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MEASURING AND MONITORING AMPHIBIAN DIVERSITY IN TROPICAL FORESTS. I. AN EVALUATION OF METHODS WITH RECOMMENDATIONS FOR STANDARDIZATION

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Abstract: The need for standardization of field methods within and across studies has been recognized by the majority of ecologists throughout the world. However, comparable studies based on a standardized protocol are still scarce. We provide a guideline for effectively sampling and monitoring tropical forest amphibians and give recommendations for standardization. Based on a four-year study on amphibians in Taï National Park, Côte d'Ivoire, we evaluate commonly used techniques, and offer a catalogue of efficient techniques, along with suggestions for improvement of particular methods, with regard to study objectives and specific amphibian guilds. For simple short-term surveys we recommend visual and acoustic encounter surveys, accompanied by opportunistic trapping. The transect design introduced here proved to be most adequate for representative sampling and appeared to be appropriate for most studies that involve multivariate data. It is especially useful for long-term studies. Transects furthermore provide an effective method of investigating at least leaf litter frogs, not only at their breeding sites but also throughout the whole range of habitats used by them, thus generating a much more complete picture of an amphibian community than is possible with other methods. *Accepted 4 February 2004.*

Key words: *Tropical amphibian monitoring, standardization, method evaluation, Taï National Park, West Africa.*

INTRODUCTION

In theory there is no disagreement about the necessity to standardize ecological field methods and data acquisition in order to guarantee comparability between different studies, as well as to enhance the power of predictions resulting therefrom. The need for standardization of techniques across and within studies has continuously been emphasized by several authors (e.g., Heyer *et al.* 1994, Adis *et al.* 1998). Those who are involved in community ecological field research know well that this is a crucial factor when it comes to generalizing results in order to make them accessible to those who urgently need scientific guidelines to back up their practical efforts. This becomes especially important when looking at phenomena such as the well known world-wide amphibian decline, which seems to have affected even populations in pristine habitats and continues to affect or even wipe out whole populations with terrifying rapidity (Houlahan *et al.* 2000, Kiesecker *et al.* 2001, Pounds 2001). In these cases synergistic efforts are urgently needed, calling for unified methods and data output (Alford & Richards 1999, Parris 1999, DAPTF 2002).

However, in reality there still is a lack of studies that can be compared without reservations, especially studies that were conducted in different parts of the world, although precisely this kind of comparison is

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essential for academic and practical purposes alike. Given the lack of time for the development of effective conservation programs, standardization of methods that yield broad-scale comparative data is now needed more than ever. A number of recently published regional field monitoring manuals for amphibian surveys (Latin America: Lips *et al.* 2001, Africa: Howell 2002) reflect this need. The intention of this paper is thus to provide a guideline to choosing effective and comparable methods for the monitoring of tropical forest amphibian assemblages in general. We thereby evaluated several methods that are already commonly used and present a set of techniques that, on the basis of our experience in the field as well as with consecutive data analyses, proved to be most effective for forest amphibians. We report on our experiences with already existing methods and with methods that we thought needed modifications to enhance their effectiveness and to enable the use of new statistical analysis methods. All evaluations and recommendations are based on a study of tropical amphibian assemblages conducted over four years (1999–2002) in Taï National Park, Côte d'Ivoire. We aim to present a methodology that i) provides quantitative and qualitative data useful for rapid surveys as well as long-term monitoring programs, that ii) is easy to handle, also for para-ecologists, iii) is efficient concerning time and money, and iv) has a low environmental impact. Thus widely used techniques, such as standard plot sampling (Allmon 1991, Vonesh 2001, Doan 2003) or total removal plots (Barbault & Trefaut Rodrigues 1978, 1979a, b; Rodda *et al.* 2001) were *a priori* excluded from testing, as they may result in severe disturbance to the system under investigation.

MATERIAL AND METHODS

Study site

The study was conducted in Taï National Park (TNP), situated in western Côte d'Ivoire (5°08'-6°07'N, 6°47'-7°25'W). TNP is the largest remaining protected area of rain forest in West Africa. It can be characterized as humid tropic seasonal (Riezebos *et al.* 1994, Parren & de Graaf 1995, Richards 1996). Precipitation is distributed across two more or less distinct periods. A minor rainy season lasts from March/April to July, followed by a short dry season in July/August. The major rainy season stretches from September to October. The core dry season lasts from November until February/March. Mean annual precipitation in the study area was 1806 mm during 1988–2002 (± 297 mm; data: Taï Monkey Project). Daily temperatures vary between 20 and 33° C. The mean annual temperature is about 25° C (Rompaey 1993). Our study site was located 23 km southeast of the small town of Taï and comprised about 30 km^2 of primary and secondary rain forest around the Station de Recherche en Ecologie de Taï (SRET, 5°50'N, 7°20'W). Parts of the habitats on the park's periphery were subject to more or less intense logging and cultivation until 1998 (P. Formenty pers. comm. and unpubl. map "Projet OMS Forêt de Taï"). Our study sites are either pristine forest areas or have not been logged or cultivated since 1978. Floristically the TNP belongs to the Guinean-Congo-Region (Guillaumet 1967, Lawson 1986, PACPNT 2000). TNP is part of the Upper Guinea forest block, that stretches west of the Dahomey Gap from Ghana into Sierra Leone and Guinea (Schiøtz 1967, Poynton 1999). More detailed descriptions of TNP are provided by Rompaey (1993), Riezebos *et al.* (1994) and PACPNT (2000).

Selection of sites and design of sampling units

We chose sites within existing macrohabitats (primary/secondary forest) to establish a total of ten rectangular transects (six in primary forest, four in secondary forest). Each had a north-south extension of 200 m and an east-west extension of 100 m. For data acquisition the complete transect length of 600 m was subdivided in 25 m subunits (24 subunits/transect). Every subunit was marked with numbered colored flag-tape. Transect paths were kept open so that walking at a constant speed was possible at all times. We avoided extensive cutting and thus manipulation of important habitat features. The starting coordinate for each transect always marked the southeast corner to ensure identical geographic orientation between sampling units. Transects were arranged in pairs, thus ensuring that all habitat types of a certain area within the very inhomogeneous forest were covered. The minimum distance between adjacent transects was 200 m. The maximum distance between transects was 6.3 km. The rectangular transect design is a combination of two widely used standard techniques. The first, known as quadrat sampling (plot design), consists of a series of small squares (quadrats) that are laid out at randomly selected sites within a habitat then thoroughly searched for amphibians. The second, known as transect sampling, uses linear transects instead of squares. Whereas quadrat sampling can be used to determine the species present in a homogenous area, as well as their relative abundances and densities, transect sampling can provide similar data across habitat or dis-

turbance gradients (Jaeger 1994, Jaeger & Inger 1994). Compared to linear transects, rectangular ones provide the possibility of easily up- or downscaling data without neglecting local habitat diversity (e.g., for comparison of local with regional species pools). For a discussion of the advantages of rectangular sample units over quadratic or circular ones see Krebs (1989) and McCune & Grace (2002).

Sampling methods and sampling effort

Habitat characterization. To assess habitat preferences of particular species (e.g., to assign them to particular guilds), and to investigate correlations of species assemblages with environmental variables, we characterized all habitats using several variables that were recorded at two defined points within each 25 m subunit (beginning and midpoint). These parameters included vegetation density in four strata (canopy: > 20 m, lower tree stratum: 3–10 m, bush and shrub stratum: 0.5–1.5 m, understory: < 0.5 m), divided into seven categories corresponding to particular densities. Edaphic parameters were registered as general substrate types according to Lieberoth (1982). A simplified method originally developed by Braun-Blanquet (1964) for determination of vegetation coverage in vegetation analyses was used to estimate the percentage of leaf litter coverage. In addition, the vegetation of all 25 m segments within a distance of about 100 cm left and right of the transect was recorded by counting the number of plants belonging to a certain category (diameter at breast height, dbh). We assumed that the number of plants with small dbh is greater in degraded, secondary forests, whereas primary forests show increasing numbers of plants of larger dbh (Chatelain *et al.* 1996, Pearman 1997). Definitions of habitat variables are summarized in Table 1. In order to quantify the availability of potential aquatic breeding sites, every aquatic habitat (lentic and lotic) located at a maximum distance of 25 m from either side of the transect was recorded with respect to type, surface and depth. Additionally, substrate moisture was determined in four categories during every transect walk.

Standardized visual transect sampling (SVTS). Sampling was performed independent of prevailing weather conditions. Usually four to six transects per day were sampled during daytime. A maximum of four transects was patrolled at night. Repeated controls of identical transects on consecutive days were avoided to ensure independence of samples. Transects were intensively patrolled at a constant speed (0.30–0.35 m/s), thereby recording all amphibians within a distance of 100 cm from either side of the path. As far as possible all individuals were captured. Specimens heard but not seen within this distance were not searched for and not included in the SVTS data sets (see below). In addition to species identity we recorded sex and snout-vent-length (SVL) of every individual, thus providing data that are useful to test for sex- or age-specific differences in habitat use, both in time and space.

Sampling was interrupted for the duration of the recording in order not to overestimate locations in which animals had previously been captured. To avoid duplicate recordings, captured frogs were marked by

TABLE 1. Categories of habitat variables measured on transects; dbh = diameter of plants at breast height; vegetation density was measured in four strata (see text).

	definition			
category	vegetation density	substrate types	dbh [cm]	leaf cover (%)
1	absent	forest soil	0–5	0–20
1.5	transition			
2	gaps predominating	arenaceous forest soil	6–10	21–40
2.5	transition			
3	closed areas predominating	loamy soil	11–20	41–60
3.5	transition			
4	closed	arenaceous soil	21–50	61–80
5		sabulose soil	> 50	81–100
6		muddy soil		
7		swampy soil		

toe clipping (Donnelly *et al.* 1994, Henle *et al.* 1997). Recaptures were excluded from the analyses. Individuals below nine mm SVL were not marked due to their small size. Coding schemes used for individual recognition were not applied. Removal of additional toes may decrease the recapture rate of marked individuals by more than 6–18 % for each additional toe removed after the first (Parris & McCarthy 2001). Thus, individual marking should be restricted to studies in which individual recognition is indispensable. At capturing sites a thorough description of the microhabitat was recorded, following the characterization routine used for general habitat description.

Standardized acoustic transect sampling (SATS). Since in the majority of frog species males use species-specific calls to advertise their position to potential mates and rivals (Wells 1977), this behavior can be exploited for acoustic monitoring. Audio strip transects represent a commonly used method for acoustic monitoring (Zimmerman 1994). Counts can be used to estimate relative abundance of calling males, species composition, as well as breeding habitat use and breeding phenology of species (Zimmerman 1994). Furthermore, this technique allows the detecting of cryptic species that, despite their potential abundance, may be underestimated when exclusively using visual techniques.

Throughout transect walks a combination of visual and acoustic techniques was applied at all times, keeping the transect routine identical for both techniques. As opposed to visual sampling, during SATS it was often impossible to determine individual parameters, other than sex and species. Likewise microhabitat description was not always possible. In those cases, habitat analyses can be based on data obtained from the general habitat characterization for single transects or segments. The width of the acoustic transect depends on the ability to detect each species' advertisement call. For that reason a maximum recording distance of 12.5 m to either side of the transect was defined, thus creating 25 m x 25 m acoustic sampling plots. Calls from greater distances cannot be unambiguously identified and the chance of duplicate recordings in neighboring segments increases. In the transect corners, only calls coming from the right-hand side in the first segments were registered (i.e., beginning with segment 1: segment 1, 8, 12 and 20). For both SVTS and SATS, data can be expressed in numbers of individuals per time and surface units. From February 1999 to December 2000 we compiled 382.5 hours of transect sampling. This corresponds to 765 transect walks.

Visual (VES) and acoustic (AES) encounter surveys. Due to the simplicity of the method, VES and AES are frequently used for rapid assessments and the evaluation of larger areas. An area or habitat is searched systematically for individuals in a defined time period. The resulting data are expressed in numbers of individuals of a certain species found in an area per unit time. For practical reasons "man-hours" can be used, which can be adjusted to the complexity of the habitats being sampled. This technique has been formalized as the time-constrained technique of Campbell & Christman (1982), and as the time-constrained searches of Corn & Bury (1990). It can be used to determine the species richness of an area and the species composition of a local assemblage, and to estimate relative abundances of species within an assemblage (Crump & Scott 1994). According to Corn & Bury (1990), VES can only provide information on the presence or absence of a species in an area but are inadequate for determining abundances.

In concordance with these authors the methods were only used as a qualitative or semi-quantitative tool within the scope of our studies. We used these methods continuously in all habitats of the study area including the transect areas. VES and AES thus could be used to evaluate if the randomly chosen transects represented the regional species pool, and also for evaluating if species that are rarely found on a transect belong to a particular local species pool or represent single migrating specimens that have habitat preferences not covered by the transects. Total VES- and AES-effort was kept comparable to the time spent on SVTS and SATS surveys throughout the entire study period.

Trapping with pitfall or funnel traps along drift fences. Pitfall traps with drift fences were installed in two of the primary forest transects from March to April 1999, and additionally in only one of these transects from January 2001 to September 2002. This device is useful to determine species richness of epigaeic organisms (Corn 1994). Capture success may vary greatly between species (Corn & Bury 1990, Dodd 1991). Anurans that are strong jumpers (e.g., *Ptychadena* species) are more difficult to trap than terrestrial species that lack these abilities (e.g., *Bufo* species). Drift fences consisted of durable green plastic gauze, 0.5 m high and stapled vertically onto wooden stakes. An array of fences and traps consisted of a central trap (buckets:

275 mm deep, 285 mm top diameter, 220 mm bottom diameter) and two triangular fence segments (total length 16 m). Each segment was tightened around a plastic bucket with an opening angle of 45°. The ends of each segment were flanked with additional plastic buckets, one on either side. Duct tape was used to reduce the diameter of the buckets and construct funnel-like openings in order to impede escaping from traps. Traps were checked at least on a daily basis.

In the course of this study, funnel traps (see Branch & Rödel 2003) were installed in a primary forest transect from 18 to 27 September 2002, and in a forest fragment (Paulé-Oula 2) outside TNP from 30 August to 12 September 2002 (A. Hillers *et al.*, unpubl. data). They were checked at least every morning. Additionally, we applied that method during a herpetological survey of the Haute Dodo and Cavally forests, which are situated south and west of TNP respectively (Rödel & Branch 2002, Branch & Rödel 2003). The data from pitfall and funnel traps can be expressed as number of individuals per trap-day. Pitfall trapping time summed to a total of approximately 4000 trap-days. Funnel traps summed to a total of 384 trap-days.

Data from each sampling method were compared with each other and to a list of species records that we gathered through January 1999 to September 2002 for the forest parts of the SRET region (Appendix 1). Sampling success is referred to as number of species within families recorded, using a particular sampling method. In addition, results were analyzed for leaf litter, arboreal, fossorial and aquatic species independent of families, as sampling success and efficiency may vary with regard to the particular biology of a species.

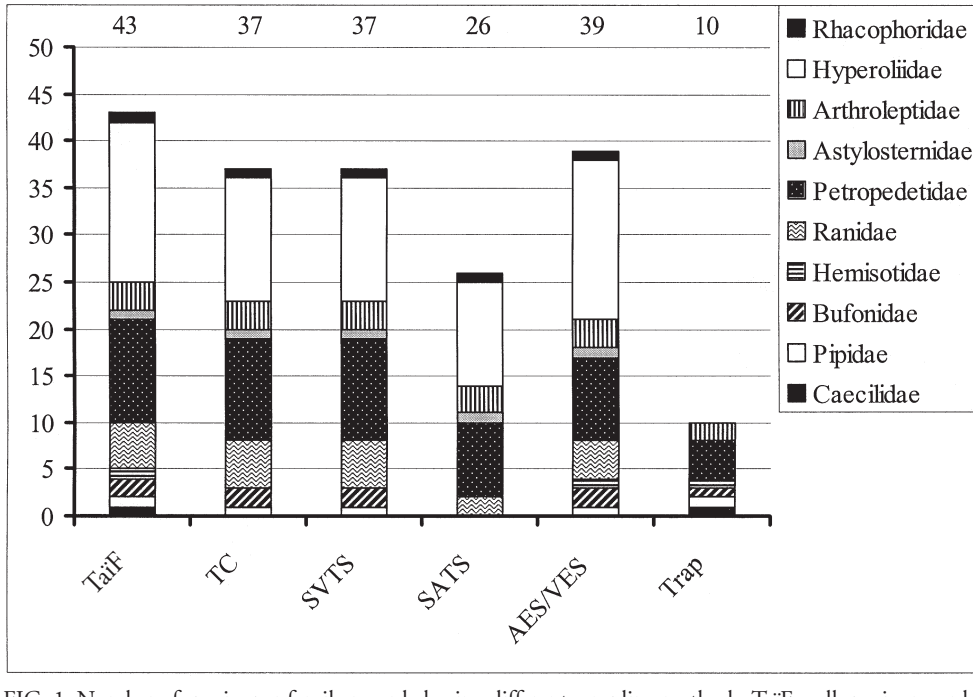

FIG. 1. Number of species per family recorded using different sampling methods. TaïF = all species recorded with all methods in forest habitats around SRET station; TC = species recorded during transect walks (SVTS and SATS combined); SVTS = species recorded during visual transect walks; SATS = species recorded during acoustic transect walks; AES/VES = visual and acoustic encounter surveys (only species that have been recorded in forest habitats around SRET station); Trap = pitfall and funnel traps. Numbers above bars represent total number of species recorded with the respective method.

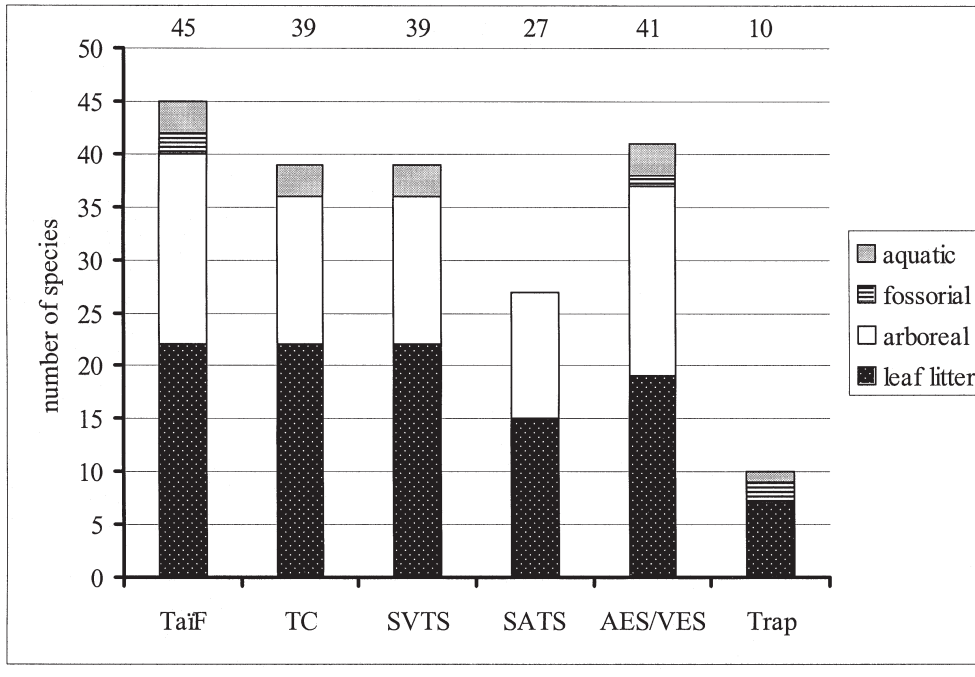

FIG. 2. Number of species per amphibian guild recorded using different sampling methods. For abbreviations see Fig. 1; two species were each listed in two guilds (compare Appendix). Numbers above bars represent total number of species recorded with the respective method.

RESULTS

In total, 56 amphibian species are known to occur in TNP (Schiøtz 1967, Perret 1988, Rödel 2000, Rödel & Ernst 2000, 2002; Rödel *et al.* 2003, see Appendix 1). Using all methods we recorded 50 species in the region of the SRET (89.3 % of TNP species). Failure to detect particular species in this region was most probably due to their general scarcity (e.g., *Bufo superciliaris*) or simply absence in the area under investigation (e.g., *Phrynobatrachus calcaratus*, *Hyperolius guttulatus*), rather than actual sampling method insufficiency. Seven species (*Bufo maculatus*, *B. regularis*, *Hoplobatrachus occipitalis*, *Ptychadena pumilio*, *P. bibroni*, *P. mascareniensis*, and *P.* sp.) were recorded exclusively outside forest habitats (e.g., clearing around SRET) and thus ignored in the analysis. Taking all methods into account, 43 species were recorded in forest habitats within the study region (Fig. 1, Appendix 1).

Sampling success and data quality varied between different methods, and between different amphibian families or guilds (Figs. 1, 2). Families containing only a few species in the TNP area showed the highest recording rates. Sampling efficiency in families containing higher numbers of genera and/or species was only marginally lower, thus making overall sampling success very high (Tab. 2; compare Appendix 1). During transect sampling (SVTS, SATS) we recorded a total of 15007 individual amphibians belonging to 37 species (86.0 % of TaïF) in eight families. Three leaf litter species (*Amnirana occidentalis*, *Phrynobatrachus fraterculus*, *P. annulatus*) were exclusively recorded during transect walks. VES/AES revealed 39 forest species (90.7 %) of nine families. Four arboreal frogs were exclusively recorded with these methods (*Hyperolius picturatus*, *H. nienokouensis*, *H. fusciventris*, *Phlyctimantis boulengeri*). Ten species (23.2 %) were recorded with pitfall and funnel trapping. Two fossorial species were exclusively detected either with VES and pitfall traps (*Hemisus* sp.) or pitfalls only (*Geotrypetes seraphini*).

Effectiveness in detecting species within given families differed significantly between methods (Friedman test; $\chi^2 = 19.199$, df = 5, p = 0.002, N = 10; tested for TaïF, TC, SVTS, SATS, AES/VES, Trap).

TABLE 2. Percentage of species within an amphibian family or guild that were recorded using a particular method. Reference is the number of species that were recorded using all methods in forested habitats around the SRET station (TaïF). For other abbreviations see text and Fig. 1.

Family / guild	TaïF	TC	SVTS	SATS	AES/VES	Trap
Caecilidae	1	0.0	0.0	0.0	0.0	100.0
Pipidae	1	100.0	100.0	0.0	100.0	100.0
Bufonidae	2	100.0	100.0	0.0	100.0	50.0
Hemisotidae	1	0.0	0.0	0.0	100.0	100.0
Ranidae	5	100.0	100.0	40.0	80.0	0.0
Petropedetidae	11	100.0	100.0	72.7	81.8	36.4
Astylosternidae	1	100.0	100.0	100.0	100.0	0.0
Arthroleptidae	3	100.0	100.0	100.0	100.0	66.7
Hyperoliidae	17	76.5	76.5	64.7	100.0	0.0
Rhacophoridae	1	100.0	100.0	100.0	100.0	0.0
leaf litter	22	100.0	100.0	68.2	86.4	31.8
arboreal	18	77.8	77.8	66.7	100.0	0.0
fossorial	2	0.0	0.0	0.0	50.0	100.0
aquatic	3	100.0	100.0	0.0	100.0	33.3

We could not detect a statistical difference in sampling efficiency between different amphibian guilds using the methods employed (Friedman test; $\chi^2 = 10.294$, df = 4, p = 0.067, N = 4; tested for TaïF, TC, SVTS, SATS, VES/AES, Trap). Schaich & Hamerle *post hoc* multiple comparisons revealed no significant differences between methods at $\alpha = 0.05$, neither between given family or guild. However, this was most probably due to the small overall sample size and high heterogeneity of species numbers in families and guilds (Bortz *et al.* 1990).

VES and AES revealed highest species numbers. Quantification of these data, other than based on time units, was difficult as detectability of species varied considerably with (e.g.) vegetation density. In contrast, transect walks made it possible to search for amphibians in a very comparative way. A distance of 1 m (visual) and 12.5 m (acoustic) proved to work equally well in all habitats investigated. Diurnal ground-dwelling frogs were best recorded quantitatively using SVTS. Most arboreal frogs could be recorded with SVTS, but that concerned mostly single specimens. With the exception of *Acanthixalus sonjae*, which is mute, quantitative data for all arboreal species were best assembled with SATS. Likewise, nocturnal leaf litter frogs (arthloeptids, asytlosternids) were best recorded with SATS.

The traps proved to be inadequate in qualitative and quantitative sampling since even small species such as *Phrynobatrachus villiersi* (SVL: 10–15 mm) managed to escape regularly (several direct observations). In Haute Dodo and Cavally forests we captured 38 % of the recorded amphibian species (16 of 42) with a combination of pitfall and funnel traps. Most specimens were captured with funnel traps (0.47 specimens per trap-day in contrast to 0.03 specimens per trap-day in pitfall traps). Trapping success was highest in leaf litter frogs (56.5 % of recorded leaf litter frogs), but very low in arboreal species (6.7 % of recorded arboreal species). As in TNP, the fossorial *Geotrypetes seraphini* was recorded with pitfall traps only. All other species were recorded with VES/AES (Rödel & Branch 2002, Branch & Rödel 2003). In TNP funnel traps were ineffective. We only captured a few leaf litter frogs; all were recorded using other methods as well, in a primary forest transect with none in the forest fragment (Hillers *et al.*, unpubl. data). No additional species were detected with funnel traps.

As aquatic sites were only taken into account, when being a part of the transect line itself, presence and abundance of purely aquatic species and tadpoles of all species were underestimated with all methods used here.

DISCUSSION

Choice of methods should reflect the best compromise between i: practicability, ii: specific aims, iii: efficiency, and iv: environmental impact. Standard plot sampling and total removal plots were not tested, as they impose a severe disturbance on the system under investigation and thus were not suitable to our goals. In addition, these methods do not seem to sample a given fauna adequately well (Allmon 1991, Vonesh 2001, Doan 2003). Compiling data on presence and abundance of aquatic species and tadpoles was outside the scope of this study and these species and stages were inadequately sampled with all methods used here. Simple presence/absence data of aquatic species and stages can best be gathered by direct observation (surfacing individuals) and with dip-netting. Methods of collecting quantitative data for aquatic amphibians and for tadpole assemblages have been described by Shaffer *et al.* (1994), Olson *et al.* (1997) and Rödel (1998a). Migrating pipid frogs can also be easily recorded with pitfall and funnel traps.

The methods tested within this study proved to perform with varying degrees of efficiency. VES and AES yielded highest species numbers. However, a combination of SVTS and SATS, as well as SVTS alone, were nearly as successful in detecting species. According to Pearman *et al.* (1995) a simple comparison of species numbers may not be sufficient to evaluate the efficiency of different sampling methods. They suggest using relative species richness within taxonomic entities, such as species groups, genera or families, as an adequate measure. The percentage of species within supraspecific taxonomic units, determined by using a particular sampling method, can then be compared to the real conditions in an area or habitat. In this study this has been done by determining relative species richness with reference to families or guilds.

The differences in efficiency of visual versus acoustic sampling varied between taxa. Some taxa, such as species of the genus *Acanthixalus*, which are mute (Drewes 1984, Schiøtz 1999, Rödel *et al.* 2003), could be detected exclusively using visual sampling methods. SVTS was generally the best method for detecting diurnal leaf litter frogs. Nonetheless, in order to sample particularly secretive leaf litter species, such as the very abundant *Arthroleptis* sp.1, *Arthroleptis* sp.2, *Cardioglossa leucomystax*, or *Phrynobatrachus alticola*, acoustic sampling appeared to be indispensable since these species were more readily detected by their calls than by sight. This was also true for most of the arboreal species belonging to the families Hyperoliidae and Rhacophoridae, and will likewise hold true for other arboreal anurans throughout the tropics, such as the Hylidae. In general SATS was very efficient in detecting nocturnal leaf litter frogs and treefrogs but less successful in detecting diurnal leaf litter frogs, and failed to detect aquatic and fossorial species. Pitfall trapping was only useful in detecting fossorial species that were not encountered during transect walks. We found no additional species and only very few specimens by funnel trapping.

Although the combination of AES and VES provided an adequate approximation to real conditions (see also Doan 2003), this only holds true if species numbers alone are considered. When including relative abundance measurements these methods were insufficient. The combined transect sampling methods provided a close approximation to the real presence and abundance of species, whereas visual sampling appeared to be superior to acoustic sampling. The advantage of transect sampling was especially obvious when focusing on leaf litter species. Therefore transect sampling can be considered to be the method of choice when sampling leaf litter anurans, but is certainly just as well suited for the investigation of tropical anuran assemblages in general.

The methods VES and AES in combination with pitfall traps with drift fences were useful in sampling additional, especially arboreal and fossorial, species not encountered during transect sampling, but appear not to be appropriate when standardized quantitative sampling is required. We found it impossible to quantify VES and AES other than in relation to time. Whereas transect walks provide the possibility of monitoring amphibians in a very comparative way, data acquisition varies considerably depending on habitat type in VES and even AES. Thus even time-based quantification of these data is questionable. We found it more realistic to apply a (clearly subjective) measure for habitat complexity on which to base collection effort during VES/AES, spending more time in complex, inaccessible areas than in areas that are easy to monitor. However, VES and AES are useful tools for the compilation of species inventory lists, e.g., during rapid assessment surveys (for recent West African examples see Rödel & Branch 2002, Rödel 2003, Rödel & Ernst 2003). Although widely used and recommended, especially in long-term field studies within temperate regions (e.g., Bury & Corn 1987, Semlitsch *et al.* 1996), pitfall traps and drift fences

proved to be the least effective method. Donnelly *et al.* (2001) report on similar experiences using this method in a herpetological survey in Guyana. They collected only six species (out of a total of 132 species of amphibians and reptiles being recorded), none of them uniquely found by this method. Burger *et al.* (2004) had high trapping success with pitfalls in Gabon when considering numbers of individuals. However only two species, the fossorial *Hemisus perreti* and the aquatic *Silurana epitropicalis*, accounted for 72.6 % of all individuals captured with this method. Data from both trapping methods can, in theory, be quantified in relation to time, e.g., as trapping success per trap per time unit. However trapping success depends very much on choice of site, experience of investigator and prevailing weather conditions (see Branch & Rödel 2003). A comparison of trapping data with data other than those of the observer in question seems to be difficult. When considering the relatively high costs and time investment due to the high level of maintenance required (Parris 1999), one should test the efficiency at a particular site in advance before installing these traps on a broad scale. In our experience, this method cannot be recommended for standardized sampling of tropical anurans.

SVTS and SATS have been proven to be the only methods that provided quantitative data on forest amphibians with regard to space and time. With the exceptions of aquatic and fossorial species they provided data that cover the whole community very well. SVTS and SATS provided data on species and habitats und thus may reveal changes in composition and species abundance, as well as environmental changes. Data can be used for comparisons between habitats, seasons and years.

Costs with regard to time spent for data acquisition was highest in trapping and in transect walks. Traps have to be checked at least daily. If the investigation is interrupted for some time, traps have to be uninstalled or closed and reopened when starting again. Transect walks are time intensive. It is advisable to perform them randomly independent of prevailing weather conditions. Thus data should be gathered throughout a whole season to obtain a thorough knowledge of the local fauna. However, in consecutive field seasons, the frequency of sampling can be reduced when general phenological traits of the species recorded have been clarified. VES and AES are less time consuming; however, generalization of data with regard to phenology or abundances is less possible.

VES and AES had probably the lowest environmental impact. The impact of traps and drift fences was difficult to judge. Theoretically it might well be that trapping will result in dislocating at least some species from the area where traps have been established. Transects will have an environmental impact, if not on amphibians then on other organisms. We observed (e.g.) that leopard (*Panthera pardus*) tracks

TABLE 3. Effectiveness of methodology in regard to type of data required, amphibian guild and environmental impact. QS/TR = quadrat sampling/total removal sampling (data from Allmon 1991, Parris 1999, Rodda *et al.* 2001, Vonesh 2001, Doan 2003); for other abbreviations see text and Fig. 1.

	TC	SVTS	SATS	AES/VES	Trap	QS/TR
leaf litter frogs	+++	+++	++	+++	+	+++
arboreal frogs	++	++	++	+++	–	–
fossorial amphibians	–	–	–	+	+++	–
aquatic frogs	+++	+++	–	+++	+	–
qualitative data	+++	+++	+++	+	+	+++
quantitative data	+++	++	++	+	–	+++
environmental impact	low	low	low	very low	medium	very high
costs (time)	high	high	high	low	very high	high
costs (material)	low	low	low	very low	low	low
utility (ecology)	very high	high	high	low	very low	very low
utility (conservation)	very high	high	high	high	low	low

were more often seen on the transect path than in undisturbed forest. This might affect densities of other mammals including possible seed dispersers with, in the worst case, consequent long-term effects on forest structure. After using transects intensively for some time, a well visible path becomes established that at least in primary forests remains so for years. Transect cutting and the use of transects should therefore be done with the necessary precautions.

Advantages and disadvantages of different methods are summarized in Tab. 3. For simple short-term surveys we recommend VES and AES, possibly accompanied by opportunistic trapping. The presented transect design proved to be adequate for representative sampling and appeared to be appropriate for most studies involving multivariate structure data. SVTS and SATS are especially useful for long-term studies. Furthermore transects provide an effective method of investigating leaf litter frogs in particular, not only on their breeding sites but throughout the whole range of habitats used by them, thus generating a much more complete picture of an amphibian community than is possible with other methods. However, for specific questions (*cf.* Lips *et al.* 2003) transects should be supplemented by specifically investigating aquatic breeding sites with the appropriate set of standardized techniques (Heyer *et al.* 1994, Olson *et al.* 1997, Rödel 1998a).

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APPENDIX. List of amphibian species recorded in Taï National Park (TNP); TaïF = species recorded in forest habitats around the SRET station; G = species recorded in southern TNP (Guiroutou, 5°25' N, 7°10' W); SRET = species recorded with VES/AES on the clearing around the SRET station; TC = all species recorded on transects; TP = all species recorded on transects in primary forest; TS = all species recorded on transects in secondary forest; VES/AES = species recorded via visual and acoustic encounter surveys in forest habitats near SRET, other than transects; Trap = species recorded with pitfall and funnel traps; l = leaf litter species; a = arboreal species; f = fossorial species; aq = aquatic species; [1] = known from TNP (Schiøtz 1967, Perret 1988) but not recorded by us; [2] = determination not possible at present time; [3] = *Phrynobatrachus guineensis* is a leaf litter frog but reproduces in small water-filled tree holes (Rödel 1998b); [4] = *Acanthixalus sonjae* lives aquatically in large water filled tree holes but forages in surrounding vegetation (Rödel *et al.* 2003); [5] = treated as full species and not as subspecies of *Hyperolius fusciventris* due to sympatric occurrence in TNP (see Rödel & Branch 2002); [6] = recorded north of area under investigation.

species	TaïF	G	SRET	TC	TP	TS	VES/AES	Trap	guild
Gymnophiona									
Caecilidae									
Geotrypetes seraphini	1	0	0	0	0	0	0	1	f
Anura									
Pipidae									
Silurana tropicalis	1	1	0	1	1	0	1	1	aq
Bufonidae									
Bufo regularis	0	1	1	0	0	0	0	0	l
Bufo maculatus	0	1	1	0	0	0	0	0	l
Bufo togoensis	1	1	0	1	1	1	1	1	l
Bufo taiensis	1	0	0	1	1	0	1	0	l
Bufo superciliaris	0	1	0	0	0	0	0	0	l
Hemisotidae									
Hemisus sp.[2]	1	0	0	0	0	0	1	1	f
Ranidae									
Hoplobatrachus occipitalis	0	1	1	0	0	0	0	0	aq
Amnirana albolabris	1	1	0	1	1	1	1	0	l
Amnirana occidentalis	1	1	0	1	1	1	0	0	l
Aubria occidentalis	1	0	0	1	1	0	1	0	aq
Ptychadena pumilio	0	1	1	0	0	0	0	0	l
Ptychadena bibroni	0	0	1	0	0	0	0	0	l
Ptychadena mascareniensis	0	0	1	0	0	0	0	0	l
Ptychadena superciliaris	0	1	0	0	0	0	0	0	l
Ptychadena aequiplicata	1	1	0	1	1	1	1	0	l
Ptychadena longirostris	1	1	1	1	0	1	1	0	l
Ptychadena sp.[2]	0	1	1	0	0	0	0	0	l
Petropedetidae									
Phrynobatrachus accraensis	1	1	1	1	0	1	1	0	l
Phrynobatrachus gutturosus	1	1	0	1	1	0	1	0	l
Phrynobatrachus fraterculus	1	0	0	1	1	1	0	0	l
Phrynobatrachus guineensis[3]	1	1	0	1	1	1	1	0	l, a
Phrynobatrachus phyllophilus	1	1	0	1	1	1	1	1	l
Phrynobatrachus liberiensis	1	1	0	1	1	1	1	0	l
Phrynobatrachus alticola	1	1	0	1	1	1	1	0	l
Phrynobatrachus alleni	1	1	0	1	1	1	1	1	l
Phrynobatrachus plicatus	1	1	1	1	1	1	1	1	l

Appendix continued

species	TaïF	G	SRET	TC	TP	TS	VES/AES	Trap	guild
Phrynobatrachus calcaratus	0	1	0	0	0	0	0	0	l
Phrynobatrachus taiensis[1]	0	0	0	0	0	0	0	0	l
Phrynobatrachus villiersi	1	1	0	1	1	1	1	1	l
Phrynobatrachus annulatus	1	0	0	1	1	0	0	0	l
Astylosternidae									
Astylosternus occidentalis	1	1	0	1	1	1	1	0	l
Arthropleptidae									
Cardioglossa leucomystax	1	1	0	1	1	1	1	0	l
Arthroleptis sp. 1[2]	1	1	1	1	1	1	1	1	l
Arthroleptis sp. 2[2]	1	1	0	1	1	1	1	1	l
Hyperoliidae									
Leptopelis hyloides	1	1	1	1	1	1	1	0	a
Leptopelis occidentalis	1	1	0	1	1	1	1	0	a
Leptopelis macrotis	1	1	0	1	1	1	1	0	a
Hyperolius concolor	1	1	1	1	1	0	1	0	a
Hyperolius guttulatus[6]	0	0	0	0	0	0	0	0	a
Hyperolius picturatus	1	1	1	0	0	0	1	0	a
Hyperolius sylvaticus	1	1	0	1	1	1	1	0	a
Hyperolius zonatus	1	1	0	1	1	1	1	0	a
Hyperolius fusciventris[5]	1	0	1	0	0	0	1	0	a
Hyperolius lamtoensis[5]	1	1	0	1	1	0	1	0	a
Hyperolius nienokouensis	1	1	0	0	0	0	1	0	a
Hyperolius wermuthi[1]	0	0	0	0	0	0	0	0	a
Hyperolius chlorosteus	1	1	0	1	1	1	1	0	a
Afrixalus dorsalis	1	1	1	1	0	1	1	0	a
Afrixalus nigeriensis	1	1	0	1	1	1	1	0	a
Afrixalus vibekae	1	0	0	1	1	0	1	0	a
Kassina lamottei	1	1	0	1	1	0	1	0	l
Phlyctimantis boulengeri	1	0	0	0	0	0	1	0	a
Acanthixalus sonjae[4]	1	0	0	1	0	1	1	0	a, aq
Rhacophoridae									
Chiromantis rufescens	1	1	0	1	1	1	1	0	a
total 56 species in TNP	43	41	16	37	33	28	39	10	