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Evaluation of bird survey methods and estimators for species inventory in dry sclerophyll forest

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A species inventory aims to list all of the species present in an area over some period of time. Complete results are rarely practical and estimators can be applied to predict total species richness. In this study four survey methods were compared in a northern New South Wales dry sclerophyll forest: standardised search, two-hectare search, transects and point counts. Total sampling time was equal (560 minutes) for all methods. Three non-parametric estimators were evaluated: Chao2, first-order jacknife and second-order jackknife.

The quality of inventories and estimates was strongly affected by search method and sampling effort. True species richness was approximately 42 species. The standardised search recorded 35 species, transects 34, point counts 32 and the two-hectare search 27 species. Estimates of total species richness were more accurate at high completeness (when more than 75 per cent of species present were recorded) and when there were few unique records. The first-order jackknife was most accurate at high completeness and the second-order jackknife at low completeness. Large area, active search methods, patch-scale sampling, results-based stopping rules and species richness estimation are recommended to improve bird species inventories.

INTRODUCTION

Species richness (the number of species) is a simple and practical measure of biodiversity (Gaston and Spicer 2004). Species richness has been widely used in biogeography (e.g. Macarthur and Wilson 1967), ecological research (e.g. Mittelbach *et al.* 2001), conservation planning (e.g. Kerr 1997) and environmental impact assessment (e.g. Waltert *et al.* 2004). This paper concerns the evaluation of species richness within sites or habitats (alpha diversity, Whittaker 1972).

Natural species-abundance distributions in large assemblages typically contain many rare species (Magurran and Henderson 2003) and the effort required to record complete species inventories has commonly been underestimated (Colwell and Coddington 1994). Preston (1979) estimated that a single reasonably skilled observer would miss 50 per cent of individual birds and 15 per cent of species when searching wooded habitats.

Another challenge for species inventories is to present meaningful results (Remsen 1994). 'Core species' should be distinguished from wandering or dispersing individuals. Core species are persistent, often abundant and are biologically associated with habitats in the site (Magurran and Henderson 2003). In forests, open-country birds, waterbirds, aerial foragers, nocturnal birds and raptors might be excluded from the main list (Watson 2004, 2010). These birds were not included in this study and the complete inventory refers only to core species.

Field ornithologists have traditionally attempted to control bias in bird surveys with rigid protocols and observer training (e.g. Kavanagh and Recher 1983), a combination of methods (e.g. Recher *et al.* 1983) and corrections (e.g. Bart and Earnst 2002). Or they have assumed that opposing biases approximately cancel out (e.g. Craig and Roberts 2001) and especially with large sample sizes (Johnson 1981). Variable bias has long prevented inter-study comparisons (Recher 1988).

The effects of habitat and bird behaviour on detectability are beyond the observer's control and modern approaches to bird surveys apply modelling and estimation to account for the 'invisible birds' (e.g. Buckland *et al.* 1993). Species richness estimators attempt to correct for negative bias due to incomplete sampling effort by: fitting statistical distributions to species-abundance data; extrapolation of species accumulation curves; or non-parametric models (Chao 2005). Non-parametric estimators are based on sampling theory and use the relative abundance of rare species to estimate the number of species not yet recorded. Estimators are not a substitute for poor fieldwork, however. They do not correct for measurement error (e.g. overlooked species) and sampling bias (unrepresentative sampling, Walther and Moore 2005).

Watson (2003, 2004, 2010) has promoted a 'standardised search' bird survey method that combines active, timed searches with a results-based 'stopping rule' to indicate when sampling is satisfactorily complete (i.e. to standardise completeness). He has recommended entire-patch searching, which may not be practical in large patches and when boundaries are indistinct. The standardised search has not been widely adopted, likely because the popular bird survey methods (transects and point counts) and fixed-effort sampling are entrenched in ornithology (Watson 2003).

Watson (2004) compared the standardised search and fixed-effort transects in four small patches (9 to 42 ha) of grassy, box woodland in southern New South Wales (NSW). He reported that the standardised search accumulated species more rapidly and achieved higher completeness (73 to 78%) than transects (34 to 46%). He did not investigate species richness estimation.

While numerous comparative evaluations of species richness estimators have been published (Walther and Moore 2005 and references therein), field research into the effects of sampling methods and design on estimation is lacking. This study evaluated four popular bird survey methods and three estimators in a medium-sized 570-hectare patch of dry sclerophyll forest. The patch was sampled rather than searched entirely. Performance with extended sampling time was investigated.

This paper follows previous authors (e.g. Colwell and Coddington 1994) and uses the general term ‘sample’ to refer to a sampling occasion (e.g. a fixed period of time, quadrat, transect or point) or to a subset of observations from a population (the statistical definition, e.g. Zar 1999).

METHODS

Study Site

Surveys were performed during winter 2010 in Carwong State Forest (SF), 22 kilometres south of Casino, in the Richmond River catchment, NSW (29°03'S, 152°57'E; Fig. 1). Carwong SF has an area of 570 hectares and a relatively flat topography with elevation 50 to 90 metres asl (Department of Lands 2006). There are no permanent watercourses. The forest is located in a subtropical climate zone with a warm, humid summer (Bureau of Meteorology 2010a). Minimum-maximum temperature averages at Casino are 6.7 to 20.7°C in July and 19.0 to 30.9°C in January. Mean annual rainfall is 1046 millimetres, wet in summer and dry in winter-spring (Bureau of Meteorology 2010b).

Carwong SF is grassy, dry sclerophyll forest. Canopy trees are *Eucalyptus variegata* with *E. siderophloia*, *E. tereticornis* and *E. moluccana*. Scattered eucalypts were flowering during the fieldwork. Mistletoe spp. were common but few were flowering. Grass cover was mature *Imperata cylindrica* and knee-high over much of the site. *Themeda australi*s and other mostly native grasses occurred in low-lying areas. Sparse *Acacia falcata, A. irrorata*, *Alphitonia excelsa* and *Lantana camara* grew in the understorey. Adjacent to Carwong SF are young *Pinus radiata* plantations to the south and north-east, *Acacia* shrubland to the north-west and grazing land to the west. The edge of Braemar SF (c. 1390 ha of dry sclerophyll forest) is 1.5 kilometres to the east. Carwong SF is managed for forestry. There was no evidence of recent logging, fires or cattle grazing during the fieldwork.

Carwong SF was selected for this study because the habitat is simpler and more uniform than nearby dry sclerophyll forests, the patch size is relatively small and it has distinct boundaries. Seasonal movements of birds into and out of sclerophyll forests in the Richmond River district are minimal in winter and summer (Gosper 1992). With these conditions, the winter assemblage of birds in Carwong SF was presumed to be reasonably stable.

Standardised search

The standardised search has no fixed area. The observer moves freely through the patch and lists all bird species seen or heard. Distant calling birds are recorded if estimated to be inside the patch. Standardised searches of 15 to 60 minutes are suitable for most conditions (Watson 2003). Forty-minute searches were used in this study and birds flying overhead were recorded if less than one canopy height above the treetops. Visual identifications were aided by 8 x 32 binoculars.

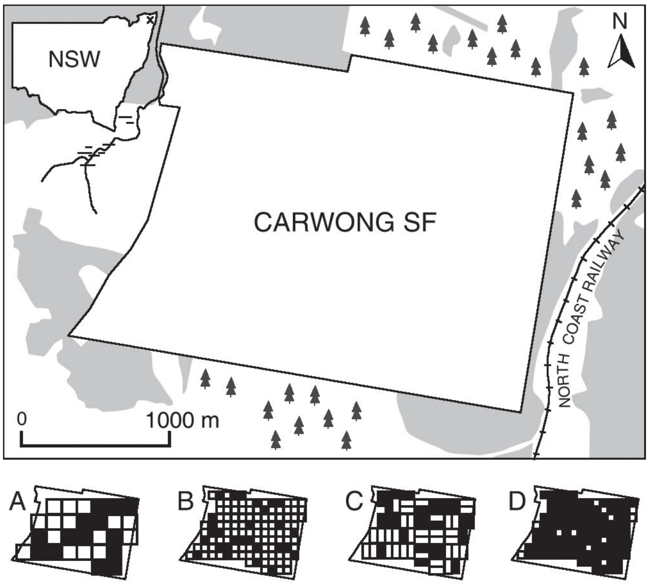

Figure 1. *Carwong State Forest (redrawn from Department of Lands 2006). Cleared and grazing land outside Carwong SF white. Native vegetation remnants and secondary growth light-grey. Pine plantations to south and northeast. Lower figures (1/4 scale) illustrate sampling grids for standardised search (A), two-hectare search (B), transects (C) and point counts (D). Black grid cells were sampled.*

Two-hectare search

The standard survey in the *New Atlas of Australian Birds* (Barrett *et al.* 2003) is a fixed-effort two-hectare, 20-minute active search. Species are recorded as present or absent, including birds flying over the area. The recommended 200 by 100 metre quadrat was used in this study.

Transect

Most birds can be detected up to 60 metres in eucalypt forests (Recher *et al.* 1983). Transects were 400 metres long with lateral distances grouped in two bands: from zero to 25 metres and from 25 to 75 metres. The inner strip area was two hectares (400 × 50 m) and the total area six hectares (400 × 150 m).

Transect duration was nominally 20 minutes (speed 20 m per min.). Birds seen or heard ahead and to the sides were counted. To avoid causing movements of birds, deviations from the transect centreline were restricted to less than five metres.

Point count

Point counts were grouped in two bands: from zero to 25 metres and from 25 to 75 metres. The inner circular plot area was 0.2 hectares and the total area 1.8 hectares. Waiting time was three minutes, followed by a five-minute count. Short duration counts reduce the effect of bird movements (Bibby *et al.* 2000). Any birds that were flushed upon arrival were added to the counts.

Transect and point count methods were not modified for species inventory except that birds flying overhead were recorded, which can usefully add to the species list. Exact distances are not required in a species inventory and the methods are equivalent to distance-sampling with measurements truncated at 75 metres. Abundance data were collected for a separate analysis. In this paper, species richness is estimated from incidence results (presence/absence) and count data are not presented.

Sampling design

Samples were selected randomly and without replacement. Sampling grids were 400 by 400 metres for the standardised search, 400 by 200 metres for transects and 200 by 200 metres for the two-hectare search and point counts (Fig. 1). Large grid squares located focal areas for standardised searches. Transects and two-hectare searches followed the centreline of grid cells and were orthogonal to the topographic contours which improves coverage of habitat features (Sinclair *et al.* 2006). Point counts were located at the centre of squares. To avoid recording open country birds, grid cells that overlapped the forest edge were discarded.

Global Positioning System (Garmin GPS 76) was used to locate sites. Transects and points were marked at least one day before counting. The centreline of each transect was flagged and distance references were flagged 25 metres parallel on both sides. Point counts were marked similarly. Width was measured in paces, because GPS without corrections is not accurate over such short distances. The 75-metre distance limit was estimated. Visual distance estimates can be accurate within 10 to 15 per cent after practise (Emlen 1977).

Surveys were between 0700 and 1030 hours in the morning and with rotation between methods. Starting time was 30 minutes after sunrise, when light levels were adequate for visual identification and to avoid high variance in counts near dawn (Dawson 1981). Activity of forest birds and their detectability generally declines toward late morning, although the number of species observed is less sensitive to time of day than counts (Robbins 1981).

Total sampling time was equal for all methods, with two 20-minute searches and eight five-minute point counts to every 40-minute standardised search. Transect duration increased slightly when there were many birds to count (e.g. flocks in flowering eucalypts) and total sampling time was monitored for this method. The standardised search can be considered reasonably complete when no additional species are recorded in three consecutive samples ('strict stopping rule', Watson 2004). Sampling continued for an additional 160 minutes to evaluate long-term performance for other methods.

Rare species that have been recorded incidentally (i.e. outside of formal surveys) on a number of occasions may be considered for the species inventory (Watson 2004). A separate list was maintained for incidental records.

The birds of dry sclerophyll forests south of Casino were familiar to the observer. A similar nine-day study had been performed in nearby Camira SF (29°17'S 152°56'E) in March 2010. Two days were spent exploring Carwong SF and marking transects and points before starting the inventory.

Species richness estimation

The Chao2 (Chao 1987) and first- and second- order jackknife (Burnham and Overton 1978) non-parametric estimators were applied. These have generally performed well for species richness estimation (Walther and Moore 2005) and are easy to calculate:

$$\hat{S}_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$$

$$\hat{S}_{jack1} = S_{obs} + Q_1 \left(\frac{m-1}{m}\right)$$

$$\hat{S}_{jack2} = S_{obs} + \left[\frac{Q_1\,(2m-3)}{m} - \frac{Q_2\,(m-2)^2}{m\,(m-1)}\right]$$

where $\hat{S}$ = estimated species richness, S_{obs} = observed species richness (number of species recorded), Q_1 = frequency of uniques (number of species seen in exactly one sample unit), Q_2 = frequency of duplicates (number of species seen in exactly two sample units) and m = sample number.

The software EstimateS (Version 8.2, Colwell 2009) was used to calculate variance. EstimateS randomises the accumulation curve many times (default 50 runs) and averages the results to remove sample order effects. EstimateS 8.2 reports analytical variance for Chao2 and first-order jackknife and 'runs variance' for second-order jackknife. Sampling without replacement is used for analytical variance (Colwell 2009). Sampling with replacement is for runs variance and 1000 runs was used to improve precision. With these variance results log-transformed (asymmetric) 95 per cent confidence intervals were calculated for species richness estimates. The log-transformation is appropriate when variance is high and usually provides better coverage probability (Chao 1987).

Incidence rates (frequency or reporting rates) provide an index of abundance and were used to compare species sensitivity of different methods:

$$p_k = \frac{N_k}{m}$$

where p_k = incidence rate (proportion of samples that contain species) and N_k = number of samples that contain species k.

Performance evaluation

There was no reference bird species list for Carwong SF. Lists from the four survey methods were merged and used as reference. Performance of survey methods and estimators was quantified with mean absolute error:

$$MAE = \frac{1}{n}\sum_{i=1}^{n} |\hat{S}_i - S_{true}|$$

where MAE = Mean Absolute Error, $\hat{S}_i$ = estimated species richness, S_{true} = true species richness (reference value) and n = number of estimates averaged. Mean absolute error combines the effects of bias and precision (Walther and Moore 2005).

RESULTS

Carwong SF was surveyed over 24 days: from 28 June to 15 July and from 19 July to 24 July 2010. The weather during these periods was mostly fine. Two days had more than two millimetres of rain and two had wind speeds at 0900 hrs exceeding 20 kilometres per hour (Bureau of Meteorology 2010c).

The standardised search accumulated species rapidly and satisfied the strict stopping rule at 400 minutes, with no new species in three consecutive samples (Fig. 2). Four additional searches added only one more species. Wide transect (0–75 m) and large circular plot (0–75 m) results approached the standardised search observed richness at 560 minutes.

Total sampling time was equal for all methods, but patch coverage (the fraction of the patch area sampled) was low for the two hectare search, narrow transect and small circular plot (Table 1). Sampling intensity (the fraction of the grid sampled) was low for the two-hectare search (20-minute searches restricted in area) and very high for the point count method (with many short five-minute counts).

Forty-two bird species were recorded overall (Table 2). With 37.6 combined survey hours and good patch coverage, this inventory should be quite complete. Incidental records are summarised in Table 3. One or two species might be subtracted from the inventory (e.g. the single Pied Currawong *Strepera graculina* may have been a wanderer), one or two incidentals might be added (e.g. Grey-crowned Babblers *Pomatostomus temporalis* may have been daily in the patch) and the total richness will hardly change.

Incidence rates for some species were markedly different between methods. Birds with loud and repeated calls (e.g. Grey Shrike-thrush *Colluricincla harmonica*) were more frequently detected by standardised searches than by fixed-area methods. Stationary, short-duration point counts had poor sensitivity towards inconspicuous birds (e.g. Painted Button-quail *Turnix varius*).

Final observed species richness and estimates at 560 minutes are presented in Table 4. Higher completeness delivered estimates with greater consistency and the standardised search gave the lowest mean absolute error. The first-order jackknife was the most accurate (unbiased and precise) estimator at high completeness.

Early-time results are presented in Table 5 at 200 minutes, which might be considered a reasonable survey effort for a 570-hectare patch like Carwong SF. Gosper (1992) applied single 2.5 to 3 hour (150 to 180 minutes) searches in similar habitats. Chao (1987) recommended at least five samples for species richness estimation (five 40-minute standardised searches equals 200 minutes). At 200 minutes the standardised search was far ahead (completeness 69 per cent) and small-area methods had not yet recorded half of the species present. Chao2 and second-order jackknife early-time estimates for the standardised search and wide transect were close to total species richness although confidence intervals were wide.

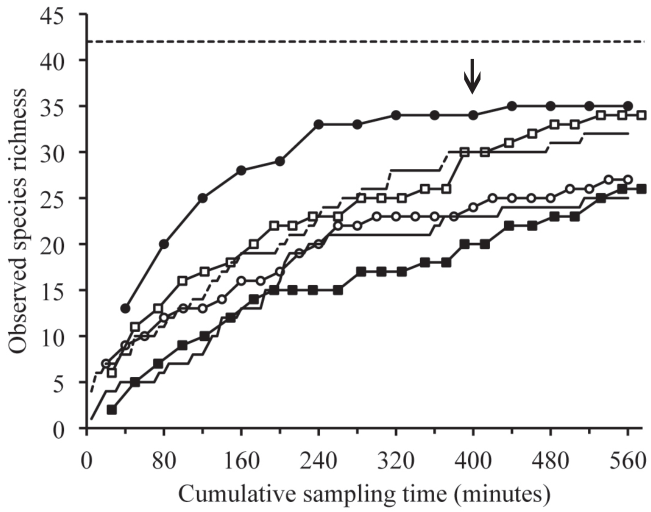

Figure 2. *Species accumulation curves (field data, not smoothed) for standardised search (solid circles), two hectare search (open circles), transect 0-25 m (solid squares), transect 0-75 m (open squares), point count 0-25 m (long-dashed line) and point count 0-75 m (short-dashed line). Total observed species richness was 42 (dotted line). The arrow indicates where the standardised search strict satisfied the strict stopping rule, with no additional species in three consecutive samples.*

TABLE 1

Sampling effort for different survey methods. Time is total sampling time in minutes. Area is total area sampled. Coverage is the fraction of the 570-ha patch sampled. Intensity is the fraction of the sampling grid sampled. Sampling grids are illustrated in Figure 1.

	Sample size	Time (min.)	Area (ha)	Coverage	Intensity
Standardised search	14	560	112[A]	0.2	0.5
Two hectare search	28	560	56	0.1	0.23
Transect 0-25 m	25	574	50	0.09	0.42
Transect 0-75 m	25	574	150	0.26	0.42
Point 0-25 m	112	560	22	0.04	0.93
Point 0-75 m	112	560	202	0.35	0.93

[A]Standardised search area approximately 8 ha in 40 minutes. Detections of distant calling birds would effectively increase this area.

Early estimates at 200 minutes were imprecise however and a doubling of effort was required before the strict stopping rule was satisfied.

DISCUSSION

Efficiency of the different survey methods

The number of species observed increases with the number of individuals in a sample (Preston 1979). Larger search areas and longer searching time will encounter more birds and more species. Active searching helps find inconspicuous birds (Loyn 1986). For all of these reasons, the standardised search accumulated species more rapidly than other survey methods.

Wide transects (0 to 75 m) recorded 31 per cent more species than narrow transects (0 to 25 m). Harden *et al.* (1986) evaluated strip transects in rainforest and wet sclerophyll forest and reported similar increases in species observed with transect width. Results from Carwong SF suggest that wide transects (and distance sampling) can deliver useful species inventories for moderate effort in dry sclerophyll forests. A hidden cost for transects is the additional time spent surveying transect lines.

TABLE 2

Composite species list from Carwong SF, Winter 2010. The total number of species recorded during formal surveys was 42. Nearly all of these were recorded on multiple occasions and are considered core species of this patch. Non-core species (NC) included one diurnal raptor, one dove of adjacent habitats and one possible wanderer. Blank cells are species not recorded by a particular search method (zero incidence).

Species	Incidence rates					
	Stan. search	Two hectare search	Transect 0-25 m	Transect 0-75 m	Point 0-25 m	Point 0-75 m
Common Bronzewing *Phaps chalcoptera*			0.08	0.08		0.01
Bar-shouldered Dove *Geopelia humeralis* (NC)	0.07					
Wonga Pigeon *Leucosarcia picata*	0.43	0.04		0.08	0.01	0.02
Brown Goshawk *Accipiter fasciatus* (NC)	0.07				0.01	0.01
Painted Button-quail *Turnix varius*	0.07	0.11	0.08	0.08	0.01	0.01
Rainbow Lorikeet *Trichoglossus haematodus*	0.64	0.43	0.12	0.12	0.08	0.08
Scaly-breasted Lorikeet *Trichoglossus chlorolepidotus*	0.71	0.36	0.32	0.36	0.03	0.04
Little Lorikeet *Glossopsitta pusilla*	0.93	0.82	0.84	0.92	0.42	0.49
Australian King-Parrot *Alisterus scapularis*	0.21	0.04	0.04	0.08		
Eastern Rosella *Platycercus eximius*	0.14	0.04				
Horsfield's Bronze-Cuckoo *Chalcites basalis*				0.04		
Laughing Kookaburra *Dacelo novaeguineae*	0.29		0.04	0.16		0.01
Rainbow Bee-eater *Merops ornatus*	0.36			0.04	0.01	0.04
Brown Treecreeper *Climacteris picumnus*	0.86	0.25	0.32	0.76	0.01	0.15
Superb Fairy-wren *Malurus cyaneus*	0.43	0.36		0.08	0.04	0.13
Red-backed Fairy-wren *Malurus melanocephalus*	1	0.61	0.28	0.64	0.11	0.35
Variegated Fairy-wren *Malurus lamberti*	0.14	0.11			0.01	0.01
Fuscous Honeyeater *Lichenostomus fuscus*	0.93	1	1	1	0.75	0.94
Noisy Miner *Manorina melanocephala*			0.08	0.12	0.01	0.03
Scarlet Honeyeater *Myzomela sanguinolenta*	0.43	0.07	0.08	0.12	0.02	0.12
White-throated Honeyeater *Melithreptus albogularis*	0.71	0.04	0.04	0.08	0.01	0.03
Noisy Friarbird *Philemon corniculatus*	0.29	0.14		0.12	0.01	0.08
Little Friarbird *Philemon citreogularis*			0.08	0.12	0.01	0.01
Spotted Quail-thrush *Cinclosoma punctatum*	0.07					0.01
Black-faced Cuckoo-shrike *Coracina novaehollandiae*	0.29	0.18	0.12	0.16	0.01	0.03
White-bellied Cuckoo-shrike *Coracina papuensis*	0.36	0.14	0.12	0.2	0.01	0.03
Crested Shrike-tit *Falcunculus frontatus*	0.07		0.04	0.08		
Golden Whistler *Pachycephala pectoralis*			0.04	0.04		
Grey Shrike-thrush *Colluricincla harmonica*	0.86	0.29	0.16	0.28	0.05	0.13
Olive-backed Oriole *Oriolus sagittatus*	0.21	0.04		0.2		0.03
Dusky Woodswallow *Artamus cyanopterus*		0.07	0.04	0.04	0.02	0.02
Pied Butcherbird *Cracticus nigrogularis*	0.29	0.04	0.04	0.04	0.02	0.04
Australian Magpie *Cracticus tibicen*	0.57		0.04	0.08		0.01
Pied Currawong *Strepera graculina* (NC?)	0.07					
Grey Fantail *Rhipidura albiscapa*	0.07					
Willie Wagtail *Rhipidura leucophrys*	0.79	0.29	0.16	0.28	0.01	0.13
Torresian Crow *Corvus orru*	0.64	0.07		0.04	0.03	0.03
Restless Flycatcher *Myiagra inquieta*	0.21	0.04		0.08		0.06
Hooded Robin *Melanodryas cucullata*		0.04				0.01
Jacky Winter *Microeca fascinans*	0.29		0.04	0.04		
Eastern Yellow Robin *Eopsaltria australis*	0.14	0.07	0.04	0.08		
Red-browed Finch *Neochmia temporalis*	0.14	0.11	0.04	0.04	0.01	0.02

TABLE 3

Incidental species list from Carwong SF, Winter 2010. These are additional records outside of formal surveys. The total number of incidental species recorded was 11. Most are non-core species (NC) and were recorded only once.

Species	Records in 24 days	Remarks
Brown Falcon *Falco berigora* (NC)	1	Edge, along the railway line.
Yellow-tailed Black-Cockatoo *Calyptorhynchus funereus* (NC)	2	Present in a wider area around Carwong SF.
Southern Boobook *Ninox novaeseelandiae* (NC)	1	Nocturnal birds are not part of the inventory.
White-throated Treecreeper *Cormobates leucophaea* (NC?)	1	Heard once, usually very vocal.
Striated Pardalote *Pardalotus striatus*	2	Edge, along the railway line.
Blue-faced Honeyeater *Entomyzon cyanotis*	3	Occasional afternoon visitor in SE of patch.
Grey-crowned Babbler *Pomatostomus temporalis*	4	Visitor to south of patch.
Eastern Whipbird *Psophodes olivaceus* (NC)	2	Associated with creek over the NE boundary.
White-winged Chough *Corcorax melanorhamphos*	1	Party moving through the patch.
Welcome Swallow *Hirundo neoxena* (NC)	1	Aerial birds are not part of the inventory.
Tree Martin *Petrochelidon nigricans* (NC)	1	Aerial birds are not part of the inventory.

TABLE 4

Final species richness results and estimates at 560 minutes. Total observed species richness was 42 by merging results from the four survey methods (Table 2). Estimated species richness ± s.d. with 95 per cent confidence intervals in brackets.

	Observed species richness						Estimated species richness			
	Observed richness	Completeness	Uniques	Duplicates						All estimators Mean Abs. Error
	Sobs	Sobs/42	Q1	Q2	Q1/Q2	Q1/Sobs	Chao2	Jackknife1	Jackknife2	MAE
Stan. search	35	0.83	7	4	1.8	0.2	41 ± 6 [36 - 66]	42 ± 3 [38 - 49]	44 ± 5 [38 - 61]	1.2
Two-hectare search	27	0.64	8	4	2	0.3	35 ± 7 [29 - 65]	35 ± 2 [31 - 41]	39 ± 5 [32 - 52]	5.9
Transect 0-25 m	26	0.62	11	5	2.2	0.42	38 ± 10 [29 - 74]	37 ± 3 [32 - 45]	42 ± 6 [34 - 60]	3.2
Transect 0-75 m	34	0.81	8	10	0.8	0.24	37 ± 3 [35 - 50]	42 ± 3 [38 - 49]	40 ± 6 [35 - 65]	2.3
Point 0-25 m	25	0.6	14	3	4.7	0.56	58 ± 26 [33 - 156]	39 ± 3 [34 - 48]	50 ± 6 [41 - 64]	8.8
Point 0-75 m	32	0.76	9	3	3	0.28	46 ± 12 [35 - 95]	41 ± 3 [37 - 50]	47 ± 6 [39 - 62]	3.1
All search methods MAE							6	3	3.4	
High completeness (>0.75) MAE							3.1	0.6	3	
Low completeness (<0.75) MAE							8.9	5.3	3.8	

Watson (2004) found that observed species richness from standardised searches was nearly twice as complete as transects. Transects performed much better in the present study because of increased effort (equal total sampling time), longer (400 versus 250 m) and wider (150 versus 80 m) transects and with additional records of birds flying over the transect. Watson (2004) addressed 'effort-based stopping rules' and halted transect sampling at just 80 minutes.

While intensive sampling increased point count species richness, the large sample size (n = 112) was unwieldy and the many unique records (birds seen only once) limit confidence in the results. Arnold (1984) has similarly reported, from Wandoo Woodland in Western Australia, that point counts have poor sensitivity towards rare and inconspicuous birds compared to transects. A hidden cost for point counts is the non-surveying time spent moving between stations, which is often large compared to counting time.

TABLE 5

Early smoothed species richness results and estimates at 200 minutes. Total observed species richness was 42 by merging results from the four survey methods (Table 2). Estimated species richness ± s.d. with 95 per cent confidence intervals in brackets.

	Observed species richness						Estimated species richness			
	Observed richness	Completeness	Uniques	Duplicates						All estimators Mean Abs. Error
	Sobs	Sobs/42	Q1	Q2	Q1/Q2	Q1/Sobs	Chao2	Jackknife1	Jackknife2	MAE
Stan. search	27	0.64	9	6	1.5	0.33	37 ± 8 [29 - 67]	35 ± 2 [32 - 41]	38 ± 6 [31 - 61]	5.8
Two-hectare search	19	0.45	8	3	2.7	0.42	32 ± 13 [21 - 86]	26 ± 2 [22 - 31]	29 ± 5 [22 - 45]	13.2
Transect 0-25 m	16	0.38	9	3	3	0.56	8 ± 21 [21 - 123]	24 ± 3 [20 - 31]	29 ± 7 [21 - 49]	11.7
Transect 0-75 m	23	0.55	11	5	2.2	0.48	40 ± 14 [27 - 94]	33 ± 3 [28 - 41]	38 ± 8 [29 - 62]	4.9
Point 0-25 m	14	0.33	8	2	4	0.57	39 ± 25 [19 - 145]	22 ± 3 [19 - 31]	29 ± 6 [21 - 47]	12
Point 0-75 m	23	0.55	8	4	2	0.35	33 ± 10 [25 - 73]	31 ± 3 [26 - 38]	34 ± 7 [26 - 55]	9.3
						All search methods MAE	5.7	13.6	9.1	

The two-hectare search recorded a low 26 species. Small-area searches (200 by 100 m) cannot effectively sample birds with large home ranges or clumped distributions. The 20-minute search was developed for forests in Gippsland, Victoria and optimal survey parameters may be different in other forest types. Loyn (1986) also suggested recording species heard calling outside the search area to add to the species inventory, which is not allowed by the *New Atlas of Australian Birds* protocols (Barrett *et al.* 2003).

Incidence rates are a more useful index of relative abundance when both search time and area are fixed (Verner 1984). Standardised search incidence rates reflect site preference rather than relative abundance (Watson 2003). Herzog *et al.* (2002) suggested that a 50 metre distance cut-off (in tropical forests) avoids overestimation of common, noisy birds and only very occasionally results in rare and loud species being excluded. Experimentation with fixed-area searches larger than two hectares is recommended.

Species richness estimation and stopping rules

The results suggest that around 80 per cent completeness is required for stable estimates. Watson (2010) suggested 75 to 85 per cent. Consistent with the recommendations of Brose *et al.* (2003), at low completeness the second-order jackknife was more accurate than other estimators. At high completeness, precision becomes more important than bias reduction and the first-order jackknife was more accurate.

Observed species richness shows negative bias and a flattening species accumulation curve does not reliably indicate completeness (Colwell and Coddington 1994). Various rules have been suggested to control for sampling effort: stability in observed richness ('strict stopping rule'; Watson 2004), stability in estimated richness (Peterson and Slade 1998), estimated completeness thresholds (Herzog *et al.* 2002; Peterson and Slade 1998), variance estimate thresholds (Walther and Martin 2001) and a threshold for the ratio of uniques to duplicates ('lenient stopping rule', Watson 2004). Many of these have not been critically evaluated or field tested.

Model-based stopping rules (estimated completeness, richness or variance) are limited by the choice of estimator and may not be reliable at low completeness and if unique records are persistent. The strict stopping rule was effective for the standardised search in this study although it is not clear how it can be applied to other methods. Applying the strict stopping rule to the narrow transect data, it would have tripped prematurely after just 15 species had been recorded. The lenient stopping rule appears more useful in controlling variance for second-order estimators (by reference to the analytical variance equation in Chao 1987). The standardised search achieved 83 per cent completeness and accurate estimates even though the ratio of uniques to duplicates was greater than one.

Colwell and Coddington (1994) noted that an inventory is theoretically complete when all species have been observed 'multiple' times. For the Chao2 and first-order jackknife estimators, estimated richness equals observed richness when there are zero uniques. On this basis, a novel stopping rule is proposed: stop sampling when 'most' species have been observed more than once. Results from the present study suggest that the proportion of uniques in the observed species richness (Q_1/S_{obs}) should be less than 0.25. Applied to the first-order jacknife equation, minimum estimated completeness is 75 per cent. This stopping rule can be applied successfully to the data from this study (Fig. 3).

A second recommendation is that estimated species richness be used for comparisons between inventories rather than observed species richness results of standardised completeness (Watson 2003). Estimates should be less affected by the choice of survey methods and stopping rules and confidence intervals can be used to account for uncertainty.

The fact that high completeness is required for accurate estimates should not cause disillusionment. Most of the common species can be discovered quickly and species richness estimation proves most useful when the accumulation rate slows. Applying the extrapolation methods of Chao *et al.* (2009), 15 hours would have been required for the standardised search to reach 95 per cent completeness. Accurate estimates of total species richness were available at 400 minutes (6.67 hours) and 81 per cent completeness.

A robust estimate of total species richness may not be completely satisfying. Undiscovered species (equal in number to the difference between estimated and observed richness) might be identified from incidental observations (Watson 2004) and supplementary surveys: e.g. sound-recordings (Parker 1991), mist-net sampling (e.g. Gram and Faaborg 1997) and call playback.

Sampling design

Random, patch-scale sampling (i.e. selection of units from a sampling universe that covers the whole patch) is recommended for reliable results. Patch-scale sampling is necessary to make inferences about the patch rather than sites within the patch (Watson 2003). Random sampling helps to satisfy the assumptions and limitations of the estimator models (Chao *et al.* 2009, Kendall 1999). While this study has shown that entire-patch sampling is not required for species richness estimation, and would be impractical for very large sites, one should be aware of within-patch heterogeneity. When there is fine-scale heterogeneity (e.g. a moist gully in dry forest) the freedom of the standardised search can be advantageous (Watson 2003). When there is large-scale heterogeneity (i.e. when there are different habitat patches in a study area, each with their own assemblage of core species) then stratified sampling designs are appropriate. Fixed-area methods are suitable for stratified designs.

CONCLUSIONS

Considerable effort is needed to record complete bird species inventories, even for simple sites like Carwong SF. Small-area and short duration methods (two-hectare search, narrow transect and point count) were shown to be inefficient.

Bird species inventories can be improved with large area, active searching, patch-scale sampling and robust stopping rules. The standardised search method is maximally efficient but not the only choice. Useful results are possible from large-area transects. More detailed abundance data from transects can be important to some studies.

Species richness estimation is a useful addition to the ecologist's 'toolbox'. Modern species inventories should be reported with estimates of total species richness, completeness and precision. Results should be defined in terms of the species, habitats, area, and time periods covered (Remsen 1994).

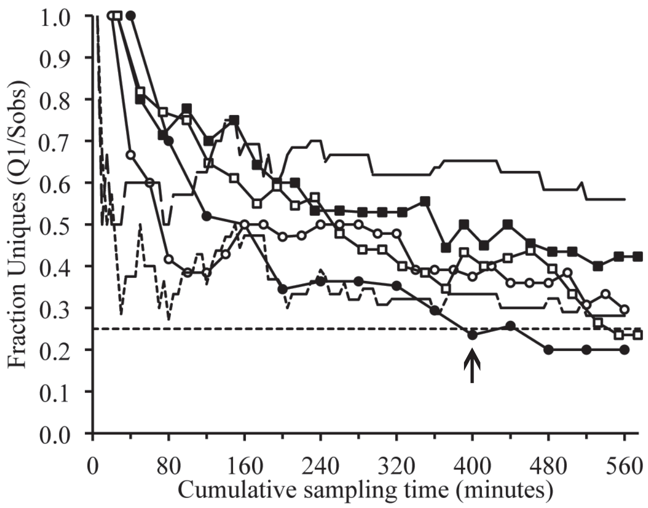

Figure 3. *Stopping rule plot of the fraction of uniques (field data, not smoothed) for standardised search (solid circles), two-hectare search (open circles), transect 0-25 m (solid squares), transect 0-75 m (open squares), point count 0-25 m (long-dashed line) and point count 0-75 m (short-dashed line). Suggested stopping rule cut-off at 0.25 (dotted line). The arrow indicates where the standardised search satisfied the strict stopping rule (Fig. 2).*

This study was from a single patch, without replicate sites, and the conclusions drawn might be criticised as context specific. The results were all reasonable and consistent with previous studies however and repeating this study in similar habitats (i.e. Australian open forests and woodlands) is expected to produce similar conclusions. Future work can be directed towards comparative evaluations in other forest types (e.g. wet sclerophyll and rainforest) and optimising fixed-area searches (search area and shape).

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