

## On the measure of sampling effort used in species accumulation curves

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### Summary

1. We agree with Willott (2001) that number of individuals would be an appropriate measure of sampling effort to compare species accumulation curves among sites, but the reason is not sampling bias. It has been shown theoretically that number of individuals is an unbiased effort unit when density varies among sites, although our results with bats do not prove this.

2. We compared our results using nights and individuals as measures of effort in bat species accumulation curves, but did not detect changes in the estimated richness using the two measures.

3. We maintain our position about the utility of species accumulation curves as practical tools for inventory assessment, even for very diverse groups. To compare curves from different sites, we agree that number of individuals may be an unbiased measure of effort. But to give practical recommendations for sampling, we suggest that effort also be expressed in standard sampling units.

*Key-words:* bats, biodiversity inventories, density, species richness estimation.

*Journal of Applied Ecology* (2001) **38**, 487–490

We have used species accumulation models to evaluate the completeness of inventories of bats, and to provide valid comparisons among inventories (Moreno & Halffter 2000), and argue that this method can be used to assess the inventories of any other group. Willott (2001) is concerned that the measure that we used as sampling effort (cumulative number of sampling nights over sampling period) is not the appropriate one to compare species accumulation curves among different habitats.

We are completely in agreement with the opinion of Willott that the number of individuals is the appropriate measure to construct species accumulation curves, when the objective is to compare these curves among different sampling units. However, the reason is not sampling efficiency or observer bias, as Willott suggests. During the design of the sampling protocol, knowledge about the natural history of the study group is essential. As Willott argues, for some groups, mainly vertebrates, we know much about their behaviour, as in the case of

the lunar phobia of bats. This kind of knowledge should be used to plan data gathering, so that sampling bias may be avoided. Although for hyperdiverse or less known groups we do not have many data about their behaviour, the selection of sampling techniques and the sampling design should be based on the available knowledge of the biology of the group. Even if we select an adequate measure of sampling effort for the species accumulation curves, no subsequent analysis can avoid the biases derived from the observer or from sampling efficiency.

Number of individuals is the appropriate measure to compare species accumulation curves among different sampling units because this measure avoids biased comparisons when the density of individuals varies among such sampling units. This aspect has been discussed by Chazdon, Colwell & Denslow (1999) and Kobe (1999) as a problem with the conclusions drawn by Hubbell *et al.* (1999). Hubbell *et al.* compare tropical tree richness in gaps and in continuous forest, based on the number of species per stem (the number of species in a quadrat divided by the number of stems). With this measure, Hubbell *et al.* find that tree richness is equal in gaps and in non-gap control sites of equal area. Chazdon, Colwell & Denslow (1999) and Kobe (1999) indicate that, although both kinds of sites may have the

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**Table 1.** Estimated richness of bats (asymptotes) in seven habitats computed with two species accumulation models, using cumulative number of nights and cumulative number of individuals as sampling effort

Vegetation type	Asymptote using nights	Asymptote using individuals	Rank using nights	Rank using individuals	Difference between asymptotes
Linear dependence model					
Subdeciduous forest	17·1182	17·4456	1	1	-0·3273
Deciduous forest	10·6637	10·6791	7	7	-0·0154
Riparian vegetation	12·3828	12·4101	6	6	-0·0273
Palm stand	15·2713	14·3274	3	4	0·9439
Secondary vegetation	15·5726	15·6728	2	2	-0·1003
Mango plantation	14·4793	14·5202	4	3	-0·0409
Corn field	13·5286	13·5040	5	5	-0·0246
Clench model					
Subdeciduous forest	19·6660	19·7031	3	3	-0·0372
Deciduous forest	12·6225	12·6625	7	7	-0·0401
Riparian vegetation	14·3934	14·4363	6	6	-0·429
Palm stand	22·5221	20·4313	1	2	2·0908
Secondary vegetation	20·8512	21·0732	2	1	-0·2220
Mango plantation	17·1835	17·2754	4	4	-0·0919
Corn field	16·1753	16·1577	5	5	0·0177

same number of species per stem, the cumulative number of species in gaps can be greater than the richness of non-gap sites, if the gap sites have greater stem density than the non-gap site. Thus, the measure used by Hubbell *et al.* can influence their conclusions, and in fact it does, as Hubbell (1999) indicates, because gap and non-gap sites have distinct tree density. Normalizing richness by stem number produces an upward-biased estimate of the species richness in low-density sites, and downward-biased estimate of richness in high-density sites (Kobe 1999).

Re-analysing our own data of Phyllostomidae and Mormoopidae bats (Moreno & Halffter 2000), we fitted the linear dependence and the Clench models to species accumulation curves. Data were randomized using the Estimates program (Colwell 2000), with cumulative number of individuals as a measure of effort. We ordered the seven habitats by rank, from highest to lowest species richness, according to the asymptote of both models, and compared the results using nights and the results using individuals as units of sampling effort (Table 1). With both species accumulation models, the species richness of the palm stand showed the most divergent result according to both measures of effort (Table 1). With the linear dependence model, the palm stand had a higher richness than the mango plantation when nights were used as sampling effort, but the opposite relation appeared when number of individuals was used as sampling effort. Likewise, with the Clench model the palm stand had higher richness than the secondary vegetation when nights were the measure of effort, but the opposite relation appeared when individuals were used as sampling effort.

When bats are captured with mist nets, density is very difficult to estimate due to the problem of identifying the area that is being sampled in any array of nets. Even when we know the area of each habitat where we carried out the bat inventories, such area does not correspond with the sampling area, and we cannot

estimate density with precision. However, with this method of capture, the standardized abundance of bats in each habitat can be estimated by dividing the number of captured individuals by the sampling effort invested in that habitat. In our work (Moreno & Halffter 2000), sampling effort was estimated as the product of the net area (total net metres) and the total number of hours that the nets remained open each night for a given site ( $\text{m h}^{-1}$ ). For each sampling site, we summed the effort of all nights during the sampling period. Then, we added the effort of all sampling sites for a given habitat and increased the number of sampling nights for those habitats where effort was less, to standardize sampling effort per habitat (Moreno & Halffter 2000). Thus, with the total number of individuals captured, we estimated the standardized abundance of bats in each habitat using two measures of effort: the product of the net metres and hours ( $\text{m h}^{-1}$ ), and the number of nights (Table 2). With both measures, the higher standardized abundance of bats corresponded to the subdeciduous tropical forest, and the lower one to the palm stand.

We used linear regressions ( $n = 7$ ) to test whether the standardized abundance (Table 2) determines the differences (Table 1) detected between the estimated richness produced by the two measures of effort. With the linear dependence model, the regression line explained more variance in the data than with the Clench model, but neither of these regressions was significant for either of the two measures of abundance (Table 3).

Our results do not show conclusively that in habitats with different abundance or density, the estimation of species richness is biased by the measure of sampling effort used to construct the species accumulation curves, as has been shown theoretically by Chazdon, Colwell & Denslow (1999). However, we believe that more empirical examples are needed (with groups in which it is possible to estimate density, and with a greater number of samples) to explore this relationship.

**Table 2.** Sampling effort invested in inventories and the relative abundance of bats in seven habitats

Vegetation type	m h <sup>-1</sup>	Number of nights	Number of individuals	Relative abundance using m h <sup>-1</sup>	Relative abundance using nights
Subdeciduous forest	3858	24	761	0.20	31.71
Deciduous forest	3850	20	99	0.03	4.95
Riparian vegetation	3858	14	221	0.06	15.79
Palm stand	3858	14	65	0.02	4.64
Secondary vegetation	3858	18	89	0.02	4.94
Mango plantation	3846	16	365	0.09	22.81
Corn field	3873	14	273	0.07	19.50

**Table 3.** Results of linear regression analysis of differences between asymptotes (dependent variable) and bat relative abundance (independent variable), using two species accumulation models

	Asymptote based on the linear dependence model	Asymptote based on the Clench model
Relative abundance using m h <sup>-1</sup>	$r^2 = 0.321$ , $P = 0.185$	$r^2 = 0.113$ , $P = 0.461$
Relative abundance nights	$r^2 = 0.309$ , $P = 0.195$	$r^2 = 0.150$ , $P = 0.390$

Although we concur with the opinion of Chazdon, Colwell & Denslow (1999), Kobe (1999) and Willott (2001), that to compare habitats with different abundance or density, the number of individuals is an unbiased measure of effort, we think that to apply accumulation curves in the design of future inventories, sampling effort should also be expressed in standard sampling units. In this way, other investigators can plan the minimum effort required to carry out the inventory of a group under certain conditions. For example, the bat accumulation curves based on the number of nights indicate that 5–18 sampling nights are required (each night with 225 m h<sup>-1</sup>) to reach an acceptable level of efficiency (90%) in inventories within each habitat type (Moreno & Halffter 2000). Researchers interested in carrying out inventories of Phyllostomidae and Mormoopidae with mist nets can use an equivalent effort each night and can invest the minimum sampling effort required to have an acceptable representation of these bats. If this effort had been expressed only as the number of individuals, it would be very difficult to plan the sampling effort required, and to estimate its cost at the beginning of an inventory project. It is of greatest importance to use a standard sampling unit that directly measures capture effort. The number of individuals depends on population density and on less predictable factors such as temporal responses to ecological conditions.

In our work with bats (Moreno & Halffter 2000), the species accumulation curves reached an asymptotic phase in all the habitats, except the palm stand. Willott (2001) argues that for hyperdiverse groups, such as moths, this is very infrequent, and he questions the applicability of accumulation curves in these cases. Fortunately, mathematical models such as those described by Soberón & Llorente (1993) are predictive ones. That is to say, based on the accumulation pattern of species with a given effort, it is possible to extrapolate the curve to

know the necessary effort to reach the asymptotic phase of the curve, although such an asymptote had not been reached with the invested sampling effort.

We wish to emphasize that species accumulation curves are particularly valuable for biodiversity indicator groups: taxonomically well-defined and ecologically restricted groups, with a relatively well-known natural history. For very diverse groups there could be many identification or sampling mistakes, and they usually do not have ecological or historical congruence. In this case, species accumulation curves will have a limited utility for comparisons among collections, giving an incomplete picture.

In conclusion, species accumulation curves, estimated with models like those used by Soberón & Llorente (1993), or with non-parametric models such as those described by Colwell & Coddington (1994), are very practical tools to assess species inventories, even for hyperdiverse groups. To compare the curves of different sites an unbiased measure of effort (i.e. cumulative number of individuals) should be used if density varies across these sites. But if we wish to give practical recommendations to other researchers, effort should be also expressed in sampling units to simplify the design of sampling procedures. However, independent of the unit used to measure the sampling effort, or of the mathematical model used to describe the accumulation curves, knowledge of the natural history of the group is essential to avoid biased estimations. Empirical examples with different groups and under distinct conditions will be needed to determine the minimum effort required to reach complete inventories.

### Acknowledgements

We are truly grateful to Robert Colwell for his valuable comments and suggestions. We also wish to thank the Theodore Roosevelt Memorial Fund, Idea Wild and

the International Foundation for Science for financial support for bat research. We have also received support from CONABIO (project K038) and UNESCO-ORCYT (project 884.639-9).

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*Received 18 May 2000; revision received 18 August 2000*