

# Inventoring and Estimating Subcanopy Spider Diversity Using Semiquantitative Sampling Methods in an Afromontane Forest

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Environ. Entomol. 31(2): 319–330 (2002)

**ABSTRACT** We investigated the effect of plot-based and unrestricted (plot-less) sampling on an inventory of a megadiverse taxon, spiders, in an Afrotropical forest for the purpose of species richness estimates. We also investigated the efficiency of human-based sampling methods and the effect of allocation of sampling effort to different sampling methods to cover as many microhabitats as possible. In the 10-d sampling period in the montane forest of the Uzungwa Scarp Forest Reserve in Tanzania, eight collectors sampled spiders for 350 h and 800 pitfall “trap-days.” Two hundred hours of sampling were restricted to a 1-ha plot and 150 h of sampling took place outside the plot. The sampling team included both experienced and inexperienced collectors using five different hand collecting methods during day and night sampling periods. Sampling yielded 9,096 adult spiders representing 170 species in total. Number of species and adult spiders per sample and overall species composition depended mainly on the sampling methods used and time of day. Whether the sampling took place within or at random outside the plot did not affect species composition or number of species per sample. Collector experience did affect the number of species collected per hour and thereby overall species composition of the sample but was less important than sampling methods used and time of day.

**KEY WORDS** montane forest spiders, sampling methods, sampling intensity, species richness estimation

THE NUMBER OF species and their relative abundances are the two classic, widely-used measures used to describe communities (Magurran 1988, Krebs 1989). Methods using these measures to produce results supporting conservation and management decisions of natural resources would be valuable. Simple counts of the number of species are usually negatively biased by undersampling in the case of tropical arthropods; even in intensive and thorough inventories, species accumulation curves often do not asymptote (Novotny and Basset 2000). Failure to detect rare species can dramatically underestimate the true local species richness and will often result in many apparently rare species (here defined as “singletons,” species represented by only one individual). However, if a limited fraction of a specific taxonomic group is sampled quantitatively, undersampling bias can theoretically be reduced, if not completely eliminated, by using statistical extrapolations to estimate species richness from such data (Heltshe and Forrester 1983; Colwell and Coddington

1994; Olivier and Beattie 1996; Walther and Morand 1998).

The current study is part of a long-term project to develop rapid and reliable sampling methods for arthropods that will yield data adequate to estimate local species richness at a given time, essentially measuring the ‘point parametric richness’ (Coddington et al. 1991, 1996). The ability to estimate local species richness reliably at a given point in time is fundamental, because all more complex sampling designs depend on it. For example, annual studies directed at phenology or seasonal species turnover are effectively studies of complementarity in species composition in time. Geographic studies along elevational or ecological transects are likewise studying complementarity of the species composition in space, or beta diversity. Both sorts of studies assume the accuracy of the local point estimates on which the turnover measures are based.

Coddington et al. (1991) proposed a sampling protocol that attempted to render semiquantitative a suite of methods known to be highly effective in tropical arthropod surveys. These are the methods of choice used by museum personnel and other experts on the natural history of their target groups. For any group the range of methods available varies from cheap to expensive, from high to low yield, and in the diversity of the fauna sampled. Economical surveys might use only the most efficient methods that sample the broadest range of species; elaborate surveys might use the

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full known range. Richness estimates based on a particular suite of methods obviously estimate only the sampling universe defined by the methods chosen. The initial trials used only vegetation beating, hand collecting and litter sifting because they effectively sample most microhabitats of the target taxon, spiders (Coddington et al. 1991, 1996). Sampling effort was standardized by time (1 h) or area. The underlying goal was to generate a series of replicate samples sufficient to estimate the local species richness. Because of its low cost and simple design, the protocol is suitable for biodiversity surveys in areas where resources are scarce. The basic concept, making "natural history" collecting methods statistically tractable, can easily be applied to other groups of organisms. After a moderate training period, collectors with little or no previous field experience should be able to use the sampling methods effectively.

Use of the protocol on the Northern (Coddington et al. 1996, Dobyns 1997, Toti et al. 2000) and Southern Hemisphere (Coddington et al. 1991, Silva 1996, Silva and Coddington 1996) have shown that in both areas it performs well both in terms of richness and abundance of species sampled. As noted above, the sampling methods developed thus far have been directed at obtaining estimates of local species richness at a given time and in a restricted area. Dobyns (1997) argued that the size of sampling area and sampling intensity would affect the species composition of spiders. He found that "repetitive" sampling (repeated applications of the same method in a restricted area) resulted in more species and more rare species than "nonrepetitive" sampling (each method applied only once to each area), given the same sampling intensity. The latter obviously will require a much larger area to accumulate the same number of samples as repetitive sampling. Point sampling events can provide valuable data for comparison of sites and for conservation decisions, but the biota sampled by an inventory will always depend on the methods used, the site and habitats selected, and the duration and timing of inventory relative to faunal phenologies. The reliability of short, limited time inventories has also been tested (N.S., unpublished data) in Denmark at a locality where the spider fauna and phenology is extremely well understood. In that case, the inventory gave reasonably accurate species richness estimates of the fauna that occurred during the period the sampling took place.

In this article, we summarize the results of a spider inventory in a Tanzanian montane forest, and investigate the performance of the different sampling methods (sweep netting, vegetation beating, different types of hand collecting and pitfall trapping). We also discuss the effect of collector experience on the results. We present species richness estimates of the area sampled based on nonparametric estimators and evaluate how well the sampling covered the fauna available to the methods used. We also test the effect of restricted sampling area by comparing "plot-based" sampling to a less controlled sampling in which the

collectors are free to wander and select the microhabitats in the locality sampled ("plot-less" sampling).

## Materials and Methods

**Study Site.** The fieldwork was carried out 17–27 May 1997 on a ridge in the Uzungwa Scarp Forest Reserve, Iringa District, in a Tanzanian primary montane forest at the end of the rainy season. The mountain is part of the Eastern Arc Mountains, known for their high degree of endemism among animals and plants (Lovett and Wasser 1993). The site is situated 11 km southeast of Masiwe Village, above Kihanga Stream (08° 22' 05.7" S, 35° 58' 41.6" E) at 1800–1900 m above sea level.

The forest was undisturbed, mature and homogeneous (Fjeldså 1999) with a canopy dominated by a few species of trees and a fairly open understory with *Tabernaemontana* sp. (Apocynaceae), other bushes, cycads, and ferns. Mean canopy height was  $\approx 25$  m. The slope of the sampling area was  $\approx 30^\circ$  or less. For plot-based sampling a square area of 1 ha was bounded by string. The plot was divided into four equally sampled 0.25-ha subplots (A–D). Sampling outside the plot (plot-less sampling) used identical methods. The latter area was adjacent to the plot on the same mountain ridge and in the same forest area. We estimate that collectors ranged over  $\approx 5$  ha during plot-less sampling. Areas with gaps, permanent streams, swampy ground, or outcrops were avoided.

**Sampling Team.** The team comprised four experienced professional arachnologists (collectors 1–4), and a group with much less experience: two graduate students in arachnology (collectors 4 and 5), and three collectors with no field experience and no familiarity with spiders (collectors 6–8). Two additional persons participated, but sampled primarily canopy (Sørensen 2000) and contributed few (3%) samples to the ground samples. Their samples are excluded from statistical comparisons between methods and collectors but were included in the estimation of species richness.

**Sampling Methods.** Sampling of the forest (not canopy) followed the concept of Coddington et al. (1991), with minor modification and included additional methods: pitfall trapping, sweep-netting, and hand searching for cryptic fauna. Sweep netting was used in the inventory of Silva (1996) but not as a repeated method.

**Method 1. Pitfall Trapping (Pitfall).** Pitfalls were 9 cm wide by 10 cm deep, one-third filled with a 0.5% formaldehyde solution and a few drops of liquid soap to break the surface tension, and sheltered by lids on stilts 2–3 cm above trap level. In total, 100 pitfalls running for 8 d were set in two series adjacent to but outside the plot boundary to avoid disturbance of the traps. Groups of five pitfall samples were pooled to reduce variation between samples in the abundance of adult spiders.

**Method 2. Cryptic Searching (Cryptic).** Hand collection of species living in cryptic habitats (e.g., within litter, small holes in trees or fallen logs, bark crevices, within rotting logs or trees, under logs, bark, and stones, within and under moss). Sampling from the

litter was either done through direct search, or by search of unsifted or sifted litter ( $\approx 1$  cm mesh) on sheets. The latter (litter sifting) was treated as a separate method in Coddington et al. (1991).

Method 3. *Sweep Netting* (Sweeping). Only low, primarily herbaceous or shrubby vegetation was swept. Areas without suitable vegetation were omitted. The net was emptied at regular intervals (after three to five sweeps) to avoid loss and destruction of the specimens.

Method 4. *Ground Hand Collecting* (Ground). Hand collection from ground to knee level ("looking down" of Coddington et al. 1991, 1996). This method accesses spiders visible on (but not hiding in) the leaf litter and on the ground, low buttresses, logs and the lowest vegetation that requires kneeling or crawling to access. "Looking down" in the previous test of the protocol included searches for cryptic species (Coddington et al. 1991, 1996), but is here segregated as a distinct method to reduce variance.

Method 5. *Aerial Hand Collecting* (Aerial). Hand collection from knee level to as high as one can reach ("looking up" of Coddington et al. 1991, 1996). This method accesses web-building and/or free-living spiders on the foliage and stems of living or dead shrubs, high herbs, tree trunks, or lianas.

Method 6. *Vegetation Beating* (Beating). The method accesses spiders living in the shrub, high herb vegetation, bushes, and small trees and branches. The spiders were collected by tapping the vegetation with a heavy stick while holding a collecting tray underneath from which the spiders were sampled (Coddington et al. 1996).

Most methods were applied during night and day, but sweep netting was impractical at night. Each sample for methods 2–6 comprised 1 h active sampling, measured with a stopwatch. Activity not directly involved in sampling was excluded by pausing the watch (e.g., travel time to a different area within the subplot, logistical problems, equipment maintenance, personal tasks). Collecting occurred continuously and steadily while watches were running; a "1-hour" sample typically required 75–90 min to complete. All putatively adult animals seen were collected. The mean number of samples per collector per day was four and the maximum seven.

Dusting webs with cornstarch to enhance their visibility improved the efficiency of hand collecting, and aspirators were generally used to transfer small animals to vials without damaging them. All spiders obtained via one method in 1 h were transferred to a single ethanol vial and labeled with date, time of day, method, collector, and replicate number.

*Treatment of Specimens.* Collected specimens were transferred to 70% alcohol. All adult specimens were identified to at least family level and sorted to morphospecies and assigned a unique species-code. When possible the spiders were identified to genus and species. The morphospecies concept was necessary, as the majority of the species were undescribed. Species were distinguished by examination of genitalia. Sexes were matched by color patterns and somatic features,

but co-occurrence and relative abundance were also considered. If species were represented only by females with indistinguishable epigynes, clear somatic differences were used to establish species boundaries. Voucher specimens were selected for all species and deposited at the Zoological Museum, University of Copenhagen (ZMUC). Duplicates are deposited at the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA, and will be deposited in Tanzania when facilities for an arthropod collection are in place.

*Performance of the Protocol.* The number of species represented by only one specimen (singletons) was used to evaluate the completeness of the inventory in Coddington et al. (1996), who also introduced the concept of "sampling intensity": the ratio of specimens to species. As an alternative measure of completeness of the inventory, we calculated the ratio of observed richness to the Chao1 estimate of species richness (see below).

Because date of collection did not influence the number of species per sample for the sampling methods (analysis of variance [ANOVA],  $P > 0.05$ ), we combined the plot-less and plot-based sampling data to test for the effect of collector, method, and time of day of sampling on the number of species and specimens per sample.

We used ANOVA as a full general linear model (SAS Institute 1989–1996) to test for effect of collector, sampling methods and time of day on number of species (model 1) and specimens (model 2) per sample. The Tukey studentized range honestly significant difference (HSD) test was used to test for differences among collectors (collectors 1–8) and methods (excluding pitfalls) (both  $P < 0.05$ ). For the ANOVA on number of specimens the data from collectors 1–8 and the methods beating, aerial and cryptic were used. Data were log-transformed before the analysis to reduce heteroscedasticity. To evaluate the effect of collector experience on number of species per sample, the same full model on collector, method and time of day was run separately for the group of experienced collectors (1–4) and for the remaining group of less and inexperienced collectors (5–8).

A diverse community might possibly yield fewer species and specimens per sample than a less diverse community, even though the former total species number was greater (Lande et al. 2000). Therefore, we randomly selected 13 d and night samples of each method (except sweeping and pitfalls) and used chi-square test on the total numbers of species and adults between night and day for each method.

*Complementarity.* Complementarity is the extent to which two samples, or lists complementarity rather than supplement each other. "Beta" diversity is complementarity along a spatial gradient. We assessed the distinctiveness of plot-less compared with plot-based sampling by complementarity as defined by Colwell and Coddington (1994). For analysis of complementarity between plot-based and plot-less sampling, equal numbers of samples or specimens were chosen at random to reduce the effect of sampling intensity.

**Table 1.** Summary table of results and species richness estimates for total, plot-based, and plot-less sampling data

	Total data	Plot-based sampling	Plot-less sampling
No. samples	370	200	170
No. specimens	9,096	4,708	4,388
Observed richness	170	148	145
No. singletons	32	35	32
% singletons	18.8	23.6	22.1
Sampling intensity	53.5	31.8	30.3
Richness estimates			
ACE	197.07	184.27	175.21
ICE	195.51	184.27	171.02
Chao1	196.95 ± 12.49	175.84 ± 12.31	177 ± 14.97
Chao 2	196.95 ± 12.49	180.6 ± 14.07	170.6 ± 11.84
Jackknife 1	201.91 ± 6.26	184.82 ± 6.84	176.81 ± 5.64
Jackknife 2	214.89	200.76	188.79
Bootstrap	185.04	164.97	159.98
% completeness	86	84	82

The same technique (13 randomly chosen night and day samples, or 1,016 specimens) was used to investigate how well different methods samples different microhabitats and also the degree of overlap between the methods. The number of species uniquely obtained by a particular method was also used to measure how well methods complemented each other.

**Effect of Area on Number of Rare Species.** For each of the increasingly larger sampling areas (subplot A-D, total plot-based and plot-less samples) the number of rare species was calculated as the number of species represented by only one specimen.

**Species Richness Estimation.** We chose to use the following nonparametric species richness estimators, ICE (Lee and Chao 1994), ACE (Chao et al. 1993), Chao1 (Chao 1984), Chao 2 (Chao 1987), Jackknife 1, Jackknife 2 (Burnham and Overton 1978, 1979), and Bootstrap (Smith and van Belle 1984), because they involve fewer assumptions about the underlying species abundance distribution. Species richness estimates were computed using EstimateS 5.0.1 (Colwell 1997). Detailed descriptions of the estimators can also be found in Colwell (1997) and Colwell and Coddington (1994).

## Results

**Species Composition and Abundance.** A combined total of 370 samples comprising 9,096 adult specimens (170 species; 33 families) were collected inside and outside the 1-ha plot, including all methods (Table 1; Appendix 1). Thirty-two species (19%) were singletons (one specimen each) and 19 species (11%) were doubletons (two specimens each). Within the 1-ha plot, 200 samples were taken totaling 4708 adult specimens and 148 species; of these, 35 species (24%) were singletons and 22 (15%) were doubletons. Outside the plot a total of 170 samples (including 20 pitfall samples) were taken, resulting in 4388 adult specimens and 145 species, of which 32 species (22%) were singletons and 16 (11%) were doubletons. Approximately 80% of the species were undescribed.

Species composition of the samples taken with the different methods is summarized in Appendix 1. A few very common species dominated the fauna. Two species of pholcids (sp. 1 and sp. 2) made up >34% of the total number of specimens caught. The third most abundant species (4.6% of total) was the cyatholipid *Isicabu henriki* Griswold, 2000, and the fourth most abundant species (4.5% of total) was the linyphiid *Ophrynia* sp. A. All of these represent new species. In contrast to these results, previous neotropical studies typically have found that the families Araneidae, Theridiidae, and Salticidae dominate in both richness and abundance. Pholcidae and Linyphiidae have usually been relatively minor components of the spider community (Silva 1996, Silva and Coddington 1996).

**Complementarity of Methods and Their Unique Species.** A rough comparison of the methods (Table 2) showed that all methods contribute unique species, but beating, cryptic and pitfall contribute more unique species per number of specimens collected.

To compare the distinctiveness of the faunas sampled by the different collecting methods, we randomly subsampled the total dataset to produce equal-sized samples from all methods, measured both as total specimens and number of samples. Ground and cryptic sampling, and beating and aerial sampling were least distinct in species composition (see footnote, number of specimens Table 3). Pitfall trapping overlapped most with ground and a little less with cryptic in both analyses. Sweeping was more similar to aerial and beating samples when data were adjusted for differences in number of samples and more similar to ground and beating when number of specimens were taken into account. The results suggest that ground, cryptic and pitfall collecting target rather similar spider faunas (forest floor), whereas aerial and beating target a different fauna (understory). Sweeping seems to access both and overlaps with ground, aerial and beating (Appendix 1).

**Protocol Performance: Efficiency of Methods, Collectors, and Time-of-Day Effect.** The number of species per sample did not decrease (or increase) significantly over the sampling period for any of the methods either inside or outside the plot. Intensive sampling did not measurably deplete the spider population in the plot and density of species was the same both inside and outside the plot. Based on this result we combined the data for the analyses of variance.

Collector, method, and a method × time of day interaction significantly affected both the number of species and the number of individuals per sample (models 1 and 2, Table 4). Time of day affected number of species but not number of specimens. As the matrix was nonorthogonal, significance in interaction effects should be treated cautiously. Although all two-way interactions significantly affected number of species, the relatively small sum of squares and *F* values indicate that interactions involving collector were much less important (Table 4) than method × time of day. None of the collector interactions significantly affected the number of adult specimens per sample (model 2, Table 4).

**Table 2. Numbers of unique species and other statistics by method**

	Beating	Cryptic	Ground	Aerial	Pitfall	Sweeping	Total
<b>Total data</b>							
No. samples	91	76	67	85	20	31	370
No. specimens	3,336	1,016	1,068	2,146	278	2,362	9,096
No. species	110	73	77	85	29	57	170
Sampling intensity	30.3	13.9	13.9	25.2	9.6	41.4	53.5
Unique species	27	7	5	8	5	3	55
Unique species, day	8	3	0	0	NA	3	14
Unique species, night	12	0	5	8	NA	0	25
Singletons	23	15	21	33	14	22	32
<b>Random draw of 26 samples</b>							
No. specimens, day	450	145	169	171	278 <sup>a</sup>	472 <sup>b</sup>	NA
No. species, day	48	35	36	22	29 <sup>a</sup>	51 <sup>b</sup>	NA
No. specimens, night	503	154	220	331	NA	NA <sup>b</sup>	NA
No. species, night	54	37	44	45	NA	NA <sup>b</sup>	NA
Unique species	23	7	3	8	6	2	49
Unique species, day	8	3	1	0	NA	2	14
Unique species, night	10	1	1	8	NA	NA <sup>b</sup>	20
Singletons	22	20	17	20	14	12	
<b>Random draw of 1,016 specimens</b>							
Unique species	21	7	10	5	5 <sup>a</sup>	3 <sup>b</sup>	51

NA, Not applicable.

<sup>a</sup> Pitfall traps sampled for 8 days.

<sup>b</sup> Only sweep net day samples included.

A chi-square test on the difference between methods by night and day (Table 2) adjusted for sample numbers showed that the abundance of active spiders was higher at night (test = 26.54; df = 1, 3;  $P < 0.0001$ ), but a chi-square test on number of species by night and day sampling was not significant.

Comparison of the mean number of species per sample for the sampling methods (Tukey HSD test) discriminated three significantly ( $P < 0.05$ ) different groups of methods: beating and sweeping caught most, followed by ground, and finally cryptic, with aerial not significantly different from ground or cryptic. The same test on mean number of specimens per sample also discriminated three significantly ( $P < 0.05$ ) different groups. Beating and sweeping produced most specimens per sample, followed by aerial, and ground and cryptic produced the least.

**Collector Experience.** The Tukey HSD test on number of species per sample identified three significantly different but overlapping groupings of collectors ( $P < 0.05$ ): one group of mainly experienced collectors (2, 1, 4, 3, 5, and 8, arranged high to low) caught more species per sample than the second group (6 and 7). The third group overlapped the first two and consisted only of inexperienced collectors (5, 8, 6, and 7, ar-

anged high to low). The Tukey HSD test on the mean number of specimens per sample also showed three overlapping groups ( $P < 0.05$ ): a group of mainly experienced collectors (1 2, 3, 4, 1, 8, and 7) caught more animals than the second group 2 (3, 4, 1, 8, 7, and 5); a third group of inexperienced collectors (8, 7, 5, and 6) also caught fewer animals. Together, the two tests suggest that, in this case, all collectors were able to collect nearly equal number of specimens per hour, but experienced collectors caught more species per sample than inexperienced collectors.

The same ANOVA model run just on experienced or inexperienced collectors confirmed these results. Number of species or specimens per sample did not differ among the experienced collectors ( $P > 0.05$ ), or

**Table 4. ANOVA for effect of method, collector, time of day and all interactions on number of species (model 1) and specimens (model 2) per sample**

	F value	df	Pr > F	R-square
Model 1. Dependent variable: species	8.99	47	0.0001	0.68
Method	75.97	2	0.0001	
Collector	12.43	7	0.0001	
Time of day	19.57	1	0.0001	
Collector × time of day	2.78	7	0.0088	
Method × time of day	13.94	2	0.0001	
Collector × method	2.31	14	0.0059	
Collector × method × time of day	1.44	14	0.1383	
Model 2. Dependent variable: abundance	6.24	47	0.0001	0.60
Method	80.00	2	0.0001	
Collector	4.36	7	0.0002	
Time of day	1.65	1	0.2009	
Collector × time of day	0.61	7	0.7487	
Method × time of day	9.59	2	0.0001	
Collector × method	1.46	14	0.1304	
Collector × method × time of day	0.44	14	0.9584	

**Table 3. Complementarity (Colwell and Coddington 1994) between methods: lower triangle, random draw of 1,016 specimens; upper triangle, random draw of 26 samples**

	Cryptic	Pitfall	Ground	Aerial	Beating	Sweeping
Cryptic		73	39 <sup>a</sup>	78	67	68
Pitfall	69		66	94	92	92
Ground	43 <sup>a</sup>	67		74	64	66
Aerial	84	94	68		48 <sup>a</sup>	77
Beating	77	92	68	38 <sup>a</sup>		57
Sweeping	76	92	62	55	58	

<sup>a</sup> The samples most similar (<50%).

the collector  $\times$  time of day interaction, or the three-way interaction. For inexperienced collectors, the picture changed. For number of species per sample, all factors except the three-way interaction were significant. For number of specimens per sample, only method and the interaction method  $\times$  time of day were significant ( $P < 0.05$ ). Inexperienced collectors were equally good at sampling spiders (abundance), but varied in their ability to catch species. Training in collecting spiders may reduce the effect of inexperienced collectors, but in this case was insufficient to remove all collector bias. Even among experienced collectors, we found a significant interaction with method, even though the overall effect of collector was not significant. One collector did relatively much better at hand searching in the understory than for cryptic fauna.

**Effect of Plot-Based Sampling and Area.** No significant differences in number of species per sample were found between the 25 randomly chosen samples from the four subplots within the 1-ha plot ( $F = 1.23$ ;  $df = 3, 108$ ;  $P = 0.30$ ), but number of specimens per sample differed significantly ( $F = 3.1$ ;  $df = 3, 108$ ;  $P = 0.03$ ). Plot-based versus plot-less samples did not differ significantly in the number of species ( $F = 0.68$ ;  $df = 1, 298$ ;  $P = 0.41$ ) or specimens ( $F = 1.91$ ;  $df = 1, 298$ ;  $P = 0.17$ ) per sample.

We found 148 species in the plot-less sampling and 145 in the plot-based, with 123 species shared between the two areas. To reduce bias resulting from unequal sample numbers, 13 samples were randomly chosen for each method for the analysis of complementarity between the two areas. We then found 111 species in the plot-based sampling and 119 in the plot-less sampling with 88 species shared (complementarity 38%). If singletons and doubletons are disregarded, the complementarity drops to 8.8%. Within the four subplots the proportion of singletons remained roughly constant at 31–34%. At the scale of the entire 1-ha plot, percentage singletons dropped to 24%. If plot-based and plot-less samples were combined, the proportion of singletons dropped to 19%.

**Estimates of Species Richness.** As the plot-based and plot-less sampling apparently assessed the same spider community, the species richness estimates presented here (Table 1; Fig. 1) are based on the combined data (including pitfalls), thus estimating the species richness of this mountain ridge ( $\approx 6$  ha sampled). The bootstrap estimate is lowest at 185; other estimates range from  $197 \pm 12$  SD to 215 species. Although the number of samples and individuals is only half the total if the data are partitioned into plot-based and plotless sampling, the richness estimators decrease only by  $\approx 10\%$  and are similar (Bootstrap: 160, the rest  $171 \pm 12$  to 189 species, versus Bootstrap: 165, the rest  $176 \pm 12$ –201 (Table 1)) despite 17% less sampling outside the plot and over a much larger area. The relatively slight increase in richness with doubled sampling effort suggests that even enormous increases in effort would not be sufficient to make estimates and observed richness coincide.

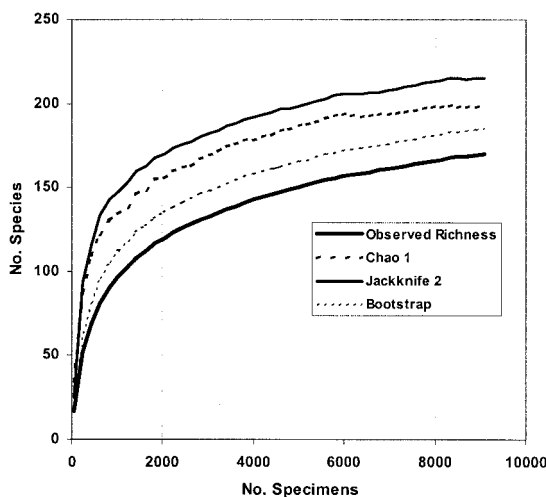


Fig. 1. Observed species richness and estimated richness for the estimators, Chao 1, Jackknife 2, and Bootstrap based on 200 randomized samples (Colwell 1997) for the total data.

## Discussion

The inventory presented here is the most elaborate to date based on the protocol outlined by Coddington et al. (1991) both in terms of numbers of samples and specimens (Coddington et al. 1991, 1996, Dobyns 1997, Toti et al. 2000). A main objective of this study was to estimate the total species richness at the sampling site and at the time of sampling. Thus, methods were selected to sample as many different microhabitats as resources allowed. Judged by complementarity, the inventory revealed two substantially different spider communities: one at the forest floor (accessed by the methods: ground, cryptic and pitfall) and one in the low vegetation (accessed by the methods: aerial and beating). Sweeping as a method accesses both forest floor and the low vegetation and overlaps greatly with other methods that provide many more unique species.

**Protocol Performance.** Of the three primary factors in the analysis (method, collector, and time or day), method explains by far the most variance in results, followed by time of day and collector experience. Methods differ greatly in the numbers of species per sample. This is partly due to the intrinsic nature of the methods. These results may also reflect real differences in species richness between microhabitats, although our data can only weakly and indirectly test that hypothesis. Beating understory vegetation yielded many animals and species, but hand searching for cryptic fauna yielded many fewer specimens and species per sample unit (Table 2).

All methods contributed unique species (Table 2), thereby complementing each other and reducing the overall sampling effort required for a complete inventory. The comparison of methods showed that beating obtained by far the most unique species, followed by aerial, cryptic and pitfall, then ground and sweeping (Table 2). The ratio of unique species to specimens

showed that pitfall trapping is an important method. Combining these results and the complementarity between the methods (Table 3), it seems that the effectiveness of the inventory in this case would have been improved by allocating more sampling effort to beating.

We recorded fewer but more abundant species during the day. Measured as species per h, richness was higher at night, but although the total nighttime species list for a method was always higher, the difference was not significant (Tables 2 and 4). The ANOVA showed that time of day (differential availability or activity of spiders) strongly influenced the number of species per sample and strongly interacted with method (Table 4). Time of day effects with a method are sometimes greater than differences between methods. The chi-square test on the total number of species caught during day and night for each method verified only an effect of time of day on the abundance, not richness, of spiders. However, each method-time of day combination contributes unique species (Table 2), which also indicates differences in activity patterns and thus the advisability of sampling during day and night. This effect is consistent when sample numbers are adjusted for unequal sampling effort (both as number of samples and specimens) (Table 2).

Collector experience significantly affected number of species per sample. Inexperienced collectors tended to collect fewer species and focus on the more common ones. However, even experienced collectors differed by method, although there was no detectable overall difference between collectors. More mechanical methods like sweeping, beating and pitfall or Winckler extraction or Berlese funnel traps are less subject to human bias, however the latter two require that appropriate facilities are available. Furthermore, the operator must still choose which litter to collect, where to beat or sweep, or where to place pitfalls. These methods require less training compared with, for example, cryptic, which requires more collectors with more experience and knowledge about the biology of the organisms. Of the hand collecting methods, aerial and ground are probably easier for inexperienced collectors than cryptic.

**Effect of Area.** Most of the previous samplings with the protocol have been restricted to a defined area (Coddington et al. 1991, 1996; Dobyns 1997). The results of plot-less sampling in this inventory did not differ from plot-based sampling. Perhaps restriction of sampling area is not required in a homogeneous areas, although it would require use of standardized quantifiable methods, and to be sure that additional habitat types were not included in the sampling. However, it is possible that many small plots randomly scattered throughout a homogeneous area might sample community variation better than a single large plot. It would also ensure true replicate sampling and strengthening the statistical power.

Enlarging the area sampled, at least at this scale, decreased rather than increased the proportion of rare species, and thus improved the quality of the inven-

tory, probably because sampling effort increased. If singleton species reflect insufficient sampling effort, then a 1-ha plot may be representative for this forest type. If so, inventory completion is just a matter of even more sampling effort. However, the result could also indicate that the nearest neighbor distance between individuals of these rare species is much larger than expected and that a 1-ha plot is unlikely to contain two conspecifics. Either explanation could potentially explain the increased species richness observed when samples are combined (Table 1).

**Species Richness.** Previous tests of species richness estimators have disagreed on which of the estimators included in the program EstimateS (Colwell 1997) are most accurate or efficient (Palmer 1990, Colwell and Coddington 1994, Condit et al. 1996, Chazdon et al. 1998, Poulin 1998, Walther and Morand 1998). We chose to present the results of the Bootstrap, Chao 1, and Jackknife 2 (Fig. 1), as upper, lower, and mediate estimates, respectively.

Good estimators should asymptote accurately and early (Colwell and Coddington 1994). Neither of the estimators other than Chao 1 show much tendency to asymptote. Chao 1 performs better compared with the other estimators when number of specimens was large. However, the relatively slight but constant final slope of the Chao 1 curve suggests that many more samples will be necessary to improve significantly the estimates presented here. Although, the behavior of the estimates can also be due to the species abundance distribution between samples.

The estimated number of species based on the plot-less and plot-based data are roughly comparable (Table 1). Combining the data results in only a slight increase in estimated species richness. Knowing that many spiders can show a patchy distribution (both due to rarity and seasonality) the estimated species richness will always be a minimum estimate of the species richness in the area sampled. Indeed, mathematically these estimators are "lower bound" estimates, so that persistent negative bias in richness estimators should be no surprise (Chao 1984). It thus seems possible to obtain a relative reasonable "point" estimate of the species richness of a diverse group of organisms, which can be used to assess the completeness of the inventory. The inventory apparently sampled >80% of the fauna accessible by the methods tested during the sampling period (Table 1), which compares well to the level (82%) of the comprehensive study by Dobyns (1997) on a rich temperate forest at Ellicott Rock (Georgia, USA). In comparison, sampling in three forest sites in Bolivia obtained <60% of the estimated available fauna (Coddington et al. 1996). A second inventory at Ellicott Rock obtained 70% of the estimated available species (Coddington et al. 1996). Percentage singletons show the same pattern. If one wants to include reasonably reliable information on richness from the most diverse groups of organisms, then one must accept that such inventories will require considerably more resources than has hitherto been the case. Although previous "rules of thumb" had suggested that a sampling intensity of 10:1

(specimens: species) for mature tropical wet forest conditions might suffice for a reliable richness estimate (Coddington et al. 1991), the present inventory suggests that 30–50:1 might be more realistic, especially in high diversity sites. This statistic, of course, assumes that tropical lowland faunas tend to have the same underlying species abundance distribution.

**Design of Sampling Protocol.** The proposed sampling design by Coddington et al. (1991) is flexible and can be adapted to fit purposes for which data on total species richness is required. This sampling design does not measure absolute species density, and thus is no substitute for quadrat-based sampling if measuring species density is a goal.

For long-term monitoring programs the design of a sampling protocol should be considered carefully. It should cover sufficient area and encompass seasonal variation. The current study showed that even intense sampling was insufficient to observe the entire spider fauna in the area. Any monitoring program will probably have less resources, and therefore the scope of the inventory must be reduced. It is therefore, suggested that long-term monitoring should focus on a single or a few families, or a single feeding guild, and use a few standardized methods which are absolute and practical. This will ensure comparable data; undersampling bias can be assessed and ameliorated by use of nonparametric richness estimators. The latter can give some indication of how well the total fauna was sampled. Permanent plots would provide baseline data for future surveys.

For total species richness estimates the sampling design must maximize the number of species in the samples. Because methods are differentially efficient and because species richness varies among habitats, unequal allocation of effort among methods is typically required. This conflicts with the need for balanced designs in ANOVA, which is fundamental for questions about methodology or comparisons between strata or habitats. The efficiency and importance of the coverage of the different habitats must be balanced against the use of resources to obtain the most species in the shortest time.

### Acknowledgments

We especially thank team members Per de Place Bjørn (ZMUC), Johanna Heinonen (University of Helsinki), Scott Larcher and Jeremy Miller (USNM, Washington, DC.), Elia Mulungu (Parabiologist, Iringa), Bruno Nyundo (University of Dar es Salaam) and Innocent Zilihona (Tanzania Forestry Research Institute) for their invaluable help in the field. We thank the Commission of Science and Technology (COSTECH) for kindly granting research permits; Wildlife Department for granting Cites permits, and the Tanzania Catchment Forestry Office, Iringa, for allowing the expedition to work in forests under their jurisdiction. We gratefully acknowledge the Felista M. Urassa, Jacob G. Yarro, Kim M. Howell (University of Dar es Salaam) and the Enreca program (Danish International Development Assistance, Danida) for support to Tanzanian students, the North/South Priority Research Area (University of Copenhagen), the Danish National Research Council (grant no. 9502155 to NS),

the Smithsonian Biodiversity and Neotropical Lowlands Research Programs, and British Airways for funding and air transport. Finally, we thank the Danish Center for Tropical Biodiversity (CTB) and David Moyer for logistical support, Renner Baptista (USNM, Washington, DC) for assisting with the sorting; and Robert Colwell (University of Connecticut), Peter M. Hammond (The Natural History Museum), Henrik Enghoff, Mary E. Petersen (ZMUC), and Jens N. Kristiansen for comments on the manuscript.

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*Received for publication 17 April 2001; accepted 29 October 2001.*

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**Appendix 1. Summary table of data sampled during day (D) and night (N) in the spider inventory of montane forest of the Uzungwa Mountains, Tanzania, 1997**

Species	Code	Beating		Aerial		Cryptic		Ground		Pitfall		Sweeping		Forest floor	Understory	Total
		D	N	D	N	D	N	D	N	D	N	D	N			
Agelenidae																
<i>Agelena</i> sp. 1	ta001	1	1	6	20	2	12	2	14	.	.	.	.	30	28	58
<i>Agelena</i> sp. 2	ta002	.	3	.	1	.	.	.	.	.	.	.	.	.	4	4
Amaurobiidae																
Amaurobiid sp. N	ta033	1	6	.	.	.	.	.	.	.	.	.	.	.	7	7
Anapidae																
Anapid sp. 1	ta003	.	.	.	.	.	.	.	1	.	.	.	.	1	.	1
Anapid sp. 2	ta004	3	.	.	.	.	.	.	.	.	1	.	.	1	3	4
Anapid sp. 3	ta005	1	.	.	.	.	.	.	.	.	1	.	.	1	1	2
Araneidae																
Araneid sp. 1	ta007	4	16	2	20	2	.	1	34	.	85	2	124	42	166	
Araneid sp. 2	ta008	1	3	.	6	.	.	.	1	.	.	.	1	10	11	
Araneid sp. 3	ta009	1	15	.	13	.	.	.	.	.	.	.	.	29	29	
Araneid sp. 4	ta010	1	3	.	5	.	.	.	.	.	.	.	.	9	9	
Araneid sp. 5	ta011	.	.	.	1	.	.	.	.	.	.	.	.	1	1	
<i>Caerostris</i> sp. 1	ta193	.	3	.	.	.	.	.	.	.	.	.	.	3	3	
<i>Cyclosa</i> sp. 1	ta013	2	5	.	3	.	.	.	.	.	.	.	.	10	10	
<i>Cyrtophora</i> sp. 1	ta808	.	.	.	1	.	.	.	.	.	.	.	.	1	1	
Barychelidae																
Barychelid sp. 1	ta016	.	.	.	.	1	2	.	1	5	.	.	.	9	.	9
Barychelid sp. 2	ta017	.	.	.	.	1	1	.	.	.	.	.	.	2	.	2
Barychelid sp. 3	ta062	.	2	.	.	.	.	.	.	.	.	.	.	.	2	2
Clubionidae																
<i>Clubiona</i> sp. 1	ta018	5	40	2	5	.	.	.	.	.	1	.	1	52	53	
<i>Clubiona</i> sp. 2	ta019	6	21	.	2	1	.	.	1	.	.	.	2	29	31	
<i>Clubiona</i> sp. 3	ta020	.	4	.	.	1	.	.	1	.	.	.	2	4	6	
<i>Clubiona</i> sp. 4	ta021	1	1	.	.	.	.	.	.	.	.	.	.	2	2	
Clubionid sp. 1	ta022	18	142	4	39	1	3	.	10	.	20	3	37	203	240	
Corinnidae																
Corinnid sp. 12	ta186	.	.	.	.	.	.	.	.	1	.	.	1	.	1	
Corinninae sp. 1	ta023	.	.	.	.	1	3	.	2	1	.	.	7	.	7	
Corinninae sp. 2	ta807	.	.	.	.	.	.	.	1	.	.	.	1	.	1	
Trachelinae sp. 1	ta024	3	7	.	.	2	.	.	.	.	16	.	18	10	28	
Trachelinae sp. 2	ta025	1	9	.	.	.	.	.	.	.	1	.	1	10	11	
Trachelinae sp. 3	ta026	.	5	.	.	.	.	.	.	.	.	.	.	5	5	
Trachelinae sp. 5	ta806	1	.	.	.	.	.	.	.	.	.	.	.	1	1	
Ctenidae																
<i>Ctenus</i> sp. 1	ta027	.	5	.	10	1	3	.	19	.	.	.	23	15	38	
<i>Ctenus</i> sp. 2	ta028	.	.	.	.	3	4	1	13	1	.	.	22	.	22	
<i>Isoctenus</i> sp. 1	ta029	.	.	.	1	1	8	1	11	.	.	.	21	1	22	
Cyatholipidae																
<i>Ilisoa</i> sp. 1	ta030	1	.	.	2	.	.	.	10	.	1	.	11	3	14	
<i>Isicabu henriki</i> Griswold, 2000	ta031	66	186	14	135	1	1	1	4	.	6	.	13	401	414	
<i>Isicabu magrathae</i> Griswold, 2000	ta032	34	62	1	38	.	1	.	29	.	52	.	82	135	217	
Cyrtacheniiidae																
Cyrtacheniiinae sp. 1	ta971	.	.	.	.	.	.	.	.	1	.	.	1	.	1	
Dictynidae																
Dictynid sp. 1	ta034	5	12	.	1	.	.	.	.	.	2	.	2	18	20	
Gnaphosidae																
cf Echeminae sp. 2	ta970	.	.	.	.	.	.	.	.	1	.	.	1	.	1	
Gnaphosid sp. 1	ta035	.	.	.	.	2	6	.	1	1	.	.	10	.	10	
Hahnidae																
<i>Hahnia</i> sp. 1	ta036	.	.	.	.	158	117	31	48	20	3	.	377	.	377	
<i>Hahnia</i> sp. 2	ta037	2	1	.	.	2	.	.	.	.	.	.	2	3	5	
<i>Hahnia</i> sp. 3	ta038	.	.	.	26	7	.	.	.	.	.	.	33	.	33	
<i>Hahnia</i> sp. 4	ta039	1	4	1	.	19	7	4	15	9	.	.	54	6	60	
Heteropodidae																
Heteropodid sp. 1	ta040	.	2	.	.	.	.	.	.	.	.	.	.	2	2	
Heteropodid sp. 2	ta951	.	3	.	.	.	.	.	.	.	.	.	.	3	3	
Idiopidae																
Idiopid sp. A	ta913	.	.	.	.	.	.	.	.	5	.	.	5	.	5	
Linyphiidae																
<i>Callitrichia criniger</i> Scharff, 1990	ta154	.	.	.	1	.	.	.	.	.	.	.	.	1	1	
<i>Callitrichia sellafontis</i> Scharff, 1990	ta041	69	135	.	26	1	1	1	8	.	24	.	35	230	265	
<i>Callitrichia</i> n. sp.	ta054	.	1	.	.	.	.	.	.	.	.	.	.	1	1	
Erigoninae sp. 1	ta809	.	.	.	.	.	.	.	.	.	1	.	1	.	1	



## Appendix 1. Continued

Species	Name	Code	Beating		Aerial		Cryptic		Ground		Pitfall	Sweeping		Forest floor	Understory	Total
			D	N	D	N	D	N	D	N		D	N			
<i>Scytodes</i> sp. 2		ta803	.	1	.	1	.	.	.	.	.	.	.	.	2	2
Segestriidae																
<i>Ariadna</i> sp. 1		ta096	.	1	2	2	.	.	.	5	9	.	.	14	5	19
<i>Ariadna</i> sp. 2		ta097	.	.	.	.	1	2	1	.	.	.	.	4	.	4
<i>Ariadna</i> sp. 3		ta098	.	.	.	.	.	2	.	.	12	.	.	14	.	14
Selenopidae																
Selenopid sp. 1		ta099	.	.	.	12	.	.	.	2	.	.	.	2	12	14
Selenopid sp. 2		ta804	.	1	.	1	.	.	.	.	.	.	.	.	2	2
Tetragnathidae																
cf <i>Cardimia</i> sp. 1		ta100	.	7	.	3	6	3	3	27	1	106	4	150	10	160
cf <i>Chrysometa</i> sp. 1		ta101	1	1	1	2	.	.	.	2	.	.	.	2	5	7
<i>Leucauge</i> sp. 1		ta102	6	10	10	22	2	.	5	12	.	78	.	97	48	145
<i>Pachygnatha</i> cf <i>palmqvisti</i> Tullgren, 1910		ta105	.	2	.	3	9	23	2	16	12	4	.	66	5	71
<i>Pachygnatha</i> sp. 1		ta103	1	.	.	.	37	43	3	43	13	1	.	140	1	141
<i>Pachygnatha</i> sp. 2		ta104	.	1	.	.	1	8	.	10	2	1	.	22	1	23
Theridiidae																
<i>Achaearanea</i> sp. 1		ta106	.	1	3	19	.	3	2	5	.	.	.	10	23	33
<i>Achaearanea</i> sp. 2		ta107	3	8	1	5	.	.	.	.	.	.	.	.	17	17
<i>Achaearanea</i> sp. 3		ta108	.	.	.	1	.	.	.	.	.	.	.	.	1	1
<i>Anelosimus</i> sp. 1		ta109	1	5	.	1	.	.	.	.	.	2	.	2	7	9
<i>Anelosimus</i> sp. 2		ta178	.	2	.	3	.	.	.	.	.	.	.	.	5	5
<i>Argyrodes</i> sp. 1		ta110	4	6	.	11	.	.	.	.	.	1	.	1	21	22
<i>Argyrodes</i> sp. 2		ta111	4	15	1	10	.	.	.	.	.	.	.	.	30	30
<i>Argyrodes</i> sp. 3		ta112	.	.	.	2	.	.	.	.	.	.	.	.	2	2
<i>Argyrodes</i> sp. 4		ta947	1	.	.	.	.	.	.	.	.	.	.	.	1	1
<i>Chryso</i> sp. 1		ta113	1	6	5	8	.	.	.	.	.	1	.	1	20	21
cf <i>Crustulina</i> sp. 1		ta115	2	2	.	1	.	.	.	.	.	3	.	3	5	8
<i>Dipoena</i> sp. 1		ta117	2	3	.	1	.	.	.	.	.	.	.	.	6	6
<i>Dipoena</i> sp. 2		ta118	1	.	.	1	.	.	.	1	.	.	.	1	2	3
<i>Dipoena</i> sp. 3		ta119	2	2	.	2	.	.	.	1	.	.	.	1	6	7
<i>Dipoena</i> sp. 10		ta114	.	1	.	.	.	.	.	.	.	.	.	.	1	1
<i>Episinus</i> sp. 1		ta120	2	6	.	11	1	16	2	85	.	39	.	143	19	162
<i>Euryopis</i> sp. 1		ta121	9	11	.	19	.	.	.	4	.	9	.	13	39	52
<i>Phoroncidia</i> sp. 1		ta122	23	19	3	54	1	1	.	8	.	16	.	26	99	125
<i>Phoroncidia</i> sp. 2		ta123	.	3	.	7	.	2	1	5	.	5	1	14	10	24
<i>Phoroncidia</i> sp. 3		ta124	4	12	.	9	.	.	.	.	.	.	.	.	25	25
<i>Phoroncidia</i> sp. 4		ta125	.	3	.	.	.	.	.	.	.	.	.	.	3	3
<i>Phoroncidia</i> sp. 5		ta954	.	2	.	.	.	.	.	.	.	.	.	.	2	2
<i>Steatoda</i> sp. 1		ta126	.	.	.	1	2	7	.	6	1	.	.	16	1	17
Theridiid sp. 1		ta116	1	4	.	1	.	.	.	.	.	1	.	1	6	7
Theridiid sp. 2		ta128	.	1	.	.	.	.	.	.	.	.	.	.	1	1
Theridion sp. 1		ta129	39	50	1	10	1	.	1	4	.	5	.	11	100	111
Theridion sp. 2		ta130	1	.	.	2	.	.	.	.	.	2	.	2	3	5
Theridion sp. 3		ta131	9	16	2	10	.	9	7	16	1	17	2	52	37	89
Theridion sp. 5		ta133	1	2	2	.	.	.	.	.	.	1	.	1	5	6
Theridion sp. 6		ta134	.	1	.	.	.	.	.	.	.	.	.	.	1	1
Theridion sp. 7		ta127	2	.	.	.	.	.	.	.	.	.	.	.	2	2
Theridion sp. 8		ta802	1	1	.	.	.	.	.	.	.	.	.	.	2	2
<i>Thuaitesia</i> sp. 1		ta135	11	20	.	28	2	.	.	10	.	16	.	28	59	87
<i>Thymoites</i> sp. 4		ta132	1	.	.	.	.	.	.	.	.	.	.	.	1	1
<i>Tidarren</i> sp. 1		ta801	1	.	.	.	.	.	.	.	.	.	.	.	1	1
Thomisidae																
<i>Borboropactus</i> sp. 1		ta195	.	6	.	3	1	6	.	6	3	.	.	16	9	25
Misumeninae sp. 1		ta136	6	21	.	3	.	.	.	1	.	3	.	4	30	34
Misumeninae sp. 2		ta137	.	.	.	1	.	.	.	1	.	.	.	1	1	2
<i>Synema</i> sp. 1		ta138	5	19	.	.	.	.	.	.	.	3	.	3	24	27
<i>Tmarus</i> sp. 1		ta140	.	.	.	.	.	.	.	1	.	.	.	1	.	1
<i>Tmarus</i> sp. 2		ta141	.	1	.	.	.	.	.	.	.	.	.	.	1	1
<i>Tmarus?</i> sp. 1		ta800	.	.	.	.	.	.	.	.	.	1	.	1	.	1
Theridiosomatidae																
Theridiosomatid sp. 1		ta142	.	.	2	9	5	5	5	18	.	8	1	42	11	53
Theridiosomatid sp. 2		ta143	.	.	1	.	.	.	2	.	.	.	.	2	1	3
Uloboridae																
<i>Miagrammopes</i> sp. 1		ta144	2	11	1	7	.	1	.	.	.	2	.	3	21	24
Zodariidae																
Zodarid sp. 1		ta145	.	.	.	1	1	2	1	2	1	.	.	7	1	8
Zodarid sp. 2		ta146	.	.	.	.	2	.	.	.	1	.	.	3	.	3