

Assessing biodiversity with species accumulation curves; inventories of small reptiles by pit-trapping in Western Australia

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Abstract We examined 11 non-linear regression models to determine which of them best fitted curvilinear species accumulation curves based on pit-trapping data for reptiles in a range of heterogeneous and homogeneous sites in mesic, semi-arid and arid regions of Western Australia. A well-defined plateau in a species accumulation curve is required for any of the models accurately to estimate species richness. Two different measures of effort (pit-trapping days and number of individuals caught) were used to determine if the measure of effort influenced the choice of the best model(s). We used species accumulation curves to predict species richness, determined the trapping effort required to catch a nominated percentage (e.g. 95%) of the predicted number of species in an area, and examined the relationship between species accumulation curves with diversity and rarity. Species richness, diversity and the proportion of rare species in a community influenced the shape of species accumulation curves. The Beta-P model provided the best overall fit (highest r^2) for heterogeneous and homogeneous sites. For heterogeneous sites, Hill, Rational, Clench, Exponential and Weibull models were the next best. For homogeneous habitats, Hill, Weibull and Chapman–Richards were the next best models. There was very little difference between Beta-P and Hill models in fitting the data to accumulation curves, although the Hill model generally over-estimated species richness. Most models worked equally well for both measures of trapping effort. Because the number of individuals caught was influenced by both pit-trapping effort and the abundance of individuals, both measures of effort must be considered if species accumulation curves are to be used as a planning tool. Trapping effort to catch a nominated percentage of the total predicted species in homogeneous and heterogeneous habitats varied among sites, but even for only 75% of the predicted number of species it was generally much higher than the typical effort currently being used for terrestrial vertebrate fauna surveys in Australia. It was not possible to provide a general indication of the effort required to predict species richness for a site, or to capture a nominated proportion of species at a site, because species accumulation curves are heavily influenced by the characteristics of particular sites.

Key words: abundance, diversity, fauna surveys, lizards, rarity, reptiles, species accumulation curve, species richness.

INTRODUCTION

Many ecological studies require accurate estimates of species richness for an area. For example, a prerequisite for the preparation of an environmental impact assessment (EIA) is knowledge of the species composition for the area. Similarly, comparative analyses of assemblages in various habitats using presence–absence data require a near-complete list of species for each area.

Soberón and Llorente (1993) argued that a sound theoretical basis for understanding the relationship

between collecting time (effort) and number of species accumulated gives formality to fauna studies, provides a planning tool for collecting expeditions, and is a predictive tool for conservation and biodiversity studies. Colwell and Coddington (1994) argued that species accumulation curves based on trapping effort represent a uniform process, without bias of a collector's attention being given to uncollected species.

The pattern of species accumulation during habitat sampling has been described in various ways, including species diversity curves (Sanders 1968), species richness curves (Hurlbert 1971), collector's curves (Pielou 1975), species effort curves (Hayek & Buzas 1997), species accumulation curves (Soberón & Llorente 1993) and species individual curves (Hubbell

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2001). In the present paper we use the term 'species accumulation curves'.

Colwell and Coddington (1994) indicated that different curve-fitting models predict different species richness values (for a given amount of effort) and extrapolation to a total species count increases error, with certain models being more effective for different groups of organisms, or in different environments, or with different amounts of effort. Soberón and Llorente (1993) argued for *a priori* choice of models for species accumulation curves, whereas Colwell and Coddington (1994) suggested a more practical approach. Soberón and Llorente (1993) also argued that only asymptotic models should be considered, as at any particular time there is only a finite number of species in a given area (although, over time this asymptotic number might fluctuate as species move in and out of an area as part of natural ecological processes). Non-asymptotic models have no upper limit, and therefore theoretically should not be used to estimate a finite number of species for an area. From a practical perspective, non-asymptotic regression models might still prove to be useful predictors of trapping effort to secure a nominated proportion of the species within an area or even an area's species richness if a very high upper limit is set for the catch effort, as there is usually very little increase in the predicted species count for a site once the accumulation curve has 'flattened', even for non-asymptotic models.

Numerous non-linear models have been proposed for the relationship between species diversity and trapping effort (Miller & Wiegert 1989; Palmer 1990, 1991; Bunge & Fitzpatrick 1993; Soberón & Llorente 1993; Colwell & Coddington 1994; Flather 1996; DeVries *et al.* 1997; Longino & Colwell 1997; Moreno & Halffter 2000). Two issues in considering the usefulness of non-linear models are the extent to which a regression model fits the data, and the capacity of the model to predict species richness accurately. Miller and Wiegert (1989) reported for vascular plant species in the southern Appalachian region that the negative exponential function was the most 'appropriate' (best fit) model for species accumulation patterns. Palmer (1990, 1991) reported that the log-log model overestimated true species richness, and log-linear models performed better but still overestimated species richness. Choice of an appropriate non-linear model is influenced by the size of the area sampled, the heterogeneity/homogeneity of the habitat and temporal considerations (Connor & McCoy 1979; Soberón & Llorente 1993). Soberón and Llorente (1993) suggested for sampling well-known taxa in a small or homogeneous area with few rare species that the Exponential model was most appropriate. If sampling occurred in a large or heterogeneous area containing relatively unknown taxa, the Clench or logarithmic models may be more appropriate. Recently, Flather

(1996) compared eight non-linear regression models, and reported that the Weibull cumulative distribution function best fitted landscape-scale species accumulation data. Moreno and Halffter (2000) reported for bat sampling that the Linear Dependence model best predicted the 'lower limit' asymptote and that the Clench model best predicted the 'upper-limit' asymptote, with the true relationship lying between these two curves. Willott (2001) and Moreno and Halffter (2001) suggested that the number of individuals caught, not sampling effort (e.g. pit-trapping days) should be used for faunal comparison purposes.

Palmer (1990) and Hubbell (2001) argued that species accumulation curves have different forms at different scales (e.g. biotope *vs* landscape *vs* regional) and should not be used for extrapolation (although interpolation and comparison among similar sized habitats may be valid). Variations in curve shape were also due to the heterogeneity of habitats sampled and the proportion of the fauna assemblage considered 'rare'. Palmer (1990) suggested that computer-generated patterns might not mimic real patterns, a problem that can only be addressed by intensive and extensive sampling of real assemblages. There was also no obvious consensus in the literature for which model best fits field data for small reptile fauna, and which should be used to match effort with increases in the number of species caught or to predict species richness. Nor was there a consensus on how habitat heterogeneity, spatial and temporal variables, and the proportion of 'rare' species in assemblages likely to influence the choice of models to predict species diversity at a given site, or the effort required to record a proportion of the total number of species in an area.

Assessing biodiversity of reptiles can be undertaken on a biotope, landscape or regional scale. Typically, pitfall trapping regimes are used to sample small reptiles in most habitats. This is often supplemented by other trapping or search strategies, particularly to capture rare or difficult to pit-trap species, and as might be expected inadequate sampling can provide a misleading indication of diversity and species richness at a site. How much effort is required to inventory accurately or even estimate diversity of reptiles in a particular habitat is unknown.

Our purpose was to give direction to researchers who are sampling areas for small reptiles (and perhaps other small terrestrial vertebrates). Questions regularly asked include how many species are in an area, and how much effort is required to predict species richness for an area (Colwell & Coddington 1994). An appropriate species accumulation curve should provide answers to these questions. Our first objective was to determine which of the available non-linear regression models would best fit actual species accumulation data for a range of homogeneous (α diversity) and heterogeneous (γ diversity) sites in Western Australia (WA). To answer

this question we selected data sets that enabled us to test: (i) which curves best fit α and γ diversity sites (Soberón & Llorente 1993); and (ii) whether different non-linear models are better estimates of species accumulation curves when pit-trap days is substituted for number of individuals caught as a measure of effort. We chose to consider only parametric models, but are aware that non-parametric estimates of species richness are also available (Colwell 2000). These answers enabled us to examine the extent to which data from real reptile assemblages reflect theoretical models. Having identified the most appropriate non-linear regression models, our second objective was to describe the usefulness of species accumulation curves as indicators of effort required to determine different proportions of species richness for various habitat types. We then considered the relationship between the slope and shape of species accumulation curves, and diversity and rareness, because both these parameters influence curve shape (Connor & McCoy 1979; Soberón & Llorente 1993; DeVries *et al.* 1997; Lande *et al.* 2000; Thompson & Withers 2003). We examined data from seven reptile trapping studies for this investigation, because species richness in a given semi-arid region of WA is generally high for reptiles, and higher than for mammals and amphibians (Pianka 1986; McKenzie & Hall 1992).

METHODS

Study sites

We analysed reptile diversity for 33 databases, five heterogeneous sites and 28 homogenous sites. The total number of trap-days and total number of individuals caught are shown in Table 1. The location of study sites and the layout of pit-traps at Bungalbin and Ora Banda are shown in Fig. 1.

Great Victoria Desert (GVD) L area ($28^{\circ}31'S$, $122^{\circ}46'E$) is typical western Great Victoria Desert habitat: a flat, gently rolling, red sand plain, which is dominated by spinifex (*Triodia basedowii*), with large marble gum eucalypt trees (*Eucalyptus gongylocarpa*), and some scattered bushes (*Acacia aneura* and others).

Redsands ($28^{\circ}12'S$, $123^{\circ}35'E$) is also in the Great Victoria Desert of WA. It is characterized by red sand plains and long east-west sand ridges (Shephard 1995). Redsands 'flat' was the swale between the dunes, Redsands 'base' was the area at the base of sand ridges, Redsands 'slope' was the area on the slope of sand ridges and Redsands 'crest' was the top of the sand ridges. Each of these habitats was treated as a homogenous site. Lizard fauna varied significantly among these four habitats (Pianka 1986, 1996). Great Victoria

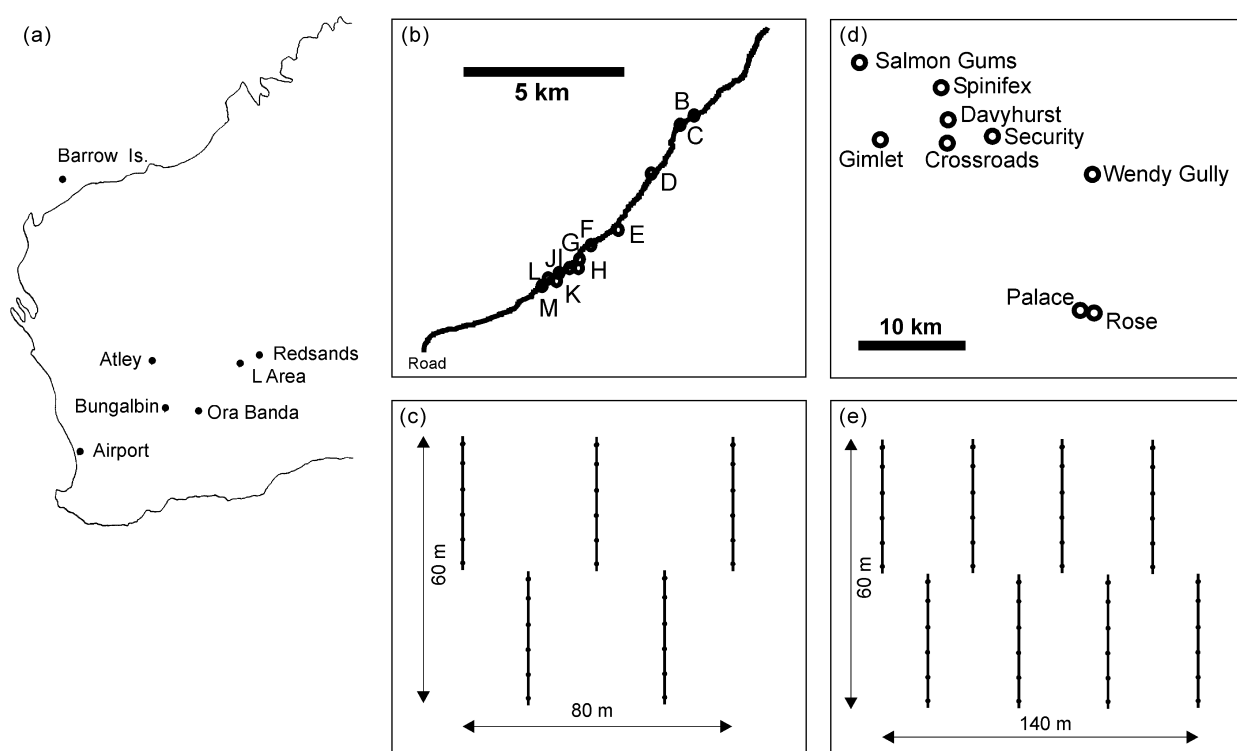


Fig. 1. Location of pit-trap sites, with inserts showing the location of the 12 sites at Bungalbin and nine sites at Ora Banda, and the layout of pit-traps. (a) Location of study sites; (b) Bungalbin sites; (c) Bungalbin pit-trap layout; (d) Ora Banda sites; (e) Ora Banda pit-trap layout.

Table 1. Total number of pit-trap days and number of caught individuals for each site, along with predicted and recorded species richness for each site

	No. pit-trap days	No. individuals caught	Measurement of effort	Predicted species richness*											Recorded species richness
				A	B	Ch	Cl	Ex	LD	P	R	W	L	H	
Heterogeneous sites															
GVD L area	6306	1652	Pit-traps	26	29	28	28	32	26	34	28	29	32	29	31
			Individuals	27	32	28	28	32	26	33	28	30	32	31	31
Redsands	25429	17080	Pit-traps	46	55	49	48	60	45	66	48	50	60	55	51
			Individuals	46	51	50	47	52	45	54	48	49	52	57	51
Ora Banda	13200	1567	Pit-traps	46	47	46	51	69	45	87	52	46	70	52	46
			Individuals	45	47	46	52	64	45	77	50	45	65	52	46
Barrow Island	2198		Individuals	23	24	24	23	30	22	33	24	23	30	29	25
Bungalbin	41400	2817	Pit-traps	43	52	46	44	51	39	61	48	45	52	50	46
			Individuals	40	57	59	38	51	35	59	44	49	51	164	41
Homogeneous sites															
Great Victoria Desert sites															
GVD B area	5325	841	Pit-traps	29	32	30	31	34	28	37	31	34	34	36	30
			Individuals	30	37	32	33	38	29	46	33	32	39	39	30
Redsands flat	2813	720	Pit-traps	34	41	38	34	42	32	46	34	39	42	46	36
			Individuals	33	40	35	36	43	33	48	36	36	43	39	36
Redsands base	9053	2288	Pit-traps	38	40	40	40	43	38	44	40	39	43	43	41
			Individuals	38	40	39	40	42	38	43	40	40	42	45	41
Redsands slope	4299	856	Pit-traps	36	41	38	38	43	34	51	38	41	44	49	36
			Individuals	37	43	42	40	45	35	55	41	41	48	70	36
Redsands crest	8274	2592	Pit-traps	47	61	60	47	50	42	63	51	49	54	269	48
			Individuals	47	56	56	47	49	43	59	50	46	53	158	48
Ora Banda sites															
Salmon Gums	1344	193	Pit-traps	22	24	23	26	32	21	52	28	20	35	33	20
			Individuals	22	24	23	27	36	21	67	28	22	40	31	20
Spinifex	1344	191	Pit-traps	34	35	34	41	48	32	83	44	30	55	50	29
			Individuals	34	35	34	43	54	32	113	45	29	63	48	29
Gimlet	1344	164	Pit-traps	34	31	32	42	40	31	91	47	25	56	51	24
			Individuals	71	86	98	67	48	45	206	103	26	94	24	24
Davyhurst	1344	192	Pit-traps	36	54	43	40	44	31	84	48	41	54	115	28
			Individuals	39	61	49	45	51	33	124	54	29	65	115	28
Security	1296	132	Pit-traps	20	33	22	26	29	20	58	25	41	35	31	18
			Individuals	19	27	23	23	28	18	71	24	30	37	35	18
Palace	1296	168	Pit-traps	21	20	20	30	34	23	70	27	19	42	22	19
			Individuals	21	22	22	25	30	20	68	26	20	38	30	19
Rose	1296	201	Pit-traps	39	27	32	63	34	48	129	58	25	76	44	20
			Individuals	29	87	87	32	28	23	87	41	26	28	20	20
Wendy Gully	1296	221	Pit-traps	24	27	26	31	34	24	69	32	28	42	38	21
			Individuals	25	64	61	28	31	22	69	33	44	28	21	21
Crossroads	1296	91	Pit-traps	58	32	38	81	15	74	120	68	32	86	60	16
			Individuals	355	167	166	48	25	34	167	54	54	68	16	16

Table 1. (continued)

	No. pit-trap days	No. individuals caught	Measurement of effort	Predicted species richness*													Recorded species richness
				A	B	Ch	Cl	Ex	LD	P	R	W	L	H			
Bungalbin sites																	
B	351		Individuals	24	30	30	23	26	21	30	25	20	27	145	24		
C	196		Individuals	29	62	49	34	38	26	92	39	49	50	123	26		
D	269		Individuals	25	37	30	27	35	23	55	31	38	38	57	25		
E	239		Individuals	23	27	25	26	35	22	53	27	28	37	33	23		
F	193		Individuals	24	38	33	26	35	21	62	28	39	38	53	23		
G	165		Individuals	23	38	23	28	39	23	80	27	24	45	27	24		
H	278		Individuals	33	85	85	36	35	27	85	45	58	49	-	25		
I	308		Individuals	115	66	66	32	28	25	66	92	-	40	-	24		
J	307		Individuals	23	38	27	26	31	21	52	28	26	35	44	23		
K	202		Individuals	23	24	23	27	38	23	58	27	24	40	27	23		
L	120		Individuals	18	33	19	22	32	18	61	22	23	35	24	19		
M	189		Individuals	27	63	63	25	32	21	63	35	33	37	21	21		
Atley	1800		Pit-traps	22	22	22	27	35	23	47	26	22	36	22	22		
Airport	7436		Pit-traps	13	14	13	12	13	12	14	13	13	13	74	12		

*Predicted species richness for all sites at 100 000 pit-trap days and 25 000 caught individuals for heterogeneous habitats, and 10 000 pit-trap days and 2500 caught individuals for homogenous habitats. A, Asymptotic model; B, Beta-P model; Ch, Chapman-Richards model; Cl, Clench model; Ex, Exponential model; LD, Linear Dependence model; P, Power model; R, Rational model; W, Weibull model; L, Logarithmic B model; H, Hill model. GVD, Great Victoria Desert; -, indicates that the model would not fit data.

Desert B area (28°13'S, 128°36'E) is approximately 4 km south of Redsands, and has a habitat that is similar to Redsands flat, except that there are no trees, very few shrubs and the swale is covered with spinifex.

Ora Banda (30°27'S, 121°4'E) is on Archaen granites or gneisses that underlie lateritic gravel soils. The vegetation is heterogeneous, ranging from eucalypt-casuarina-mulga woodlands interspersed with *Acacia*, to sparsely distributed spinifex (*Triodia* spp.) and shrubs (*Acacia* spp.), to dense shrubs (*Acacia* spp., *Atriplex* spp., *Allocasuarina* spp.). Nine study sites (Salmon Gums, Spinifex, Gimlet, Davyhurst, Security, Palace, Rose, Wendy Gully and Crossroads) are within 50 km of each other. Each was an α diverse site and collectively they form the γ diverse Ora Banda site.

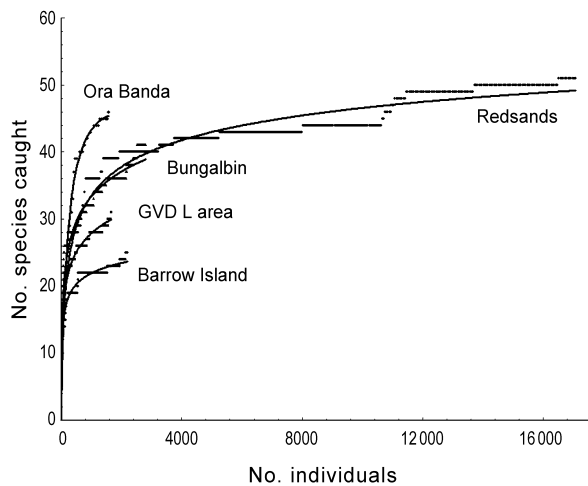


Fig. 2. Species accumulation curves for five heterogeneous sites (dots show actual data points). GVD, Great Victoria Desert.

Barrow Island (20°45'S, 115°22'E) is an extensive coastal dune swale system, located in 'John Wayne Country' on the west coast of the island. The western edge of the trapping grid abuts coastal white sand dunes, the eastern edge abuts red sand dunes, and the centre of the grid is primarily a low red earth swale. The coastal dune is well vegetated primarily with *Acacia coriaca* and occasionally spinifex (*Spinifex longifolius*), but has some open patches of beach sand. The red earth swale is mostly covered with spinifex (*Triodia angusta* and *T. wiseana*). The red sand dune is sparsely vegetated with shrubs such as *Acacia* spp. and *Olearia* spp.

Bungalbin (30°24'S, 119°38'E) is a gently undulating kwongan sand plain, which is covered with small shrubs (predominantly *Melaleuca* and *Acacia*), sedges and perennial grass clumps of spinifex (*Triodia* spp.). Twelve α diverse sites (B, C, D, E, F, G, H, I, J, K, L, M) lie within the general study site (γ diverse), and each contained five arrays of six pit-traps (30 pit-traps in total per site) that were sampled from December 1989 to April 2001 for periods of 3–20 days each spring–autumn when reptiles were active. The 12 sites were placed in different vegetation habitats within 10 km of each other (Fig. 1).

Atley (28°25'S, 119°07'E) is a relatively homogeneously vegetated habitat (α diversity) on red loamy soils that support patches of spinifex grasses (*Triodia* spp.) and small trees (*Acacia* spp., *Eucalyptus* spp.).

Airport (32°08'S, 115°57'E) is a banksia woodland (mostly *Banksia attenuata*) on the Bassendean dune system near Jandakot Airport, south of Perth, WA. Data were collected between March and May 1978 and reported in Davidge (1979). Individuals were caught

Table 2. Non-linear regression models examined as suitable to represent the species accumulation data collected at a number of heterogeneous and homogeneous habitat sites

Models	Name	Source
Two parameters		
$(a z)/(1 + (b z))$	Clench, Eadie-Hofstee	Clench (1979); Soberón and Llorente (1993), Moreno and Halffter (2000)
$a/b (1 - \exp((-b) z))$	Linear dependence*	Soberón and Llorente (1993), Moreno and Halffter (2000)
$a (1 - \exp((-b) z))$	Negative exponential*	Miller and Wiegert (1989); Flather (1996);
$a + (b \log_{10}(z))$	Exponential	Gleason (1922); Flather (1996)
$a z^b$	Power	Preston (1962); Connor and McCoy (1979)
$\log(1 + (a b z))/b$	Logarithmic B	Longino and Colwell (1997)
Three parameters		
$a - (b (c^z))$	Asymptote	Flather (1996)
$a ((1 - \exp(-b z))^c)$	Chapman-Richards	Flather (1996)
$(a + (b z))/(1 + (c z))$	Rational	Flather (1996)
$(a b z^c)/(1 + b^c)$	Hill	Withers (1992)
Four parameters		
$a (1 - (1 + (z/c)^d)^{-b})$	Beta-P	Connor and McCoy (1979); Flather (1996); Lande <i>et al.</i> (2000)
$a (1 - \exp(-(b (z - c))^d))$	Weibull	Flather (1996)

Estimated parameters are *a*, *b*, *c* and *d*; trap days (effort) or number individuals caught (return) are *z*. *These two equations provide similar outcomes, and the Linear Dependence model was used in the analyses.

in 169 pit-traps. Data are taken from Fig. 2 in Davidge (1979).

Species-accumulation curve models

We examined 12 asymptotic and logarithmic models suggested by various authors (Gleason 1922; Preston 1962; Clench 1979; Connor & McCoy 1979; Miller & Wiegert 1989; Soberón & Llorente 1993; Flather 1996; Lande *et al.* 2000; Moreno & Halffter 2000; Table 2). The Linear Dependence and Negative Exponential models provided the same r^2 ; as a consequence only the Linear Dependence model was used. Thus the analyses compared 11 alternative models. Asymptotic curves assume a finite number of trappable species in a particular area, and when sufficient effort is applied this number of species will be caught. Logarithmic and exponential models presume the number of trappable species will continue to increase; however, there is a point where yield increases very slowly with continued trapping effort. We also included the Hill model for oxygen dissociation curves (Withers 1992) for three reasons, although we could find no record of it having been used before for species accumulation curves. First, the Hill model has three variables: essentially one is for shape, one for slope and one for the asymptote; second, it has the benefit that the line of best fit passes through the origin (which must be the situation when the number of individuals caught is used as the measure of effort). Third, the Hill model can be easily transformed into a straight line, enabling a comparison of slopes.

Species accumulation curves can be calculated from two sets of data: all of the data points, or alternatively only those data points where the number of species increased. As we could find no commentary on which method was preferred, we chose to use all available data points as this generally provided the better estimate of species richness for each site for the better models (see Discussion section below).

We judged goodness of fit using adjusted r^2 , mean square error (MSE) and a visual examination of how each model fitted field data, in that order. Adjusted coefficient of multiple determination r^2 was used as it accounts for a varying number of parameters in different models, enabling us to compare performances of different non-linear models (Hair *et al.* 1995). Analyses were undertaken with NLREG (Sherrod 2001) and the non-linear estimation module in Statistica (StatSoft 1995). Initially, NLREG was used to find a solution using the ratio of sequential sum of squared residual values (Sherrod 2001). Where a solution could not be found, the non-linear estimate module in Statistica was used. In Statistica, the quasi-Newton estimation method was initially used to find a solution, but if an appropriate solution was not identi-

fied, then the simplex, simplex and quasi-Newton, Hooke-Jeeves pattern or Rosenbrock pattern searches were used. The maximum number of iterations was 1000, but the model was often re-run with new initial values to obtain a better fit. Having determined an approximate model in Statistica, the model was then run in NLREG to determine adjusted r^2 and MSE. Statistica and NLREG both graphically present observed scores and the curve that best fits the data. Statistica does not provide an adjusted r^2 value for its non-linear regression models, and where a solution could not be reached in NLREG, but could be obtained in Statistica (these programs obviously use different algorithms), adjusted (adj.) r^2 was subsequently calculated after Kenkel (1996).

For Redsands, Bungalbin and Ora Banda the actual number of species caught at a particular location and for a particular catch effort was compared with the predicted number of species for the location for a given level of effort to determine the likely accuracy of each model for estimating a location's species richness. The predicted species number for a homogenous site was compared with the total number of species in the larger heterogeneous site of which it was a part. The number of species in a homogenous site cannot exceed the number in the larger, more habitat diverse, heterogeneous site, thus enabling us to indicate that the species richness prediction for some models for some sites was too high.

We estimated asymptotes (species richness) for each regression equation at 100 000 pit-trap days and 25 000 individuals caught for heterogeneous sites, and 10 000 pit-trap days and 2500 individuals caught for homogeneous sites, for equations that do not have an asymptote. We know of only one other study (Gibbons *et al.* 1997) that has collected more than 100 000 pit-trap days or 25 000 individuals for a heterogeneous site, or 10 000 pit-trap days or 2500 individuals for a homogeneous site, so we considered these measures of effort to be reasonable upper limits of what could be achieved. We calculated the trapping effort required to obtain 50, 75 and 95% of the predicted number of species at each site for the four best-fit regression equations.

RESULTS

No species accumulation curve plateaued for our heterogeneous sites (Fig. 2), despite considerable trapping effort. For Redsands (including flat, base, slope and crest), where we had data in excess of 25 000 pit-trap days and 17 000 individuals caught, a new species was caught after 24 500 pit-trap days and 16 500 individuals. The same was true for Bungalbin where a new species was caught after 41 400 pit-trapping days. It was also evident from inspection of

Fig. 2 that species accumulation curves for Ora Banda and GVD L area were still increasing relatively rapidly, whereas the curve for Barrow Island had begun to plateau. Similarly, although we had large data sets for many homogenous sites, few of the species accumulation curves had a well-defined plateau (see homogenous sites at Redsands: Fig. 3).

Plateaus and predictions

The ability of non-linear regression models to predict species richness, and thus allow estimation of the trapping effort required to achieve a nominated percentage of the total number of species at a particular site, depends on the eventual accuracy of the plateau value. Hence the accuracy of prediction improved as a species accumulation curve approached an obvious plateau. If the species accumulation curve did not approach a plateau, then projections of species richness varied considerably between the different non-linear regression models. This can be illustrated for three sites at Bungalbin (Fig. 4). For site K, adjusted r^2 values for Beta-P, Chapman-Richards, Rational, Hill and Weibull models (the better performers) were between 0.984 and 0.986, indicating a high level of fit by models for field data. However, each model provided a slightly different estimated species richness at 2500 individuals caught (Beta-P was 24, Hill was 23, Chapman-Richards was 27, Rational and Weibull were 24; Fig. 4). For site I (Fig. 4) the species accumulation curve did not plateau, with the consequence that the five best non-linear regression models predicted a continued increase in number of species caught with further trapping effort. The extrapolation of the Rational model was not plotted, as the value was negative at

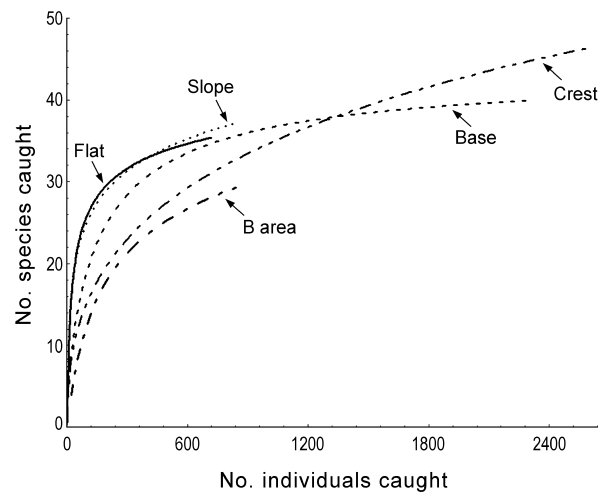


Fig. 3. Species accumulation curves for five homogenous sites in the Great Victoria Desert (GVD), drawn using the Beta-P model.

2500 individuals caught, having risen to a level above 1000 at 1150 individuals caught. Data for site G provided a further example and an exaggeration of the effect shown for site K (species richness being 38, 23, 27, 27, 24 for five models, respectively; Fig. 4). Data must be examined visually to determine the extent of plateauing in the species accumulation curve to interpret any extrapolation accurately; analysis therefore incorporates an element of subjectivity.

Goodness of fit for alternative models

The goodness of fit for the 11 models using the two alternative measures of trapping effort, number of pit-trap days (time \times number of pit-traps) and number of individuals caught (returns) were examined.

Number of pit-trap days as a measure of effort

When pit-trapping effort was used as the measure of effort, the Beta-P model provided the best overall fit for heterogeneous and homogeneous sites (adjusted

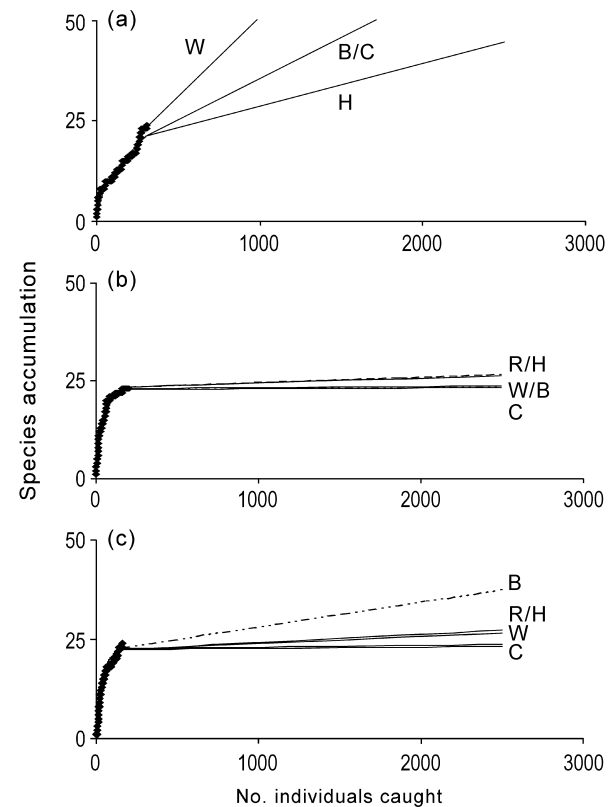


Fig. 4. Comparison of species accumulation curves for the (a) I, (b) K, and (c) G sites at Bungalbin showing the different predicted species richness values at 2500 individuals caught using the Weibull (W), Rational (R), Chapman-Richards (C), Beta-P (B) and Hill (H) models; R not shown for site I, see text for explanation.

$r^2 = 0.97$ and 0.96 , respectively; Table 3). For heterogeneous sites, the Hill, Rational, Clench, Exponential and Weibull models were the next-best models (adj. $r^2 = 0.96$ for Hill and 0.95 for the others). For homogeneous sites, the Weibull, Hill and Chapman–Richards models were the three next-best models to fit the data (both adj. $r^2 = 0.96$). For homogeneous sites at Ora Banda, nine models had a mean adjusted r^2 value greater than 0.95 (Asymptote, Beta-P, Chapman–Richards, Clench, Linear Dependence, Rational,

Weibull, Logarithmic B and Hill). For homogeneous sites at Redsands, the best model was Beta-P ($r^2 = 0.98$), closely followed by Hill, Weibull, Logarithmic B and Chapman–Richards (all adj. $r^2 = 0.97$). The lowest three MSE values concur with the highest adjusted r^2 values and support conclusions drawn above. For heterogeneous sites, the worst performing models were Power (adj. $r^2 = 0.90$), Linear Dependence (adj. $r^2 = 0.90$) and Asymptote (adj. $r^2 = 0.91$). For homogeneous sites, the worst performing models

Table 3. Adjusted r^2 values for the 11 models for heterogeneous and homogeneous habitat sites using number of pit-trap days as the metric of effort

	A	B	Ch	Cl	Ex	LD	P	R	W	L	H
Heterogeneous sites											
GVD L Area	0.871	0.964*	0.898	0.941	0.919	0.870	0.839	0.941	0.928	0.912	0.943
Redsands	0.869	0.962*	0.924	0.929	0.950	0.832	0.896	0.937	0.947	0.947	0.954
Ora Banda	0.986	0.987	0.988	0.986	0.969	0.996*	0.919	0.986	0.987	0.963	0.986
Bungalbin	0.935	0.977	0.964	0.952	0.978*	0.879	0.951	0.946	0.965	0.977	0.974
Mean	0.915	0.973*	0.944	0.952	0.954	0.894	0.901	0.953	0.957	0.950	0.964
SD	0.056	0.012	0.040	0.025	0.026	0.071	0.047	0.023	0.025	0.028	0.019
Median	0.903	0.971*	0.944	0.947	0.960	0.875	0.908	0.944	0.956	0.955	0.964
Homogeneous sites											
Great Victoria Desert sites											
GVD B area	0.956	0.972*	0.967	0.967	0.969	0.928	0.941	0.971	0.957	0.969	0.972*
Redsands flat	0.836	0.970*	0.940	0.888	0.969	0.765	0.933	0.906	0.955	0.966	0.956
Redsands base	0.964	0.990*	0.980	0.987	0.967	0.946	0.902	0.989	0.985	0.964	0.990*
Redsands slope	0.929	0.973*	0.958	0.950	0.964	0.897	0.939	0.951	0.962	0.967	0.963
Redsands crest	0.952	0.988*	0.988*	0.911	0.932	0.824	0.988*	0.963	0.981	0.973	0.988*
Mean	0.927	0.979*	0.966	0.941	0.960	0.872	0.941	0.956	0.968	0.968	0.974
SD	0.053	0.010	0.019	0.041	0.016	0.076	0.031	0.031	0.014	0.004	0.015
Median	0.952	0.973*	0.967	0.950	0.967	0.897	0.939	0.963	0.962	0.967	0.972
Ora Banda sites											
Salmon Gums	0.967*	0.960	0.963	0.957	0.940	0.952	0.947	0.962	0.970	0.957	0.959
Spinifex	0.943	0.932	0.936	0.931	0.899	0.934	0.920	0.935	0.958*	0.929	0.930
Gimlet	0.928	0.919	0.923	0.922	0.846	0.926	0.916	0.924	0.952*	0.920	0.919
Davyhurst	0.962*	0.950	0.953	0.942	0.895	0.939	0.953	0.959	0.946	0.946	0.952
Security	0.962	0.968	0.966	0.968	0.957	0.963	0.959	0.967	0.959	0.970*	0.967
Palace	0.976	0.984*	0.983	0.957	0.943	0.967	0.919	0.967	0.984*	0.946	0.981
Rose	0.952*	0.949	0.950	0.950	0.840	0.950	0.946	0.948	0.947	0.949	0.950
Wendy Gully	0.964	0.969*	0.965	0.965	0.943	0.963	0.956	0.964	0.962	0.965	0.964
Crossroads	0.963	0.962	0.964*	0.964*	0.841	0.964*	0.964*	0.963	0.960	0.964*	0.964*
Mean	0.957	0.955	0.956	0.951	0.900	0.951	0.942	0.954	0.960*	0.950	0.954
SD	0.015	0.020	0.018	0.016	0.048	0.015	0.019	0.015	0.012	0.017	0.019
Median	0.962	0.960	0.963*	0.957	0.899	0.952	0.947	0.962	0.959	0.949	0.959
Atley	0.974	0.984*	0.983	0.928	0.913	0.958	0.822	0.953	0.973	0.886	0.983
Airport	0.971	0.971	0.972*	0.900	0.954	0.804	0.972*	0.971	0.971	0.961	0.972*
All homogeneous sites											
Mean	0.950	0.965*	0.962	0.943	0.923	0.917	0.936	0.956	0.964	0.952	0.963
SD	0.033	0.020	0.018	0.027	0.046	0.063	0.038	0.020	0.012	0.023	0.019
Median	0.962	0.970*	0.964	0.950	0.941	0.942	0.943	0.962	0.961	0.962	0.964
Overall											
Mean	0.942	0.966*	0.957	0.945	0.929	0.914	0.928	0.955	0.961	0.951	0.963
SD	0.040	0.018	0.024	0.026	0.044	0.063	0.041	0.020	0.016	0.023	0.019
Median	0.959	0.969	0.963	0.950	0.943	0.936	0.938	0.960	0.960	0.962	0.963

A, Asymptotic model; B, Beta-P model; Ch, Chapman–Richards model; Cl, Clench model; Ex, Exponential model; LD, Linear Dependence model; P, Power model; R, Rational model; W, Weibull model; L, Logarithmic B model; H, Hill model. Mean, standard deviations and medians are shown for heterogeneous, homogeneous and for all sites. GVD, Great Victoria Desert. *Highest value for the site.

were the Linear Dependence (adj. $r^2 = 0.92$) and Exponential models (adj. $r^2 = 0.92$).

Some models generally over-predict, whereas others under-predict, species richness. Data for the Airport site had plateaued and most closely represent the typical shape for a species accumulation curve (Hubbell 2001), and are therefore a useful example to show the variability in the predictive ability of the various models. Figure 5 shows extrapolations from field data to 10 000 pit-trap days for all 11 models for the Airport site. The ranking (high to low) of predicted species richness for each model for the Airport site was typical of the relative prediction of species richness when the species accumulation curve had obviously begun to plateau (e.g. Power model generally predicts the highest and Linear Dependence model the lowest species richness).

For heterogeneous and homogenous sites, the Power model generally predicted much higher species richness than other models, and predicted values were often clearly above the number of species likely to be caught in these habitats irrespective of trapping effort (Table 1). Exponential and Logarithmic B models also sometimes predicted species richness above what could be expected in the area. The Hill model also generally over-predicted species richness. The Asymptotic and Linear Dependence models consistently predicted species richness values less than the known number of species for an area. An underestimation of species richness for a site generally occurred for even the better models when the rate of increase in species accumulation was relatively high toward the end of the pit-trapping effort. See, for example, Fig. 6 where two new species were captured in the last 108 individuals caught, and three new species were recorded in the last 274 individuals caught. The line of best fit from model Beta-P (which has the highest adj. r^2) probably underestimates species richness for the site.

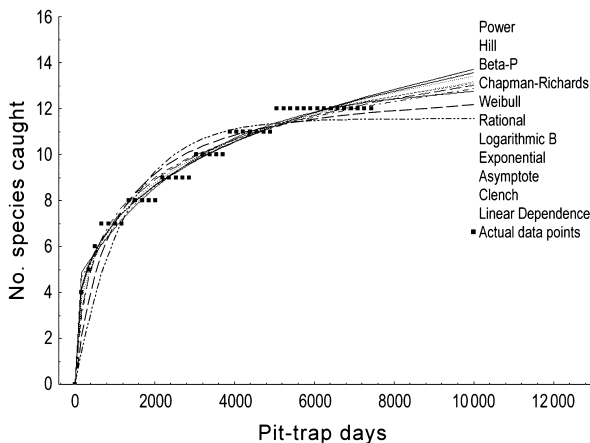


Fig. 5. Species accumulation curves for 11 models and actual data showing the different predictions for each model at 10 000 pit-trap days for the Airport site.

Number of individuals caught as the measure of effort

When number of individuals caught, rather than pit-trapping days, was used as the measure of effort, then for heterogeneous sites the Beta-P model provided the best fit (adj. $r^2 = 0.96$; Table 4). The worst performing were the Linear Dependence, Asymptotic and Clench models (adj. $r^2 = 0.75, 0.88$ and 0.89 , respectively). The lowest MSE generally corresponded with models with highest adjusted r^2 values.

For homogeneous sites, the best models were Weibull, Beta-P, Hill, Chapman-Richards and Rational models (adj. $r^2 = 0.98, 0.97, 0.97, 0.97$ and 0.97 , respectively). The worst performing models were the Exponential and the Linear Dependence (adj. $r^2 = 0.92$ and 0.93). Models with highest adjusted r^2 values generally had the lowest MSE values, although the order was not the same.

For the four homogeneous sites at Redsands, the Beta-P model provided the best fit (adj. $r^2 = 0.98$), followed by Hill, Weibull, Chapman-Richards, Logarithmic B and Rational models (adj. $r^2 = 0.98, 0.98, 0.97, 0.97$ and 0.97 , respectively; Table 4). For the nine homogeneous sites at Ora Banda, the Weibull, Rational, Asymptotic, Chapman-Richards, Beta-P and Hill models had adjusted r^2 values greater than 0.97. For the 12 homogeneous sites at Bungalbin, the Weibull, Beta-P and Chapman-Richards models had adjusted r^2 values above 0.97, and the Rational model adjusted r^2 was just below 0.97. From these data, we concluded that the Weibull, Beta-P, Hill, Chapman-Richards and Rational models were generally the better fits when the number of individuals caught was used as the measure of effort.

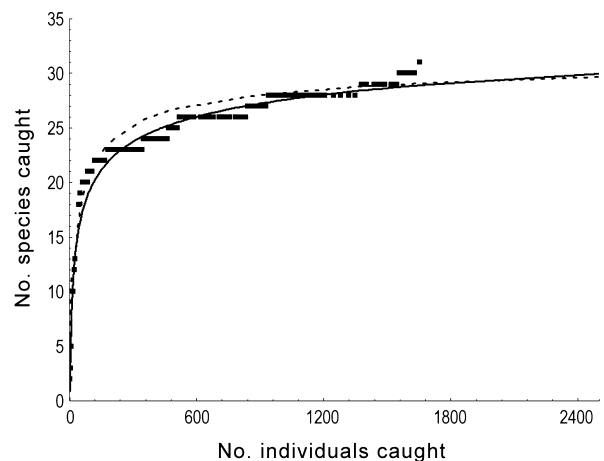


Fig. 6. Actual data and the species accumulation curve (Beta-P model) for Great Victoria Desert L area showing the increase in number of species caught late in the trapping program, and how the shape of the species accumulation curve differs depending on which data are used to calculate the curve (see text for explanation). (—), Predicted species accumulation curve based on all data points; (■), actual data points; (- - -), predicted species accumulation based on data points when a new species is caught.

Table 4. Adjusted r^2 values for the 11 models for heterogeneous and homogeneous habitat sites using number of individuals caught as the metric of effort

	A	B	Ch	Cl	Ex	LD	P	R	W	L	H
Heterogeneous sites											
GVD L Area	0.864	0.976*	0.930	0.942	0.961	0.854	0.887	0.944	0.959	0.954	0.962
Redsands	0.847	0.959*	0.926	0.904	0.953	0.798	0.912	0.921	0.931	0.953	0.952
Ora Banda	0.982	0.985*	0.985*	0.985*	0.969	0.957	0.923	0.985*	0.963	0.964	0.985*
Barrow Is	0.855	0.936*	0.915	0.826	0.927	0.587	0.898	0.892	0.897	0.926	0.928
Bungalbin	0.866	0.937*	0.934	0.799	0.937*	0.572	0.934	0.881	0.934	0.936	0.935
Mean	0.883	0.959*	0.938	0.891	0.949	0.754	0.911	0.925	0.937	0.947	0.952
SD	0.056	0.022	0.027	0.078	0.017	0.169	0.019	0.042	0.027	0.015	0.022
Median	0.864	0.959*	0.930	0.904	0.953	0.798	0.912	0.921	0.934	0.953	0.952
Homogeneous sites											
Great Victoria Desert sites											
GVD B area	0.951	0.961*	0.957	0.960	0.958	0.942	0.943	0.960	0.956	0.960	0.960
Redsands flat	0.903	0.980*	0.948	0.962	0.967	0.880	0.912	0.963	0.964	0.962	0.971
Redsands base	0.967	0.991*	0.986	0.985	0.971	0.942	0.925	0.990	0.990	0.976	0.991*
Redsands slope	0.959	0.982	0.983*	0.967	0.971	0.939	0.977	0.971	0.980	0.980	0.982
Redsands crest	0.958	0.991*	0.990	0.949	0.928	0.888	0.989	0.972	0.991*	0.985	0.991*
Mean	0.948	0.981*	0.973	0.964	0.959	0.918	0.949	0.971	0.976	0.973	0.979
SD	0.026	0.012	0.019	0.013	0.018	0.031	0.033	0.012	0.016	0.011	0.013
Median	0.958	0.982*	0.983	0.962	0.967	0.939	0.943	0.971	0.980	0.976	0.982
Ora Banda sites											
Salmon Gums	0.979*	0.977	0.979*	0.978	0.968	0.974	0.966	0.978	0.977	0.977	0.978
Spinifex	0.987*	0.984	0.985	0.983	0.961	0.984	0.973	0.984	0.997	0.981	0.982
Gimlet	0.979	0.978	0.976	0.976	0.867	0.976	0.977	0.979	0.989*	0.976	0.976
Davyhurst	0.985	0.981	0.982	0.977	0.943	0.975	0.982	0.984	0.987*	0.979	0.982
Security	0.949	0.956	0.955	0.955	0.882	0.945	0.955	0.955	0.953	0.959*	0.957
Palace	0.984*	0.981	0.983	0.980	0.917	0.978	0.970	0.982	0.982	0.980	0.981
Rose	0.977*	0.975	0.976	0.960	0.813	0.957	0.977*	0.977*	0.975	0.833	0.976
Wendy Gully	0.971	0.978	0.979*	0.962	0.915	0.952	0.980	0.973	0.977	0.843	0.979*
Crossroads	0.950	0.935	0.938	0.922	0.808	0.921	0.941	0.955*	0.954	0.924	0.938
Mean	0.973	0.972	0.973	0.966	0.897	0.962	0.969	0.974	0.977*	0.939	0.972
SD	0.014	0.016	0.016	0.019	0.059	0.020	0.014	0.012	0.015	0.060	0.015
Median	0.979*	0.978	0.979*	0.976	0.915	0.974	0.973	0.978	0.977	0.976	0.978
Bungalbin sites											
B	0.897	0.952	0.951	0.871	0.948	0.737	0.951	0.915	0.976*	0.949	0.952
C	0.990	0.995*	0.994	0.983	0.919	0.972	0.994	0.992	0.994	0.990	0.995*
D	0.969	0.979	0.979	0.952	0.952	0.915	0.976	0.973	0.980*	0.975	0.979
E	0.966	0.983*	0.979	0.972	0.972	0.939	0.966	0.977	0.981	0.983*	0.982
F	0.943	0.970	0.967	0.949	0.953	0.908	0.966	0.956	0.971	0.970	0.969
G	0.969	0.986*	0.971	0.978	0.959	0.970	0.945	0.980	0.974	0.973	0.978
H	0.983	0.984*	0.984*	0.971	0.869	0.965	0.984*	0.984*	0.983	0.976	0.984*
I	0.962*	0.926	0.927	0.859	0.773	0.841	0.927	0.967	0.965	0.880	0.927
J	0.974	0.983*	0.982	0.970	0.941	0.947	0.978	0.980	0.979	0.981	0.983*
K	0.985	0.986*	0.986	0.984	0.963	0.981	0.925	0.984	0.986*	0.966	0.984
L	0.973	0.984	0.980	0.982	0.973	0.969	0.956	0.982	0.981	0.991*	0.983
M	0.945	0.958	0.959	0.904	0.904	0.863	0.960	0.947	0.949	0.938	0.959*
Mean	0.963	0.974	0.972	0.948	0.927	0.917	0.961	0.970	0.977*	0.964	0.973
SD	0.025	0.019	0.019	0.045	0.057	0.072	0.021	0.021	0.011	0.031	0.019
Median	0.969	0.983*	0.979	0.970	0.950	0.943	0.963	0.978	0.979	0.974	0.980
All homogenous sites											
Mean	0.964	0.974	0.972	0.957	0.923	0.933	0.961	0.971	0.977*	0.957	0.974
SD	0.023	0.017	0.017	0.033	0.056	0.055	0.022	0.016	0.013	0.042	0.016
Median	0.969	0.980*	0.979	0.968	0.945	0.946	0.966	0.977	0.979	0.975	0.979
Overall											
Mean	0.951	0.972*	0.967	0.947	0.927	0.904	0.953	0.964	0.970	0.955	0.970
SD	0.042	0.018	0.022	0.048	0.052	0.104	0.028	0.028	0.021	0.039	0.019
Median	0.967	0.979*	0.979*	0.962	0.948	0.942	0.960	0.973	0.977	0.970	0.978

A, Asymptotic model; B, Beta-P model; Ch, Chapman–Richards model; Cl, Clench model; Ex, Exponential model; LD, Linear Dependence model; P, Power model; R, Rational model; W, Weibull model; L, Logarithmic B model; H, Hill model. Mean, standard deviations and medians are shown for heterogeneous, homogeneous and for all sites. GVD, Great Victoria Desert. *Highest value for the site.

Shape of accumulation curves

Species accumulation curves for five heterogeneous sites indicated a rapid increase in initial number of species caught (Fig. 2). The species accumulation curves had almost plateaued for Redsands and most probably had plateaued for Barrow Island. The shape of species accumulation curves for Redsands and Bungalbin, when plotted using the Beta-P model with number of individuals caught as the measure of effort, and up to 40 species caught are similar. However, the slightly higher 'shoulder' and earlier plateauing of the Redsands species accumulation curve compared with Bungalbin suggests that species richness at Bungalbin will exceed that of Redsands with additional trapping effort (Fig. 2).

The shape of species accumulation curves for homogeneous sites in the Great Victoria Desert are different when plotted using the Beta-P model (Fig. 3). The same was true for the nine homogeneous sites at Ora Banda. We normalized species accumulation (*y* axis) to 100% at 225 individuals caught for the nine homogeneous sites at Ora Banda using the Weibull model (the better performer) to display variation in shape of species accumulation curves (Fig. 7) and examined the relationship between aspects of curve shape and species diversity and rareness. We selected Ora Banda sites, as the trapping effort for all nine sites was identical, eliminating any effects of variation in trapping effort. The Simpson (1949) and Shannon–Weaver diversity (Shannon & Weaver 1963) indices were calculated for each of the nine homogeneous sites (Salmon Gums 0.64, 2.53; Spinifex 0.92, 4.10; Gimlet 0.92, 4.01; Davyhurst 0.92, 4.14; Security 0.87, 3.41; Palace 0.89, 3.63; Rose 0.89, 3.57; Wendy Gully 0.83, 3.24; Crossroads 0.85, 3.25, with Shannon–Weaver index (the second value) calculated to \log_2).

In the Weibull equation:

$$\text{species accumulation} = a(1 - \exp(-(b(z - c))^d)),$$

where z is trapping effort, a is the asymptote, c is the intercept on the x -axis, and values for b and d reflect the curve's shape. Values for b indicate the rate of increase in species accumulation. A high b indicates a more rapid initial increase in number of new species caught (Brown & Mayer 1988). For any value of b , the value of d modifies the shape of the curve. Values for b and d were not significantly correlated with Simpson's diversity index ($r = -0.33$ and 0.47 , respectively) for the nine homogeneous sites at Ora Banda. However, the Shannon–Weaver index was significantly correlated with d ($r = 0.72$, $P < 0.05$) but not with b ($r = -0.27$).

To test if the shape component (d) of the species accumulation curve was related to species evenness (or rarity; James & Rathbun 1981; Brewer & Williamson 1994), we correlated d with an index of evenness. Evenness, which is the inverse of rarity, is calculated as

$H'/\log_2 S$, where H' is the Shannon–Weaver species diversity index and S is species richness (Tramer 1969). There was no significant correlation between the index of evenness and shape of species accumulation curves (d) in the Weibull equation ($r = 0.42$, $P = 0.58$). To test if the slope component of the species accumulation curve was related to evenness, we correlated both b and the initial slope of the Weibull curve with the measure of evenness. The correlation between the slope b and the evenness index was not significant ($r = -0.20$, $P = 0.61$). Lande *et al.* (2000) argued that the initial slope of species accumulation curves is related to Simpson's diversity index but not species richness. To measure the slope of the initial part of the accumulation curve, we used data for the first five pit-trapping days and the number of individuals caught as the measure of effort for all homogeneous sites at Ora Banda. There was no significant correlation between the initial slope of the curve and the evenness index ($r = 0.07$, $P = 0.57$) but there was a significant relationship with species richness for the Ora Banda sites ($r = 0.68$, $P < 0.05$). There was also no significant correlation between Simpson's diversity index and the initial slope of the nine species accumulation curves ($r = 0.1$, $P = 0.79$), or Shannon–Weaver diversity index and the initial slope ($r = 0.35$, $P = 0.36$).

Species richness was significantly positively correlated with Shannon–Weaver diversity index ($r = 0.71$, $P < 0.05$), the shape of the curve (d ; $r = 0.82$, $P < 0.01$) but not the evenness index ($r = 0.30$, $P = 0.43$) for the nine Ora Banda sites.

Trapping effort

Two measures of trapping effort were analysed: pit-trap days (effort) and number of individuals caught

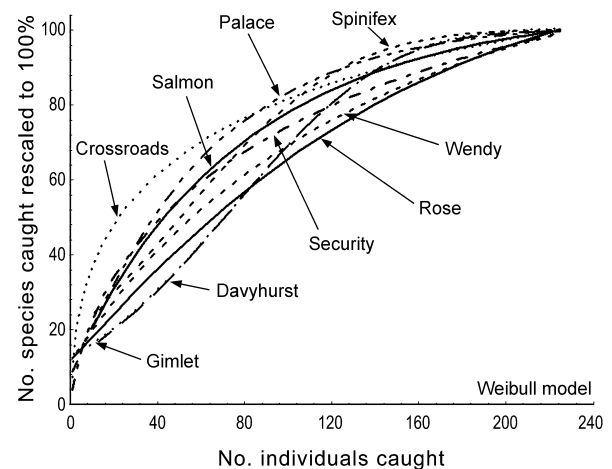


Fig. 7. Species accumulation curves normalized to 100% showing variations in curve shape (Weibull model) for the nine homogeneous sites at Ora Banda.

(returns). The pit-trapping required to catch a nominated percentage of the total predicted number of species at a site was similar for the two alternative measures of trapping effort (Table 5). Trapping effort required to capture a nominated percentage of the predicted total number of species was generally higher for heterogeneous sites than for homogeneous sites (Table 5). This was most probably the effect of increased species richness (and the area sampled) at heterogeneous sites (MacArthur 1965), or may indicate a higher propensity for 'rare' species to be found in heterogeneous (larger area) sites (see Hubbell 2001).

The effort required to catch a nominated percentage of the total predicted number of species in a γ diversity habitat varied considerably among sites (Table 5). For GVD L area and Barrow Island, the effort required to catch a nominated percentage of the total number of predicted species was less (e.g. a catch effort of approximately 3000 pit-trap days and 1200 individuals caught, respectively, for 95% of species at GVD L area) than for the more habitat diverse sites (e.g. Bungalbin and Ora Banda), which required a much higher trapping effort to secure a nominated percentage of the total species. For Ora Banda, the trapping effort to capture 95% of species was approximately 12 300 pit-trap days or 1370 individuals. For Bungalbin, trapping effort to capture 95% of species was approximately 55 000 pit-trap days or 12 200 individuals, using the trapping protocols described above.

Species richness can vary considerably for different sites within the larger heterogeneous area. For sites in the Great Victoria Desert, sand ridge crests generally had a higher species richness than the adjacent swales or slopes (e.g. for Redsands, crests = 48 species,

flats = 36 species, ridge bases = 41 species and ridge slopes = 36 species). Sand ridge crests required a greater trapping effort to catch 95% of species (14 850 pit-trap days or 4000 individuals caught) than at the other sites with lower species richness.

Effort required to catch a nominated percentage of species at homogeneous habitat sites at Ora Banda and Bungalbin varied considerably (Table 1). The layout of pit-traps and drift fences among Bungalbin sites and among Ora Banda sites were essentially identical, thus controlling for spatial effects (Hubbell 2001). Species richness values for these homogeneous sites in these two areas were similar (Table 1), but the shape of the curve (less steep *vs* flatter; Fig. 2) indicates there are more relatively rare or difficult to trap species at Bungalbin, which means that a greater effort must be applied to catch a nominated percentage of the total number of species at that site.

An examination of the species accumulation curve for Bungalbin (Fig. 8) indicated that the rapid increase in species captured changed (inflection point) to a much more gradual rate of increase at about 3770 pit-trap days. There was no obvious plateauing of the species accumulation curve up to 36 600 pit-trap days of effort.

General issues

If the general shape of a species accumulation curve does not display the characteristic shape of a 'typical' curve (e.g. Figures 5 and 6; a steep initial increase in the number of new species recorded, with a gradual plateauing of the curve as fewer new species are recorded with increased catch effort), then models that generally fit the 'typical' species accumulation curve well (e.g. Beta-P, Chapman-Richards, Weibull and Rational models) generally overestimate species richness. When the shape of the curve is 'atypical' (e.g. Bungalbin, Fig. 8), it may be impossible to find a model that accurately represents the data and predicts species richness.

There were insufficient data for some sites to be able to predict species richness using some models (e.g. a solution for the Weibull model for data from site I and for the Rational model at Crossroads could not be determined). Another problem sometimes encountered was that the Weibull and Beta-P models sometimes provided two alternative solutions with very similar adjusted r^2 values, when different starting points were used for the four parameters. The Weibull model was often not able to provide a solution for a data set in the NLREG software package, and sometimes a solution generated in NLREG for the Chapman-Richards model could not be graphically represented in Statistica.

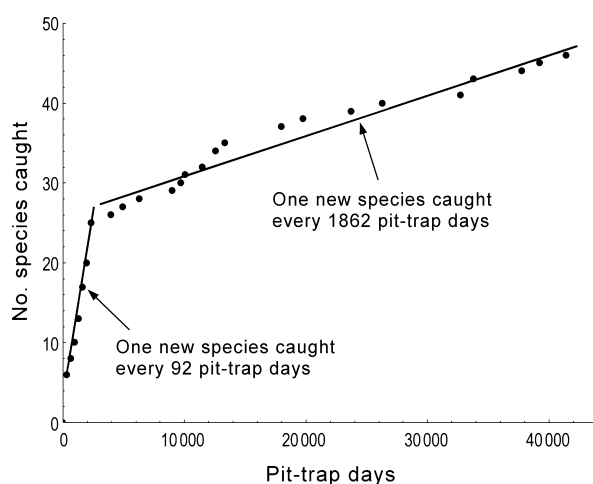


Fig. 8. Actual data for the heterogeneous Bungalbin site showing the change in the rate of species caught at about 3770 pit-trap days (see text for explanation).

Table 5. Required amount of pit-trapping to catch 50, 75 and 95% of the predicted species richness for heterogeneous and homogeneous sites using two alternative measures, effort (pit-trap days) and return (number of caught individuals)

	Pit-trap days			Individuals caught		
	50%	75%	95%	50%	75%	95%
Heterogeneous sites						
GVD L area						
Beta-P	152	618	4448	50	355	1692
Chapman–Richards	166	613	2044	43	190	711
Rational	157	446	2254	41	125	637
Weibull	154	624	3062	43	235	1623
Redsands						
Beta-P	737	5220	47280	268	2139	14446
Chapman–Richards	304	2231	11215	295	2154	10448
Rational	667	2196	12880	360	1229	6464
Weibull	587	2943	17704	330	1836	10095
Ora Banda						
Beta-P	1344	3391	9488	150	398	1179
Chapman–Richards	1335	3327	8465	147	382	1004
Rational	1562	4616	23561	170	510	2568
Weibull	1351	3443	7696	154	377	716
Bungalbin						
Beta-P	5570	20950	75350	434	4236	17872
Chapman–Richards	4200	13160	38660	558	5158	18870
Rational	4410	15000	40800	124	956	6042
Weibull	3790	11140	38700	284	1471	6067
Barrow Island						
Beta-P				28	200	1421
Chapman–Richards				22	232	1410
Rational				33	230	1697
Weibull				79	223	824
Homogeneous sites						
Redsands flat						
Beta-P	90	843	5960	38	207	1358
Chapman–Richards	79	606	3090	31	118	398
Rational	68	246	1470	36	107	559
Weibull	89	724	4931	31	120	470
Redsands base						
Beta-P	368	1184	5085	113	374	1409
Chapman–Richards	367	1101	3186	116	368	1091
Rational	389	1122	4491	121	352	1288
Weibull	306	1175	4730	113	371	1273
Redsands slope						
Beta-P	485	1836	5329	55	376	1699
Chapman–Richards	473	1453	4236	142	445	1280
Rational	466	1329	4969	138	392	1360
Weibull	513	1714	7572	133	406	1396
Redsands crest						
Beta-P	1724	6938	16463	518	1820	4138
Chapman–Richards	1727	6820	16277	545	1867	4135
Rational	1108	3578	11963	393	1151	3356
Weibull	1306	5056	14693	514	1779	4096
GVD B area						
Beta-P	640	2126	6960	212	679	1895
Chapman–Richards	572	1637	4536	159	403	1034
Rational	607	1722	5746	175	472	1500
Weibull	758	2791	7710	164	421	1154
Salmon Gums						
Beta-P	331	831	2293	53	125	328
Chapman–Richards	306	731	1800	50	113	272
Rational	443	1293	4902	72	209	923
Weibull	277	541	860	48	106	246

Table 5. (continued)

	Pit-trap days			Individuals caught		
	50%	75%	95%	50%	75%	95%
Spinifex						
Beta-P	360	902	2035	61	131	311
Chapman-Richards	350	782	1838	60	128	293
Rational	554	1564	5446	99	282	1119
Weibull	308	554	924	51	90	145
Gimlet						
Beta-P	516	1038	2260	375	812	1455
Chapman-Richards	544	1124	2493	437	922	1859
Rational	1042	2644	6973	436	1023	2037
Weibull	406	691	1076	67	109	160
Davyhurst						
Beta-P	1082	2972	7305	219	582	1553
Chapman-Richards	682	1715	4362	140	336	834
Rational	846	2505	6594	172	471	1500
Weibull	608	1561	4366	62	112	190
Security						
Beta-P	993	3192	7964	67	194	630
Chapman-Richards	472	1057	2489	51	132	345
Rational	565	1518	5305	53	154	743
Weibull	1539	3929	8150	91	285	979
Palace						
Beta-P	325	538	915	45	108	287
Chapman-Richards	342	566	1047	42	96	232
Rational	512	1319	4841	61	178	825
Weibull	33	526	857	39	81	175
Rose						
Beta-P	675	1153	2091	737	1505	2283
Chapman-Richards	752	1448	2888	736	1503	2282
Rational	1916	3998	7390	1173	2117	3213
Weibull	614	974	1772	86	174	356
Wendy Gully						
Beta-P	501	1128	2780	541	1284	2212
Chapman-Richards	442	1026	2374	493	1204	2169
Rational	661	1768	5760	135	383	1348
Weibull	530	1251	3304	271	794	1925
Crossroads						
Beta-P	1242	2251	4357	960	1689	2229
Chapman-Richards	1541	2908	5866	961	1680	2327
Rational	3088	5718	8940	–	–	–
Weibull	1253	2285	4455	152	233	359
Site B						
Beta-P				136	713	1988
Chapman-Richards				162	803	2044
Rational				41	166	844
Weibull				14	54	250
Site C						
Beta-P				310	877	1987
Chapman-Richards				190	508	1325
Rational				111	320	1219
Weibull				184	532	1514
Site D						
Beta-P				113	433	1529
Chapman-Richards				67	218	665
Rational				67	214	958
Weibull				126	499	1655
Site E						
Beta-P				43	137	499
Chapman-Richards				36	105	295
Rational				42	130	659
Weibull				47	159	621

Table 5. (continued)

	Pit-trap days			Individuals caught		
	50%	75%	95%	50%	75%	95%
Site F						
Beta-P				112	425	1500
Chapman–Richards				80	261	796
Rational				47	148	728
Weibull				126	489	1645
Site G						
Beta-P				85	415	1709
Chapman–Richards				32	68	156
Rational				40	112	565
Weibull				33	77	197
Site H						
Beta-P				733	1508	2296
Chapman–Richards				727	1496	2279
Rational				226	597	1729
Weibull				400	1008	2103
Site I						
Beta-P				–	–	–
Chapman–Richards				–	–	–
Rational				–	–	–
Weibull				–	–	–
Site J						
Beta-P				197	736	1939
Chapman–Richards				86	249	702
Rational				1145	2069	3065
Weibull				70	198	638
Site K						
Beta-P				25	58	144
Chapman–Richards				25	56	133
Rational				31	90	477
Weibull				25	59	151
Site L						
Beta-P				79	445	1778
Chapman–Richards				19	48	120
Rational				24	72	397
Weibull				28	88	320
Site M						
Beta-P				464	1243	2209
Chapman–Richards				465	1243	2208
Rational				114	350	1301
Weibull				95	273	825
Atley						
Beta-P	279	445	867			
Chapman–Richards	276	444	796			
Rational	308	770	3323			
Weibull	284	441	790			
Airport						
Beta-P	848	3519	8260			
Chapman–Richards	853	4185	8106			
Rational	864	3059	7608			
Weibull	807	3029	7843			

GVD, Great Victoria Desert.

Non-linear regression models that asymptote (and use least MSE scores as the criterion for determining the ‘best-fit’ solution) will often place the asymptote below the total number of species caught if new species are caught toward the end of the catching period

(Fig. 6), and are therefore not good predictors of species richness.

Models with two parameters have less flexibility in defining the shape of the curve than do models with three or four parameters. As a consequence,

models with three or four parameters generally were better at fitting actual data sets and had higher r^2 values.

DISCUSSION

We began this study believing that we had sufficient data for at least some of these study sites to develop reasonably accurate species accumulation curves. For example, the Bungalbin and Redsands sites had considerably more trapping effort than had been undertaken for most large landscape-scale surveys of small vertebrate fauna in Australia (Morton & James 1988; McKenzie *et al.* 1989; 2000; McKenzie & Hall 1992; Hobbs *et al.* 1994; Masters 1996; Read 1998; 1999; Read & Owens 1999; Paltridge & Southgate 2001). So, one of the surprising and significant findings of this investigation was the very high trapping effort that was required to estimate species richness accurately for both heterogeneous and homogeneous habitats. A surprising and disappointing finding was that sufficient species need to have been captured, so that the species accumulation curve had passed the inflection point and commenced to plateau, before species richness could be estimated with confidence. However, as the number of species captured approached the total number of species at the site, the value of species accumulation curves to predict species richness decreased.

A high proportion of rare or 'transient' species at a site can result in a significant underestimate of species richness using species accumulation curves. For example, after 12 000 and 14 000 pit-trap days for the heterogeneous Redsands site (Fig. 9; Table 6) species richness was predicted to be 44, but additional trapping recorded an unexpected increase

in the number of new species between 14 000 and 16 000 pit-trap days; the consequence was that species richness predictions increased appreciably. The GVD L area (Fig. 6) was another good example: the species accumulation began to plateau at approximately 600–800 individuals caught, providing an early indication of a plateau with the total number of species in the high 20s. However, with further pit-trapping more (rarer) species were caught, and this increased the estimate of species richness. This progressive increase in the number of species caught could also be an effect of time (Rosenzweig 1995; discussed later).

Atypical shaped species accumulation curves

The species accumulation curve for Bungalbin was atypical (Fig. 8). There was a near-linear relationship between pit-trapping effort and number of new species caught after the first 25 species were caught, and no plateau was apparent (Fig. 8). Between zero and 2310 pit-trapping days, the number of new species caught increased at the rate of one per 92 pit-trapping days, then after this point of discontinuity a new species was caught every 1862 pit-trapping days. The shape of the species accumulation curve for Redsands (Fig. 9) was similar to that for Bungalbin, with approximately one new species being caught every 57 pit-trap days up to 2230 pit-trap days, after which the rate of increase in new species being caught decreased to one every 1933

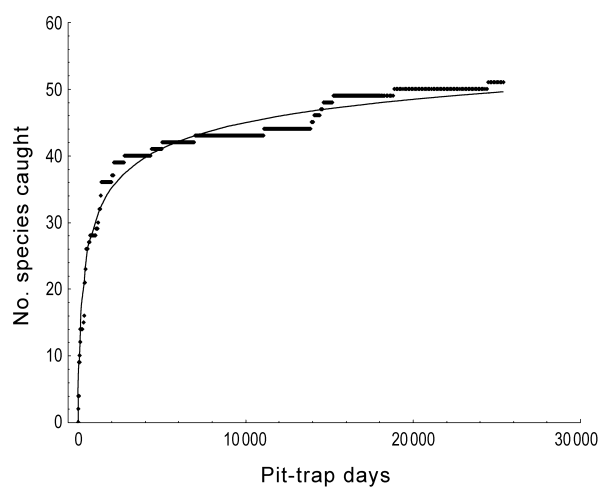


Fig. 9. (●) Actual data and (—) species accumulation curve (Beta-P model) for heterogeneous Redsands site with predicted species richness values (Table 6) based on different trapping efforts.

Table 6. Changes in predicted species richness at Redsands for 100 000 pit-trap days (Fig. 9) for different levels of trapping effort.

Pit-trap days	Predicted number of species at 100 000 pit-trap days
25 000	55
22 500	54
20 000	52
19 000	52
18 000	51
17 000	49
16 000	48
15 000	46
14 000	44
13 000	44
12 000	44
11 000	43
10 000	43
9000	43
8000	43
7000	42
6000	42
5000	42
4000	42
3000	45
2000	59
1000	37

pit-trap days until the end of the trapping program. Variation in the relative abundance of species and a time effect were the primary reasons for the change in the rate of new species being caught at Bungalbin. Relatively common (or more abundant) species were caught in the initial survey period (rapidly rising slope of the species accumulation curve) and the less common species in latter flatter part of the curve (Thompson & Withers 2003). The first 25 species caught, and represented in the rapidly rising initial stage of the curve, generally had a relative abundance greater than 0.5% (i.e. number of individuals per species caught/total number of individuals caught presented as a percentage; Fig. 10). Because they were more common, they had a higher propensity to be caught and were generally caught early in the trapping effort. The more difficult to catch (rarer, range-restricted or difficult to pit-trap) species required considerably more trapping effort, thus the change from one new species for every 92 pit-trap days in the early part of the trapping to one new species for every 1862 pit-trapping days at Bungalbin. This progressive increase in the number of new species caught was probably also a result of combining two curves: a species accumulation curve and a species–time curve. Preston (1960) and Rosenzweig (1995) demonstrated that species richness for an area generally increased with time. Rosenzweig (1995) suggested the increase in species richness with time was linear for a semilogarithmic plot, which would account for the near-linear increase after the inflection point for the species accumulation curve for Bungalbin (Fig. 8). The effect of time might also be a contributing factor in the progressive increase of species at Redsands. The combining of a species accumulation curve and a species time curve into a single curve can obscure the estimate of species richness for a site at a particular time.

Rareness and evenness

Rare species have a low propensity for being caught, and sites with high species evenness had a high proportion of species with a similar propensity for being caught. There is considerable discussion in the literature on the importance of rareness in understanding community assemblages. Main (1982) suggested that both biological and social issues must be considered. In the biological context, rareness can be defined as species that are: (i) broad ranging but generally sparsely distributed; (ii) locally dense but with a very restricted range; and (iii) locally sparse with a very restricted range. In a pit-trapping program, three additional categories of rareness can be identified: (iv) when the sampling area is on the boundary of the distribution of a common species so only occasional specimens are caught; (v) when ‘transient’ individuals pass through an area that is not typical of their habitat; and (vi) when species are difficult to pit-trap. Rare, in the context of influencing a species accumulation curve, is any of these, that is, when capture frequencies are low. Depending on the survey purpose, some field surveys incorporate additional search strategies to ensure they catch ‘difficult to pit-trap species’. Some of these strategies are difficult to quantify, and surveyor experience can influence results. The inclusion of data from different search strategies will probably change the shape of species accumulation curves and therefore make it difficult to compare data collected using different search strategies.

There is little commentary on the importance of recording rare species when undertaking survey work that leads to the preparation of an EIA in any of these biological contexts. If rare species are considered important, then it behoves an investigator to apply sufficient sampling effort to predict with reasonable

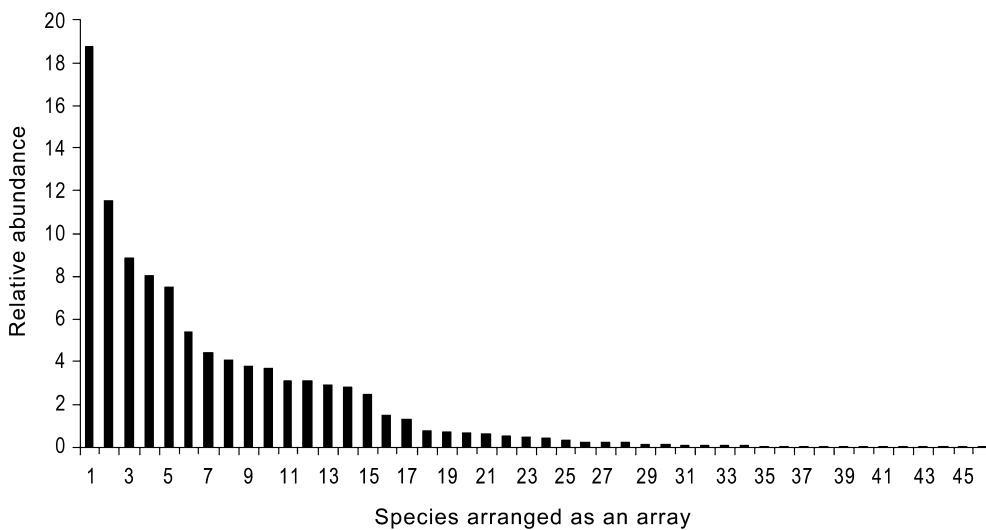


Fig. 10. Relative abundance of species caught at Bungalbin. Relative abundance is calculated as number of individuals/total number of individuals × 100.

accuracy the total number of species in an area and to have identified most, if not all of these species, including rare ones. If this is the case, then sufficient field trapping effort needs to be applied to develop the species accumulation curve past the point of inflection such that it is obviously progressing toward a horizontal plateau (asymptote) to accurately estimate species richness. The proportion of species that are rare at a site affects the species accumulation curve in two ways. Sites with a high proportion of rare species will have species accumulation curves that begin to plateau early, but the slope of the latter part of the curve will be steeper than at sites that have a more even distribution of relatively abundant species (Thompson & Withers 2003). Greater trapping effort is required at sites with a high proportion of rare species compared with sites with a more even distribution of species, to achieve a plateauing of the species accumulation curve. Bungalbin is an example of this, where there was no evidence that the curve was about to flatten even after 40 000 pit-trap days (Fig. 8). As a consequence, a greater trapping effort is required at sites with a high proportion of rare species before the species accumulation curve can be used to predict species richness.

Trapping effort for fauna surveys

Where accurate estimates of biodiversity or species richness are required for an EIA or a comparison of community assemblages among different sites (habitats), species accumulation curves provide a useful tool to indicate required trapping effort and a complete species list. Trapping effort required for estimating species richness is generally much higher than the effort currently employed to survey the terrestrial fauna for an area. For example, McKenzie *et al.* (2000) surveyed the herpetofauna of the Carnarvon Basin, an area of 75 000 km² on the central west coast of Western Australia. Reptiles and frogs were caught with pit-traps and hand foraging at 13 relatively homogeneous sites that were considered 'typical' of the habitats in the area during spring–autumn (13 164 pitfall trap nights). These researchers subsequently undertook a comprehensive comparative analysis of assemblages among these 13 sites based on presence–absence of species. Species accumulation curves for many of these homogenous sites had not reached a plateau. Although they did not use species accumulation curves to estimate species richness, it is evident (as they acknowledge) that they had collected insufficient data to estimate species richness, the basis for much of their analyses.

Because slopes of species accumulation curves varied considerably between habitats, particularly for homogeneous sites, it is not possible to provide a 'general rule-of-thumb' as to how much effort is required to catch a

nominated percentage of the total number of species for an area. Heterogeneous sites with relatively low species richness (e.g. 25–31 species) require comparatively less trapping to obtain 75% of the predicted total number of species than those sites with a larger number of species. This is probably because species-rich sites generally have more 'rare' species (Hubbell 2001). Species richness, and its link with rareness, therefore has an important influence on the effort required to capture a nominated proportion of the predicted species at a site.

Based on our analysis of the various databases, we concur with Lande *et al.* (2000) that actual species richness cannot be accurately extrapolated by any method using small samples that contain only a minority of species in a community. This has serious implications for field surveys used to prepare an EIA. If knowledge of diversity is important, then rapid surveys with small samples are inadequate to estimate species richness. We acknowledge that diversity is only one consideration in preparation of an EIA; other important issues include habitat integrity, maintenance of viable populations of focal species, and overall ecosystem function. Determining the amount of effort required to assess diversity at a particular site is a two-stage process: (i) an initial sampling of the area sufficient to construct a species accumulation curve that is past the point of inflection and is gradually increasing toward the asymptote; and (ii) using this species accumulation curve projected to the asymptote, to determine the additional effort (*x*-axis) required to catch a nominated percentage of predicted species at the site.

For five heterogeneous sites examined, sufficient data to estimate species richness were available for Redsands where a plateau was evident (Fig. 2), and there were almost enough field data for Barrow Island as a plateau was commencing. However, there were not sufficient data for Bungalbin, Ora Banda, and for GVD L area to predict species richness accurately. Two examples illustrate this point and its consequences. Although predicted species richness for GVD L area using all four models (Beta-P, Chapman–Richards, Rational and Weibull) suggested that 95% of the predicted total number species in the area would be caught with between 637 and 1700 individuals caught (Table 5), an inspection of the fit of these models with field data indicated that these models did not cope well with an increase of three new species within the last 274 individuals caught (Fig. 6). The 'curved line of best fit' (Beta-P) did not adequately fit the increase in number of species caught in the latter part of the trapping effort. A predicted lower-than-actual species richness value will invariably also underestimate the trapping required to capture a nominated percentage of species in an area. The GVD L area is an excellent example of the importance of visually inspecting data to interpret

its meaning. The second example was the predicted effort required to capture a nominated percentage of species in three heterogeneous areas: Redsands, Ora Banda and Bungalbin. Based on the predicted species richness for each of the areas to catch 50, 75 and 95% of species, the following numbers of individuals need to be caught (based on the means of the four best models): Redsands, 313, 1840 and 10 363; Ora Banda, 155, 417 and 1367; and Bungalbin, 350, 2955 and 12 213. Effort to catch a nominated percentage of species for Bungalbin and Redsands were reasonably similar, compared with Ora Banda where the effort was appreciably less. Western Australian Museum records and biological survey data available for the areas around Bungalbin and Ora Banda (Dell *et al.* 1985, 1988; McKenzie & Hall 1992) indicate similar species richness for the areas: approximately 52 lizards and 10 snakes at each site. Variation in predicted effort appears to be a function of two important variables: insufficient data to consolidate the plateau in the species accumulation curves (thereby improving the accuracy of the predicted species richness for these sites) and the proportional abundance of various species at each of the sites (Thompson & Withers 2003). It is also influenced by when the trapping was undertaken. Trapping reptiles in periods when species are inactive (e.g. winter), or less active (e.g. autumn) than during the warmer summer months results in lower captures per pit-trap day; this may not affect the shape of the curve if the number of individuals caught is used as the measure of effort. If most species at a site are abundant, they will be caught with little trapping effort, whereas if a high proportion of species are rare, difficult to pit-trap or transient (i.e. reptiles that are caught out of their normal habitat and are possibly just passing through) then the catch effort required will be much higher. In contrast, data for Atley and the Airport sites had clearly plateaued, indicating that for homogeneous habitats with low species richness (21 for Atley (Pianka 1986 found 28 species nearby) and 12 for Airport) the median pit-trap days for 50, 75 and 95% are 281, 444 and 831 (from Beta-P, Rational and Weibull models) for Atley and 850, 3289 and 7974 for the Airport site; the difference in effort between these two sites presumably reflects the proportion of rare species at each site.

Common species will be caught early in sampling, as part of the steep initial incline in the species accumulation curve. Conversely, the propensity to catch a rare species is low and a greater catch effort will be required before a representative for each rare species is caught, and these species are more likely to be represented in the 'tail' of the species accumulation curve (Thompson & Withers 2003). The initial slope of the species accumulation curve is not, however, influenced by the proportion of rare species (Ora Banda nine sites, $r = 0.07$, $P = 0.57$), but this will influence the slope of

the curve after the inflection point. Species accumulation curves that have a steep initial increase followed by a near horizontal 'tail' after the inflection point have a high proportion of common species, few rare species and a relatively high Shannon–Weaver diversity index (the correlation between the Shannon–Weaver index of diversity and the shape of the curve d was significant ($r = 0.72$, $P < 0.05$) for the nine Ora Banda homogeneous sites), indicating that at least one measure of diversity is associated with the shape of the species accumulation curve. Simpson's index gives relatively little weight to rare species and more weight to common species (Krebs 1985), and thus might be expected to not be correlated with the shape of the curve, which is influenced by the number of rare species. In contrast, the Shannon–Weaver index is influenced by both species richness and evenness (Krebs 1985). A species accumulation curve that is less steep should indicate that the abundance of available species varies on more of a continuum, from very common to very rare. Lande *et al.* (2000) reported that an intersection of two species accumulation curves is expected when the community with the lower actual species richness has the higher Simpson's diversity score. For example, intersecting species accumulation curves for Bungalbin sites B and E (Fig. 11) showed that the curve for site E had a flatter slope and a higher species richness with Simpson's and Shannon–Weaver diversity indices of 0.88 and 3.61, respectively, and an evenness index (\mathcal{J}) of 0.80. In comparison, site B has a steeper curve, indicating more abundant species than site B, but lower species richness, diversity (Simpson's and Shannon–Weaver diversity indexes of 0.85 and 3.46, respectively) and fewer rare species (i.e. evenness index of 0.76) than site E. Species accumulation curves are therefore influenced by species richness, rarity and diversity (also see Thompson & Withers 2003).

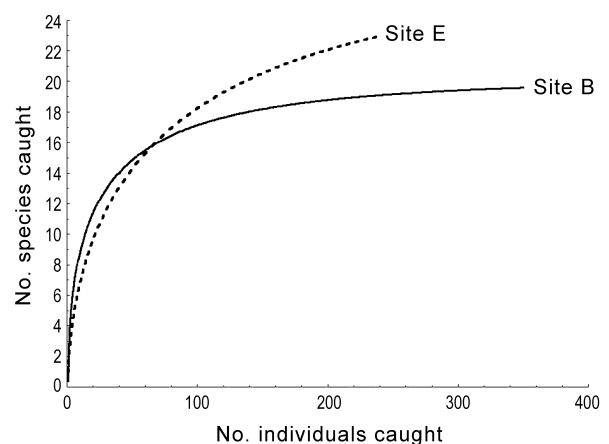


Fig. 11 Species accumulation curves (Beta-P model) for sites B and E at Bungalbin showing intersection of species accumulation curves that differ in shape.

Measures of trapping effort affect species accumulation curves

There was little difference in adjusted r^2 values for various models when comparing the two measures of trapping, pit-trapping days and number of individuals caught. The better performing non-linear models were equally applicable for both measures, so either measure could be used. However, activity patterns of reptiles are affected by ambient conditions, reproductive status, age and foraging strategy, so pit-trapping effort might yield varying results based on sampling season, daily weather conditions and other location-specific variables, and as a consequence may not be a consistent measure of trapping effort (e.g. extensive pit-trapping in cooler *vs* warmer months). Measuring trapping effort by number of individuals caught avoids this problem. However, number of individuals caught does not provide a useful indication of how much field time (and expense) is required to capture a nominated percentage of the predicted number of species in an area. This would be most noticeable when comparing a site that had a relatively high abundance (e.g. sand ridge crests in the Great Victoria Desert) with a site with low abundance (e.g. unvegetated gibber plains). In areas where reptiles are scarce, much greater effort is obviously required to catch a nominated number of individuals. If the number of individuals caught and pit-trapping days are used together, then the former can be used to determine the effort required to capture a nominated percentage of total number of species in the area and the latter to estimate the amount of field time (and expense) to catch the required number of species. For the above reasons, most texts use number of individuals caught as the measure of effort when discussing the relationship between species accumulation and effort (e.g. Hayek & Buzas 1997; Hubbell 2001).

Best models

Four non-linear models consistently performed better for both heterogeneous and homogeneous sites; Beta-P, Weibull, Chapman–Richards and Rational models. Overall, the Beta-P model, with four parameters, was the best. The Weibull model, also with four parameters, was probably the next best overall performer. Overall, the worst models were the Power, Linear Dependence and Exponential models. Flather (1996) compared nine models for avian data and found that eight had r^2 values in excess of 0.96, with the best being Weibull and Beta-P, closely followed by Chapman–Richards, Rational and Exponential models. Our ‘best-fit’ results for Weibull, Beta-P and Chapman–Richards models agreed with those of Flather (1996), but we found the Exponential model to

be a relatively poor performer with the mean adjusted r^2 of 0.95 for the heterogeneous sites and 0.92 for the homogeneous sites.

Theoretically, the species accumulation curve should pass through the origin and be asymptotic (i.e. zero trapping effort = zero species). Of the four best-fit models, the Chapman–Richards meets both criteria. The Weibull, Beta-P and Rational models do not necessarily pass through the origin, and of these only the Beta-P and Weibull models have an asymptote. The Hill model is both asymptotic and passes through the origin, but it has a tendency to overestimate species richness, and occasionally provides unrealistically high values.

The Power model (with only two parameters) generally over-predicted number of species at a site, particularly when a plateau had not been reached, and the Asymptotic model (with three parameters) and Linear Dependence model (with two parameters) consistently under-estimated predicted total number of species for a site. Models with four parameters, and consequential greater flexibility to match the shape of field data, generally perform better. However, four-parameter models can provide multiple solutions to fit field data with very similar adjusted r^2 and MSE values depending on starting values entered into the software program. For some data sets, we were unable to obtain convergence and an acceptable solution using the Weibull model. On a number of occasions, convergence and a satisfactory solution obtained in Statistica could not be replicated in NLREG software presumably because these two programs used different algorithms to derive solutions to regression equations, for example, Statistica (for Windows) provided a range of alternative approaches: quasi-Newton estimation method, Simplex, Hooke–Jeeves or Rosenbrock pattern searches; NLREG is based on minimizing the sum of the squared residuals for a set of parameter values (Sherrod 2001). This can be particularly frustrating and disconcerting, and likely to discourage some from using these models to predict species richness. Failure to converge was a problem also experienced by Brown and Mayer (1988) for the Weibull model.

How good is the prediction of species richness?

Species accumulation curves provide estimates of species richness for α and γ diversity habitats and can therefore be used to compare species richness among sites. For example, plateauing of the Redsands species accumulation curve suggested that the number of species caught was approaching the total number in the area, whereas this was not the situation for at least three of the other heterogeneous sites. The graphed Beta-P smoothed curves (Fig. 2) for Bungalbin and Redsands suggested that Bungalbin would eventually

have slightly higher species richness (note: Redsands data does not include the 16 snake species caught at the site; Bungalbin has three snake species that were included in the analyses). The total number of species caught on Barrow Island will probably be the lowest for the five heterogeneous habitats, and Ora Banda will probably have the highest number of species caught. Barrow Island was probably the least diverse habitat and being an island (i.e. unable to recruit from adjacent areas) would generally be expected to have fewer species than the other heterogeneous sites (MacArthur 1965). A landscape-scale biological survey of the Kurnalpi–Kalgoorlie area (including Ora Banda) between October 1979 and February 1981 recorded 45 species of reptiles in the area (McKenzie & Hall 1992). A similar survey undertaken again at the landscape-scale to the west of Ora Banda between 1979 and 1981 identified a total of 55 reptiles in the area (Dell *et al.* 1985). A landscape-scale biological survey north of the study site identified 63 species of reptiles (Dell *et al.* 1988). These authors reported an enormous diversity of habitat in this area with little similarity in the herpetofaunal composition for the three main habitat types (37% of the reptiles common to the three sites; Dell *et al.* 1988). A search of the Western Australian Museum records indicates in excess of 100 species of reptiles being caught within a 200-km radius of Ora Banda. Many of these species are habitat specialists and their preferred habitat was not within the trapped area around Ora Banda (e.g. sand ridges and spinifex, salt lakes), reducing the possible number of species that could potentially be caught in the area. However, these data indicate the potential to collect in excess of 60 species in the Ora Banda region, which is more than predicted by most models.

Which data points to choose?

Species accumulation curves can be calculated from the data in two ways. All of the data points can be used, or alternatively only that subset of data points where the number of species increases can be used. These two approaches result in different shaped species accumulation curves (Fig. 6). For GVD L area (and all other data sets), using only data points where the number of species increased resulted in an equal or lower predicted species richness compared with when all data points were included. This was because the use of all data points flattened the curve and in doing so increased the slope of the line after the inflection point toward a final plateau. There is no commentary in the literature on which approach to adopt. We chose to use all available data points as this generally provided the better estimate of species richness for each site for the better models.

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REFERENCES

- Brewer A. & Williamson M. (1994) A new relationship for rarefaction. *Biodivers. Conserv.* **3**, 373–9.
- Brown R. F. & Mayer D. G. (1988) Representing cumulative germination. 2. The use of the Weibull function and other empirically derived curves. *Ann. Bot.* **61**, 127–38.
- Bunge J. & Fitzpatrick M. (1993) Estimating the number of species: A review. *J. Am. Stat. Ass.* **88**, 364–373.
- Clench H. (1979) How to make regional list of butterflies: Some thoughts. *J. Lepid. Soc.* **33**, 216–31.
- Colwell R. K. (2000) *EstimateS*. Available from URL: <http://viceroy.eeb.uconn.edu/estimates>
- Colwell R. K. & Coddington J. A. (1994) Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B.* **345**, 101–18.
- Connor E. F. & McCoy E. D. (1979) The statistics and biology of the species–area relationship. *Am. Nat.* **113**, 791–833.
- Davidge C. (1979) A census of a community of small terrestrial vertebrates. *Aust. J. Ecol.* **4**, 165–70.
- Dell J., How R. A., Milewski A. V. & Keighery G. J. (1988) The biological survey of the eastern goldfields of Western Australia Part 5, Edjudina–Menzies study area. *Rec. West. Aust. Mus. Suppl.* **31**, 1–143.
- Dell J., How R. A., Newbey K. R. & Hnatiuk R. J. (1985) The biological survey of the eastern goldfields of Western Australia. *Rec. West. Aust. Mus. Suppl.* **23** (3), 1–168.
- DeVries P. J., Murray D. & Lande R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biol. J. Linn. Soc.* **62**, 343–64.
- Flather C. H. (1996) Fitting species-accumulation functions and assessing regional land use impacts on avian diversity. *J. Biodiv.* **23**, 155–68.
- Gibbons J. W., Burke V. J., Lovich J. E. *et al.* (1997) Perceptions of species abundance, distribution, and diversity; lessons from four decades of sampling on a government-managed reserve. *Environ. Manage.* **21**, 259–68.
- Gleason A. H. (1922) On the relation between species and area. *Ecology* **3**, 158–62.
- Hair J. F., Anderson R. E., Tatham R. L. & Black W. C. (1995) *Multivariate Data Analysis*. Prentice Hall, New Jersey.
- Hayek L.-A. & Buzas M. A. (1997) *Surveying Natural Populations*. Columbia University Press, New York.

- Hobbs T. J., Morton S. R., Masters P. & Jones K. R. (1994) Influence of pit-trap design on sampling of reptiles in arid spinifex grasslands. *Wildl. Res.* **21**, 483–90.
- Hubbell S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Hurlbert S. H. (1971) The nonconcept of species diversity; a critique and alternative parameters. *Ecology* **52**, 577–86.
- James C. D. & Rathbun S. (1981) Rarefaction, relative abundance, and diversity of avian communities. *Auk* **98**, 785–800.
- Kenkel J. L. (1996) *Introductory Statistics for Management and Economics*. Duxbury Press, Belmont, California.
- Krebs C. J. (1985) *Ecology: The Experimental Analysis of Distribution and Abundance*. Harper & Row, New York.
- Lande R., DeVries P. J. & Walla T. R. (2000) When species accumulation curves intersect: Implications for ranking diversity using small samples. *Oikos* **89**, 601–4.
- Longino J. T. & Colwell R. K. (1997) Biodiversity assessment using structured inventory: Capturing the ant fauna of a tropical rain forest. *Ecol. Appl.* **7**, 1263–77.
- MacArthur R. H. (1965) Patterns of species diversity. *Biol. Rev.* **40**, 510–33.
- McKenzie N. L. & Hall N. J. (1992) The biological survey of the eastern goldfields of Western Australia, Part 8 Kurnalpi-Kalgoorlie study area. *Rec. West. Aust. Mus. Suppl.* **41**, 1–125.
- McKenzie N. L., Rolfe J. K., Aplin K. P., Cowan M. A. & Smith L. A. (2000) Herpetofauna of the southern Carnarvon Basin, Western Australia. *Rec. West. Aust. Mus.* **61**, 335–60.
- McKenzie N. L., Rolfe J. K. & Carter D. (1989) Reptiles. In: *A Biological Survey of the Nullarbor Region of South and Western Australia in 1984* (eds N. L. McKenzie & A. C. Robinson) pp. 179–210. Department of Conservation and Land Management, Perth.
- Main A. R. (1982) Rare species: Precious or dross? In: *Species at Risk: Research in Australia* (ed. G. R. H. Ride & W. D. L. Ride) pp. 163–74. Australian Academy of Science, Canberra.
- Masters P. (1996) The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. *Wildl. Res.* **23**, 39–48.
- Miller R. I. & Wiegert R. G. (1989) Documenting completeness, species–area relations, and the species–abundance distribution of a regional flora. *Ecology* **70**, 16–22.
- Moreno C. E. & Halffter G. (2000) Assessing the completeness of bat biodiversity inventories using species accumulation curves. *J. Appl. Ecol.* **37**, 149–58.
- Moreno C. E. & Halffter G. (2001) On the measure of sampling effort used in species accumulation curves. *J. Appl. Ecol.* **38**, 487–90.
- Morton S. R. & James C. D. (1988) The diversity and abundance of lizards in arid Australia: A new hypothesis. *Am. Nat.* **132**, 237–56.
- Palmer M. W. (1990) The estimation of species richness by extrapolation. *Ecology* **71**, 1195–8.
- Palmer M. W. (1991) Estimating species richness: The second-order jackknife reconsidered. *Ecology* **72**, 1512–3.
- Paltridge R. & Southgate R. (2001) The effect of habitat type and seasonal conditions on fauna in two areas of the Tanami Desert. *Wildl. Res.* **28**, 247–60.
- Pianka E. R. (1986) *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure*. Princeton University Press, Princeton.
- Pianka E. R. (1996) Long-term changes in lizard assemblages in the Great Victoria Desert: Dynamic habitat mosaics in response to wildfires. In: *Long-Term Studies of Vertebrate Communities* (eds M. L. Cody & J. A. Smallwood) pp. 191–215. Academic Press, San Diego.
- Pielou E. C. (1975) *Ecological Diversity*. Wiley, New York.
- Preston F. W. (1960) Time and space and the variation of species. *Ecology* **29**, 254–83.
- Preston F. W. (1962) The canonical distribution of commonness and rarity. *Ecology* **43**, 185–215.
- Read J. (1998) Vertebrate fauna of the Nifty mine site, Great Sandy Desert, with comments on the impacts of mining and rehabilitation. *West. Aust. Nat.* **22**, 1–21.
- Read J. L. (1999) Birds, reptiles and ants as indicators of ecological impacts of mining and pastoralism at Olympic Dam in the Australian arid zone. Unpubl. PhD Thesis, University of New England, Armidale, NSW.
- Read J. L. & Owens H. M. (1999) Reptiles and amphibians of the Lake Eyre south region. In: *Lake Eyre south monographs series*, Vol. 1 (ed. W. J. H. Slaytor) pp. 111–214. Royal Geographical Society of South Australia, Adelaide.
- Rosenzweig M. L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Sanders H. L. (1968) Marine benthic diversity; a comparative study. *Am. Nat.* **102**, 242–82.
- Shannon C. E. & Weaver W. (1963) *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Shephard M. (1995) *The Great Victoria Desert*. Reed, Sydney.
- Sherrod P. H. (2001) *Nonlinear Regression Analysis Program*. Available from URL: <http://www.nlreg.com/>.
- Simpson E. H. (1949) Measurement of diversity. *Nature* **163**, 688.
- Soberón J. & Llorente J. (1993) The use of species accumulation functions for the prediction of species richness. *Conserv. Biol.* **7**, 480–8.
- StatSoft (1995) *Statistica for Windows* version 5.1. StatSoft, Tulsa, OK.
- Thompson G. G. & Withers P. C. (2003) Effect of species richness and relative abundance on the shape of the species accumulation curve. *Austral Ecol.* **28**, 355–360.
- Tramer E. J. (1969) Bird species diversity, components of Shannon's formula. *Ecology* **50**, 927–9.
- Willott S. J. (2001) Species accumulation curves and the measure of sampling. *J. Appl. Ecol.* **38**, 484–6.
- Withers P. C. (1992) *Comparative Animal Physiology*. Saunders College, Philadelphia.