP-0.20
	β [c.i.]		1.87 [1.31, 2.67]	5.12 [3.75, 6.98]	1.69 [1.29, 2.23]
	α [c.i.]		0.23 [-0.58, 1.04]	-0.28 [-2.03, 1.47]	-0.20 [-0.73, 0.34]
	r		0.84	0.82	0.89
Line transect (LT)	Model			PT=2.62LT-0.33	TH=0.95LT-0.57
	β [c.i.]			2.62 [1.83, 3.73]	0.95 [0.62, 1.45]
	α [c.i.]			-0.33 [-2.79, 2.13]	-0.57 [-1.64, 0.51]
	r			0.88	0.82
Point transect (PT)	Model				TH=0.34PT-0.15
	β [c.i.]				0.34 [0.22, 0.52]
	α [c.i.]				-0.15 [-1.03, 0.73]
	r				0.71
					14

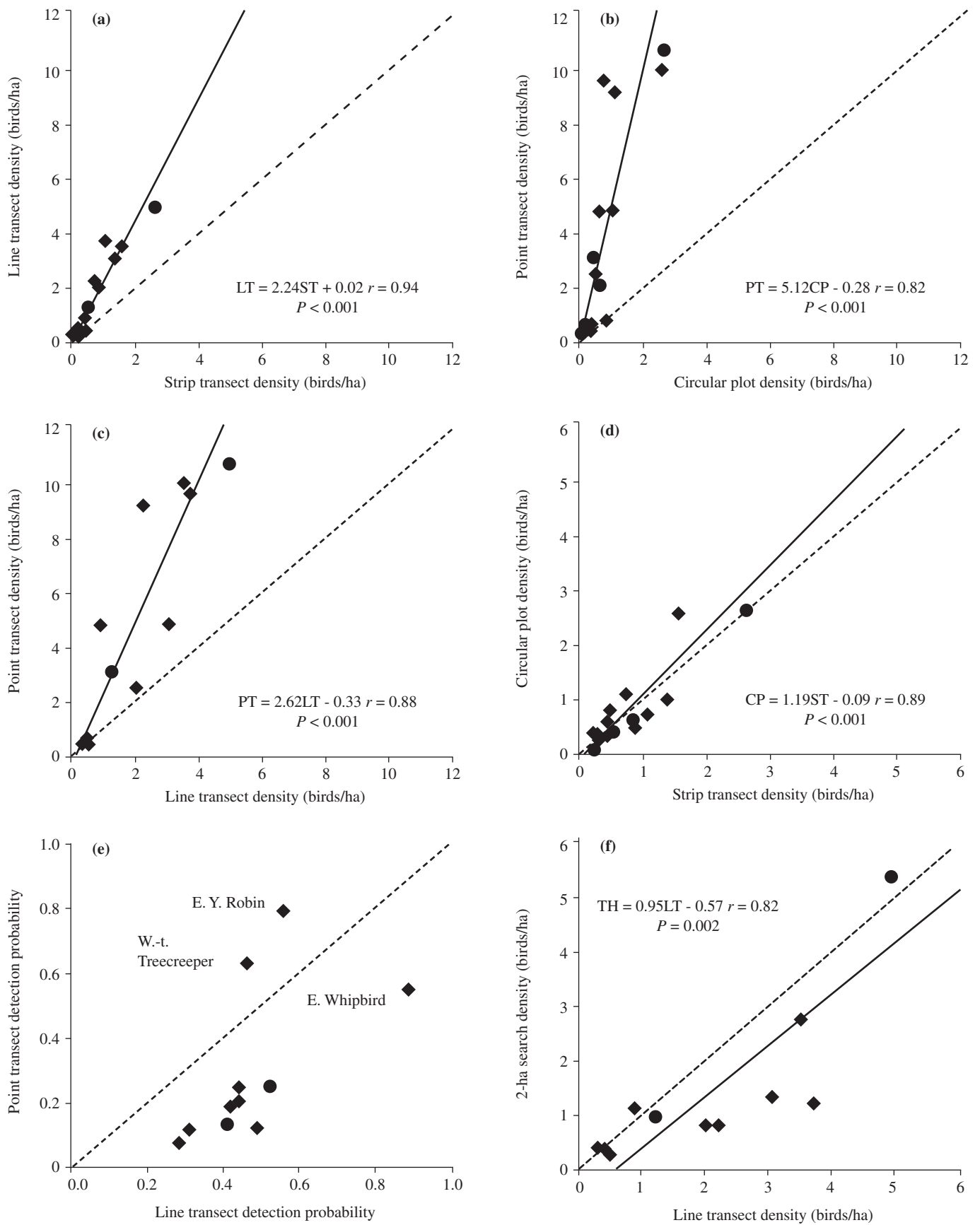


Figure 1. Scatter plots of density estimates and detection probability results at the dry sclerophyll forest (circles) and rainforest (diamonds) sites. Solid lines show standardised major axis linear regression results. Dashed lines indicate a 1:1 relationship. Three species with relatively high detection probabilities are annotated on Figure 1e.

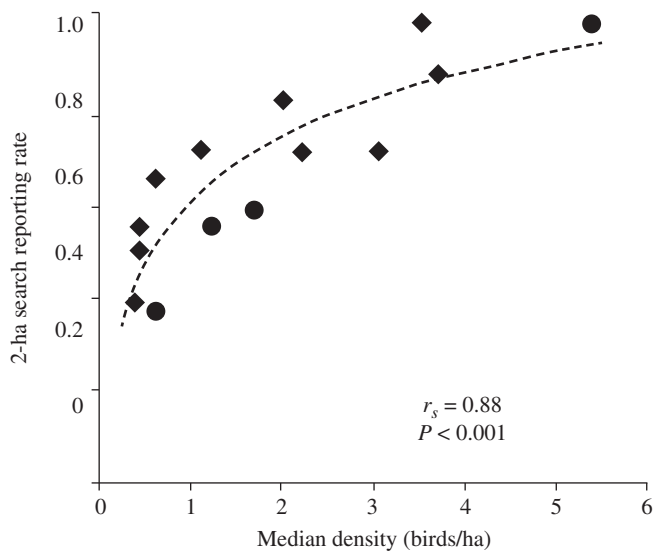


Figure 2. Correlation between reporting rate and median density at the dry sclerophyll forest (circles) and rainforest (diamonds) sites. A curvilinear relationship is suggested (dashed line).

DISCUSSION

Distance sampling evaluation

Exact distance measurements are recommended for distance sampling, however estimates based on just a few distance categories will be unbiased provided that counts are allocated to the correct category (Buckland *et al.* 2001). Line transects with two categories have produced satisfactory population size estimates for the United Kingdom Breeding Bird Survey (Newson *et al.* 2008). Bibby and Buckland (1987) studied forest succession using two-category point transects to account for differences in detectability between species and habitats. At least 60 detections are recommended for detailed modelling of the detection profile (Buckland *et al.* 2001), however simple two-category profiles might be described with fewer detections.

Distance sampling aims to estimate absolute density, however point transect densities averaged 2.62 times greater than line transects. These differences were mainly driven by differences in detection probability estimates. Several recent evaluations have reported similar overestimation of bird population densities by point transects in comparison to line transects and true reference densities (e.g. Buckland 2006; Cassey *et al.* 2007; Greene and Pryde 2012; Raman 2003). However, Gale *et al.* (2009) reported closer agreement between point transects and line transects, likely because line transect speed was extremely slow in that study (average 2 h 17 m for 500 m).

Biased estimates will result when distance sampling assumptions are violated. A first major assumption is that all objects are detected at their initial locations (Buckland *et al.* 2001). However, birds are mobile and 'random' and responsive movements are expected (Burnham *et al.* 1980). Inward movements will result in a steeper detection profile, lower detection probability and inflated density (Buckland *et al.* 2001).

For example, Fuscous Honeyeaters *Lichenostomus fuscus* were abundant in DSF, aggressive and would often approach the standing observer. Four small, active rainforest birds that may not be seen until they move closer to the standing observer are Yellow-throated Scrubwren *Sericornis citreogularis*, Large-billed Scrubwren *Sericornis magnirostra*, Brown Gerygone *Gerygone mouki* and Brown Thornbill *Acanthiza pusilla*. Buckland (2006) proposed an instantaneous point count method for randomly moving birds.

Evasive movements will reduce the distance sampling density. When more detailed distance data are acquired, evasive movements can be identified as heaping of detections at intermediate distances (Buckland *et al.* 2001). Reverse detection profiles can result in extreme cases. For example, Red-backed Fairy-wrens *Malurus melanocephalus* and Brown Treecreepers *Climacteris picumnus* moved away when approached by the observer.

A second critical assumption for distance sampling is that all objects on the point or at the line are detected (Buckland *et al.* 2001). Concealment behaviour near the line or point will result in a lower detection probability and inflated density. Reverse detection profiles can result in extreme cases. For example, Brown Cuckoo-Doves *Macropygia amboinensis* would often stop calling when approached by the observer and are difficult to see in the rainforest mid-canopy.

In this study, line transect densities are expected to be more reliable than point transects for most species. Firstly, stationary observations tend to be more strongly biased by movements (Buckland *et al.* 2001). Inward movements could explain the relatively high point transect densities. Secondly, point counts are less precise than transects for sampling clumped distributions (Sinclair *et al.* 2006). The mean c.v. for point transect densities was 1.4 times that for line transects. Backing-out sample size effects on standard errors (106 point counts versus 23 transects in DSF and 72 point counts versus 14 transects in rainforest), the mean c.v. (now standard deviation divided by mean) for point transects was 3.1 times that for line transects. Similarly, the mean c.v. for circular plot counts (again standard deviation divided by mean) was 2.5 times that for strip transect counts. One supposed advantage of point counts is the shorter count duration and relatively large sample sizes versus transects for the same total counting time. However, these results show that the reduction in standard errors with large sample sizes is countered by the high variability in circular plot counts.

Two-hectare search evaluation

The two-hectare search method is a short 200-metre long by 100-metre wide transect which is searched actively over 20 minutes. The open understorey of the DSF site allowed thorough two-hectare searches, with flushing of hidden birds and frequent visual contacts. Two-hectare search densities in DSF were similar to line transects. In rainforest, the dense vegetation restricted mobility and visibility and two-hectare search results were similar to strip transects. Active searching can be disadvantageous for between-habitat comparisons because differences in searching thoroughness will increase differences in the proportion of birds counted.

Blondel (1975) and Dawson (1981) have previously noted the curvilinear relationship between reporting rate and density. Bart and Klosiewski (1989) examined United States Breeding Bird Survey data and found that the magnitudes of changes in abundance from reporting rates did not match those from index counts. Joseph *et al.* (2006) explained that the probability of recording a species as present is sensitive to abundance when detectability and search effort are low and sensitive to site occupancy when detectability and search effort are high. The effects of abundance, detectability and search effort on reporting rates were discussed in the two preceding papers (Totterman 2012, 2014). Fixed search areas and durations are recommended for measuring reporting rates (Verner 1985). However, Szabo *et al.* (2010) applied list length analysis to approximately account for variable and unknown effort in bird species list data. Statistical modelling of the reporting rate-density relationship should also be possible (e.g. Dawson 1981), but will require some assumptions and is a poor replacement for direct counts.

Reporting rates were more precise than densities. The mean c.v. for reporting rates was 0.7 times that for two-hectare search densities. However, following the preceding discussion, the interpretation of standard errors is different for low and high reporting rates. Standard errors approach zero for binomial proportions near unity, which is sensible when it is recognised that high reporting rates indicate occupancy and not abundance.

Recognising that reporting rates confound abundance and occupancy, the lack of count data in the continuing Atlas of Australian Birds (<http://www.birddata.com.au>) is concerning. Returning to Loyn's (1986) 20-minute search method, two improvements are suggested (Totterman 2014). Firstly, counts of birds inside the two-hectare plot can provide meaningful indices of abundance and especially in more open forests and woodlands (Szabo *et al.* 2012, this study). It is recommended to count clusters for estimation of mean cluster sizes, which can then be substituted for any observations where cluster size could not be counted. Birds flying over the two-hectare plot may not be counted (Szabo *et al.* 2012, this study). Secondly, records of birds outside the two-hectare plot but still within habitat patch of interest can be useful for species inventory (Loyn 1986). The improved two-hectare search should be satisfactory for abundance and species inventory surveys in forests (Loyn 1986) and more powerful than the species list method in the continuing Atlas of Australian Birds (<http://www.birddata.com.au>). Species lists compatible with the atlas database can be generated from 20 minute search counts.

Relative densities

Strong linear correlations between the five density estimators indicated substantial agreement in relative densities. Other researchers have noted strong correlations between different methods: across species (e.g. Gale *et al.* 2009; Raman 2003), across sites (e.g. Raphael 1987) and over time (e.g. Greene and Pryde 2012). Raphael (1987) explained that 73 to 83 percent of the variation in distance sampling densities from his study was explained by variation in unadjusted counts. In the present study, coefficients of determination (r^2) were 89 per cent for line versus strip transects and 67 per cent for point transects versus circular plots.

Given the difficulty of measuring exact distances, uncertain assumptions, little additional information contributed by detectability corrections and incomplete results when the detection profile has the 'wrong' shape, distance sampling methods have not replaced unadjusted counts. Index counts can be applied when differences are much larger than errors caused by failure of the constant proportionality assumption (Thompson 2002). Users should be aware that there are two uncertainties when using unadjusted counts: 1) precision of the counts alone, and; 2) precision of the linear relationship between the counts and true density. Errors in the proportionality assumption are difficult to evaluate and usually ignored, which can lead to overconfidence and inflated statistical type I error rates.

Index counts collected over longer time scales and at multiple sites can allow a more robust and powerful analysis (Bart *et al.* 2004a). Firstly, differences in abundance are expected to be greater and sample sizes tend to be larger. Secondly, trends in relative densities are unbiased if there is no long term trend in the ratio of the index to true density (Bart *et al.* 2004b). Inferences drawn from short-term, small-scale studies with small effect sizes and especially two-sample comparisons should be treated cautiously.

CONCLUSIONS

Although true bird population densities were unknown for this study, systematic variation between the five density estimators was evidence for variable bias. The absolute accuracy of distance sampling methods is uncertain because birds are highly mobile and are responsive towards disturbance by human observers. More relevant than asking whether densities are unbiased (mostly they are not) is asking whether or not they are useful. Strong linear correlations between the five density estimators was evidence for substantial agreement in relative densities. Unadjusted counts can answer many questions and are less costly to measure than absolute densities (Verner 1985).

There are many factors to consider when planning forest bird abundance surveys including the target species (abundance, spatial distribution, mobility and behaviour), the habitat, the terrain, required accuracy, the scale of the study (geographical and temporal), the observers (numbers and proficiency), survey method time efficiency and the project budget (Greene and Pryde 2012). Issues like sampling grain size, severe violation of assumptions and confusion between abundance and occupancy are consequences of choosing a particular survey method and abundance estimator and not easily fixed. Researchers can make better informed choices after performing their own pilot studies including multiple survey methods and abundance estimators. From this study, transects were more efficient than point counts and two-hectare searches for measuring relative densities of the common bird species in one moderate-sized DSF site and one smaller rainforest site.

ACKNOWLEDGEMENTS

Bo Totterman helped with comments on early drafts. Surveys in Koreelah National Park were conducted under scientific license SL100559 authorised by the NSW Office of Environment and Heritage.

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