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THE RELIABILITY OF ESTIMATES OF DENSITY FROM TRANSECT COUNTS

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Densities were estimated from transect counts for seven species at Wollomombi, New South Wales. These estimates are compared with accurate densities derived from intensive studies of colour-banded birds. Also estimates of density of the Golden-headed Cisticola *Cisticola exilis*, at Port Moresby, Papua New Guinea, are compared with seasonal changes in behaviour of that species. Three methods of analysis were applied to the transect data: the Fixed-strip Transect, Variable-strip Transect and the Line Transect Methods. While all methods tended to underestimate density the Variable-strip and Line Transect Methods performed much better than the Fixed-strip Transect Method, because they attempted to overcome problems associated with varying detectability. However, the bias of estimates was not constant and differed greatly between species and between seasons. These results demonstrate the need for caution in using transect methods to compare densities where the detectability of birds may differ. It is concluded that no one method of censusing is appropriate to all species under all conditions and that combinations of different methods are required for accurate estimates.

Recher *et al.* (1983a) have described ways of using transect counts to measure the abundance of birds in forests. Although extensive censusing work in now being carried out in Australia few data have so far been published. There is a danger that census workers have, and may continue to, present results uncritically, leading to an (unintended) impression that their data accurately describe the absolute densities of birds present (e.g. Bell 1980a). Recher *et al.* suggest that, if methods used are consistent, transect data will at least indicate relative differences in the density of birds over time and space.

The aim of this paper is to demonstrate the need for caution in using transect methods to compare situations in which the detectability of birds may differ. Such differences may occur between species, or within the same species under varying conditions.

We will compare estimates of density derived from transect counts with known densities of seven species, derived from intensive colour-banding and mapping. This information will be used to investigate the influence of inter- and intra-specific variation in detectability on transect counts. The influence of intra-specific variation will be further investigated using transect data for the Golden-headed Cisticola *Cisticola exilis*, a species displaying marked seasonal changes in behaviour and detectability.

STUDY AREA AND METHODS

The two study areas were Wollomombi Falls Reserve (30°32′S., 152°02′E.) near Armidale, NSW, and Port Moresby (9°30′S., 147°10′E.), Papua New Guinea. Wollomombi Reserve is dense eucalypt woodland with a sparse but clumped understorey and is described by Noske (1979). The area at Port Moresby is eucalypt savanna with little understorey but a dense cover of grass (Bell 1982a).

At Wollomombi an average of five transect counts were made monthly (range 2-8, but rarely outside 3-6) from September, 1978 to May, 1982. The transect was 600 m long and was traversed from 0800 to 0830 hours. All counts were made in dry and calm conditions. All birds seen were recorded except for overhead transients (but including above-canopy foragers such as raptors and wood-swallows). For the first thousand birds counted it was found that 60% of individuals, or parties of one species, were first located by their calls. Although many or most of these birds may have otherwise been detected the influence of calling on detectability must be high. For each individual the lateral distance from the centre-line was recorded, in 10 m bands, using measured landmarks for estimation. A cumulative record of lateral distances was kept for each species. At Port Moresby the census methods used were similar except that lateral distances were recorded separately for each month, and not cumulatively. The Port Moresby study was from October 1976 to February 1978 (Bell 1982a).

At Wollomombi three species of thornbills, the Brown *Acanthiza pusilla*, the Buff-rumped *A. reguloides*, and the Striated *A. lineata* were intensively studied for over three years (Bell 1983a, in press). R. A. Noske studied treecreepers, including the White-throated *Climacteris leucophaea* and the Red-browed *C. erythrops*, for over three years (Noske 1979, 1982). In 1978/79 L. Huddy studied the Scarlet Robin *Petroica multicolor* (Huddy 1979). In addition, all three researchers colour-banded any species believed to be sedentary and this included, in 1978/1979, the total local population of the Speckled Warbler *Sericornis sagittatus*. With all seven species territory/home range was determined by spot-mapping of occurrences and of intra-specific aggression. The addition of progeny was noted and disappearances of marked birds, or intrusions of unmarked ones, were noted on a weekly, often daily, basis. Thus there were seven species, of which all individuals were colour-banded, where territorial boundaries were known and whose recruitment and loss was monitored regularly. The population of cisticolas at Port Moresby was not marked and actual numbers were unknown.

Three line transect methods were applied to the census data (terminology follows Eberhardt 1978). The actual details of how to carry out these methods are presented in Appendix A.

(1) Fixed-strip Transect Method (Recher *et al.* 1983a).

A fixed transect width of 120 m was used for all species. No adjustment was made for detectability.

(2) Variable-strip Transect Method (Emlen 1971, 1977; Ramsey & Scott 1981).

For each species, the frequency of observed detections was plotted against lateral distance from the transect line. An inner basal region of 'perfect' detectability was determined by the technique proposed by Balph *et al.* (1977). This technique selects the transect width for a species as the distance within which the highest density of observations was recorded (doubled to account for both sides of the transect). Density was then estimated only from counts obtained within this basal region.

(3) Line Transect Method (Anderson & Pospahala 1970, Burnham *et al.* 1980).

A polynomial regression equation (with the linear term set at zero) was fitted to the data on frequency of detection for each species. This equation was used to estimate density by adjusting for the influence of lateral distance on detectability.

The relative bias of the above three estimates was calculated by $RB = 100 \times \frac{(\hat{D}-D)}{D}$ where $\hat{D}$ is the transect estimate of density and D is the density determined from intensive study of colour-banded birds (Tilghman & Rusch 1981).

RESULTS AND DISCUSSION

Differences between methods at Wollomombi

Table 1 shows mean densities for each species at Wollomombi estimated using the three transect methods, compared with mean densities derived from colour-banding. Table 2 shows the relative bias of the transect estimates and summarizes results of a two-way anova testing for differences between methods and between species. All three methods tended to underestimate density. *A posteriori* tests (Sokal and Rohlf 1969) showed no significant difference in relative bias between the Variable-strip and Line Transect Methods ($p>0.05$), but suggested that both these methods were significantly less biased than the Fixed-strip Method ($p<0.001$). The Variable-strip and Line Transect Methods both attempt to compensate for detectability. These two methods nevertheless usually underestimated density probably because of violation of the assumptions made in applying such techniques (Burnham *et al.* 1980):

(a) that birds directly on or near the centre-line will never be missed;
(b) that there is no movement of birds in response to that of the observer; and
(c) that no bird is counted more than once.

Specific differences

Underestimation in itself does not necessarily affect the usefulness of transect estimates as indices of abundance. What really matters is whether or not bias is constant under all situations being compared, e.g. years, seasons, species, habitats, etc. The Wollomombi data have been used to test for differences in bias between species and between seasons. Bias was found to differ significantly between species for all three transect methods (see Table 2). This is probably because different species violated the assumptions of these methods to different degrees. Table 3 summarizes the main factors affecting detectability of the seven species. We suggest the following main reasons for differences in detectability. White-throated and Red-browed Tree-creepers were accurately estimated because they are conspicuous and not shy. Scarlet Robins were generally overestimated possibly because the same marked birds would re-appear in the

TABLE 1

Mean density (individuals/10 ha) of seven species at Wollomombi, estimated from intensive study of colour-banded birds and three transect methods.

	Brown Thornbill	Buff-rumped Thornbill+	Striated Thornbill+	Scarlet Robin	Speckled Warbler	Red-browed Treecreeper	White-throated Treecreeper	All Species
	7.0	7.5	18.5	3.2	4.0	4.2	4.5	48.9
1. Fixed-strip Transect	3.6***	3.5***	6.3***	2.9	1.4***	3.5**	4.3	25.5***
2. Variable-strip Transect	5.1***	4.9***	10.4***	4.1*	2.3***	3.9	4.4	35.1***
3. Line Transect	5.4***	5.0***	11.2***	4.4**	2.3***	3.9	4.5	36.7***

+: September 1978-May 1982 (224 transects), all other species September 1978-August 1979 (56 transects).
Significance of difference between actual and estimated density (paired t-test) *: $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 2

Mean relative bias (%) of density estimates at Wollomombi, using three transect methods.

Transect method	Brown Thornbill	Buff-rumped Thornbill	Striated Thornbill	Scarlet Robin	Speckled Warbler	Red-browed Treecreeper	White-throated Treecreeper	Average	
1. Fixed-strip Transect	-49	-53	-66	-9	-65	-17	-4	-38	
2. Variable-strip Transect	-27	-35	-44	+28	-43	-7	-2	-18	F=28.3*** (df=2,2163)
3. Line Transect	-23	-33	-40	+37	-43	-7	0	-15	
Average	-33	-40	-50	+19	-50	-10	-2		
			F = 41.1*** (df = 6.2163)						

F-values are from a two-way Anova testing for differences in relative bias between methods and between species: ***$p<0.001$: the method × species interaction was not significant ($F = 0.8$; df = 12.2163; $p>0.05$).

TABLE 3

Factors contributing to detectability and abundance of seven intensively-studied species at Wollomombi.

Species	Social groupings	Dispersal of young	Foraging station	Calling	Reference
Brown Thornbill	Permanent pairs, hold territory year-round.	Evicted in autumn.	Dense foliage of understorey	Loud, infrequent, year-round.	Bell (1983)
Buff-rumped Thornbill	Territorial non-breeding clan of 10-20, dividing into territorial breeding groups of 1 ♀, 1-3 ♂♂.	Retained until spring, ♂♂ usually added to parental group, ♀♀ usually evicted.	Ground or bark January-August; more arboreal September-December.	Quiet, infrequent, year-round.	Bell (1983)
Striated Thornbill	Similar to Buff-rumped.	As for Buff-rumped.	Foliage of canopy.	Similar to Buff-rumped.	Bell (1983)
Scarlet Robin	Pairs hold year-round territory.	As for Brown Thornbill.	Ground (autumn and winter), canopy (spring and summer).	Quiet, more frequent in spring.	Huddy (1979)
Speckled Warbler	Pairs or possibly polygamous, year-round territory?	Retained until spring. Then evicted.	Ground.	Moderately loud, infrequent, year-round.	Bell (in press)
White-throated Treecreeper	Pairs or individual. Year-round territory.	Evicted *ca* 2 months from fledging.	Trunks and branches.	Loud, frequent, more winter and spring.	Noske (1982)
Red-browed Treecreeper	Pairs or groups 1 ♀, 1-2 ♂♂, year-round territory.	Evicted *ca* 2 months from fledging, may retain young ♂.	Trunks and branches.	Quiet, frequent,?	Noske (1982)

same transect, suggesting that they were being driven forward and counted more than once. Brown Thornbills were underestimated possibly because they move away from the observer, into dense shrubbery. Striated Thornbills were underestimated because they are small inconspicuous canopy-foragers which could be overlooked even right on a transect-line. Buff-rumped Thornbills and Speckled Warblers were underestimated, because although easily located, each group would contain individuals overlooked because they were feeding behind tussocks of grass.

Seasonal differences

Seasonal differences in bias were investigated for each species using estimates derived from a basal region calculated from the total data for that species. Seasonal comparisons between actual and estimated density are presented in Figure 1. Also shown are the results of statistical analyses testing for differences in relative bias between seasons. Five out of the seven species showed significant seasonal variation in bias. To show that this variation is truly seasonal and not simply random, Figure 2 depicts estimated and known densities for Striated Thornbills over 45 months. The pattern, as shown in Figure 2, is of gross underestimation in spring and summer occurring in three successive years.

Figure 3 summarises variations in bias between species and between seasons. Not only were there marked differences between species and between seasons within species, but there were also significant differences between the patterns of seasonality displayed by different species (indicated by a significant interaction between species and seasons in a two-way anova: $F = 2.55$; d.f. $= 18{,}700$; $p<0.001$).

We can provide plausible explanations for all but one of these seasonal differences in the bias of estimates (see Table 3). The low estimates of Striated Thornbills in spring and summer conform to other reports on the species (Bell 1980a, Ford & Bell 1981, Kavanagh & Recher 1983, Recher *et al.* 1983b, Taylor 1983), which suggested a movement out of the census area. In fact there is very little evidence that Striated Thornbills at Wollomombi move outside a range

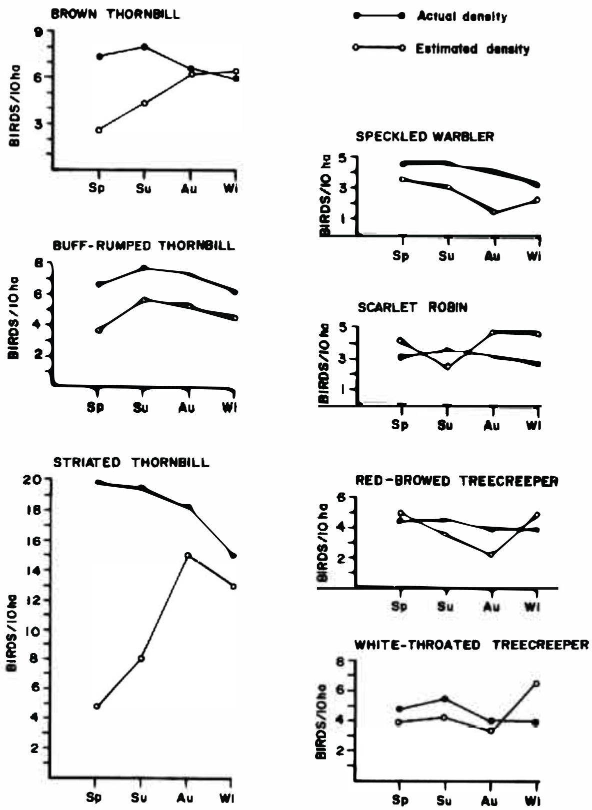

Figure 1. *Seasonal comparisons between mean actual density and mean estimated density (Variable-strip Transect) at Wollomombi. Estimated densities are derived from a fixed basal region calculated from the total data for that species. Results of one-way Anovas testing for difference in relative bias between seasons were: Brown Thornbill* $F = 8.1$, $df = 3{,}25$, $p < 0.001$; *Buff-rumped Thornbill* $F = 0.7$, $df = 3{,}220$, $p > 0.05$; *Striated Thornbill* $F = 12.7$, $df = 3{,}220$, $p < 0.001$; *Speckled Warbler* $F = 1.0$, $df = 3{,}52$, $p > 0.05$ *Scarlet Robin* $F = 3.1$, $df = 3{,}52$, $p < 0.05$ *Red-browed Treecreeper* $F = 14.1$, $df = 3{,}52$, $p > 0.001$; *White-throated Treecreeper* $F = 26.5$, $df = 3{,}52$; $p < 0.001$.

with a radius of *ca* 200 m (Bell 1983), even during spring and summer. The seasonal variation in estimates results from seasonal changes in social organization (Table 3). The large (*ca* 20 birds) non-breeding clans break up in spring into small breeding groups of 2 to 4 birds. These small groups are less noticeable; the species does not join mixed-species flocks in spring (see Bell 1980b); the abundance of food, compared with autumn and winter, results in fewer tree-to-tree movements of what is a difficult species to observe at any time; females are incubating for part of that time and adults probably moult and are less active in summer.

We can offer no explanation for the Red-browed Treecreeper being less detectable in autumn. However, the high detectability of White-throated Treecreepers in winter may relate to their violent and conspicuous territorial displays by males before the breeding season (Noske 1982). High detectability of Scarlet Robins in autumn and winter relates to their seasonal change in foraging habits. Huddy (1979) found that Scarlet Robins switched from arboreal to ground feeding in autumn and winter and also joined mixed-species flocks. Thus they became more conspicuous and, being closer to the observer than when feeding in the canopy, probably responded more to his movements. The low detectability of Brown Thornbills in spring and summer is probably because they nest and hide their young in dense undergrowth at that time, and rarely participate in mixed-species flocks. There appear to be no seasonal differences in estimates of Buff-rumped Thornbills and Speckled Warblers, the consistent underestimates probably being for reasons given earlier.

The problem of seasonal variations in detectability can be partly overcome by processing data separately for each season (or even by month if data are sufficient). This was not done at Wollomombi, because when the various studies started, the implications of the widely-differing social systems and the seasonal changes in behaviour to estimates of density were not appreciated.

Comparison of seasonal estimates with behavioural changes of cisticolas

The processing of data separately by months will be illustrated with census counts of cisticolas at Port Moresby, the data of which had not been analyzed until well after the commencement of the studies at Wollomombi. In the breeding season cisticolas are very conspicuous, calling continuously from prominent perches and frequently making soaring display flights. When not breeding they are silent, keep inside the

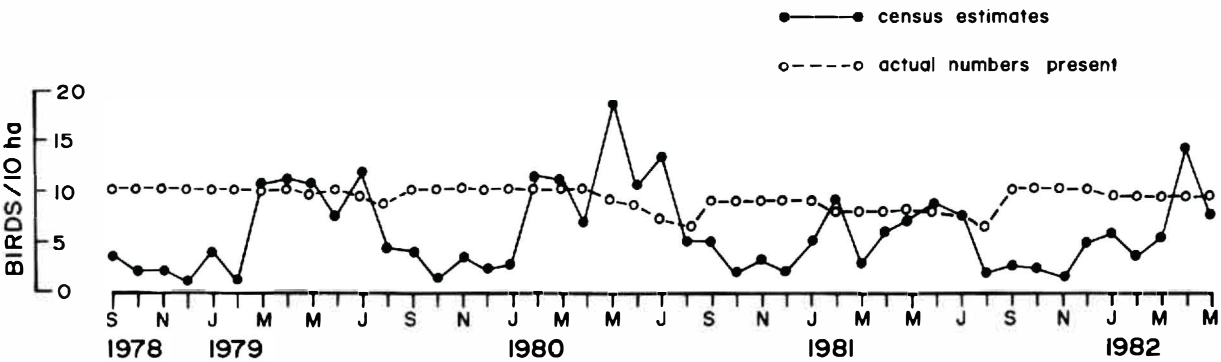

Figure 2. *Mean monthly census estimates (Variable-strip Transects) of Striated Thornbills at Wollomombi, compared with actual numbers known to be present September 1978 - May 1982.*

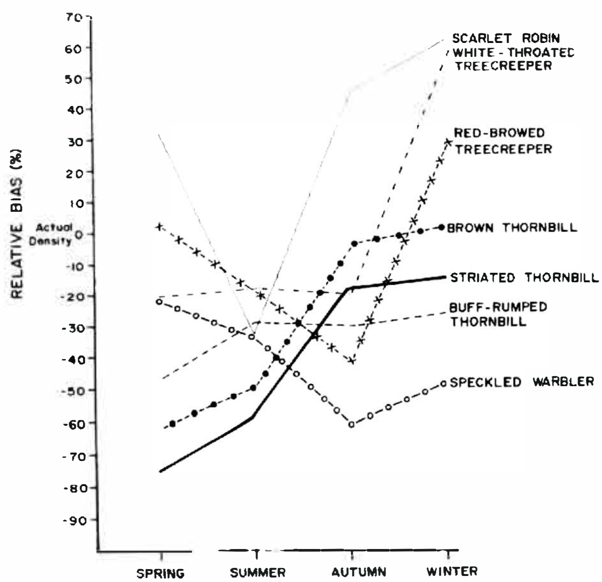

Figure 3. *Seasonal changes in relative bias of transect estimates (Variable-strip Transects) at Wollomombi. Estimates for each species were derived from a fixed basal region calculated from the total data for that species.*

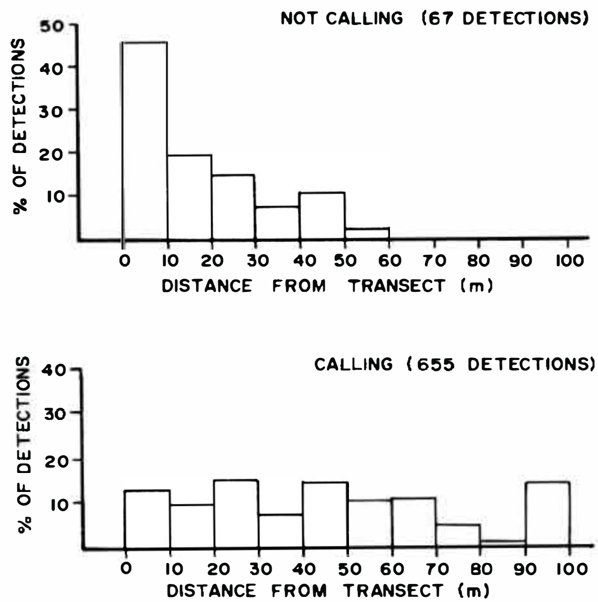

Figure 4. *Percentage frequency of detections of Golden-headed Cisticolas plotted against distance from the centre-line of transect. Data divided into whether or not cisticolas were heard calling during a particular transect.*

grass layer, and are usually only seen as a result of flushing at short distances from the centre-line of the transect. Figure 4 shows that the width of the region of detectability is greatly influenced by this variation in behaviour. When calling, the species is easily detected out to 100 m; when not calling most birds are detected within 10 m from the centre-line.

Figure 5 shows the seasonal variation in estimates of cisticolas based on a Fixed-strip Transect. This seasonal variation is significantly reduced if based on a Variable-strip Transect calculated separately for each month (coefficients of variation, fixed basal area = 92%, variable basal area = 57%; $t=2.33$, d.f. = 50, $p<0.05$; Dow 1976).

Even after using the Variable-strip Transect Method marked seasonal differences in estimates of cisticolas are still apparent. These may be real. The extent of grass-cover burnt (see Figure 5) in the dry (non-breeding season) may greatly reduced the population. Also, in the wet season when breeding occurs, there may be, unlike most tropical passerines, heavy recruitment of young. Most New Guinean birds have small clutches (Rand & Gilliard 1967) but cisticolas at Port Moresby lay four eggs and seem usually to fledge three young (Bell, unpubl. data). Moreover, unlike most tropical birds they may be double-brooded. However, seasonal fluctuations in estimates may also be due partly to variations in detectability not compensated for by the Variable-strip Method (e.g. variation in detectability directly on, or near to the transect line).

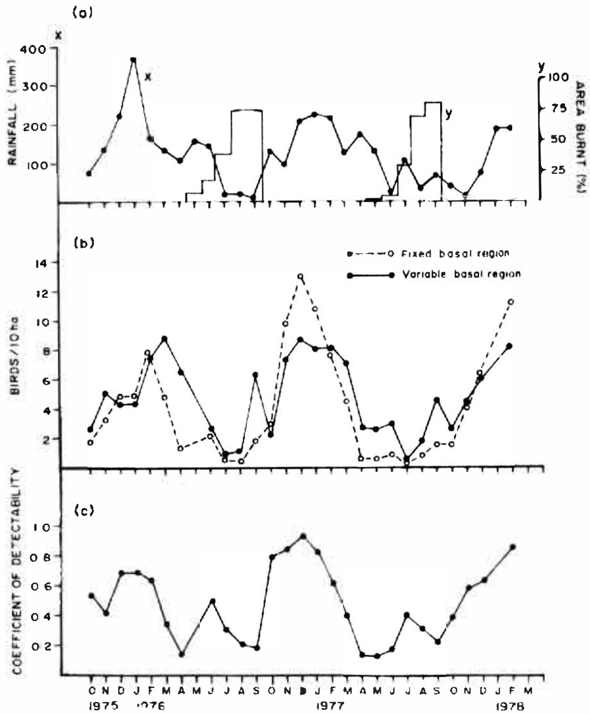

Figure 5. (*a*) *Monthly rainfall at Port Moresby* (*x*) *and percentage of transect area burnt* (*y*).

(*b*) *Monthly estimates of densities of Golden-headed Cisticolas using the Fixed-strip and Variable-strip Transect Methods.*

(*c*) *Monthly variation in the coefficient of detectability* (*Emlen 1971*) *for the Golden-headed Cisticola, i.e. the estimated proportion of birds counted within a 200 m wide transect strip.*

CONCLUSIONS

Caution is needed when using transect methods to compare situations in which detectability may differ. In this paper we have concentrated on differences between species and between seasons. Yet detectability can also be affected by time of day (Shields 1977, 1979; Robbins 1981a), weather (Ratkowsky & Ratkowsky 1979, Robbins 1981b), habitat (Dawson 1981, Richards 1981), topography (Myrberget & Stromme 1974), and differences between individual observers (Faanes & Bystrak 1981, Kavanagh & Recher 1983).

Some comparisons may not involve differences in detectability. For example, annual counts designed to assess population trends may be relatively free of detectability problems if conducted under standard conditions (e.g. time of year and day, weather and habitat). Examples of studies in which such problems are likely to be encountered include:

(a) comparisons of counts made at different times of year to assess seasonal change in abundance; (b) comparisons of counts made in different habitats, or in the same habitat subject to alteration (e.g. by logging); (c) comparisons of counts obtained for different species designed to compare their relative abundance.

Several transect methods have been specifically designed to overcome the problems associated with varying detectability (see reviews by Eberhardt 1978 and Burnham *et al.* 1980). In this paper we have concentrated on two of these, the Variable-strip Transect and the Line Transect Methods. While both techniques performed better than the Fixed-strip Transect Method, they still failed to compensate adequately for variation in detectability. This failure most likely results from the assumptions, implicit in all methods, not being satisfied. The most important ones are:

(a) birds directly on, or near to, the centre-line will always be detected; (b) there is no movement of birds in relation to that of the observer; and (c) no bird is counted more than once. The accuracy of estimates is largely determined by the degree to which these assumptions are violated. Violation of assumption (a) results in under-estimation. Violation of assumption (b) results in over-estimation if birds are attracted to the observer and underestimation if birds are repelled by the observer. Violation of assumption (c) results in overestimation. If the assumptions are violated to different degrees in different situations then comparisons of the estimates derived must be interpreted with caution.

In cases where the violation of assumptions is severe the best solution may be to calibrate transect estimates against independent estimates obtained using more intensive census techniques. This approach has already been used; for surveys of New Zealand passerines (Gill 1980), Emus *Dromaius novaehollandiae* (Caughley & Grice 1982), Noisy Scrub-birds *Atrichornis clamosus* (Smith & Forrester 1981), and Rufous Scrub-birds *A. rufescens* (Ferrier 1984). The proportions of known birds counted at Wollomombi in the present study could also be used to adjust counts made elsewhere in similar habitats and conditions. Unfortunately, calibration is time-consuming and its advantages therefore need to be carefully weighed against different methods such as colour-banding and mapping.

Above all, we should guard against dogmatic claims that any one census method is superior to another, or that a standard census method should be used for all species in all situations. The advantages of standardization may be offset by problems of varying detectability. These problems may be partly overcome by using methods that adjust for detectability. However, if the assumptions underlying such methods are severely violated then it may be necessary to consider other types, or combinations of types, of censusing techniques. For example, in a study of lowland rainforest in New Guinea, Bell (1982b) estimated densities using a combination of transects; spot-mapping; delineation of territories by colour-banding, mark and recapture; and, as a last resort, estimated distances between calling birds. The overall densities were close to those from other equatorial forests of similar structure, where different methods of census were applied to different species (e.g. Africa, Zimmerman 1972, and in Malaysia, Wells 1978).

To conclude, we can do no better than to heed the points made by Karr (1981):

'(1) Use a composite of census procedures selected to provide the best possible data for a variety of species.

(2) Select procedure(s) which do not depend on some seasonal phenomenon like breeding for their effectiveness.

(3) Identify exceptional species and use special procedures to improve knowledge of their abundances if such knowledge is appropriate to project objectives.

(4) There is no substitute for knowledge of the animal under study.

(5) Keep in mind the constraints placed on these thoughts by variability in study objectives.'

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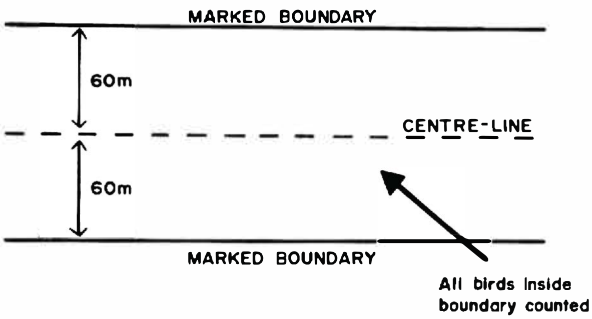
APPENDIX

This appendix shows how to carry out the three census methods, Fixed-strip Transect, Variable-strip Transect and Line Transect. We recommend the Variable-strip Transect as an easy, practicable method, yielding relatively reliable results.

Fixed-strip Transect

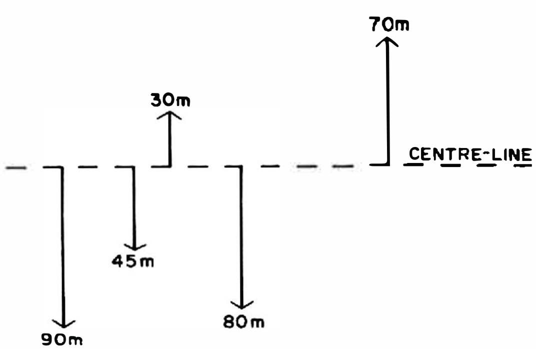


A transect of fixed-width has its boundaries marked (width of transect will depend on visibility, or type of birds being counted). All birds inside the transect are counted. Overhead transients, except aerial foragers, are not included. Density is estimated as:

$$\frac{\text{number of birds counted}}{\text{area of transect strip (i.e. length x width)}}$$

divided by number of transect counts.

Variable-strip Transect



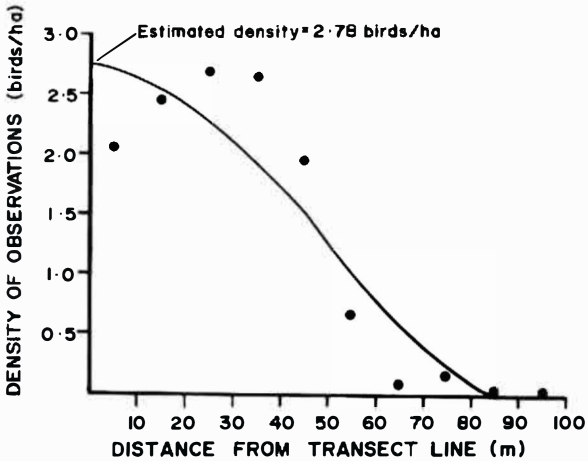
A transect with no set boundary. All birds recorded, noting their lateral distance from the centre-line. For the period under study (e.g. month, season, whole study) observations for each species are tallied in bands of equal width from the centre-line. We recommend monthly or seasonal tallies but this depends on a sufficiency of observations. The band that encompasses the greatest density from the centre-line is the outer limit of the 'basal region' containing 'useable' observations, all other observations being discarded. In the example below the 40 m band encompasses the greatest density. Estimated density for this species is therefore 2.46 birds per hectare.

Length of transect = 500 m, number of transects = 20

Band	No. of observations	Cumulative No. of observations, averaged over 20 transects	Cumulative density (birds per hectare)
10 m	41	$\frac{41}{20} = 2.05$	$\frac{2.05}{*1} = 2.05$
20 m	49	$\frac{41+49}{20} = 4.50$	$\frac{4.50}{2} = 2.25$
30 m	54	$\frac{90+54}{20} = 7.20$	$\frac{7.20}{3} = 2.40$
40 m	53	$\frac{144+53}{20} = 9.85$	$\frac{9.85}{4} = 2.46$
50 m	39	$\frac{197+39}{20} = 11.80$	$\frac{11.80}{5} = 2.36$
60 m	13	$\frac{236+13}{20} = 12.45$	$\frac{12.45}{6} = 2.08$
70 m	1	$\frac{249+1}{20} = 12.50$	$\frac{12.50}{7} = 1.79$
80 m	3	$\frac{250+3}{20} = 12.65$	$\frac{12.65}{8} = 1.58$
90 m	0	$\frac{253+0}{20} = 12.65$	$\frac{12.65}{9} = 1.41$
100 m	0	$\frac{253+0}{20} = 12.65$	$\frac{12.65}{10} = 1.27$

* = 1 ha, calculated by length (500 m) × twice the width of the band (10 m × 2) to account for both sides of the centre-line. 10,000 m^2 = 1 ha.

Line Transect



A wide variety of line transect estimators have been developed, most involving complex mathematical calculations. Burnham *et al.* (1980) provide an excellent review of these techniques. The method used in the present study was derived from that proposed by Anderson and Pospahala (1970). The steps involved are illustrated using the data presented for Variable-strip Transects above:

(a) The density of observations is calculated for each 10 m band. For example, in the 40-50 m band the average density of observations is

$$\frac{53 \text{ birds}}{20 \text{ transects x 1 ha}} = 2.65 \text{ birds/ha.}$$

(b) The density of observations within each 10 m band is plotted against the mid-point of that band. For example, in the graph below the value of 2.65 birds/ha for the 40-50 m band is plotted against 45 m.

(c) A polynomial regression line is fitted to these points. In the present study we used a third order polynomial with the linear term set at zero. The advantages of using this form of the polynomial for density estimation are outlined by Burnham *et al.* (1980). The line is most easily fitted to the data by the method of least squares (see Anderson and Pospahala 1970).

(d) The value of the regression line at zero distance from the transect is the estimated density for that species, adjusting for the influence of distance on detectability. In this example the estimate is 2.78 birds/ha.