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Using species accumulation curves to estimate trapping effort in fauna surveys and species richness

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Abstract The shape of species accumulation curves is influenced by the relative abundance and diversity of the fauna being sampled, and the order in which individuals are caught. We use resampling to show the variation in species accumulation curves caused by the order of trapping periods. Averaged species accumulation curves calculated by randomly assigning the order of trapping periods are smooth curves that are a better estimate of species richness and a more useful tool for determining the trapping effort required to adequately survey a site. We extend this concept of randomly resampling the trapping period to show that randomizing the number of individuals caught for each species over the number of collection periods (e.g. days) can provide an accurate estimate of the averaged species accumulation curve. This is particularly useful as it enables an accurate estimation of the proportion of the total number of species caught in an area during a survey from information on the number of individuals caught for each species and the number of trapping periods, and is not dependent on having knowledge of the trapping period in which each individual was caught. This calculation also enables an assessment to be made of the adequacy of fauna surveys to report a species inventory in environmental impact assessments when only a species list and relative abundance data are provided.

Key words: fauna, species accumulation curves, surveys, trapping effort.

INTRODUCTION

Governments require environmental impact assessment (EIA) be undertaken prior to major disturbances to the natural environment where the proponent is required to describe the potential impact of disturbances on the faunal assemblages at the site and in a biogeographical regional context (Environmental Protection Authority (EPA) 2002). For example, in Western Australia the Environmental Protection Authority (EPA) requires proponents of a development to use data from terrestrial biological surveys to address biodiversity and ecological function values in their EIA (EPA 2002). The EPA argues that best practice requires that biodiversity be considered to have two key aspects; (i) its biodiversity value at the genetic, species and ecosystem levels; and (ii) its ecological functional value at the ecosystem level (EPA 2002). For this to be done, terrestrial fauna surveys should result in a near complete inventory of the species for the site to be disturbed. Most EIA reports provide an overview of the methods used in fauna surveys and many provide an indication of the number of individuals for each species that have been caught during the surveys. However, there is almost never an indication of the adequacy of the faunal surveys to provide an inventory of the species in the area or an estimate of species richness.

There are numerous mathematical models developed and reviewed in the last three decades to estimate species richness (Palmer 1990, 1991, 1995; Bunge & Fitzpatrick 1993; Colwell & Coddington 1994; Hellmann & Fowler 1999; Melo & Froehlich 2001; Chiarucci *et al.* 2003). These models can be grouped into three categories: parametric, non-parametric and extrapolations of species accumulation curves (a parametric method). Melo and Froehlich (2001) argued that the parametric methods, which require information on the abundance of each species can be labourious to calculate, can perform badly and have not been heavily used in recent years. In contrast, the non-parametric methods are easier to calculate and most need no information about abundance, and as a consequence, are more frequently used. Extrapolations from non-parametric data are problematic. Environmental consultants typically do not use these tools to estimate species richness or comment on the adequacy of their faunal surveys, and fauna survey guidance statements issued by the government agency often fail to recommend the use of these tools in the data analysis aspect of preparing the EIA (e.g. Owens 2000; EPA 2004). The reason for this is unclear, but the complexity of computations without access to the

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appropriate software may be a contributing factor. Alternatively, the data collected may be inadequate to assess species richness and proponents do not wish to expose this inadequacy of the survey protocol.

The overall objective of this paper is to indicate a relatively simple method of assessing species richness and the adequacy of fauna surveys prepared for EIA reports using the summary data available in most reports.

Accumulation curves

Species accumulation curves, or collectors' curves, plot the cumulative number of species discovered within a defined sampling area with increasing levels of survey effort. Species accumulation curves provide a measure of species inventory efficacy and completeness, and can be used to compare surveys based upon standardized sampling protocols (Moreno & Halffter 2000). Species accumulation curves are also useful in estimating the minimum sampling effort required to reach a satisfactory level of completeness in a survey as judged by the proportion of the species in the area detected (Moreno & Halffter 2000), resulting in better planning and sampling protocols. Soberón and Llorente (1993) suggested that species accumulation curves lend rigour to faunal inventories, particularly in poorly collected areas.

Numerous models have been discussed in the literature for species accumulation curves (see Soberón & Llorente 1993; Thompson *et al.* 2003; Diaz-Frances & Soberon 2005). Species accumulation curves are normally based on some uniform measure of detection (e.g. trap-hours, hours of observations, pit-trap nights). For unstandardized or *ad hoc* detection strategies, it is possible that habitats, activity times and individuals for particular species already discovered are ignored, biasing the process used as a measure of effort. Some authors (Soberón & Llorente 1993; Moreno & Halffter 2001; Willott 2001) have argued that the number of individuals caught is a better measure of sampling effort than the number of trapping periods as it takes into account differences in species richness and diversity, trap efficiency and temporal variations in assemblages. Soberón and Llorente 1993) urged caution in the use of species accumulation curves, suggesting that samples biased either temporally or spatially are useless for extrapolation, and the choice of an appropriate model is critical to the accurate estimation of species richness as different models diverge significantly in their extrapolations while fitting the same data set. They went on to suggest that different models might need to be used for different sized areas and fauna being sampled (e.g. well-known taxa in a small homogeneous area *vs* an unknown assemblage in a heterogeneous area with many rare species).

Gotelli and Colwell (2001) added to this list of cautions, suggesting that there are important differences among the four taxon sampling curves (sample-based *vs* individual-based, accumulation curves *vs* rarefaction curves) and these each have a different purpose and should not be confused although they are closely related. They stressed the point that rarefaction cannot be used for extrapolation as it does not provide an estimate of asymptotic richness. Under-sampling often results in a higher number of 'rare' species (e.g. singletons and doubletons) in an area than are actually there; and the greater number of 'rare' species reported in a data set the more likely it is that other species are present and not detected (Gotelli & Colwell 2001). On the positive side, Gotelli and Colwell (2001) concluded that although extrapolation of species accumulation curves is inherently more risky than interpolation, some asymptotic estimators performed well (e.g. see Thompson *et al.* 2003). This is probably more true for species accumulation curves that have plateaued with a reasonable number of individuals being caught compared with those data sets for which the flattening of the curve is less apparent and the extrapolated species accumulation curve asymptote provides a totally unrealistic high estimate of species richness (Gotelli & Colwell 2001; Thompson *et al.* 2003).

Colwell and Coddington (1994) and Thompson and Withers (2003) reported that the shape of a species accumulation curve is influenced by both relative abundance and diversity. In addition, the shape of a species accumulation curve is also affected by the order in which individuals are caught (Colwell & Coddington 1994; Gray *et al.* 2004), as we will demonstrate below. As a consequence, day-to-day variations in the composition of catches in a trapping program will influence the shape of a species accumulation curve and its asymptote for a survey in a particular habitat. Our experience is that daily weather variables (e.g. humidity, rainfall, ambient temperature) affect the number and species of reptiles and mammals caught (Read & Moseby 2001; Brown & Shine 2002), and as weather varies from day to day so do catch rates. Because the sequence in which individuals are caught affects the shape of the species accumulation curve, extrapolation to the asymptote will provide varying estimates of species richness.

If species accumulation curves are to be used to estimate species richness and as a tool for estimating the trapping effort required to catch a nominated proportion of the species in a particular area (e.g. 90%), and they are influenced by the sequence in which individuals are caught, then it is useful to obtain an 'average' of the catch variations by repeated resampling of the data set. Colwell's (2005) EstimateS includes a module that calculates averaged species accumulation curves. Randomly resampling trapping

Table 1. Data set for simulations, showing seven pit-trapping days of captures

Species	Day A	Day B	Day C	Day D	Day E	Day F	Day G
A	3	1	6	6	6	6	7
B	1	0	0	2	6	3	5
C	2	0	4	3	2	1	0
D	3	1	0	0	3	1	2
E	0	1	0	2	1	2	3
F	2	0	2	0	2	0	2
G	1	0	0	0	2	2	3
H	0	1	0	0	0	1	3
I	2	0	1	0	0	0	1
J	0	0	0	1	0	0	2
K	2	0	0	0	0	0	1
L	1	0	0	0	0	1	0
M	1	1	0	0	0	0	0
N	0	0	0	0	0	0	2
O	0	0	0	1	0	0	0
P	0	1	0	0	0	0	0
Q	0	0	1	0	0	0	0
R	0	0	1	0	0	0	0
S	0	0	0	1	0	0	0
T	0	0	0	0	1	0	0
Count	18	6	15	16	23	17	31
Species	10	6	6	7	8	8	11

periods (without replacement) and recomputing curves, and then taking means, produces a smooth curve of best fit for the data set.

Objectives

Our first objective was to demonstrate that by reordering the 'days' in which data are collected during a fauna survey we can significantly alter the shape of a species accumulation curve, the asymptote value and the predicted species richness for an area. Based on these data we argue that species accumulation curves for the purposes of predicting species richness from terrestrial fauna surveys and for planning purposes should be randomly resampled multiple times and means calculated to provide an averaged species accumulation curve. Although this would seem obvious it is not often done (see McKenzie *et al*. 2000; How & Dell 2004).

Our second objective was to demonstrate that by randomly allocating the number of individuals caught for each species over the number of collection periods (e.g. days) we can provide an accurate estimate of the averaged species accumulation curve which can then be used to estimate the adequacy of the trapping effort to catch a nominated proportion of the species in an area. We illustrate how these estimates of species richness can have less variation than the reordering of trapping periods if a high number of random resampling of the data is used.

Table 2. Sequence of days used to create the six species accumulation curves in Figure 2 from the data in Table 1

	Data set A	Data set B	Data set C
	Day A	Day B	Day G
	Day B	Day E	Day A
	Day C	Day G	Day F
	Day D	Day A	Day B
	Day E	Day C	Day E
	Day F	Day D	Day C
	Day G	Day F	Day D
Asymptotes	23.0	72 311.4	43 091.4

METHODS

For our first objective of demonstrating the variability in species accumulation curves based on the order of collection periods we have used a simple data set. This data set has 126 individuals from 20 species caught over seven trapping periods in a single habitat (Table 1). We calculate a species accumulation curve using the Beta-P model (Thompson *et al*. 2003) in NLREG software (Sherrod 2001) for three different combinations of the seven trapping periods (Table 2). The formula for the Beta-P model is: a (1 – (1 + (*z*/c)^d)^(–b)) (Thompson *et al*. 2003).

For our second objective we have selected two of our field data sets where we have a record of the number of individuals for each species caught each day. During the Australind survey in the mesic south-west of

Western Australia, we caught 352 reptiles from 10 species over 5 days of intensive trapping (720 pit-trap nights and 1440 funnel-trap nights) in March 2005. For the Ora Banda survey we caught 942 individuals from 45 species of reptiles over 14 days of intensive trapping (6720 pit-trap nights and 6720 funnel-trap nights) in 10 undisturbed habitats, ranging from Eucalypt-Casuarina-Mulga woodlands interspersed with *Acacia*, to sparsely distributed spinifex (*Triodia* spp.) and shrubs (*Acacia* spp.) through to dense shrubs (*Acacia* spp., *Atriplex* spp., *Allocasuarina* spp.) during January 2004.

These two data sets were selected because the Australind survey was in a relatively homogenous habitat and the Ora Banda survey was in a heterogeneous habitat. Sampling periods (e.g. days), taxa, habitat types, number of individuals and number of species caught, and capture rates per unit of trapping effort used varied between the two surveys.

For each of these data sets we calculated an averaged species accumulation curve using 10 000 random iterations of the survey periods without replacement using EstimateS (Colwell 2005). A non-linear regression curve was then calculated using the Beta-P model in NLREG software (Sherrod 2001). We also calculated the upper and lower 95% confidence limits for each species accumulation curve. Then, using a list of the total number of individuals caught for each species captured over the entire survey period, we randomly assigned individuals for each species across the number of survey days using a custom software application designed for this task so as to mimic the data set of individuals caught per species per day. For example, if 10 individuals were caught for species X over a 7-day survey, then each of these 10 individuals would be randomly assigned to being caught on any one of the 7 days. This was repeated 10 times to create 10 data sets for each of the two habitats (Australind and Ora Banda). Averaged species accumulation curves were then calculated for each of these data sets.

RESULTS

Species accumulation curves for the example data set (126 individuals from 20 species) showed considerable variability in shape (Fig. 1). Asymptotes varied, and ranged between 23.0 and 72 311 (Table 2). For two of the data sets in Figure 1B and C, the flattening or plateauing of the species accumulation curve was not obvious, indicating that an inadequate number of individuals had been captured over the 7 days of survey to calculate a species accumulation curve. In contrast, the asymptote for species accumulation curve A is probably a reasonable assessment of species richness for this site.

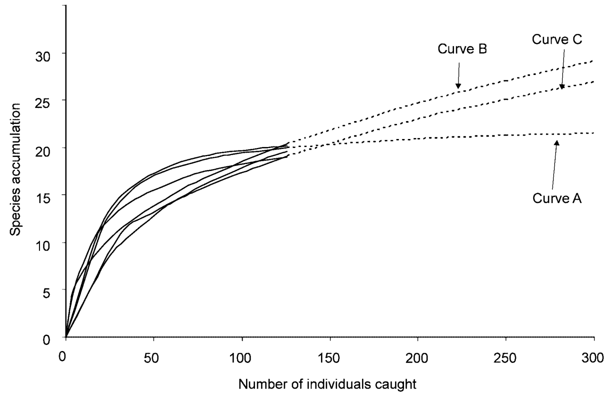

Fig. 1. Six species accumulation curves for the data in Table 1, with the order of trapping days varied as shown in Table 2.

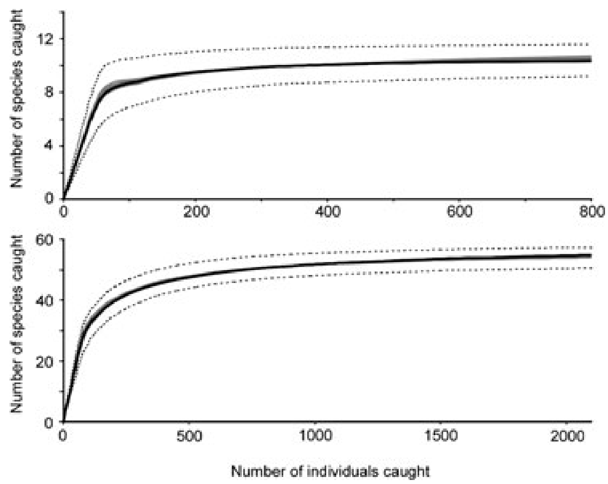

Fig. 2. Actual species accumulation curves (black line) with the upper and lower 95% confidence limits (dotted lines), and 10 species accumulation curves (grey lines) calculated by randomly allocating individuals per species across the trapping periods for two different habitats (see text).

Figure 2 shows the averaged species accumulation curve for each of the two habitats sampled based on the actual data (dark lines) and the 10 species accumulation curves (grey lines) for each habitat based on a random allocation of individuals for each species across the number of trapping days. It is apparent that for each of the habitats the species accumulation curves for each of 10 randomly allocated data sets are a very close approximation of the averaged species accumulation curve based on the actual data. For both habitats, all 10 curves fit well within the upper and lower 95% confidence limits for the actual species accumulation curve. It is difficult to identify most of the grey lines as they lie under or very close to the actual species accumulation curve. A lesser number of random iterations to calculate the mean curves will obviously provide a greater spread of scores.

DISCUSSION

Local environmental variables such as humidity, rain, cloud cover and daily temperature can affect catch rates for reptiles and mammals (Read & Moseby 2001; Brown & Shine 2002), so much so that the number of individuals and number of species caught on any day can vary considerably across the trapping period. In addition, most trapping programs only catch a small proportion of the individuals available to be caught in an area (i.e. recapture rates for sampling on multiple consecutive days is generally low for mammals and reptiles), and 'sampling error' results in considerable variation in both the number of individuals and number of species caught during a terrestrial fauna trapping program from day to day. If species accumulation curves are to be used as a tool to predict species richness and to estimate the trapping effort required to catch a nominated proportion of species in an area, then 'distortions' to the shape of the species accumulation curve attributable to daily environmental variables and sampling error need to be minimized. Although free software has been readily available for a number of years (Colwell 2005), environmental consultants rarely use any of the available measures to estimate species richness for surveyed sites and some researchers continue to represent species accumulation curves based on actual catch periods (e.g. How *et al*. 1988; McKenzie *et al*. 2000; How & Dell 2004) rather than randomizing the catch periods to provide a more accurate and smooth curve.

The use of 10 000 iterations in randomly sorting the trapping periods, which is easily achieved in the available software, provides multiple species accumulation curves that are very closely aligned and fit well within the 95% confidence limits. The larger the data set and the greater the number of days, the better the estimate of species richness when based on species accumulation curves. Species accumulation curves must have established an obvious plateau to provide reasonable estimates of species richness. Small samples collected over a limited number of trapping periods invariably provide species richness estimates based on species accumulation curves that are unrealistically high.

Terrestrial fauna surveys in Western Australia undertaken by environmental consultants for the purpose of preparing an EIA typically open a small number of traps (10–20) for 5 to 7 days in each habitat type (Biota Environmental Sciences 2004, 2005; Ecologia Environmental Consultants 2004, 2005; Environmental Protection Authority 2004; Davis *et al*. 2005; Ninox Wildlife Consulting 2005a,b). Catch rates for mammals and reptiles combined per habitat type are typically less than 100 individuals. These data are almost always presented as a list of the number of individuals caught per species. We have never seen a report that indicated what individuals were caught in each of the trapping periods, thus enabling a species accumulation curve to be calculated for the actual data set. By randomly allocating individuals for each species to the number of trapping days, it is possible to calculate an accurate species accumulation curve for each habitat sampled. This curve can then be used to estimate the proportion of the total number of species in the area that have been detected and species richness. This tool therefore enables assessors of EIA reports to determine the adequacy of the survey effort in catching the available species (e.g. if 50% of the species present were caught) and to estimate the total number of species for the habitat.

Similarly, most researchers when reporting on small vertebrate and invertebrate assemblages for a habitat normally only list the number of individuals per species caught in each habitat (e.g. Cowan & How 2004; Masters 1996; How 1998; Paltridge & Southgate 2001; How & Cooper 2002; How & Dell 2004). Using the technique of randomly assigning individuals for each species to catch periods it is possible to estimate the proportion of the total number of species in a habitat detected and to estimate species richness.

For fauna surveys where the species accumulation curve has not obviously plateaued, the only conclusion that can be reached is there was inadequate sampling effort to estimate species richness, and it is likely that the survey data are not an adequate reflection of the faunal assemblages being sampled. In these circumstances it is highly probable that the survey has not met the published EPA requirements (EPA 2002).

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