MEASURING AND MONITORING AMPHIBIAN DIVERSITY IN TROPICAL FORESTS. II. ESTIMATING SPECIES RICHNESS FROM STANDARDIZED TRANSECT CENSING

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Abstract: In the face of accelerating declines in amphibian populations, it is crucial to be able to effectively identify conservation priorities, both in terms of species and localities. Rapid assessment of amphibian community structure is therefore essential. Visual encounter survey (VES) and standardized visual transect sampling (SVTS) are becoming increasingly important in the measurement and monitoring of tropical anuran communities. In the present paper we compare the performance of SVTS along seven tropical forest transects where frog communities are currently being monitored: Lalut Birai (Borneo, Indonesia), Kakamega Forest National Reserve (Kenya, Africa), Taï National Park (Ivory Coast, Africa; two transects) and Ambolokopatrika-Betaolana Rainforest (Madagascar, three transects). We compared species lists generated from the transects with those from the entire study areas. Species richness was estimated using different incidence- and abundance-based richness estimators: ACE, ICE, Chao1, Chao2, First-order jackknife, Michaelis Menton Estimators (MMMeans and MMRuns). Only a few transect characteristics had a significant effect on species richness estimate accuracy. Species saturation was significantly enhanced by the number of transect walks (n_{counts}). The relative standard deviation of the First-order jackknife estimator significantly decreased with an increasing daily species richness and a combined effect of daily species richness and the overall abundance of frogs. Comparison of transect and forest species lists show that terrestrial species are best represented by VES/SVTS. We recommend that a transect census should be performed on at least 20 independent walks. Different species richness estimators should be applied simultaneously since their behavior/effectiveness under a wide array of transect parameters is still unknown. *Accepted 25 June 2004.*

Key words: ACE, amphibians, Borneo, Chao 1, Chao 2, diversity, First-order jackknife, ICE, Ivory Coast, Kenya, Madagascar, MM-Means, MMRuns, monitoring, rainforest, species richness.

INTRODUCTION

Potential causes of the "world-wide amphibian decline" are still embroiled in controversy (e.g., Alford & Richards 1999, Houlahan *et al.* 2000). For some years now global climatic change has been invoked to explain the rapid declines in amphibian populations occurring even in remote and pristine habitats (e.g., Lips 1999, Carey *et al.* 2001). Alternatively, synergisms among an increasing number of local causes were cited as being responsible for population declines all over the world (e.g., UV-B radiation, chytridiomycosis, pesticides, habitat destruction; Nyman 1986, Pechman *et al.* 1991, Blaustein *et al.* 1994, Alford &

Richards 1999, Houlahan *et al.* 2000, Davidson *et al.* 2002, Ron *et al.* 2003).

In confronting the decline of amphibian populations, it becomes increasingly important to recommend conservation priorities, both in terms of species and areas. Rapid habitat destruction requires a rapid assessment of community structure, even for areas as yet unaffected. Monitoring at the community level will also detect single species or groups of species that are especially prone to decline (e.g., Andean members of the bufonid genus *Atelopus*; Ron *et al.* 2003) and hence may be powerful indicators of habitat changes.

Due to its simplicity, encounter survey in a prescribed time period will often be the method-of-choice for measuring diversity of tropical anuran communities (Heyer *et al.* 1994, Lips *et al.* 2001, Doan 2003, Rödel & Ernst 2004). Surveys may be conducted

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acoustically (acoustic encounter survey, AES) or visually (visual encounter survey, VES). AES profits from the detectability of males through vocalization, which also allows for easy discrimination of species, with the cost, however, of gender and species-specific biases. In contrast, VES is less sensitive to individual detection, but it is also less prone to a gender-specific bias.

Standardized visual transect sampling (SVTS) and standardized acoustic transect sampling (SATS) are VESs and AESs that are standardized in space and time (Rödel & Ernst 2004). Species abundance can further be standardized in terms of observer number and time units of investigation (resulting in species abundance per person-hour). This allows for a determination of (*i*) community composition, (*ii*) species richness, (*iii*) relative abundance of species within a given community (e.g., Crump and Scott 1994), and (*iv*) comparison of the abundance of a particular species between transects.

In the present study we do not focus on a comparison of the overall species richness of frog communities in different parts of the world. We intend rather to analyze the overall performance of VES and SVTS by comparing the number of species that might have been detected if a census were continued over time. In turn, such analyses provide an estimation of the sufficiency of effort at the conclusion of a given

time period. By including transects from tropical rainforests in Borneo, Madagascar, West and East Africa, we are able to evaluate the performance of transect analyses under a maximum of variation in community parameters such as species richness, species composition and phylogenetic background.

Community species richness can be assessed by extrapolating the number of species observed during a field campaign to the possible outcome if the survey were extended to an infinite number of transect walks. Numerous such richness estimators have been proposed, many of which have been little used in the ecological literature. Colwell (2000) emphasized that it is premature to make any firm recommendations regarding which estimator is "best" or even under which circumstances one is better than another, although Chazdon *et al.* (1998) had made some progress in this regard (see also Magurran 2004 for an overview). Like estimators of species diversity, different richness estimators may be sensitive to different VES/SVTS parameters, such as number of species, number of specimens and number of transect walks. We therefore applied several richness estimators, which are either based on incidence or abundance of species. Depending on the transect, we analyzed the performance of VES/SVTS during day versus night and in rainy versus dry seasons (roughly corresponding to summer and winter).

TABLE 1. Characteristics of seven tropical rainforest transects. For abbreviations see Materials and Methods; n= transect walks.

Study site	Continental region	Latitude	Longitude	Altitude [mas]	Transect length [m][m]	Transect width	Data type study	Duration of	n counts
LB	SE Asia	02°52'33.8"N	115°49'10.6"E	*ca.* 500	500	2	SVTS	Sept. 12-28, 2001	13
TNP1	W Africa	05°50'03.5"N	007°20'57.0"W	150	600	2	SVTS/ SATS	March 15 –August 21, 2000	42
TNP2	W Africa	05°50'02.6"N	007°21'02.9"W	200	600	2	SVTS/ SATS	March 15 –August 21, 2000	41
KFNR	E Africa	00°21'N	034°51'E	1650	600	2	SVTS/ SATS	April 30 – Dec. 9, 2002	29
ABR1	Africa: Madagascar	14°31.8'S	49°26.5'E	810	500	5	VES	May 27 - June 3, 1997	8
ABR2	Africa: Madagascar	14°32.4'S	49°26.3'E	860	600	5	VES	June 4-12, 1997; Nov. 29 - Dec. 8, 1997	10
ABR3	Africa: Madagascar	14°32.6'S	49°25.8'E	950-1250	550	5	VES	Dec. 9-20, 1997	10

MATERIALS AND METHODS

Study sites. Amphibian communities were studied at four sites in South-East Asia, West and East Africa and Madagascar. We are limited to frogs (Anura) since salamanders are absent from all study areas and caecilians are absent from Madagascar. Transects are described in Table 1. Species lists for all transects and areas are given in the Appendix.

Lalut Birai (LB; Borneo, Indonesia). LB is the field station of the World Wide Fund for Nature (WWF) Indonesia in the Kayan Mentarang, the largest national park in South-East Asia (see Veith *et al.* 2004 for details). The LB area is dominated by small rivers and steep slopes. Vegetation cover consists of undisturbed primary rainforest. The climate of the area is predominately an ever-wet tropical rainforest climate, with high temperatures and rainfall throughout the year. Rainfall ranges between 2500 and 3700 mm per year (TAD 1983), with the driest months from July to October. The transect runs along a slope, more or less parallel to the major river, Enggeng Bio, at a distance of 50 to 100 m. It crosses several small permanent and temporary brooks. We recorded all specimens that were visible within a distance of 1 m from both sides of the transect, either sitting on the ground or attached to vegetation.

Kakamega Forest National Reserve (KFNR; Kenya). KFNR is part of the Kakamega Forest in the highlands of western Kenya (Western Province), a relict of the Pleistocene Guineo-Congolesian rainforest belt (see Lötters *et al.* in press). The general area is composed of disturbed primary and secondary montane forest as part of a highly degraded landscape. The climate is moderately warm and humid, with an annual mean temperature of ca. 19 °C and two rainy seasons from March to June and from July to September; mean annual rainfall is about 2000 mm (Jätzold & Schmidt 1982, Haupt 2000). The 600-m-long, rectangular transect (200 m x 100 m) runs through both primary and secondary forest. It is in the proximity of a permanent forest pond and crosses some swampy areas with temporary running water. All specimens that were visible within a distance of 1 m on both sides of the transect were recorded, denoting terrestrial and arboreal species. Through major parts of the survey, SVES and SVAS were not separated, so we included both in the KNFR transect analysis.

Taï National Park (TNP1; TNP2; Ivory Coast). Taï National Park (TNP), situated in western Ivory Coast,
is West Africa's largest protected area of primary rainforest (4550 km²; Guillaumet 1967, Sangaré 1995, PACPNT 2000). Our investigations were based at the Station de Recherche en Ecologie Tropical (SRET, formerly CRE and IET, 05°50.003 N, 007°20.536 W) maintained by the University of Abobo-Adjamé, Abidjan. The climate of TNP can be described as humidtropic seasonal (Riezebos *et al.* 1994, Parren & de Graaf 1995, Richards 1996). A long rainy season from March/April to July is followed by a short dry season in July or August. A second rainy season, from September to October, is usually shorter but accounts for most of the yearly precipitation. This is followed by a long dry season lasting from November to February/March. Mean annual precipitation at the SRET is 1806 mm (data from 1988–2002). Daily temperature varies between 20 and 33 °C, the mean annual temperature being 26 °C (Rompaey 1993). Humidity fluctuates between 85 % (day) and 90–100 % (night). During the dry season the humidity may occasionally drop below 40 % (M.-O. Rödel & R. Ernst, unpubl. data). Floristically, TNP belongs to the Guinean-Congo-Region (Guillaumet 1967, Lawson 1986, PACPNT 2000). The potential natural vegetation is evergreen seasonal lowland rainforest (Richards 1996). We established 10 rectangular transects, each 600 m in length. Herein we only present data from two primary forest transects, marking the extreme values of available forest types in TNP. Data collection took place from 15 March to 23 September 2000. Transect 2 (TNP2) was situated on a hill and consisted of comparatively dry forest. The understorey was open or absent, while the tree and canopy strata, in segments exceeding 50 m in height, were closed. No open water was present. Transect 1 (TNP1), in contrast, was situated in a swampy valley, drained by a small forest creek. The transect crossed the creek several times, and there were numerous puddles and ponds situated close by. Distance between TNP1 and TNP2 was only 200 m. The understory was partly very dense, while the canopy stratum was mostly open. Transects were intensively monitored (0.30-0.35 m/s walking speed) to record all individuals within 100 cm on either side. For a more detailed description of the transects and the monitoring scheme see Rödel *et al.* (2001), Rödel *et al.* (2004) and Rödel & Ernst (2004).

Ambolokopatrika-Betaolana Rainforest (ABR1-3; Madagascar). Three study sites were chosen, all occurring in the Commune Rurale d'Ambodiangezoka, Fivondronana d'Andapa, Province d'Antsiranana: "Ande-

makatsara" (ABR1), 14°31.8 S, 49°26.5 E, 810 m, 27 May–3 June 1997; "Andranomadio" (ABR 2), 14°32.4 S, 49°26.3 E 860 m, 4–12 June 1997 and 29 November–8 December 1997; "Antsinjorano" (ABR3), 14°32.6 S et 49°25.8 E, 950–1250 m, 9–20 December 1997. The forest around sites 1 and 2 is transitional between lowland and montane moist rainforest, while at site 3 it is a mid-altitude rainforest; at all sites there are patchworks of pristine and altered rainforest. For details on area and transects see Andreone *et al.* (2000). The climax vegetation is of the evergreen type, which corresponds to the eastern ombrophile primary and secondary forest and to transitional low- mid-altitude and montane wet forest. The studied forests are mosaics of fairly intact forest, "savoka" (a degraded formation mainly constituted of herbaceous species), and secondary forest. According to data for the town of Andapa (Randriamaherisoa *et al.* 1993), the region is characterized by a humid and tropical climate. The mean temperature ranges from 18°C in July to 25°C in February. The annual precipitation is slightly more than 2000 mm. The "dry" season lasts about two months (September and October). Fieldwork took place in two different periods: May–June (which is a comparatively "dry" and "cold" time), and November–December (which corresponds to the beginning of the warm rainy season, when most amphibian species are breeding). These periods were chosen to cover seasonal changes in amphibian activity patterns (Andreone 1994, 1996).

Amphibian survey. We compared VES/SVTS species lists each with two other species lists: (*i*) all species detected in the area during the same time interval of the VES/SVTS (potential number of active species) by any method, such as opportunistic searches, quadrate sampling, and pitfall traps with drift fences or funnel traps; (*ii*) all species that have ever been detected at and around the VES/SVTS site.

Estimation of species richness. We compared observed species accumulation curves with the maximum number of species estimated after randomization of observation days. Species accumulation curves (observed n species) were calculated for 1000 randomizations without replacements (see Colwell & Coddington 1994).

The incidence-based first-order jackknife estimator of species richness was introduced by Burnham & Overton (1978, 1979) and Heltshe & Forrester

(1983). *Chao1* (Chao 1984) and *Chao2* (Chao 1987) are species richness estimators that are based on abundance and incidence data, respectively. We also calculated coverage-based species richness estimators: the abundance-based coverage estimator (*ACE*; Chao *et al.* 1993; Chazdon *et al.* 1998) for the quantitative census, and the incidence-based coverage estimator (*ICE*; Lee & Chao 1994, Chazdon *et al.* 1998) for the incidence data of the combined census. Standard deviations for *ACE* and *ICE* are based on the variance of sample-order randomization (a kind of bootstrap estimate). The maximum number of species that might be recorded under the given transect sampling conditions was also estimated through two different Michaelis Menten (*MM*) richness estimators (Raaijmakers 1987). Both estimators represent the asymptote based on one, two, three ... maximum number of samples (Colwell & Coddington 1994). *MMRuns* computes estimates for values for each pooling level for each randomization run, and then averages over randomization runs. *MMMeans* computes the estimate for each pooling level just once from the mean species accumulation curve. In general, *MM* estimators are regarded as robust estimators of species richness (e.g., León-Cortés *et al.* 1998, Peterson & Slade 1998, Süssenbach & Fiedler 1999). All calculations were made with the EstimateS software (version 6.0b1; Colwell 2000). All species richness estimators were run with 1000 permutations.

Influence of species saturation curves and the variability of species richness estimates. To assess the accuracy of species observation and species richness estimation, we calculated variability estimates (as dependent variables) and compared them with several characteristics of transect counts (independent variables). Dependent variables were: (*i*) the difference between the last and the last but one observed number of species relative to the observed number of species ($\Delta S_{obs}/S_{obs}$); this is an indicator of how well S_{obs} converges on a plateau; (*ii*) the range of all species richness estimators relative to the observed number of species (range$_{est}$/S_{obs}); we interpret this as an indicator of the overall robustness of species richness estimation; and (*iii*) the relative standard deviation of the First-order jackknife estimator (sdJN$_{rel}$; here we confined to the First-order jackknife estimator since in several comparative analyses jackknife estimators perform particularly well; see Magurran 2004); it exemplifies the goodness of this estimate. Indepen-

TABLE 2. Composition of frog communities from seven tropical rainforest transects.

Abbre-viation	All Species			Arboreal Species			Terrestrial Species			Aquatic Species		
	for-est[1]	cam-paign[2]	tran-sect	for-est[1]	cam-paign[2]	tran-sect	for-est[1]	cam-paign[2]	tran-sect	for-est[1]	cam-paign[2]	tran-sect
LB	33	20	13	4	1	1	28	18	12	1	1	0
TNP1	45[3]	26	23	15	9	9	28[4]	16	14	2	1	0
TNP2	45[3]	26	9	15	9	1	28[4]	16	8	2	1	0
KFNR	23	21	12	8	8	7	13	11	4	2	2	1
ABR1	18	18	15	10	10	10	7	7	4	1[5]	1	1
ABR2$_{cold-dry}$	33	17	16	21	11	11	10	5	4	2	1	1
ABR2$_{hot-rainy}$	33	32	20	21	20	14	10	10	4	2	2	2
ABR3	28	28	18	16	16	14	11	11	3	1	1	1

[1] All species ever found in the forest area around the transect
[2] All species recorded during the field campaign when the transect census was conducted
[3] Within a radius of 2 km around the SRET
[4] The fossorial *Hemisus* was only recorded through the presence of aquatic tadpoles.
[5] Two species are considered as aquatic: *Mantidactylus* cf. *guttulatus* (a large torrenticolous frog), and *M.* cf. *betsileanus* (a rather small species inhabiting marshes).

dent variables were the number of transect walks (n_{counts}), the number of observed species (S_{obs}), the mean number of species per day, S_{mean} (calculated as the mean of the first day over all 1000 randomized input orders), its respective variance (sdS_{mean}^2), the relative number of observed species per day (S_{mean}/S_{obs}), and the total number of specimens counted along a transect (n_{ind}). We performed a multiple linear regression analysis with forward inclusion of independent variables.

RESULTS

Here we present and discuss summarized statistics on transect data and species richness estimates, rather than detailed descriptions of all richness estimators per transect.

The LB transect community of frogs comprises 40 % of all species known for the area (see Appendix). It mainly consists of terrestrial species. Only one arboreal species, *Pedostibes hosii*, was recorded. Semi-aquatic species (e.g., most *Limnonectes* species) and arboreal species (Rhacophoridae) were absent. Typical leaf litter species (e.g., *Kalophrynus, Leptobrachella, Leptollalax, Leptobrachium*) were rare or even absent within the whole area of LB (Veith *et al.* 2004).

At KFNR, about 50 % of all taxa known could be confirmed through SVES and SVAS. Due to their circadian activity, all of these could by traced during night walks, while only some of them – in very low

numbers – were also found during day walks (Tab. 3). The species record includes seven nocturnal arboreal taxa of the family Hyperoliidae as well as four terrestrial species belonging to different families (see Appendix). Among them, *Phrynobatrachus* cf. *natalensis* and *Ptychadena* cf. *mascareniensis* are both diurnal and nocturnal. *Kassina senegalensis* and *Bufo* cf. *maculates* are crepuscular to nocturnal with facultative diurnality. *Xenopus borealis* is the only aquatic species recorded through transect walks (it is active during day and night). All species are species that can also occur in bushland or even savannah, except the elusive forest species *Leptopelis* cf. *modestus*. Some of the nine species not found along, but in the vicinity of the study transect, and the two reported in literature from the study site within KFNR (see Appendix), can be similarly grouped, apart from *Hoplobatrachus occipitalis*, *Leptopelis* cf. *bocagii* and *Phrynobatrachus* cf. *minutus*. The first of these is a semi-aquatic to aquatic savannah inhabitant, while the other two are nocturnal ground-dwellers of open areas. Fossorial, riparian or small leaf litter frogs (e.g., *Arthroleptis* spp.) are unknown from this part of KFNR. All life history information was taken from Lötters *et al.* (in press) or unpublished field notes.

At TNP in 2000 we recorded 51% (TNP1) and 20% (TNP2) of the species known to live in that area of the national park through transect walks (see Appendix). However, the percentage of recorded species potentially occurring along a particular transect was

much higher (82 % on TNP1; 90 % on TNP2). Nocturnal, diurnal, terrestrial and arboreal species were equally well represented in our data. Only aquatic, *Silurana tropicalis*, and fossorial species, *Hemisus* spp., were not recorded with SVES and SVAS. For most species not encountered on the transects, suitable habitats were absent. Because of the lack of open water, TNP2 did not provide breeding sites for anurans, except for two species that have direct development (*Arthroleptis* spp. 1 and 2). Species assemblage in TNP2 consisted almost exclusively of the two *Arthroleptis* and juvenile specimens of various other leaf litter frogs. Species with particular needs, e.g., large water-filled tree-holes (*Acanthixalus sonjae*) or a preference for open or disturbed forest (e.g., *Phrynobatrachus alticola*, *Phlyctimantis boulengeri*) were absent along both transects.

Looking at data presented in Table 2 it is evident that – regarding the Madagascan sites (see Appendix) – the number of arboreal species remains almost equal in the three sampling sites. However, during the cold season the number of arboreal species is low at the transect. Also, as a general rule, it can be observed that there are many more arboreal than terrestrial species. In the "forest" the highest number of arboreal species is 21, versus 11 terrestrial and 2 aquatic. In the "field campaign" the situation is similar (20, 11, 2), but in the "transect" the number of arboreal and terrestrial frogs is much smaller (14, 4), while the number of aquatic species remains constant (2).

The observed number of species converged on a plateau at TNP1, TNP2, LB and $KFNR_{night}$. For all other transects, the number of observed species continued to increase at a considerable rate (Fig. 1). There was no consistent pattern for which species richness estimator provided the highest or lowest estimates. With the exception of *MMMean*, each estimator could give the highest or the lowest estimate, depending on the transect (Tab. 3). The lowest range of species richness estimators were found for LB (1.85) and TNP1 (1.95), while the highest ranges were estimated for $KFNR_{day}$ (19.38) and ABR1 (27.77) (Tab. 4). The average per-count-increase stabilized at a minimum level from counts 21, 21 and 26 for transects $KFNR_{night}$, TNP1 and TNP2 respectively.

How species richness estimators converge at stable levels is exemplified for the First-order jackknife estimator for all transects (Fig. 2). Only at TNP1 do the mean and 95 % confidence intervals converge at a constant level. Constancy seems to have been reached at $KFNR_{night}$ and LB, while estimates for $KFNR_{day}$, $ABR1_{winter}$ and $ABR2_{summer}$ continue to increase.

Transect characteristics had only a few significant effects on estimate accuracy. Convergence on a plateau of the observed number of species, i.e., species saturation, was significantly enhanced by either the number of transect walks (n_{counts}) or by the combined effect of transect walks and the relative number of species recorded per transect walk. The relative standard deviation of the First-order jackknife estimator sig-

TABLE 3. Observed and estimated number of frog species, based on different species richness estimators (*ACE*, *ICE*, *Chao1*, *Chao2*, First-order jackknife (*Jack1*), *MMRuns*, *MMMeans*) for seven tropical rainforest transects; means and standard deviations (sd) are derived from 1000 random input permutations; n counts = number of transect walks; $days_0$ = days with no frog records; n campaign = total number of species observed around the transect during the field campaign; S_{obs} = number of species observed on the transect; n_{ind} = number of individuals observed on the transect; $range_{est}$ = range of species richness estimates.

|	n counts	$days_0$	n campaign	S_{obs}	n_{ind}	*ACE* mean	*ICE* mean	sd	*Chao1* mean	sd	*Chao2* mean	sd	*Jack1* mean	sd	*MM Runs*	*MM Means*	$range_{est}$
LB	13	0	20	13	139	13.41	13.45	0.00	13.25	0.73	13.17	0.54	13.92	0.92	15.02	14.79	1.85
$KFNR_{night}$	29	0	21	12	265	15.75	15.35	0.01	14.25	3.40	14.25	3.40	14.90	1.61	12.56	12.48	3.19
$KFNR_{day}$	26	19	21	7	12	20.57	28.50	0.00	19.50	17.14	25.00	23.62	12.77	2.11	17.97	26.21	15.73
TNP1	42	7	26	20	1130	20.00	20.92	0.00	20.00	0.00	21.00	1.87	21.95	1.36	21.34	21.42	1.95
TNP2	41	7	26	9	391	16.60	13.20	0.02	12.92	6.62	12.92	6.62	11.93	1.65	9.08	9.32	7.52
ABR1	8	0	18	18	148	38.02	26.45	0.00	50.00	39.60	50.00	39.60	25.00	2.29	23.17	22.23	27.77
$ABR2_{cold-dry}$	9	0	17	17	135	19.37	19.02	0.00	23.32	9.99	21.00	5.29	20.56	2.35	23.62	21.66	4.60
$ABR2_{hot-rainy}$	10	0	20	32	166	44.01	50.93	0.00	50.00	14.39	50.75	13.08	45.50	3.07	49.64	46.75	6.92
ABR3	10	1	28	28	179	32.29	33.58	0.00	40.25	13.15	38.13	9.02	36.10	2.83	39.47	38.12	7.96
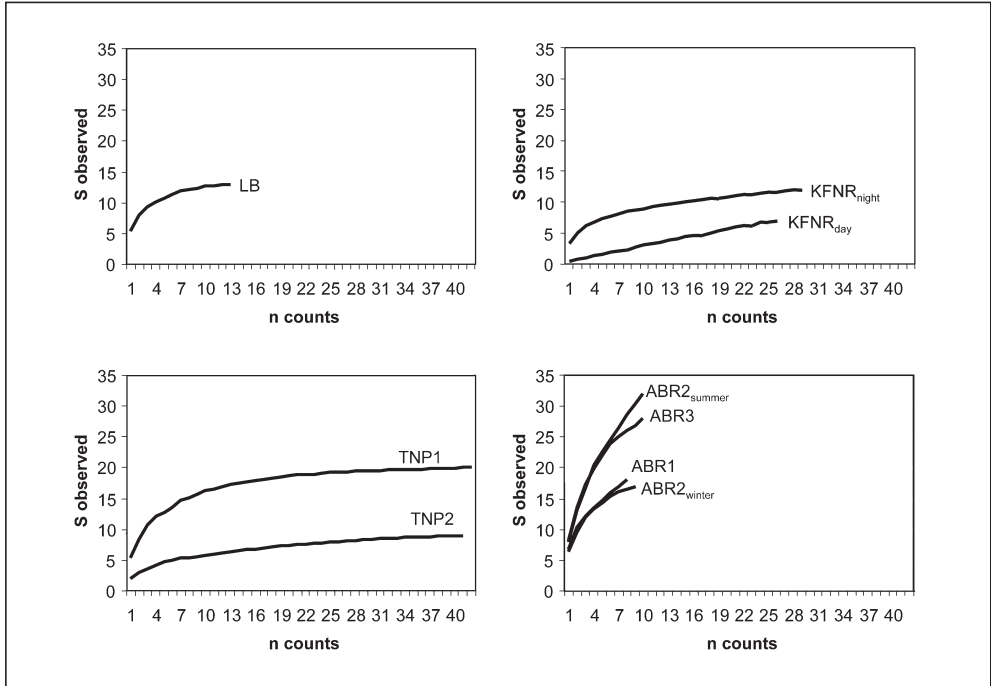
FIG. 1. Cumulative number of species observed at each transect, based on 1000 randomized input orders of transect counts.

nificantly decreased with an increasing daily species richness (S_{mean}) and a combined effect of S_{mean} and the overall abundance of frogs (n_{ind}). There was no significant effect of transect parameters on the range of species richness estimates, neither alone nor in combination.

DISCUSSION

As one would expect, the number of species observed by standardized transect sampling converges at a plateau when the number of transect walks is high. Our TNP, $KFNR_{night}$ and LB transects, all with an intermediate or high number of transect walks, reached relatively stable species number levels, with only a small expected increase in species number when the census was continued. However, even large numbers of transect walks may not result in convergence of the observed number of species when several other transect parameters are inappropriate, such as a small number of species recorded per day or a relatively low overall frog abundance.

Assessing the overall performance of the different species richness estimators is difficult. So far, their performance in a multidimensional transect parameter space has not yet been thoroughly studied. Therefore, and in order not to over-interpret the absolute numbers of species estimated, we regard them at best as estimators of how well the real species number is reflected by transect walks. Nevertheless, it is worth mentioning that the range covered by all species richness estimators tentatively decreases with an increasing number of frogs found along a transect.

However, to determine the reliability of species richness estimators it is possible to compare the number and type of species missed along a transect. At LB, mainly terrestrial species were counted along the transect. Only the terrestrial *Microhyla berdmorei*, that was found to be active in the close vicinity of the transect, was not observed. In contrast, arboreal (e.g., all Rhacophoridae), aquatic (*Staurois* spp.) and terrestrial species that mainly live along rivers and brooks (e.g., *Limnonectes* spp.) were mostly missed along the tran-

TABLE 4. Summary statistics of species diversity and species richness estimators; the last increase in the observed number of species ($\Delta S_{obs}/S_{obs}$), the relative range of all species richness estimators ($range_{est}/S_{obs}$) and the relative standard deviation of the 1st order jackknife estimator ($sdJN_{rel}$) are indicators of estimate quality.

	n_{counts}	S_{obs}	n_{Ind}	ΔS_{obs}	$S_{mean} \pm sd$	$varS_{mean}$	S_{mean}/S_{obs}	$\Delta S_{obs}/S_{obs}$	$range_{est}/S_{obs}$	$sdJN_{rel}$
LB	16	13	139	0.100	5.32±1.72	2.96	0.41	0.0077	0.142	0.066
KFNR$_{night}$	29	12	265	0.100	3.25±1.15	1.32	0.27	0.0100	0.359	0.092
KFNR$_{day}$	26	7	12	0.200	0.34±0.48	0.23	0.05	0.0286	2.153	0.141
TNP1	42	20	1130	0.000	5.40±1.92	3.69	0.27	0.0000	0.098	0.062
TNP2	41	9	391	0.040	2.00±1.50	2.25	0.22	0.0044	0.836	0.062
ABR1	8	18	148	1.020	6.86±1.83	3.35	0.38	0.0567	1.543	0.092
ABR2$_{winter}$	9	17	135	0.480	6.32±2.33	5.43	0.37	0.0282	0.271	0.114
ABR2$_{summer}$	10	32	166	1.580	7.88±2.50	6.25	0.25	0.0494	0.211	0.060
ABR3	10	28	179	1.140	8.12±2.73	7.45	0.29	0.0407	0.284	0.078

sect. Since species richness was estimated to a maximum of 15 species (Tab. 3), we may conclude that for terrestrial species transect census at LB worked almost perfectly.

At KFNR, night walks were more efficient than day walks (Tabs. 3, 4), clearly due to the fact that most species are crepuscular or nocturnal (see results). For the arboreal species of KFNR (i.e., hyperoliids), SVES and SAES data are almost complete (merely the rare *Afrixalus quadrivittatus* is missing; see Appendix). The majority of these species called during our studies from inside the forest (e.g., *Hyperolius kivuensis*, *Leptopelis* cf. *modestus*) or near water (e.g., *Hyperolius acuticeps*, *H. lateralis*). Therefore the high number of hyperoliids is basically due to SAES during nighttime. In contrast, species belonging to Bufonidae, Petropedetidae, and Ranidae were usually not vocalizing and less well recordable by SAES. They were mainly recorded by SVES and therefore number less. Even though two of them (i.e., *Phrynobatrachus* cf. *natalensis*, *Ptychadena* cf. *mascareniensis*) are primarily diurnal (with facultative nocturnal activity), we suggest that night walks are more effective. According to our observations, both are terrestrial and relatively remote. They show a tendency to escape several meters before an observer approaches. During the day their visual abilities are probably higher than at night. In addition, these taxa are highly cryptically colored and easier to see when spotted with a torch at night than in sunlight. However, for some of the terrestrial species of KFNR, neither day nor night walks resulted in presence data (see Appendix). Apart from other reasons, in frogs of the genera *Afrana*, *Phrynobatrachus* (except

P. cf. *minutus*) and *Ptychadena* (but not for the comparatively "slow" moving *Bufo kisoloensis*) this may be due to timidity and primary diurnality, while three other species are not to be expected in forests (see results). The aquatic *Xenopus borealis* was only found while migrating during both day and night. This seems more related to weather conditions, especially rain frequency and duration.

The percentages of recorded and suspected arboreal and terrestrial (leaf litter) frogs were equally high on TNP transects. We presume the recorded assemblage of local species from the two transects analyzed herein to be more or less complete. However, arboreal species were almost exclusively acoustically recorded during night walks, whereas terrestrial species were most often recorded visually during daytime (Rödel & Ernst 2004). Only fossorial species (*Hemisus* spp.; *Geotrypetes seraphini*) could not be recorded with this method. Aquatic species were likely to be observed during normal walks. Dip-netting and pitfall traps proved to be efficient additional tools in monitoring these species (Rödel & Ernst 2004).

Data for the Malagasy batrachofauna at ABR as shown in Tab. 2 indicate that the studied transects show high species richness. We had the opportunity to sample the forest during two seasonal periods (dry and rainy seasons), and one transect (ABR2) was sampled twice (in both seasons). The number of species found during the dry season was comparatively lower than during the rainy season, when most of the species are active and breeding. As has been demonstrated in other studies (Andreone 1994, Andreone & Luiselli 2003), the number of arboreal species observed dur-

ing the cold period was comparatively higher than terrestrial ones. This is likely due to a pre-adaptation of arboreal species to unpredictable climatic variation. On the other hand, terrestrial species are more active during the wet season. The few species that were active during the dry period (e.g., *Mantidactylus albofrenatus*, *M. rivicola*) are associated with riverine habitat which is more stable in terms of temperature and humidity than the surrounding forest, and are also oriented towards scansoriality. The more sensitive species are the fossorial species, which move almost entirely during the rainy period. The number of aquatic species was very limited, and in essence was restricted to *Mantidactylus guttulatus* (a torrenticolous
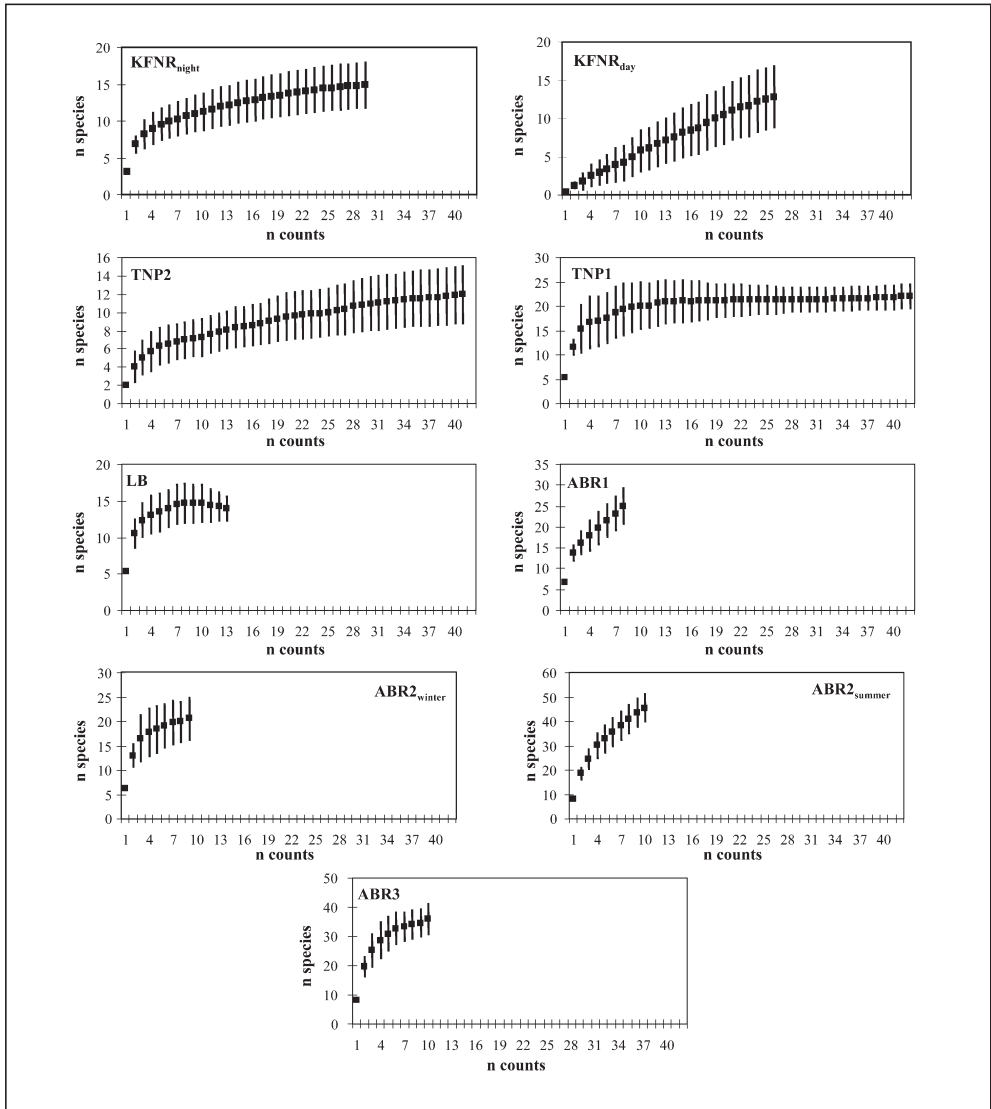
FIG. 2. First-order jackknife species richness estimator, based on 1000 randomized input orders of transect counts; mean (black square) and 95% confidence intervals (bar: mean ± 1.96 sd) are estimated for each count.

TABLE 5. Multiple linear regression analyses for parameters of estimate accuracy (range$_{est}$/S$_{obs}$, ΔS$_{obs}$/S$_{obs}$, sdJN$_{rel}$) with forward addition of six transect characteristics (independent variables); partial correlation coefficients are given for independent variables that were included in the multiple canonical regression.

	ΔS$_{obs}$/S$_{obs}$	range$_{est}$/S$_{obs}$	sdJN$_{rel}$
n$_{counts}$	r = -0.852 p = 0.007	not included	not included
S$_{mean}$	not included	not included	r = -0.816 p = 0.025
sd$_{mean}$^{2}	not included	r = -0.614 p = 0.106	r = 0.510 p = 0.242
S$_{obs}$	not included	not included	not included
S$_{mean}$/S$_{obs}$	r = -0.477 p = 0.232	not included	not included
n$_{ind}$	not included	r = -0.475 p = 0.234	r = -0.662 p = 0.105
multiple regression	r = 0.856 p = 0.019	r = 0.686 p = 0.149	r = 0.917 p = 0.019

large frog), and *M. betsileanus* (a frog living in marshes and small water bodies).

It is obvious that different species richness estimators may produce highly divergent results. Unfortunately, our analyses do not enable us to recommend one estimator over another, and to the best of our knowledge no equivalent empirical studies exist that covers all the different estimators. We think that it is still premature to recommend one estimator to use under particular field conditions (see also Colwell 2000, Magurran 2004). While empirical studies like ours can best describe how species richness estimators behave under varying field conditions, simulation studies should clarify to which transect parameter different species richness estimators are sensitive.

Nevertheless, we can draw some preliminary recommendations for the application of standardized transect sampling to tropical forest frog communities: (*i*) SVTS allows for a reasonable estimate of the number of terrestrial species; (*ii*) it enables ecologists to measure and monitor frog community structure away from breeding ponds, especially when leaf litter species are concerned; (*iii*) transect census should be performed on at least 20 independent walks; (*iv*) for the time being, we recommend the application of different species richness estimators to determine the effectiveness of SVTS.

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APPENDIX. Transect species lists; information on major frog life styles is provided in parentheses (A = arboreal, T = terrestrial, F = fossorial, Q = aquatic).

Lalut Birai (LB). Nomenclature follows Iskandar & Colijn (2000) and Frost (2002).

Thirteen species were observed along the transect: *Ansonia albomaculata* Inger, 1960 (T); *Ansonia* cf. *leptopus* (Guenther, 1872) (T); *Ansonia spinulifer* (Mocquard, 1890) (T); *Bufo juxtasper* Inger, 1964 (T); *Chaperina* cf. *fusca* Mocquard, 1892 (T); *Pedostibes hosii* (Boulenger, 1892) (A); *Leptobrachium abbotti* (Cohran, 1926) (T); *Leptolalax gracilis* (Guenther, 1872) (T); *Limnonectes finchi* (Inger, 1966) (T); *Meristogenys phaeomerus* (Inger and Gritis, 1983) (T); *Occidozyga* cf. *baluensis* (Boulenger, 1896) (T); *Rana hosii* Boulenger, 1891 (T); *Rana picturata* Boulenger, 1920 (T).

Seven additional species were active during the census period in the vicinity of the transect (less than 1 km apart): *Microhyla berdmorei* (Blyth, "1855" 1856) (T); *Limnonectes* cf. *asperatus* (Inger, Boeadi and Taufik, 1994) (T); *Limnonectes ibanorum* (Inger, 1964) (T); *Limnonectes kuhlii* (Tschudi, 1838) (T); *Limnonectes leporinus* (Andersson, 1923) (T); *Limnonectes* cf. *rhacodus* (Inger, Boeadi and Taufik, 1994) (T); *Staurois latopalmatus* (Boulenger, 1887) (Q; they live attached to stones in the current of small rivers and have never been observed outside rivers; Inger and Stuebing 1997). Most *Limnonectes* species are semi-aquatic and strictly restricted to brooks or river banks; nevertheless we regard them as terrestrial.

Thirteen additional species were not recorded by us but have been previously recorded at or around the transect site (according to Veith *et al.* 2004): *Kalophrynus pleurostigma* Tschudi, 1838 (T); *Leptobrachella mjöbergii* Smith, 1925 (T); *Fejervarya limnocharis* (Gravenhorst, 1829) (T); *Huia cavitympanum* (Boulenger, 1893) (T); *Megophrys nasuta* (Schlegel, 1858) (T); *Meristogenys whiteheadi* (Boulenger, 1896) (T); *Meristogenys* sp. (T); *Rana chalconota* (Schlegel, 1837) (T); *Rana nicobariensis* (Stoliczka, 1870) (T); *Staurois natator* (Günther, 1859 "1858") (T); *Polypedates otilophus* (Boulenger, 1893) (A); *Rhacophorus appendiculatus* (Günther, 1958) (A); *Rhacophorus pardalis* Guenther, 1859 (A).

Kakamega Forest National Reserve (KFNR). Nomenclature follows Lötters *et al.* (in press).

Twelve species were observed on the transect (d = during day walks, n = during night walks): *Afrixalus oso-rioi* (Ferreira, 1906) (n; A), *Bufo* cf. *maculatus* Hallowell, 1885 "1854" (d, n; T), *Hyperolius acuticeps* Ahl, 1931 (n; A), *Hyperolius* cf. *cinnamomeoventris* Bocage, 1866 (d, n; A), *Hyperolius kivuensis* Ahl, 1931 (n; A), *Hyperolius lateralis* Laurent, 1940 (n; A), *Hyperolius viridiflavus* Duméril and Bibron, 1841 (d, n; A), *Kassina senegalensis* Duméril and Bibron, 1841 (n; T), *Leptopelis* cf. *modestus* (Werner, 1898) (d, n; A), *Phrynobatrachus* cf. *natalensis* (Smith, 1849) (d, n; T), *Ptychadena* cf. *mascareniensis* (Duméril and Bibron, 1841) (d, n; T), *Xenopus borealis* Parker, 1936 (d, n; Q).

Nine additional species that were active in a radius of 1 km of the transect throughout census period but that were not recorded by SVES and SVAS (Lötters *et al.* in press): *Afrana angolensis* (Bocage, 1866) (T), *Afrixalus quadrivittatus* (Werner, 1907) (A), *Bufo kisoloensis* Loveridge, 1932 (T), *Hoplobatrachus occipitalis* (Günther, 1859) (Q), *Leptopelis* cf. *bocagii* (Günther, 1864) (T), *Phrynobatrachus* cf. *minutus* (Boulenger, 1895) (T), *Ptychadena anchietae* (Bocage, 1867) (T), *Ptychadena tellinii* (Perraca, 1904), (T), *Ptychadena taenioscelis* Laurent, 1954 (T).

Two additional species that were not recorded by us but that were previously recorded at or around the transect site (Lötters *et al.*, in press): *Amnirana albolabris* (Hallowell, 1856) (T); *Phrynobatrachus graueri* (Nieden, 1911) (T).

Taï National Park (TNP1 and 2). Nomenclature follows Frost (2002) and Rödel & Branch (2002). Twenty-four species were observed during transect walks: *Bufo togoensis* Ahl, 1924 (TNP1 and 2; T), *Amnirana albolabris* (Hallowell, 1856) (TNP1; T), *Aubria occidentalis* Perret, 1995 (TNP1; T), *Ptychadena aequiplicata* (Werner, 1898) (TNP1; T), *Phrynobatrachus gutturosus* (Chabanaud, 1921) (TNP1; T), *Phrynobatrachus phyllophilus* Rödel and Ernst, 2002 (TNP1 and 2; T), *Phrynobatrachus liberiensis* Barbour and Loveridge, 1927 (TNP1; T), *Phrynobatrachus alticola* Guibé and Lamotte, 1961 (TNP2; T), *Phrynobatrachus alleni* Parker, 1936 (TNP1 and 2; T), *Phrynobatrachus plicatus* (Günther, 1859 "1858") (TNP1 and 2; T), *Phrynobatrachus villiersi* Guibé, 1959 (TNP1 and –2; T), *Cardioglossa leucomystax* (Boulenger, 1903) (TNP1; T), *Arthroleptis* sp. 1 (TNP1 and 2; T), *Ar-*

Appendix continued

throleptis sp. 2 (TNP1 and 2; T), *Leptopelis hyloides* (Boulenger, 1906) (TNP1; A), *Leptopelis occidentalis* Schiøtz, 1967 (TNP1; A), *Leptopelis macrotis* Schiøtz, 1967 (TNP1; A), *Hyperolius sylvaticus* Schiøtz, 1967 (TNP1; A), *Hyperolius zonatus* Laurent, 1958 (TNP1; A), *Hyperolius fusciventris* Peters, 1876 (TNP1; A), *Hyperolius chlorosteus* (Boulenger, 1915) (TNP1; A), *Afrixalus nigeriensis* Schiøtz, 1967 (TNP1 and 2; A), *Kassina lamottei* Schiøtz, 1967 (TNP1; T), *Chiromantis rufescens* (Günther, 1868) (TNP1; A).

Five additional species were found on both transects, but not during regular transect walks: *Geotrypetes seraphini occidentalis* Parker, 1936 (TNP1; F), *Silurana tropicalis* Gray, 1864 (TNP1; Q), *Hemisus* sp. (TNP1; T/F), *Phrynobatrachus fraterculus* (Chabanaud, 1921) (TNP1; T), *Phrynobatrachus guineensis* Guibé & Lamotte, 1961 (TNP2; T).

Sixteen additional species were found in a radius of 2 km around the transect: *Bufo regularis* Reuss, 1833 (T), *Bufo maculatus* Hallowell, 1885 "1854" (T), *Bufo taiensis* Rödel and Ernst, 2000 (T), *Hoplobatrachus occipitalis* (Günther, 1859) (Q), *Amnirana occidentalis* (Perret, 1960) (T), *Ptychadena pumilio* (Boulenger, 1920) (T), *Ptychadena bibroni* (Hallowell, 1845) (T), *Ptychadena mascareniensis* (Duméril and Bibron, 1841) (T), *Ptychadena longirostris* (Peters, 1870) (T), *Ptychadena* sp. (T), *Phrynobatrachus accraensis* (Ahl, 1923) (T), *Phrynobatrachus annulatus* Perret, 1966 (T), *Astylosternus occidentalis* Parker, 1931 (T), *Hyperolius concolor* (Hallowell, 1844) (A), *Hyperolius picturatus* Peters, 1875 (A), *Afrixalus dorsalis* (Peters, 1875) (A), *Afrixalus vibekae* Schiøtz, 1967 (A), *Phlyctimantis boulengeri* Perret, 1986 (A), *Acanthixalus sonjae* Rödel, Kosuch, Veith and Ernst, 2003. (A).

Ambolokopatrika-Betaolana Rainforest. Transect only: *Platypelis* sp. 1, *Boophis brachychir* (Boettger, 1882), *Boophis madagascariensis* (Peters, 1884), *Boophis* cf. *mandraka* Blommers-Schlösser, 1979, *Boophis marojezensis* Glaw & Vences, 1994, *Mantidactylus albofrenatus* (Müller, 1892), *Mantidactylus* cf. *asper* (Boulenger, 1882), *Mantidactylus femoralis* (Boulenger, 1882), *Mantidactylus fimbriatus* Glaw & Vences, 1994, *Mantidactylus grandisonae* Guibé, 1974, *Mantidactylus* cf. *guttulatus* (Boulenger, 1881), *Mantidactylus luteus* Methuen & Hewitt, 1913, *Mantidactylus pseudoasper* Guibé, 1974, *Mantidactylus redimitus* (Boulenger,

1889), *Mantidactylus rivicola* Vences, Glaw & Andreone, 1997.

Additional species active throughout census period: *Plethodontohyla alluaudi* (Mocquard, 1901), *Stumpffia* sp. 1, *Stumpffia* sp. 2. Additional species that have ever been recorded around the transect site: None.

Ambolokopatrika-Betaolana-Rainforest 2 (ABR2), cold-dry season. Transect only: *Platypelis grandis* (Boulenger, 1889), *Boophis brachychir* (Boettger, 1882), *Boophis* cf. *septentrionalis* Glaw & Vences, 1994, *Boophis madagascariensis* (Peters, 1884), *Boophis* cf. *mandraka* Blommers-Schlösser, 1979, *Boophis marojezensis* Glaw & Vences, 1994,, *Mantidactylus albofrenatus* (Müller, 1892), *Mantidactylus* cf. *asper* (Boulenger, 1882), *Mantidactylus femoralis* (Boulenger, 1882), *Mantidactylus fimbriatus* Glaw & Vences, 1994, *Mantidactylus* cf. *guttulatus* (Boulenger, 1881), *Mantidactylus luteus* Methuen & Hewitt, 1913, *Mantidactylus opiparis* (Peracca, 1893), *Mantidactylus pseudoasper* Guibé, 1974, *Mantidactylus redimitus* (Boulenger, 1889), *Mantidactylus rivicola* Vences, Glaw & Andreone, 1997.

Additional species active throughout census period: *Stumpffia* sp. 3. Additional species that have ever been recorded around the transect site: None.

Ambolokopatrika-Betaolana-Rainforest 2 (ABR2), hot-wet season. Transect only: *Platypelis grandis* (Boulenger, 1889), *Platypelis* cf. *barbouri* Noble, 1940, *Platypelis* sp. 4, *Boophis albilabris* (Boulenger, 1888), *Boophis brachychir* (Boettger, 1882), *Boophis* cf. *septentrionalis* Glaw & Vences, 1994, *Boophis* cf. *mandraka* Blommers-Schlösser, 1979, *Boophis marojezensis* Glaw & Vences, 1994, *Mantidactylus aglavei* (Methuen & Hewitt, 1913), *Mantidactylus albofrenatus* (Müller, 1892), *Mantidactylus* cf. *asper* (Boulenger, 1882), *Mantidactylus* cf. *betsileanus* (Boulenger, 1882), *Mantidactylus femoralis* (Boulenger, 1882), *Mantidactylus fimbriatus* Glaw & Vences, 1994, *Mantidactyls* cf. *guttulatus* (Boulenger, 1881), *Mantidactylus luteus* Methuen & Hewitt, 1913, *Mantidactylus opiparis* (Peracca, 1893), *Mantidactylus pseudoasper* Guibé, 1974, *Mantidactylus redimitus* (Boulenger, 1889), *Mantidactylus rivicola* Vences, Glaw & Andreone, 1997. Aditional species active throughout census period: *Platypelis tuberifera* (Methuen, 1920), *Platypelis* sp. 1, *Platypelis* sp. 2, *Platypelis* sp. 3, *Plethodontohyla notosticta*

Appendix continued

(Günther, 1877), *Plethodontohyla serratopalpebrosa* (Guibé, 1975), *Stumpffia* sp. 3, *Stumpffia* sp. 2, *Stumpffia* sp. 1, *Mantidactylus klemmeri* (Guibé, 1975), *Mantidactylus punctatus* Blommers-Schlösser, 1979. Additional species that have ever been recorded around the transect site: *Mantidactylus salegy* Andreone, Aprea, Vences & Odierna, 2003.

Ambolokopatrika-Betaolana-Rainforest 3 (ABR3). Transect only: *Platypelis grandis* (Boulenger, 1889), *Platypelis* cf. *barbouri* Noble, 1940, *Boophis albilabris* (Boulenger, 1888), *Boophis* cf. *septentrionalis* Glaw & Vences, 1994, *Boophis* cf. *mandraka* Blommers-Schlösser, 1979, *Boophis marojezensis* Glaw & Vences, 1994, *Boophis reticulatus* Blommers-Schlösser, 1979, *Boophis rufioculis* Glaw & Vences, 1997, *Mantidactylus albofrenatus* (Müller, 1892), *Mantidactylus* cf. *asper* (Boulenger, 1882), *Mantidactylus femoralis* (Bou-

lenger, 1882), *Mantidactylus fimbriatus* Glaw & Vences, 1994, *Mantidactylus* cf. *guttulatus* (Boulenger, 1881), *Mantidactylus luteus* Methuen & Hewitt, 1913, *Mantidactylus phantasticus* Glaw & Vences, 1997, *Mantidactylus pseudoasper* Guibé, 1974, *Mantidactylus redimitus* (Boulenger, 1889), *Mantidactylus rivicola* Vences, Glaw & Andreone, 1997.

Additional species active throughout census period: *Platypelis tuberifera* (Methuen, 1920), *Platypelis* sp. 1, *Plethodontohyla alluaudi* (Mocquard, 1901), *Plethodontohyla laevipes* (Mocquard, 1895), *Plethodontohyla coudreaui* Angel, 1938, *Plethodontohyla serratopalpebrosa* (Guibé, 1975), *Stumpffia* sp. 1, *Mantidactylus klemmeri* (Guibé, 1975), *Mantidactylus pulcher* (Boulenger, 1882). Additional species that have ever been recorded around the transect site: *Mantidactylus salegy* Andreone, Aprea, Vences & Odierna, 2003.