# Focus

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Thorsten Koerner was at the Department of Historical Studies, University of Bristol, Bristol, UK BS8 1TB. (Current address: Medizinische Hochschule Hannover, D-30625 Hannover, Germany.) Peter de Raadt is at the CTD, WHO, CH-1270 Geneva, Switzerland. **Ian Maudlin** is at the Tsetse Research Group, Department of Clinical Veterinary Science, Langford, Bristol, UK BS18 7DU. **Tel: +44 117 928 9495, Fax: +44 1934 853485, e-mail: ian.maudlin@ bristol.ac.uk**

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# Sampling Effort and Parasite Species Richness

## B.A. Walther, P. Cotgreave, R.D. Price, R.D. Gregory and D.H. Clayton

*Comparative studies of parasite species richness among host taxa can be confounded by uneven sampling effort. Sampling ceases to be a confounding factor when extrapolation methods are used to estimate true species richness. Here, Bruno Walther and colleagues review examples of sampling bias and the use of extrapolation methods for circumventing it. They also discuss the confounding effects of phylogenetic association on estimates of species richness.*

Ecologists often must rely on comparisons of species richness that are not controlled for the confounding effects of uneven sampling effort[1,2]. Sampling artefacts can have severe effects on richness estimates, particularly in parasite communities. For example, the number of helminth species found among 37 species of British waterfowl is highly correlated with the number of individuals examined per host species (Fig. 1a). Host body size, population density and geographic range are also correlated with helminth richness, but after controlling for sample size, only the relationship between geographic range and helminth richness remains significant[3].
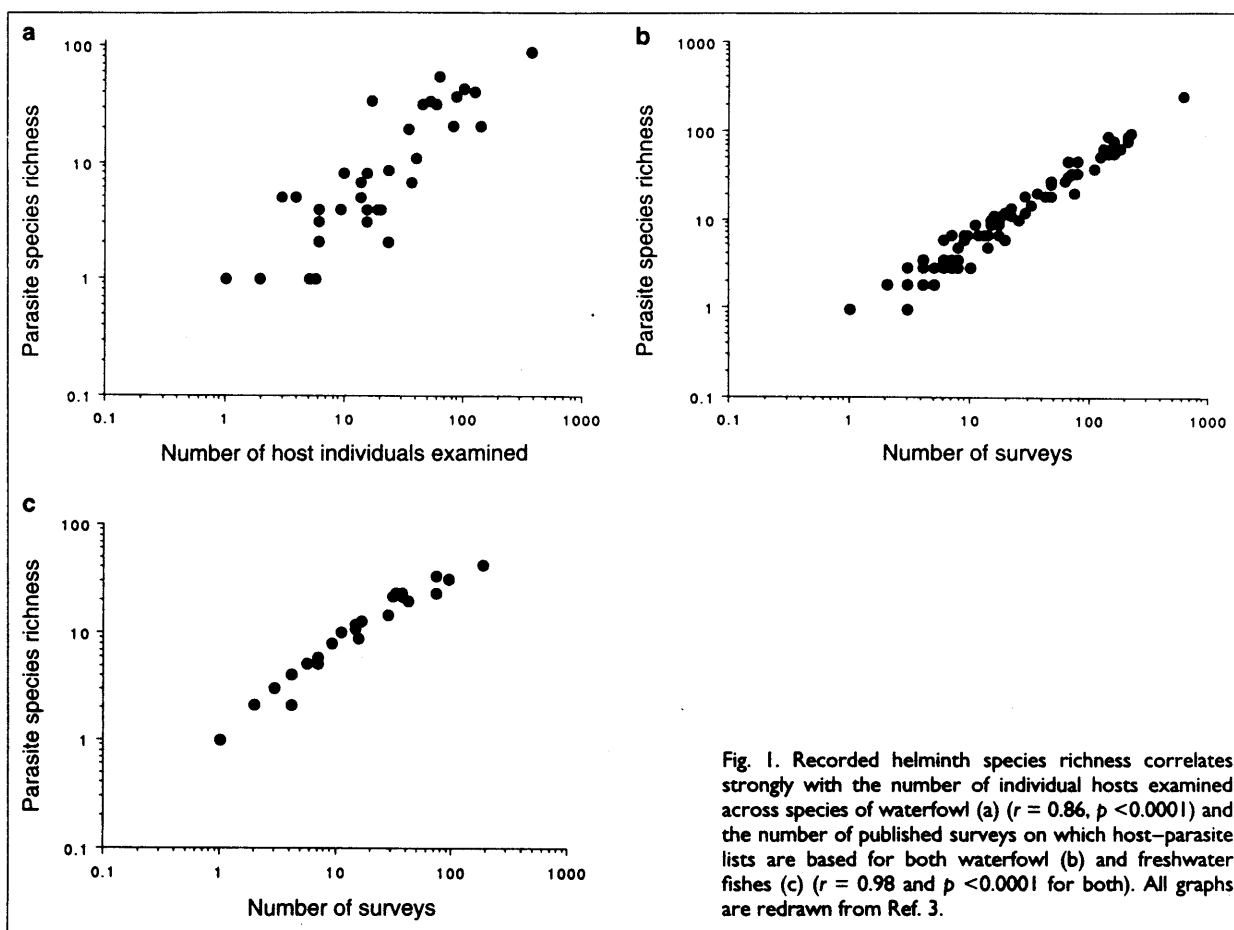
Indirect measures of sampling effort also covary with recorded species richness. The number of parasite surveys per host species is highly correlated with the recorded helminth species richness across waterfowl and fish (Fig. 1, b and c) as well as across vertebrate hosts in general (R.D. Gregory, unpublished). The time spent searching, the number or size of localities visited, the number of collecting trips, and the number of microhabitats examined have also been shown to correlate with species richness in plant, bird and insect communities[1,2,4–7]. Even the number of general literature citations on any aspect of host biology correlates with the recorded species richness of ectoparasitic mites on rodents[8] as well as lice on birds (Ref. 9 and Box 1).

These examples and others[10] show that estimates of parasite species richness are seriously influenced by uneven sampling effort. It is therefore critical to control for sampling effort in comparative studies of parasite richness.

## Controlling for Uneven Sampling Effort

A number of extrapolation methods have been developed to control for the influence of uneven sampling effort on estimates of true species richness. These methods allow one to extrapolate the true species richness with some degree of statistical certainty from incomplete collections, to estimate how much sampling effort is needed to discover a certain proportion of all species, and to estimate the accumulation rate of new species if sampling is continued. The methods can be categorized broadly into: (1) the extrapolation of accumulation curves; (2) the fitting of species-abundance distributions; and (3) non-parametric estimators.

*The extrapolation of accumulation curves.* Graphically, an accumulation curve is a plot of cumulative species richness against sampling effort (Box 2). Asymptotic accumulation curves approach an asymptote as sampling increases. The asymptote represents the true species richness. Non-asymptotic accumulation

Fig. 1. Recorded helminth species richness correlates strongly with the number of individual hosts examined across species of waterfowl (a) ($r = 0.86$, $p < 0.0001$) and the number of published surveys on which host–parasite lists are based for both waterfowl (b) and freshwater fishes (c) ($r = 0.98$ and $p < 0.0001$ for both). All graphs are redrawn from Ref. 3.

## Box 1. Relationship of Ectoparasite Richness to Number of Papers Published on the Host

Kuris and Blaustein[8] demonstrated that the number of publications on a rodent species correlates with the recorded species richness of ectoparasitic mites from that species. We used an independent data set concerning birds and their chewing lice (*Phthiraptera*, formerly *Mallophaga*) to test for a similar relationship. To assess louse species richness we used an unpublished checklist of lice from birds of the world compiled by R.D. Price over the past several decades. Going down the list, we counted the number of louse species recorded from the first bird species mentioned in each bird genus. The result was a compilation of: (1) louse species richnesses; and (2) louse generic richnesses across 952 bird species.

Sampling effort was assessed using the number of citations in the Bids ISI Data Service, Science Citation Index. The Latin binomial for each of the 952 bird species, as given in Ref. 33, was typed after 'T - Word(s) In Title' had been chosen. The computer search was repeated for each of the years 1984 to 1993.

Felsenstein's[34] independent contrasts method, as extended by Harvey and Pagel[35], was used to control for the effects of phylogenetic association between species. The method identifies sets of phylogenetically independent comparisons within the branching pattern of a phylogenetic tree. A set of independent differences (called linear contrasts) is created by comparing only the values for sister taxa in the phylogeny. Values for ancestral nodes in the phylogeny are estimated by averaging the values for extant taxa. Differences that evolved since the sister lineages split are considered independent evolutionary events. These independent contrasts meet the assumptions of ordinary regression and correlation[36]. The CAIC program developed by Purvis[36] using Pagel's[37] method was used to generate 239 independent contrasts within the phylogeny of Sibley and Ahlquist[38]. The independent contrasts were analysed using a Model 1 regression fitted through the origin[39]. All data were logarithmically transformed.
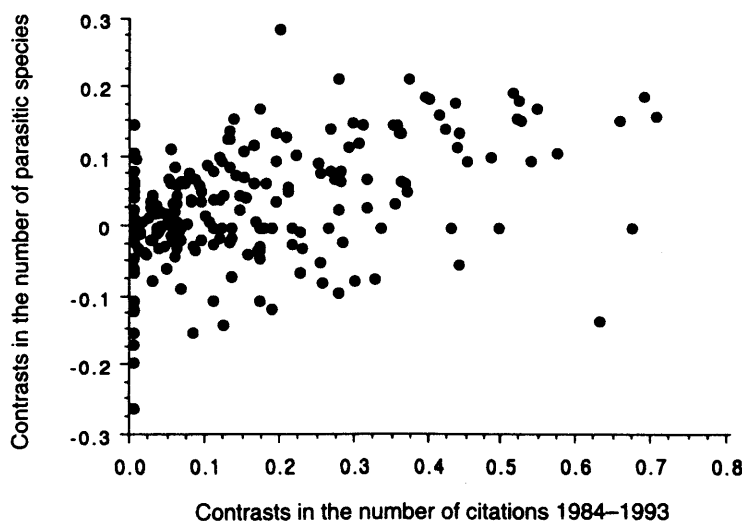
Contrasts in the richnesses of louse species and genera were both positively correlated with contrasts in the number of citations [d.f. = 1.238, $r = 0.53$, $p < 0.001$ (F-test)] (see Fig. left).



Contrasts in the number of citations 1984–1993

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**Box 2. Accumulation Curves**

Accumulation curves (see Fig. right) for five hypothetical host species (or host populations). For each species, the number of parasites recorded approaches a different asymptotic value as sampling effort increases. The asymptote (closed squares) represents the true parasite species richness for that host species. Differences in parasite richness values can be caused by many variables (eg. host body mass, diet, life span, migration, social behaviour, habitat type and diversity, population density, geographic range and latitude[3,27,40,41]). Differences in slopes may be caused by either different sampling techniques or real differences in host biology, or both. For example, to record all helminth species found in the gut of a host, more samples need to be examined for species with long guts than for species with short guts, all else being equal. The accumulation curves for short-gut species may consequently rise more steeply than



Sampling effort (eg. sample size, time spent searching, etc.)

those for long-gut species in cases where the two hosts have the same parasite species richness. Differential gut morphology, blood chemistry, plumage thickness, or body size could all contribute to unequal increases in the number of parasite species recorded for equal amounts of sampling effort.
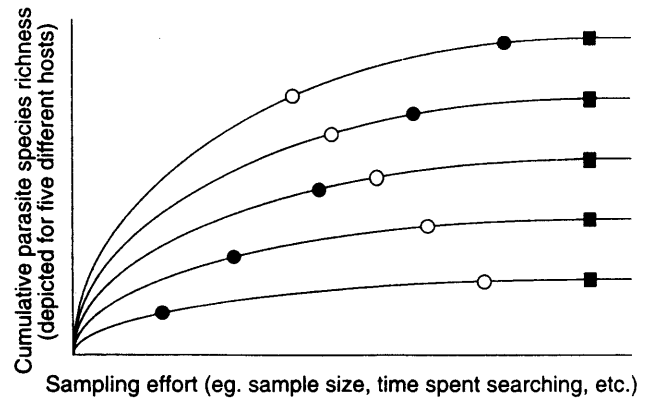
Ignorance of the shapes of these curves can yield spurious conclusions in comparative tests. For example, uneven sampling from each host species could lead to a spurious positive correlation between sampling effort and parasite species richness (closed circles). Using these data in conjunction with multiple regression to control for sampling effort, this seemingly linear relationship could lead to the erroneous conclusion that sampling effort is the sole determinant of species richness among the five hosts.

A false negative correlation between sampling effort and parasite species richness (open circles) could conceivably also result from uneven sampling effort, although it would be difficult to provide a reasonable biological explanation for such an outcome. What is worse is that any number of random patterns between sampling and richness may result, leading the investigator to assume falsely that sampling effort is unrelated to parasite species richness. Non-linear transformation of accumulation curves into straight lines does not solve this problem as different hosts would be represented by straight lines with different slopes and intercepts, which violates the assumptions of multiple regression[28].

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curves assume no such upper boundary to species richness. Only asymptotic curves can be used to extrapolate true species richness. Soberón and Llorente[11] present one non-asymptotic and two asymptotic accumulation curve models. Their exponential accumulation curve (Box 3) is suitable for sampling well-known taxa. When a host is sampled from only a limited part of its range, however, the non-asymptotic accumulation curves (Box 3) may be more realistic.

*The fitting of species-abundance distributions.* Another approach to estimating true species richness is to extrapolate a species-abundance distribution which, graphically, is a plot of the number of species against their relative abundances. Incomplete collections are truncated, ie. the species of the rare abundance classes have not been discovered, and the number of missing species can be estimated by fitting the theoretical distribution over the observed one. Four different models have been proposed[12], of which Preston's log-normal[13] is probably the best known (see Refs 14–19 for mathematical details.)

*Non-parametric estimators.* These may also be used for extrapolating true species richness. Colwell and Coddington[12] reviewed seven different non-parametric methods, and evaluated their performance using an empirical seed-bank data set. Palmer[20] also evaluated three of these methods, and compared their performance with two accumu-

lation curve models and Preston's log-normal model using a botanical data set. Although Palmer found that the non-parametric estimators performed best, his findings are not directly applicable to other data sets because performance of estimators depends on the underlying empirical species-abundance distribution of the data set being analyzed[11,12]. For example, using the exponential accumulation curve (Box 3) as a predictor, four different estimates of true species richness were calculated when four different species-abundance distributions were applied[21]. Also, the log-normal model performed worse than most other estimators on the botanical data set[20] but performed much better on a simulated data set[22]. Therefore, different extrapolation models may be more or less accurate for different data sets and sampling techniques[12,22,23].

None of the above methods has, to our knowledge, been tested on a complete data set of parasite species on different hosts. A pragmatic test to evaluate the performance of these models using known parasite data sets would increase confidence in the use of some of these methods for comparative studies of parasite species richness. Alternatively, the evaluation of estimators using simulated data can provide clues about the robustness of an estimator to changes in the distribution parameters, ie. changes in species richness and the dispersion of species abundances[22].

For example, we analyzed a data set on helminths found in black rats *Rattus rattus* with an unpublished program supplied by Robert K. Colwell (Dept of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3042, USA). Figure 2 illustrates that, for this particular data set, the Coleman estimator[24,25] quickly approaches the species-richness asymptote and remains stable while the Chao and Lee estimator[26] overshoots the asymptote.

To use these methods, estimates of sampling effort, presence/absence data for each individual host, and, for some methods, estimates of relative abundance of each parasite need to be recorded[12]. It is often the case that only summary statistics are published, rendering extrapolation methods impossible. In such cases, one way to control for sampling effort is multiple regression (see, for examples, Refs 3,9,27). In multiple regression, one (or more) specified variable (eg. sampling effort or body weight) is held constant so that the relationship between another pair of variables (eg. species richness and geographic range) can be assessed[28]. However, the use of multiple regression can be misleading (Box 2).

## Concluding Comments

The methods discussed above are useful in controlling for sampling effort

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### Box 3. Extrapolating Species Richness from Partial Accumulation Curves

The three accumulation curve models described by Soberón and Llorente[11] rely on different assumptions about the probability of finding an additional species. The first model is based on the exponential accumulation curve originally used by Holdridge et al.[42] and Miller and Wiegert[21]. This model assumes that, as new species are discovered, the probability of finding an additional species decreases in proportion to the current size of the list. Species richness as a function of sampling effort is given by:

$$S(t) = a \, (1 - e^{-bt}) \, / \, b$$

where $t$ is a unit of sampling effort such as time, $a$ is the increase in species richness at the beginning of sampling, and $b$ is a parameter that sets the species-richness asymptote $R = a/b$. The amount of sampling effort required to sample a certain proportion $q$ of the true species richness $R$ is given by:

$$t_q = -\ln(1-q) \, / \, b$$

Any particular values of the parameters $a$ and $b$ are approximations whose accuracy depends on the sampling effort expended up to that point in time[22]. The standard error associated with these parameters becomes smaller as sampling effort increases. The Marquardt procedure of SAS[43] may be used to estimate the standard errors of $a$ and $b$ (Ref. 21).

The second curve model was independently proposed by de Caprariis et al.[44] and Clench[45] and assumes that the probability of finding an additional species will improve (up to a point) as more sampling effort is expended and more experience in sampling is gained. Species richness as a function of sampling effort is given by:

$$S(t) = at / (1 + bt)$$

and sampling effort $t_q$ (see above) is given by $t_q = q / [b \, (1 - q)]$. Further details of this model and related models may be found in Refs 12,23,46.

A third model, the non-asymptotic logarithmic curve, assumes that the probability of adding a new species never approaches zero, either because the region sampled is too large or the taxa are not well-studied[11]. True species richness cannot be predicted under these conditions. Two different non-asymptotic accumulation curves originated from their biogeographic equivalents, the species-area curves. One is the log–log model[47,48] which has been incorporated into the standard species-area curve of island biogeography[49], the other is the log-linear model[50]. Continuous growth of the accumulation curve may also be due to over-sampling of a host. Over-sampling results from parasites being recorded that may have been picked up by the host accidentally, eg. by eating an unusual food item. Thus, a species-richness estimate is produced that is in excess of what can be considered meaningful in relation to the actual biological community under investigation. The problem in this situation is to determine when to stop sampling and whether to include very rare parasites in the species-richness count. One solution is to employ a modified species diversity index that is positively correlated with species richness and which can be used to rank communities comparatively (J.A. Harrison and P. Martinez, unpublished). However, the use of diversity indices is controversial[51,52], and further research is needed to determine the accuracy of this approach.

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in comparative studies of parasite species richness, but they are also relevant to other issues. Parasites are a mega-diversity group[12] with an overall species richness that could easily top ten million species, assuming that every animal and plant species has at least five host-specific parasites[29]. Since it would take several centuries to record all parasite species, given current effort levels[12], only accurate extrapolation methods will be capable of determining more precise estimates of parasite species richness on a global basis.

In the planning of research, it is important to note that sampling effort can be a confounding variable at different levels of investigation. For example, a common source of error in looking at slide preparations is the effort expended on each slide[30] and the number of slides of each faecal or blood sample examined (C. Müller-Graf, pers. commun.). To control for effects of sampling effort, one could monitor the accumulation of parasite species as the amount of time per slide increases, as the number of slides per host increases, and as the number of individuals sampled for a particular host species increases. Ideally, accumulation curves should be examined at each level of sampling and for all host species, host populations, or localities under consideration (see Refs 6,31).

Estimates of sampling effort should always be reported. The best estimate of sampling effort is sample size[3], which
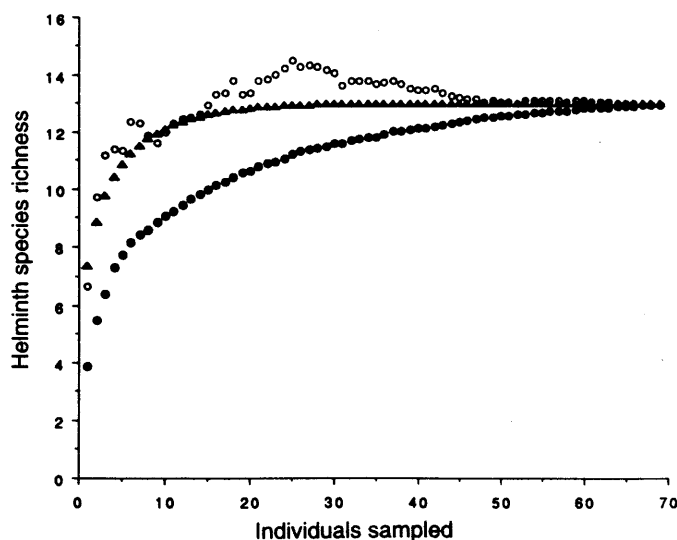


Fig. 2. Performance of two non-parametric estimators for a data set on helminths found in 69 black rats *Rattus rattus* caught in mangrove forests in Guadeloupe, French West Indies (unpublished data supplied by Serge Morand, Centre de Biologie et d'Écologie Tropicale et Méditerranéenne, Université de Perpignan, 66860 Perpignan, France). The lower accumulation curve (closed circles) gives the mean estimate of 100 curves each based on adding the samples in a random order. For this data set, the Coleman richness estimator (closed triangles) performs better than the Chao and Lee estimator (open circles).

unfortunately has often gone unreported[32]. Other estimates of sampling effort, including time spent searching, number of persons searching, number of collecting trips, amount of tissue or medium examined, host population size or range, or number of surveys or of citations, are only reliable if they correlate strongly with sample size.

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Bruno Walther, Peter Cotgreave and Dale Clayton are at the Department of Zoology, University of Oxford, South Parks Road, Oxford, UK OX1 3PS. Roger Price is at the Department of Entomology, Oklahoma State University, Stillwater, OK 74078, USA. Richard Gregory is at the National Centre for Ornithology, The Nunnery, Thetford, UK IP24 2PU. **Tel: +44 1865 271254, Fax: +44 1865 310447, e-mail: clayton@vax.ox.ac.uk**

# Techniques

# FISH Techniques for Constructing Physical Maps on Schistosome Chromosomes

## H. Hirai and P.T. LoVerde

*In an effort to provide useful information about parasites important in tropical diseases, the WHO has initiated genome mapping projects for a number of parasites. One goal of this effort is to establish physical maps of the genomes of the targeted parasites. Multicellular parasites (helminths) contain various numbers of chromosomes, some large, that condense during the cell cycle. Here, Hirohisa Hirai and Phil LoVerde present details of fluorescence in situ hybridization as a means to localize genes and DNA fragments to schistosome chromosomes. Although the techniques presented are for schistosome chromosomes, they are applicable to any system where the chromosomes condense at metaphase.*

TDR/WHO has undertaken an ambitious project to produce genome maps of preselected parasites[1]. One of the preselected organisms is *Schistosoma mansoni*, which has seven pairs of autosomal chromosomes and one pair of sex chromosomes (ZW for the female and ZZ for the male) (Fig. 1). We were able to modify standard cytogenetic techniques to initiate a genome-mapping project to localize genes and DNA elements on the chromosomes of *S. mansoni* using fluorescence in situ hybridization (FISH)[2]. The technique has been improved to localize small gene families[3]. More recently, we have established a yeast artificial chromosome (YAC) cloning system for the genome of *S. mansoni*[4]. In order to use the YAC library to develop a physical map of the *S. mansoni* genome, we improved the FISH technique to map individual recombinant YACs to specific schistosome chromosomes[4]. This review provides