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Efficiency of Adaptive Cluster and Random Sampling in Detecting Terrestrial Herpetofauna in a Tropical Rainforest

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Abstract

We sampled forest floor herpetofaunal communities in a monsoonal rainforest in South India for three consecutive years to evaluate the use of cluster sampling in estimating species composition and density. Our initial experimental design consisted of comprehensive random searches of multiple 25m^2 quadrats (SRS) for animals. After our initial season we found that most quadrats had zero animals detected and, when encountered, animals were spatially aggregated. To increase sampling efficiency and derive more precise density estimates, we shifted to adaptive cluster sampling (ACS). We compared the relative sampling efficiencies of ACS to SRS and the ability of the 2 methods to detect rare species. Adaptive cluster sampling failed to yield the more precise density estimates as predicted by statistical theory. However, ACS yielded more individual and rare species detections. Our results suggest the ACS assumptions should be carefully evaluated prior to use because it may not be appropriate for all rare, spatially aggregated populations. (WILDLIFE SOCIETY BULLETIN 34(1):59–68; 2006)

Key words

adaptive cluster sampling, amphibians, India, rainforest, reptiles, sampling efficiency, simple random sampling, species richness, rainforest.

Studies of terrestrial herpetofauna (reptiles and amphibians), a diverse group of animals with varied behaviors and habitat associations, face significant sampling challenges. Previous attempts to estimate the distribution and abundance of herpetofauna have used a variety of techniques, each with its own underlying assumptions, biases, and limitations (Heyer et al. 1994). Until recently, these deficiencies were seldom recognized or discussed. For example, sampling herpetofauna often produces estimation problems because of rarity and the patchy distribution of many species. The result is many sampling units containing zero animal-detections, and sampling becomes highly inefficient because little information is provided on the species. Recent modifications to traditional sampling methods have been proposed to address some of the often encountered problems in sampling natural populations (Thompson 1990, 1991, 2002, Thompson et al. 1992, Thompson and Seber 1996). These survey methods, collectively referred to as adaptive sampling are of interest to biologists because they have the potential to greatly increase efficiency of return of useful information (measured in terms of animals detected per unit effort and greater information on the ecology of the target species) as well as increase the precision and decrease the bias associated with estimates of population parameters. Theoretical work by statisticians demonstrates that the lack of precision in traditional sampling designs is most pronounced when sampling rare species with aggregated spatial distributions (Thompson and Seber 1996, Christman 2000).

In 1997 we initiated a study of the forest floor herpetofauna in tropical rainforests of south India. Past studies of leaf litter or forest floor/terrestrial reptiles or amphibians have used traditional random sampling procedures with rectangular quadrats of varying dimensions as the primary sampling unit (Lloyd et al. 1968, Inger 1980*a*,*b*, 1994, Campbell and Christman 1982, Jaeger and Inger 1994, Vonesh, 2001, Doan and Arriaga 2002, Hayek and Heyer, 2003). In India, the majority of herpetofaunal surveys have largely reported cumulative species lists, and studies attempting to estimate density or relative abundance are uncommon (Inger 1980*a*,*b,* Inger et al. 1984, Bhupathy and Kannan 1997, Malhotra and Davis 1991, Pawar and Birand 2001). We initially employed traditional quadrat sampling based on simple random or stratified random sampling. However, we quickly experienced sampling problems—the vast majority of our sample units contained zero detections. This experience led us to search for a more efficient sampling protocol.

The majority of herpetofaunal species are not randomly distributed but are associated with specific microhabitats (e.g., Fischer et al. 2004, Gillespie et al. 2004). If environmental variables are spatially correlated, then it is likely the animals associated with specific microhabitats also will be aggregated in their distribution. When animals are clustered, a better sampling strategy is to first stratify the populations according to expected densities (prior stratification based on preliminary survey data) and then to sample these strata in proportion to their expected abundance and variation (Cochran 1977, Hayek and Heyer 2003). However, prior information to allow stratification often is unavailable. As a result, conventional sampling designs like simple random sampling (SRS), or even stratified random sampling, often do not efficiently sample spatially aggregated populations (Thompson 1991). Therefore, estimates of population parameters (e.g., density per quadrat or population totals) are likely to be imprecise.

In such situations adaptive cluster sampling (ACS) has been proposed as a sampling design that may be more efficient (better precision for the same effort) than SRS (Thompson 1991, 2002,

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Thompson and Seber 1996). ACS allows the inclusion of additional sampling units (e.g. quadrats) in the immediate neighborhood of any quadrat in which the target species or taxonomic group is found. The advantages of ACS over SRS are believed to be 2-fold: 1) an increase in sampling efficiency resulting in more precise estimates of population parameters, and 2) an increase in the number of observations of the target species that may result in more reliable estimates of other population parameters such as species richness and composition, and relative abundance (Thompson and Seber 1996, Thompson, 2002, Hayek and Heyer 2003, Smith et al., 2003). These advantages should be especially pronounced for rare and clustered populations, such as many terrestrial and forest-floor herpetofauna.

Adaptive cluster sampling was first discussed in the statistical literature >10 yrs ago and recently reviewed by Smith et al. (2004). ACS methods are becoming better known—they have been discussed in at least 4 textbooks (Thompson and Seber 1996, Krebs 1999, Thompson 2002, Williams et al. 2002), the March 2003 issue of Ecological and Environmental Statistics was devoted exclusively to ACS, and several web sites provide examples (e.g, www.stat.lsu.edu/faculty/moser/exst7012/adaptive.pdf). However, the methods still seem to be unfamiliar to many biologists and few real-world examples have been published (Smith et al. 2004). For the most part, the literature on ACS has been theoretical (Thompson 2003) or based on simulation studies (Smith et al. 1995). We were motivated to write this paper because we believe 1) many researchers may be unfamiliar with ACS methods, and 2) these methods may prove useful in many herpetological studies.

We compared estimates of population abundance per quadrat and population totals from SRS and ACS based on data collected from forest floor herpetofauna. Our comparison of methods focused on three issues: 1) changes in sampling efficiencies as measured by the proportion of non-zero quadrats, 2) changes in the precision of density estimates comparing ACS to SRS, and 3) information content, in terms of the auxiliary information on species ecology and behavior gained through ACS. We also compared the 2 sampling methods in terms of estimates of species richness, sampling of rare species, and insights to species habitat associations.

The study results reported are not meant to be an exhaustive evaluation of ACS. A thorough discussion of studies done to date using ACS is found in Smith et al. (2004). To the best of our knowledge, however, there has not been an evaluation of the utility of ACS for sampling terrestrial herpetofauna.

Study Area

Our study was conducted from 1997–1999 in the Kalakad-Mundanthurai Tiger Reserve (KMTR) of the Western Ghats Mountains, south India (Fig. 1). The Western Ghats mountain ranges extend from near the southern tip of India (8°N) northward to River Tapti (21°N), over a distance of nearly 1600 km. KMTR contains nearly 400 km^2 of relatively undisturbed and continuous rainforests. We sampled the forest floor herpetofauna in this area at 3 sites representing 3 distinct watersheds; Kannikatti (700 m), Sengaltheri (200 m), and Kakachi (1,200 m) which represented the altitudinal and rainfall regimes in the area (Fig. 1). Within each study site, we selected a large study area (>1 km^2) to be representative of the heterogeneity in forest floor conditions at that site.

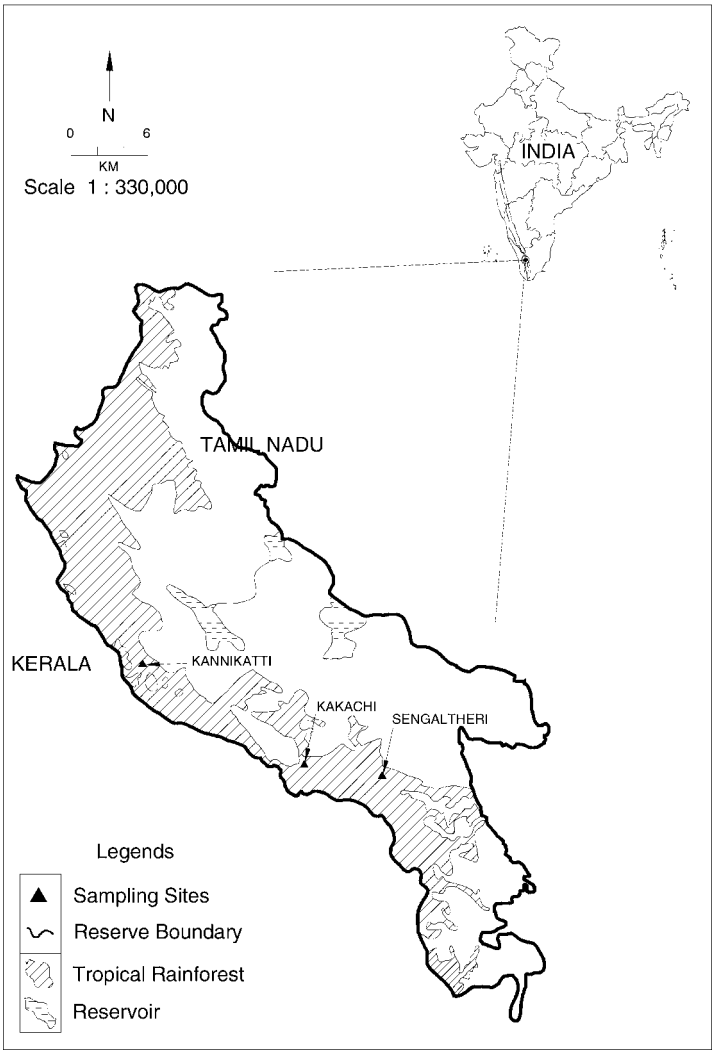


Figure 1. The Western Ghats Hill Ranges, south India, showing the location of the Kalakad-Mundanthurai Tiger Reserve and 3 areas studied from 1997–1999.

The vegetation of KMTR is primarily that of *Cullenia-Mesua-Palaquium* association, although *Dipterocarpus-Anacolosa* forests occur in the lower elevations (<800 m; Pascal 1988). Annual rainfall was around 300 cm, nearly 80% of which occurred during the southwest monsoon (June–September). Temperature ranged between 8°C in December to 31°C in March. We carried out sampling in 3 seasons (based on rainfall and temperature); the southwest monsoon (June–September), the northeast monsoon (October–January), and the dry season (February–May).

Methods

We envisioned each study area as being overlaid with a grid used to define N square sample units (quadrats). For each area, 1 boundary of the grid bordered the main drainage of the watershed and extended upslope for >1000 m. Within this area, we selected an initial sample of n quadrats via SRS.

Selection of Quadrat Size

Within each site, we used quadrat sampling to estimate density and species richness of the rainforest leaf litter herpetofauna. Quadrat sampling methods for forest litter herpetofauna were formalized by Lloyd et al. (1968), and improved upon by later researchers (Jaeger and Inger 1994, and references therein). To select an appropriate quadrat size, varying dimensions (10×10 m, 8×8 m and 5×5 m) of quadrats initially were evaluated. The final selection of quadrat size was based on the sample size that would yield the most precise estimates of density for equal effort, provide sufficient spatial replication and extent, and be efficient in detecting reptiles and amphibians in the leaf litter. We found the 10×10 m and 8×8 m quadrats to be too large for effective and efficient sampling (too high a likelihood of missing animals because of movement) and consequently, we used a quadrat size of 5×5 m.

Adaptive Cluster Sampling

Adaptive cluster sampling (ACS) has been used to address the problems associated with sampling rare, clustered populations. When such populations are sampled by conventional methods (e.g., SRS) estimates of density and population totals often are imprecise and sampling efficiency is low (Thompson 1991, 1992, Thompson and Seber 1996). ACS is based on an initial random sample of units but the sampling process is adapted based on results from the initial sample. Whenever the variable of interest satisfies a pre-specified condition (in the present case the presence of $\geq$1 individual of forest floor amphibian or reptile within the quadrat), additional units, called secondary units, sharing a common boundary with the original or primary unit are added to the sample (Thompson and Seber 1996). The process continues until the cluster of neighboring quadrats are surrounded by quadrats failing to meet the criterion.

All neighboring quadrats that collectively meet the criterion (e.g., $y > 0$) are called a network. The quadrats bordering each network that fail to meet the criterion are called edge quadrats. Network plus edge quadrats constitute the ACS cluster. Note, that if any of the quadrats in a network are included in the initial random sample, the entire cluster ultimately will be included. In addition, it is important to note that any quadrat selected in the original sample that does not meet the criterion (i.e., $y = 0$) is considered a network of size 1. The grouping of quadrats into networks constitutes a partitioning of the initial population based on the size of the initial random sample (Williams et al. 2002).

The targeted animals in our study were reptiles including geckos, skinks, agamid lizards and snakes, and four genera of amphibians (*Indirana*, *Micrixalus*, *Philautus*, and *Rana*). All amphibian genera were frogs. We carried out ACS between 0700–1730 hours for reptiles and amphibians. We included herpetofauna found on or in the leaf litter or within 2 m of the forest floor in the sample. We identified an approximate area of 1 km^2 as the target area for ACS at each of the three sites in KMTR. We carried out sampling separately for reptiles and amphibians and evaluated results individually.

Results presented in this paper treat the initial random sample (i.e., the primary sample units) as composing a SRS of the study areas. The set of primary sample units plus additional units sampled adaptively represented the ACS sample.

We separated quadrats within a network by 1 m to avoid excessive disturbance that may affect the likelihood of detecting an animal in any adjacent quadrats. We also maintained $\geq$20 m between networks because of a concern for disturbance effects arising from sampling and habitat measurements. If the 20 m spacing overlapped with a sample unit selected in the initial random sample (an unusual occurrence), we selected a new quadrat at random. Sampling within a network stopped when the network was surrounded by quadrats with no animals (edge quadrats). Additional details of ACS sampling are described in Thompson and Seber (1996: Chapter 4) and Smith et al. (2004). All reptiles and amphibians detected in a quadrat were collected to prevent their re-sightings. After identification and completion of a network sample, animals were released to the original site of collection.

Assumptions

The assumptions of quadrat sampling for herpetofauna are discussed in Jaeger and Inger (1994). Most relevant to the results reported here is the issue of detectability. Area constrained, destructive sampling generally assumes that all individuals present in a quadrat are observed. This certainly is not true for individuals that were below ground (e.g., caecilians) or arboreal at the time of sampling. We attempted to partially address this issue by sampling trees and shrubs to 2 m and by pooling samples across 3 seasons to include a range of above-ground activity periods. However, since detectability was not estimated in this study, our counts reflect an index of density and not an absolute density measure.

Thompson and Seber (1994, 1996) discuss the issue of incomplete detectability. One effect is that imperfect detectability can influence which quadrats were selected for ACS. Another is that estimates of density, or population totals, will be biased low if detectability is $<$1. The effect on variance estimates for SRS and ACS is to add an identical amount of variance to each sampling method. Therefore, our comparisons of the relative efficiency of the SRS and ACS estimators should only be slightly affected, tending to move the ratio closer to 1.0.

Search Method

The quadrat area was demarcated using a nylon rope on the forest floor, and 2 observers thoroughly searched all microhabitats. We moved fallen logs and rocks and, whenever possible, overturned them to search for animals. Two observers began searching from 2 opposite corners of the quadrat and moved toward the center in a circular fashion. As they moved, they searched leaf litter and other materials on the forest floor and then moved them toward the outside of the quadrat. We used a "search stick" to disturb animals hidden in the litter and under rocks and to move them toward the center of the quadrat, thereby helping in detection and capture. Disturbance sampling extended upward into the vegetation to a height of 2 m. We limited sampling to this height because of rapid declines in detectability beyond 2 m. Since this method was destructive and caused disturbance to the area sampled, we selected a new set of random quadrats each sampling season. This created the possibility of quadrat overlap among seasons but this did not occur.

Estimation of Population Density

Estimation methods for the mean and variance in density per quadrat or total number of animals in the study area based on SRS

are well known (e.g., Cochran 1977, Schaeffer et al. 1996). Those for ACS, however, are less familiar. Two types of ACS estimators exist (Thompson and Seber 1996): 1) one based on initial intersection probabilities between the SRS quadrats and the networks (Horvitz-Thompson estimator), and 2) one based on number of actual intersections between SRS quadrats and networks (Hansen–Hurwitz estimator). Network inclusion probabilities for the 2 methods are computed on the basis of initial intersection probabilities or initial number of intersections, respectively. To estimate mean density per quadrat ($\hat{\mu}$), we used the estimator based on number of intersections which is closely related to the Hansen–Hurwitz estimator (Thompson and Seber 1996). Greater efficiency in ACS may sometimes be achieved with the Horvitz-Thompson estimators, but there is no evidence that different estimators would have appreciably affected the results reported here.

We assumed a study area of N quadrats with a selection of n quadrats based on a SRS. For the i^{th} quadrat in the initial sample (primary sample unit i), we computed the average abundance per quadrat (w_i) based on the m_i quadrats in its network. Any quadrat that did not meet the criterion of $y > 0$ was a network of size $m_i = 1$. If a given network i included k primary sample units, we counted it k times in the estimate of the w_i's. The estimator of w_i is:

$$w_i = \frac{1}{m_i}\sum_{j=1}^{m_i} y_j, i = 1, \ldots, n$$

The estimate of the mean ($\hat{\mu}$) and variance ($\hat{\sigma}^2[\hat{\mu}]$) in density per quadrat is:

$$\hat{\mu} = \frac{1}{n}\sum_{i=1}^{n} w_i$$

$$\hat{\sigma}^2[\hat{\mu}] = \frac{(N-n)}{Nn(n-1)}\sum_{i=1}^{n}(w_i - \hat{\mu})^2$$

Adaptive cluster sampling adjusts the sampling probabilities for each primary sample unit based on the size of its neighborhood. Estimation requires calculation of the inclusion probabilities of the sample units within each network. That is, as the probability of at least 1 member of a neighborhood being selected in the initial random sample is higher for a large neighborhood than a small one, it is more likely that all sampling units of a large neighborhood eventually will be sampled. In contrast, the sampling probabilities for all units in SRS are equal.

Estimation of Species Richness

We employed 2 methods to estimate species richness (S) from our data. The first was based on interpolated estimates of S using rarefaction (Coleman 1981, Coleman et al. 1982). Rarefaction methods estimate species richness as a function of sample size n (where n = the number of quadrats in the sample) by taking repeated random samples of size k ($k = 1, 2, \ldots, n$), without replacement, from the collection of all sampled quadrats (Colwell 1997). By systematically varying k and repeating the sampling process many times for each value of k, the species accumulation curve and its variability are estimated. This curve reaches an asymptote at S, the total number of species observed in the entire sample.

Estimates of S based on survey data generally are biased low because of heterogeneity in species detectabilities and probabilities of detection <1 (Boulinier et al. 1998, Williams et al. 2002). Therefore, we used an extrapolation method to compute an asymptotic estimate of S using a second-order jackknife estimator (Burnham and Overton 1978, 1979, Colwell 1997). Extrapolation methods estimate S by including species believed to be present in the survey area but unobserved in the sample because of imperfect detectability. The sampling process, as a function of n, was simulated as for the rarefaction analyses. Randomization methods allowed us to compare SRS with ACS after controlling for the number of quadrats sampled.

Spatial Patterns in the Distribution of the Herpetofauna

Using simulated sampling methods as described above, we tested for spatial aggregation in the distribution of reptiles and amphibians by evaluating accumulation curves of the number of individuals detected as a function of number of quadrats sampled. The magnitude of difference between the slopes of the ACS and SRS accumulation curves indicates the degree of spatial aggregation of individuals at the scale of 25-m^2 plots.

We computed estimates of species richness and individual's accumulation curves separately for 3, quadrat-based data sets: SRS, ACS, and ACS network (edge quadrats removed). We based all simulation results, computed with program EstimateS Version 6.01b (Colwell 1997), on 500 randomizations of the data for each sample size n using sampling without replacement. Maximum sample sizes in each simulation were equal to the size of the smallest data set and ranged from 1–576 for reptiles and 1–200 for amphibians.

Comparing SRS and ACS

We first evaluated whether ACS and SRS provided similar estimates of taxon density by comparing their point and 95% interval estimates. We then evaluated if ACS offered advantages over SRS by addressing 4 questions: 1) Are ACS estimates more efficient as measured by the ratio of their standard errors ($\hat{\sigma}^2[\mu]_{SRS}/\hat{\sigma}^2[\mu]_{ACS}$)? 2) How do efficiency ratios change if we include information on the relative costs of obtaining ACS versus SRS samples? 3) Can we estimate other ecological parameters (i.e., $\hat{S}$) more efficiently with ACS than with SRS? and 4) Does ACS provide additional insights into the ecological relationships of the focal organisms that are less available from traditional random sampling schemes? To address question 1 required that we adjust the initial estimate of the population variance ($\hat{\sigma}^2$) from SRS to account for the larger size of the ACS sample. This was done according to: $\hat{\sigma}^2_{SRS} = (1 - \frac{n_{ACS}}{N})(\hat{\sigma}^2/n_{ACS})$, where n_{ACS} = number of quadrats in the ACS sample (including edge quadrats), and N = total number of quadrats in the study area.

To address question 2, we took into consideration the cost/quadrat which allowed us to compare the relative efficiency of ACS to SRS for fixed cost (Thompson and Seber 1996). We assumed a linear cost function with an initial set up cost of c_0, a cost c_1 and c_2 for each SRS and ACS quadrat, respectively, an initial sample size of n_1 and a total ACS sample size n_A.

To address question 3, we compared ACS and SRS estimates of species richness and cumulative detections abundances based on accumulation curves. Finally, to address question 4 we evaluated

Table 1. Estimates of leaf litter reptile density (animals ha^{-1}) and relative sampling efficiency from the Western Ghats, south India (1997–1999), based on 2 different sampling methods. The standard error (SE) estimates from a simple random sample (SRS) have been adjusted using the sample size (*n*) from adaptive cluster sampling (ACS).

	Sampling method						
	SRS			ACS			Relative efficiency
Site	*n*	Density	SE	*n*	Density	SE	Ratio[b]
KMTR[a]	576	109.03	8.52	1,095	112.83	12.01	0.71
Sengaltheri	213	122.07	14.17	425	126.25	19.91	0.71
Kakachi	218	69.72	10.82	361	71.56	14.03	0.77
Kannikatti	145	148.97	20.06	309	155.17	29.78	0.67
Taxa							
Agamids	576	10.42	3.74	530	10.42	3.50	1.07
Geckos	576	47.22	6.68	711	48.60	7.52	0.89
Skinks	576	48.61	7.22	713	49.08	7.85	0.92
Snakes	576	2.78	1.48	505	2.78	1.35	1.11

[a] Kalakad-Mundanthurai Tiger Reserve.
[b] Ratio = $\hat{\sigma}[\mu]_{SRS}/\hat{\sigma}[\mu]_{ACS}$.

information on the spatial distribution of the leaf litter herpetofauna and patterns of species co-occurrence available from SRS and ACS.

To compare sampling methods, we obtained estimates from 3 data sets: 1) the SRS quadrat sample; 2) the ACS sample including network quadrats only; and 3) the "true" ACS sample including network and edge quadrats. Data set (2) is not "true" ACS but was included because changes to the stopping rule (currently defined by edge quadrats that fail to meet the inclusion criterion) and optimal cluster sizes are active areas of research among statisticians (Brown and Manly 1998, Brown 2003, Smith et al. 2004).

Results

Density and Standard Error Estimates

For reptiles, all estimates of density from ACS fall within the 95% confidence interval of those from SRS (Tables 1, 2). Thus, the point estimates of total reptile density across all 3 study sites were similar. We observed this same pattern when we compared the density estimates by taxonomic group (Table 1). When we compared the precision of SRS and ACS estimates for reptiles, we found little evidence that ACS increased sampling efficiency relative to SRS. In fact, the ratio $\hat{\sigma}[\mu]_{SRS}/\hat{\sigma}[\mu]_{ACS}$ was <1.0 in all locations and for 2 of the 4 taxa comparisons. Surprisingly, snakes, which do not form clusters, had a ratio of 1.11. In general, these results suggest that for reptiles in KMTR, SRS provided more precise density estimates than ACS (Table 1).

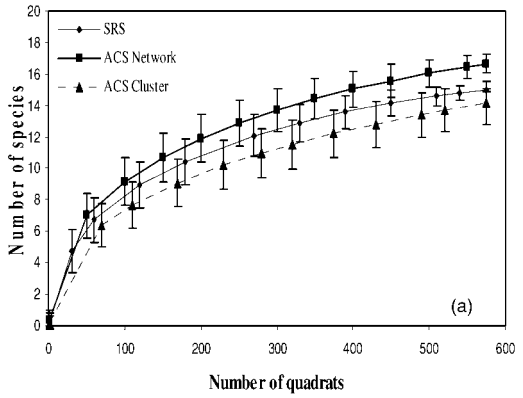
SRS and ACS density estimates for amphibian taxa also were similar; we observed similar point estimates and overlapping interval estimates for both study area and taxonomic group comparisons (Table 2). The greatest difference in point estimates occurred for Kakachi. The ACS estimate was higher at Kakachi because, on average, secondary quadrats had more animals than the primary quadrats.

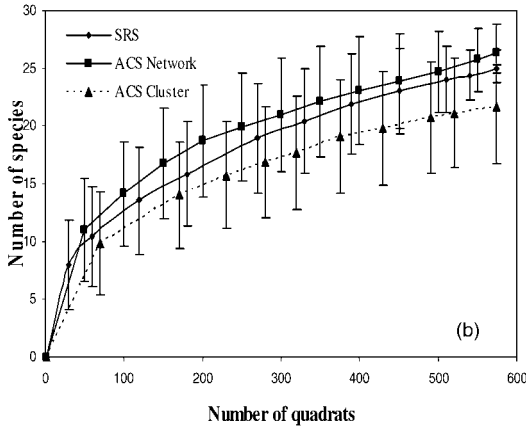
Comparisons of the relative precision of the SRS and ACS amphibian density estimates showed patterns similar to those observed for reptiles. Consistently, ACS estimates were less precise than SRS when adjusted to a common sample size

Table 2. Estimates of leaf litter amphibian density (animals ha^{-1}) and relative sampling efficiency from the Western Ghats, south India (1997–1999), based on 2 different sampling methods. The standard error (SE) estimates from a simple random sample (SRS) have been adjusted using the sample size (*n*) from adaptive cluster sampling (ACS).

	Sampling method						
	SRS			ACS			Relative efficiency
Site	*n*	Density	SE	*n*	Density	SE	Ratio[b]
KMTR[a]	102	317.65	16.30	779	349.33	42.36	0.38
Sengaltheri	24	483.33	45.71	193	485.50	116.93	0.39
Kakachi	31	296.77	21.32	234	373.42	58.34	0.37
Kannikatti	47	246.81	21.57	352	263.91	54.41	0.40
Taxa							
Rana	102	160.78	20.97	355	160.78	36.12	0.58
Micrixalus	102	117.65	14.63	290	103.02	22.83	0.64
Indirana	102	11.76	6.15	122	15.53	7.72	0.80
Philautus	102	50.98	9.40	275	42.63	14.27	0.66

[a] Kalakad-Mundanthurai Tiger Reserve.
[b] Ratio = $\hat{\sigma}[\mu]_{SRS}/\hat{\sigma}[\mu]_{ACS}$.





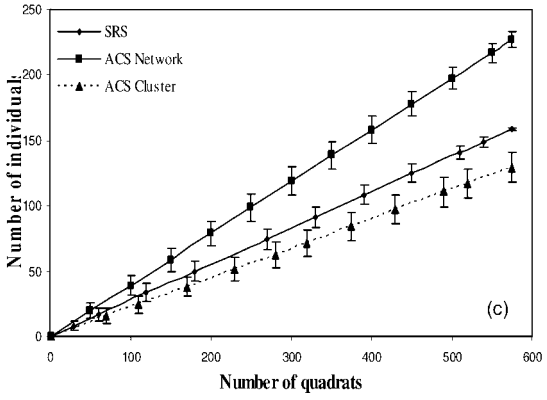


Figure 2. (a) Rarefaction species accumulation curves (±1 SE) for reptiles based on 500 random samples (without replacement) of quadrats from the simple random sample (SRS), adaptive cluster sample (ACS), and the ACS excluding edge quadrats (ACS – edge). Samples from Kalakad-Mundanthurai Tiger Reserve, 1997–1999. (b) Second-order jackknife species accumulation curves (±1 SE) for reptiles based on 500 random samples (without replacement) of quadrats from the simple random sample (SRS), adaptive cluster sample (ACS), and the ACS excluding edge quadrats (ACS – edge). Samples from Kalakad-Mundanthurai Tiger Reserve, 1997–1999. (c) Individual's accumulation curves (±1 SE) for reptiles based on 500 random samples (without replacement) of quadrats from the simple random sample (SRS), adaptive cluster sample (ACS), and the ACS excluding edge quadrats (ACS-edge). Samples from Kalakad-Mundanthurai Tiger Reserve, 1997–1999.

(Table 2). This was true for density estimates for all amphibians by study area and for taxonomic groups pooled across study areas. For almost all comparisons of relative efficiency, for both reptiles and amphibians, $\hat{\sigma}[\mu]_{SRS} > \hat{\sigma}[\mu]_{ACS}$ prior to adjusting the SRS estimate for the ACS sample size. Thus, efficiency comparisons that do not correct for different sampling intensities would be misleading.

Relative Efficiencies Considering Different Sampling Costs

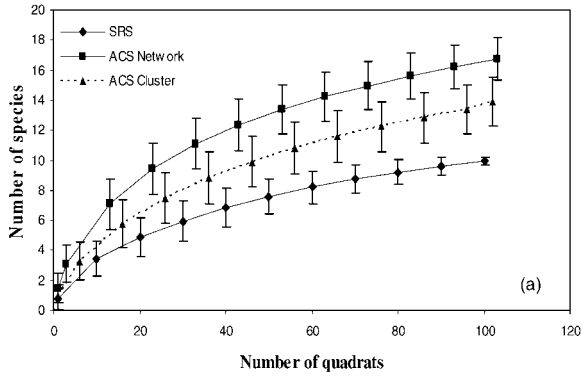
On average, we were able to sample 3 ACS for every SRS quadrat because of less equipment setup time and decreased time to locate and move between primary sample units. Including this information reduced the standard errors of the ACS estimates. Using the amphibian taxon *Rana* as an example, and setting $c_1 = 3c_2$, $n_1 = 102$, and $n_A = 355$ (Table 2) we estimated bounds on the relative efficiency of ACS to SRS of $0.58 < 0.80 < 1.08$. This led to the conclusion that the "true" value of relative efficiency lies between 0.58 and 1.08. When we carried out similar calculations for other taxa and study areas, the relative efficiency of ACS improved but the general conclusion that SRS was more efficient than ACS did not change.

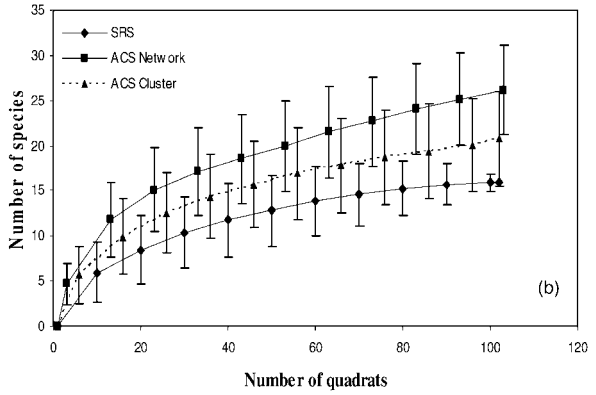
Species Richness

For reptile sampling, we sampled a total of 576 primary quadrats, 52 secondary quadrats, and 467 edge quadrats in 3 seasons and at the 3 sites in KMTR. We recorded a total of 17 species (based on 249 individuals) by ACS, and recorded 15 species (159 individuals) by SRS. The species accumulation curves and species richness estimates based on the 2 sampling methods were similar, but ACS estimates were lower for both the interpolation estimator (Fig. 2a) and the extrapolation estimator (Fig. 2b). Thus, information on the true number of reptilian species in KMTR was accumulating less quickly with ACS. However, when we restricted the richness estimators to just the network quadrats (ACS – edge), the rate of encountering rare species was greater than SRS. This result indicates that reptiles were spatially clustered but network sizes were small.

For amphibians we sampled 102 primary quadrats, 85 secondary quadrats, and 592 edge quadrats. The ACS sampling detected 20 species based on 366 individuals. In comparison, SRS detected only 10 species based on 87 individuals. Both the interpolated (Fig. 3a) and extrapolated (Fig. 3b) species accumulation curves for ACS were consistently above those for SRS indicating a faster rate of encountering new species with ACS. For fixed sampling effort, ACS resulted in higher estimates of S than SRS. This pattern was even more pronounced when we confined sampling to the network quadrats only.

Importantly, none of the estimators from either sampling method for either reptile or amphibian reached an obvious asymptote. Based on the jackknife estimator, 28 and 21 species were estimated for reptiles and amphibians, respectively. This suggests that further sampling, or use of different sampling methods, would have detected additional species.





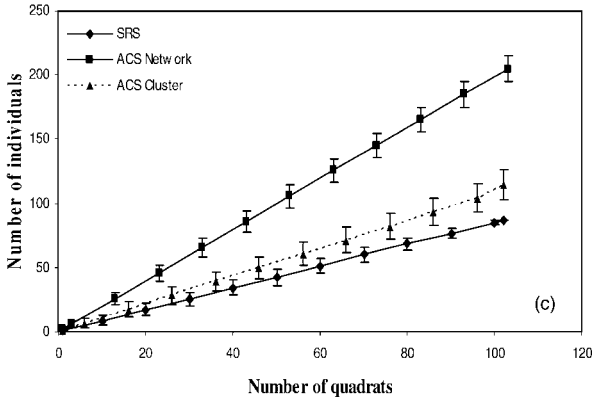


Figure 3. (a) Rarefaction species accumulation curves (±1 SE) for amphibians based on 500 random samples (without replacement) of quadrats from the simple random sample (SRS), adaptive cluster sample (ACS), and the ACS excluding edge quadrats (ACS – edge). Samples from Kalakad-Mundanthurai Tiger Reserve, 1997–1999. (b) Second-order jackknife species accumulation curves (±1 SE) for amphibians based on 500 random samples (without replacement) of quadrats from the simple random sample (SRS), adaptive cluster sample (ACS), and the ACS excluding edge quadrats (ACS-edge). Samples from Kalakad-Mundanthurai Tiger Reserve, 1997–1999. (c) Individual's accumulation curves (±1 SE) for amphibians based on 500 random samples (without replacement) of quadrats from the simple random sample (SRS), adaptive cluster sample (ACS), and the ACS excluding edge quadrats (ACS – edge). Samples from Kalakad-Mundanthurai Tiger Reserve, 1997–1999.

Encounter Rates

Many sampling designs are intended to maximize the rate of encounter with the focal organisms. This was true in the current study where we sought information on microhabitat associations of the sampled species. Sampling efficiency can be directly measured by the percent of quadrats with animals. For reptiles 91 of 576 (16%) quadrats sampled by SRS and 143 of 1,095 (13%) quadrats sampled by ACS (including edge quadrats) contained animals. For amphibians, 48 of 102 (47%) quadrats sampled by SRS and 366 of 770 (47%) quadrats sampled by ACS contained animals.

It also is possible to assess sampling efficiency by comparing the slopes of the individual's accumulation curves for ACS and SRS (Figs. 2c, 3c). A greater efficiency would be characterized by a steeper slope. For both reptiles and amphibians, the rate at which we encountered individuals in ACS and SRS were very similar. Differences in encounter rates were only evident when we removed the ACS edge quadrats from the sample. Thus, the initial gains in encounter rate, which occurred because of spatial aggregation (see below), were lost when sampling extended beyond the boundary of the network to include edge quadrats.

Spatial Distribution Patterns of Forest Floor Herpetofauna

Both sampling methods clearly demonstrate that most forest floor reptiles and amphibians taxa in KMTR were rare; the majority of quadrats sampled by either method contained no animals. In addition, by comparing the rate of detection of individuals in SRS quadrats with those in ACS network quadrats (ACS – edge) it is possible to test for spatial aggregation of the taxa. This is done, after controlling for sample size, by a visual comparison of the slopes of the individual's accumulation curves—the difference in slope between sampling methods is a measure of spatial aggregation.

For reptiles and amphibians, the individual's accumulation curves had much steeper slopes for ACS network quadrats than for SRS quadrats (Figs. 2c, 3c). This was more pronounced in amphibian taxa, perhaps a consequence of amphibians being more abundant (cf. Tables 1, 2). Both reptiles and amphibians in KMTR showed evidence of spatial clustering; they were more likely to occur in adjacent quadrats than expected at random (Figs. 2c, 3c). This result is independent of sampling intensity and occurred because some reptile and amphibian taxa were clustered at the network scale (~50–300 m^2). Thus, ACS provided information on the spatial aggregation patterns for both amphibians and reptiles that would have gone unobserved with SRS.

Measures of the relative efficiency of SRS and ACS were similar between reptile and amphibian communities (Tables 1, 2). This occurred despite the fact that amphibians showed a greater degree of spatial aggregation (Table 3). Comparison of the sizes of networks with $\geq$1 animal showed clear differences in network size. Overall, the mean size of amphibians networks were 3–4 times $>$ reptile networks (Table 3). Further, comparisons of the mean number of individuals/quadrat showed amphibians to be 3–5 times more abundant at the network scale. Both these results indicate that amphibians were more clustered (greater network

Table 3. Mean network size (number of 25 m^2 quadrats), and mean number of individuals per network for leaf litter reptile and amphibian taxa sampled via adaptive cluster sampling (ACS) in the Kalakad-Mundanthurai Tiger Reserve, south India 1997–1999.

Taxon	Mean network size (SE)	Mean number of individuals per network (SE)
Reptiles		
Geckos	1.40 (0.10)	1.63 (0.10)
Agamids	1.00 (—)	1.50 (0.22)
Skinks	1.33 (0.10)	1.79 (0.11)
Snakes	1.00 (—)	1.00 (—)
Amphibians		
Rana	3.61 (0.67)	8.00 (2.15)
Philautus	2.22 (0.64)	2.67 (0.75)
Micrixalus	2.15 (0.44)	2.70 (0.53)
Indirana	1.00 (—)	1.00 (—)

size) and more abundant (greater number of individuals/network) than reptiles.

It also is informative to compare network statistics separately by taxon within the reptile and amphibian communities. Within reptiles, we found that agamids and snakes showed no clustering (mean network size = 1.0), but geckos and skinks formed networks ranging in size from 1–5 quadrats (mean ~1.30; Table 3). At the scale of network quadrats (25-m^2), clustering was apparent for all taxa but snakes (Table 3). For amphibians, the most pronounced spatial clustering was for species in the genera *Rana* and *Philatus* with the other taxonomic groups showing patterns of spatial aggregation similar to reptiles (Table 3).

Discussion

Until the work of Thompson (1990, 1991) and Thompson and Seber (1996), classical sampling theory lacked a theoretical framework to adjust sampling location based on the spatial pattern of animal abundance. This often led to an inefficient allocation of sampling effort and imprecise estimates of abundance for animals that were rare and spatially aggregated. In fact, it was our initial experiences in KMTR of devoting considerable effort to sampling and searching many quadrats with no animals detected that led us to look for a more efficient sampling protocol.

The density estimates from the SRS and ACS sampling protocols were similar with overlap of their 95% confidence intervals occurring in all cases. Thus, estimates from adaptive sampling designs are directly comparable to previously published studies based on traditional random sampling designs. However, the precision of the estimates was not consistently better for ACS compared to SRS as expected by statistical theory for species that are rare and spatially aggregated (Thompson and Seber 1996). For reptiles, sampling efficiency, as measured by the ratio $\hat{\sigma}[\mu]_{SRS}/\hat{\sigma}[\mu]_{ACS}$, generally was better for SRS. For amphibians, sampling efficiency was consistently better for SRS. These differences are surprising given that amphibians had larger and more variable network abundances than reptiles; conditions that should favor ACS. The relatively poor performance of ACS may be attributable to the fact that few quadrats contained >3 individuals. Thus, the degree of possible aggregation and the amount of within network variance in abundance were small because almost all taxa were rare even within networks. If abundances within networks were higher and networks were larger, we believe ACS would have provided more precise estimates than SRS.

Thompson and Seber (1996) summarize characteristics of the sampled population that should lead to greater efficiency of ACS relative to SRS. These include, population rarity, high within-network variance in number of animals, similar sample sizes, edge quadrats being less "costly" to sample then network quadrats, and lower sampling costs for ACS quadrats. We address, below, the degree to which our ACS data set met these characteristics.

We generally met the first criterion because most reptile and amphibian taxa in our study areas were rare and clustered, but clusters were small and generally contained few animals. We did not consistently meet the second criterion. Within-network variance was generally low and contributed little to overall variance in the density estimates. An exception was the genus *Rana* which had relatively large within-network variance but still was more precisely sampled by SRS. Least variable were the agamids and snakes which only occurred in networks of size 1. Also, with the exception of *Rana* species, the number of individuals per network quadrat was seldom >3, even when networks were large.

We did not fully meet the third criterion. Sample sizes, ACS relative to SRS, were 1,092–576 for reptiles and 677–102 for amphibians. The large increase in ACS sample size occurred because network sizes were small for both reptiles and amphibians and we sampled many edge quadrats. We did not meet the fourth criterion of lower sampling costs for edge than network quadrats. Because most animals were hidden, all quadrats had to be searched intensely. Sampling edge quadrats added appreciably to the "costs" of ACS sampling both in time spent and in the lack of biological information gathered. Finally, we did meet the fifth criterion—sampling costs were less for ACS quadrats. However, the number of ACS quadrats was substantially larger than the number of SRS quadrats. This condition makes it unlikely that ACS will be more efficient than SRS unless cost differences are very large (Thompson and Seber 1996). In summary, our failure to achieve more precise density estimates from ACS may be a consequence of our failure to meet all the sampling characteristics listed by Thompson and Seber (1996) that favor ACS over SRS.

More precise estimates of density and abundance were not the only goals of our research. Estimating species richness and documenting the existence of rare species also were important research objectives. This information is particularly valuable for the rainforests of south India where the herpetofaunal have been poorly studied. Both sampling methods allowed us to document species composition, the spatial distribution of the herpetofauna, and whether different taxa showed similar, or distinct, habitat relationships. However, we believe that ACS helped us address these objectives more effectively than SRS. Our results suggest that ACS was marginally more efficient in 1) estimating species richness because rare species were more likely to be detected—this result was particular evident for amphibian species, 2) providing larger sample size for habitat studies of the focal taxa, and 3) documenting the degree of spatial aggregation, in terms of both multi-species assemblages and multi-individual aggregations.

Our results indicate that when edge quadrats surrounding the ACS network were excluded, differences between sampling methods were pronounced. Based on network quadrats alone, we encountered animals and detected rare species more efficiently. In our study edge units added appreciably to sample size but did not contribute to more precise estimates of density. This suggests that changes to the stopping rule, perhaps after reaching some predetermined network size, may make ACS more efficient (Brown and Manly 1998). Smith et al. (2004) describe ongoing work on adaptive sampling designs that do not require a neighborhood so as to eliminate edge units.

Our failure to observe increases in the precision of our density estimates with ACS is similar to the study by Smith et al. (2003) on freshwater mussels and for some more recent studies reviewed by Smith et al. (2004). However, we caution that it may be premature to abandon adaptive sampling methods based on the results of our studies. Admittedly, there was little evidence in support of ACS for the reptile and amphibian communities in KMTR even for the amphibian species which occurred in larger spatial aggregations than the reptiles. However, the precision of the ACS density estimates became more similar to those from SRS when we evaluated the reduced cost of sampling neighboring quadrats.

Sampling methods that provide even marginal increases in precision over traditional sampling designs are highly desirable. Increases in the precision of estimates are of obvious advantage to better understand the structure of ecological communities. They also are important for long-term monitoring programs designed to detect change in abundance of individual species or whole communities. Having more precise estimates of relevant parameters greatly increases statistical power and the likelihood of detecting a population change over time or space when one has occurred. Given the concern over global declines in amphibian populations (e.g., Wake 1991, Bury 1999, Houlahan et al. 2000), there is great need to design monitoring programs that can detect smaller changes in abundance over shorter time periods. ACS was not consistently better than SRS in our study, but research on improving its performance are actively being investigated and it should be carefully considered when sampling rare, spatially clustered populations.

Lastly, the methods we used to sample quadrats are destructive and may not be applicable to all studies. For example, studies of rare or imperiled species limited by habitat may require other sampling methods. We justified our choice of methods based on 2 considerations: 1) the area disturbed was very small relative to total habitat in the study area, and 2) less intense sampling methods may fail to detect all individuals and species present (Rodda et al. 2001). For example, in their studies of tropical herpetofaunal communities, Rodda et al (2001:24) "disassembled the forest leaf by leaf" in order to have unbiased estimates of species composition and abundance. Our methods are more destructive than traditional litter plot surveys, but less destructive than those proposed by Rodda et al. (2001). This comes at the cost of potentially failing to detect some rare species and underestimating abundance.

Acknowledgments

Funding for this project was provided by the US-India Fund, through United States Fish and Wildlife Service and Wildlife Institute of India collaborative project. We thank Drs. A. Kumar and R. Chellam for their encouragements and support; Wildlife Institute of India and Salim Ali Centre for Ornithology and Natural History for facilities provided; Tamil Nadu Forest Department for permissions to carry out the research. We also thank A. Kumar, S. Kumar and Ganesh for their valuable assistance in the field. D. R. Smith, P. F. Doherty, and 3 anonymous reviewers provided detailed comments which greatly improved the quality of our manuscript.

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Associate editor: Perry.