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Marco Antonio Ribeiro Junior
Tel Aviv University

Toby Alan Gardner
Stockholm Environment Institute (SEI)

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Evaluating the Effectiveness of Herpetofaunal Sampling Techniques across a Gradient of Habitat Change in a Tropical Forest Landscape

Marco A. Ribeiro-Júnior,[1,2] Toby A. Gardner,[3] and Teresa C. S. Ávila-Pires[1]

[1]*Museu Paraense Emílio Goeldi/Programa de Pós-graduação em Zoologia, Caixa Postal: 399, 66017-970, Belém, Pará, Brazil*
[3]*School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK*

Abstract.—**To improve our understanding of the distribution and abundance of amphibians and reptiles in tropical forests, herpetologists need to understand the relative effectiveness of different sampling techniques. However, current studies are biased by a focus on certain methods, species groups, or geographic regions. To address this problem, we conducted the first standardized comparison of patterns of species richness, rank-abundance, and community structure for both passive and active sampling methods for the study of herpetofauna in a tropical forest landscape. Moreover, we compare the effectiveness of these methods in primary and secondary forests and *Eucalyptus* plantation. Although different methods captured significantly different numbers of species and individuals, almost all techniques provided complementary benefits for the sampling of both lizards and leaf litter amphibians. The use of a limited set of methods can severely bias our understanding of changes in amphibian and lizard community structure in response to large-scale habitat change. Contrary to other studies, we recommend the use of pitfall traps in all studies, even Rapid Assessments (RAP), because they are indispensable for sampling many cryptic species, as well as being particularly cost effective for large-scale research. Because of the combination of complementary methods in sampling effectiveness, and the influence of method choice on taxon responses to habitat change, we recommend the use of multiple sampling techniques wherever possible. Synchronous adoption of multiple techniques in field studies will help improve sample representation and, thus, the understanding of species distributions and human impacts on herpetofauna in tropical forests.**

Resumo.—**Conhecer a eficácia de diferentes técnicas de amostragem é importante para o avanço nas pesquisas sobre abundância e distribuição de anfíbios e répteis em florestas tropicais. Entretanto, os estudos existentes apresentam um viés ao enfocar apenas certas técnicas, grupos de espécies ou regiões geográficas. Buscando suplantar esse problema, apresentamos a primeira comparação padronizada entre padrões de riqueza de espécies, abundância relativa e estrutura da comunidade, obtidas tanto a partir de técnicas de amostragem passiva quanto ativa, em uma paisagem de floresta tropical. Além disso, comparamos a eficácia desses métodos em floresta primária, secundária e áreas de plantio de *Eucalyptus*. Embora os diferentes métodos tenham capturado diferentes números de indivíduos e de espécies, a maioria apresentou resultados complementares, tanto para lagartos quanto para anfíbios de serrapilheira. A utilização de um número limitado de técnicas pode levar a resultados fortemente tendenciosos sobre as mudanças que ocorrem na estrutura da comunidade de lagartos e anfíbios em resposta a uma mudança de hábitat em larga escala. Contrário a outros estudos, recomendamos a utilização de armadilhas de interceptação e queda em qualquer caso, inclusive em programas de levantamentos rápidos (RAPs), pois são indispensáveis na amostragem de muitas espécies crípticas, além de apresentar custo-benefício particularmente bom em pesquisas de larga escala. Devido à complementaridade entre os métodos e à influência da técnica sobre a resposta dos táxons às mudanças de hábitat, o presente estudo recomenda a utilização, sempre que possível, de várias técnicas de amostragem. A utilização concomitante de vários métodos, nos estudos de campo, ajudará na obtenção de amostragens mais representativas e, dessa forma, contribuirá para o entendimento sobre a distribuição das espécies e os impactos antrópicos sobre a herpetofauna em florestas tropicais.**

The Amazonian region covers approximately 6 million km^2 and harbors the largest area of continuous tropical forest in the world, 60% of which is within Brazil (Capobianco, 2002; Goulding et al., 2003). However, since 1980, the region has suffered an average annual loss of 1.8 million ha of primary forest (Laurance et al., 2004).

The biodiversity of this vast region remains poorly known, even for traditionally better-studied taxa such as mammals and birds (Oren, 2001; Silva et al., 2001). In the case of amphibians, Azevedo-Ramos and Galatti (2002) reviewed 28 localities that had been inventoried. Of these,

[2]Corresponding Author. E-mail: marcoantonio@unisol.org.br

only 13 had been sampled for more than two months, whereas only five species occurred in more than 80% of the localities. Similarly, information concerning the distribution and composition of reptile fauna is lacking for most of Amazonia (Vitt, 1996), and our knowledge of the majority of species is limited to basic alpha taxonomy (Rodrigues, 2005). These data demonstrate the difficulty of making generalizations regarding ecological and biogeographical patterns based on present knowledge.

As elsewhere, the conservation of Amazonian biodiversity depends, in part, on achieving a much better understanding of the distribution of species and their sensitivity to habitat change through standardized sampling programs (Capobianco, 2002). However, the majority of research on herpetofauna in the Amazon basin has been limited to relatively pristine sites (Duellman, 2005; Gardner et al., 2007a), and we know little about the consequences of different types of habitat change for amphibians and reptiles in tropical forests (e.g., Ernst et al., 2006; Gardner et al., 2007b,c). Therefore, rigorous ecological surveys across different gradients of disturbance are necessary to improve the management of human-dominated forest landscapes for biodiversity conservation.

The success of a study aimed at sampling the biodiversity of an area is heavily dependent on the choice of sampling methods. Traditionally, herpetofauna have been sampled through active collecting techniques, searching for the animals in environments where researchers expected them to be found. For example, Vanzolini and Papavero (1967) and Corn and Bury (1990) recommended detailed searches under fallen trunks and stones, in bromeliads, within the leaf litter, at the base of tree trunks, and at stream edges. Although this approach can provide a representative sample of the species present in a given area, it is clearly biased by the ability and experience of the researcher and does not provide standardized estimates of abundance. Furthermore, the effectiveness of active sampling techniques is likely to be particularly sensitive to differences in the type of habitat through variability in detection rates (Schmidt, 2003). However, passive sampling techniques are effective at reducing researcher bias, but they generally focus on one subgroup of the total fauna (e.g., pitfall trapping is directed at leaf litter taxa and is unsuitable for sampling large, agile, or arboreal species). Indeed, it is unlikely that any single sampling technique can accurately record all resident species in proportions representative of their actual abundance (Corn, 1994). Instead, a set of complementary methods should be employed that not only provide unbiased and time-efficient assessments but also robust quantitative data that are suitable for standardized comparisons between different regions or habitats.

Despite the existence of various technical manuals detailing suitable sampling methods for herpetofauna (e.g., Vanzolini and Papavero, 1967; Heyer et al., 1994; Franco et al., 2002), and a large number of comparative studies (e.g., Rice et al., 1994; Crosswhite et al., 1999; Enge, 2001; Ryan et al., 2002), there remains a number of important sources of bias and inadequacy in our understanding of the effectiveness of different sampling techniques. First, there has been strong geographical bias, with the majority of studies evaluating different sampling techniques for reptiles and amphibians being confined to temperate and subtropical regions (e.g., Campbell and Christman, 1982; Vogt and Hine, 1982; Bury and Corn, 1987; Corn and Bury, 1990), with comparatively few from tropical regions, especially tropical forests (e.g., Pearman et al., 1995; Doan, 2003; Rödel and Ernst, 2004).

Second, there has been a focus on particular species groups, with some of the most influential tropical studies (e.g., Pearman et al., 1995) relating primarily to amphibians. However, different groups of amphibians and reptiles are sampled with varying efficiency by different methods (Crump and Scott, 1994; Jaeger and Inger, 1994; Doan, 2003).

Third, the majority of studies that have compared different sampling methodologies have focused either on comparing visual encounter techniques (quadrates, transects, plots; e.g., Pearman et al., 1995; Doan, 2003), or comparing between different passive trapping techniques (e.g., Bury and Corn, 1987; Greenberg et al., 1994; Enge, 2001), with very few having evaluated both active and passive sampling methods (e.g., Crosswhite et al., 1999; Rödel and Ernst, 2004). In particular, most methodological studies from tropical forests have not included an evaluation of trapping techniques, possibly because they are labor and time intensive, and traps may be expensive (Corn, 1994). Furthermore, some trapping techniques have received comparatively little attention, especially in tropical forests, despite the fact they have proven to be successful approaches for sampling many species elsewhere (e.g., funnel traps, Greenberg et al., 1994; Enge, 2001; glue traps, Whiting, 1998; Glor et al., 2000).

Fourth, there is very little information regarding the relative effectiveness of different sampling methods between native and anthropogenic forest types. However, understanding the sensitivity in effectiveness of different methods to changes in habitat type is of fundamental importance for implementing robust and standardized studies of land-use change (Ryan et al., 2002).

A final inadequacy in our understanding of the effectiveness of different sampling techniques concerns the growing necessity for fieldworkers to collect information about biodiversity in a relatively short period of time (Sayre et al., 2003; i.e., rapid assessments; Sobrevila and Bath, 1992). Rapid assessments are characterized by short-term surveys of a specific area and are aimed at providing information necessary to identify sites important for biodiversity conservation. However, there is considerable disagreement about the most effective methodological approach for the study of amphibians and reptiles. For example, Sobrevila and Bath (1992) have advocated active collections along 1-km transects as the most appropriate technique for providing reliable data on herpetofaunal richness and relative abundance, whereas Sayre et al. (2003) recommended using a combination of complementary techniques. Enge (1998, 2002) has argued that long-term surveys are necessary to obtain a representative sample of species within a given area.

To address these deficiencies in our understanding, we evaluated the effectiveness of four sampling techniques (pitfall traps, funnel traps, glue traps, and time-constrained searches), within three different forest types (primary forest, secondary forest, and *Eucalyptus* plantations) in the Brazilian Amazon. In particular, we were interested in comparing the performance of these methods with respect to patterns of species richness, relative abundance and community structure for both leaf litter amphibians and reptiles. In light of our results, we suggest guidelines for researchers working in tropical forests who are concerned with comparing patterns of diversity of these taxa across different habitat types, as well as implementing rapid biodiversity assessments.

Materials and Methods

Sampling Methods.—We employed four complementary sampling techniques to study reptiles and leaf litter amphibians in primary, secondary, and plantation (*Eucalyptus*) forest in the Brazilian Amazon. First, we briefly review the methods we used and then describe the characteristics of the study site and sampling design for each technique.

Pitfall Traps: Pitfall traps with drift-fences are one of the most common herpetofaunal sampling techniques, as well as being used to sample small mammals and arthropods. Typically, the traps consist of buckets embedded into the ground, connected by a drift-fence that guides the animal toward the buckets. Larger buckets are often considered to have a greater chance of success in capturing larger animals (e.g., large reptiles, Crosswhite et al., 1999; Cechin and Martins, 2000). Pitfall trapping is most effective at capturing leaf litter species (e.g., Bury and Corn, 1987; Greenberg et al., 1994; Enge, 2001), as well as some insectivorous arboreal species that descend to the leaf litter to forage (Crosswhite et al., 1999).

Funnel Traps: Funnel traps consist of a metal or plastic tube, with a single or double opening (Fitch, 1951; Enge, 2001; Franco et al., 2002). The trap is placed on the ground, either with or without drift fences. Funnel trapping can be an efficient sampling technique, although the literature is ambivalent about the relative performance of pitfall (e.g., Vogt and Hine, 1982; Enge, 2001) versus funnel traps (e.g., Greenberg et al., 1994; Jorgensen et al., 1998).

Glue Traps: Glue traps have been proposed as a possible technique for the capture of otherwise cryptic arboreal/semiarboreal lizards (Bauer and Sadlier, 1992). The traps are typically placed on the trunks of trees, fallen logs, and sometimes on the ground (Ribeiro-Júnior et al., 2006). However, the effectiveness of this method has not been compared to other sampling techniques.

Active Sampling: Active sampling (time-constrained searches, TCS; and visual encounter surveys, VES, including plot based methods) plays an important role in herpetofaunal studies, especially for agile and larger species. Comparing the efficiency of VES and quadrat plot surveys, Doan (2003) observed that for most comparisons VES yielded an equal or greater number of records than quadrats, as well as more unique species (see also Pearman et al., 1995; Adams et al., 1998; Rocha et al., 2004). Campbell and Christman (1982) and Bury and Raphael (1983) have suggested that active sampling and pitfall traps provide an effective combination for the study of herpetofaunal communities, but as yet no study has evaluated the relative performance of the two methods.

Study Area.—Sampling was conducted within a 1.7 million-ha landholding managed by Jari Celulose/Grupo Orsa, on the Jari river in the north of Pará State, Brazilian Amazonia (00°27′00″–01°30′00″S, 51°40′00″–53°20′00″W), during the wet season of 2005 (January to June). About 10% of the area has been converted into *Eucalyptus* plantations, resulting in a landscape mosaic that includes large areas of regenerating secondary forest (between 14 and 19 years since abandonment) and a larger area of undisturbed primary forest (about 1 million ha) (for site map and further details, see Gardner et al., 2007a). Average annual rainfall is 2,115 mm, with an approximate mean temperature of 26°C (Radam Brasil, 1974). Fifteen sites were sampled across the study region, with five in each of *Eucalyptus* plantations, secondary forest, and undisturbed primary forest. Sites were selected to maximize spatial independence (Gardner et al., 2007a).

Sampling Methods.—A 1.5-km linear transect was cut in each site, located at least 500 m from the edge of the forest area (although one *Eucalyptus* site had a buffer limited to 200 m). Ten 35-liter pitfall arrays, three 62-liter pitfall arrays, 20 glue traps, and 30 funnel traps were established along each transect. The pitfall arrays were arranged in Y-shaped design, formed by four buckets, with each peripheral bucket separated by 6 m from the central one. The 35-liter pitfall traps were 450 mm deep, with an upper diameter of 350 mm and a lower diameter of 250 mm; the 62-liter pitfalls traps were 570 mm deep (upper and lower diameter of 410 and 310 mm respectively). The drift fence was 0.5 m in height and passed 1 m beyond the peripheral buckets. Each pitfall array was set 100 m apart along the length of the transect (but at least 15 m distant from it) to provide spatially independent sample units (T. A. Gardner, unpubl. data). Glue traps (Rat Glue Traps, Victor®, Lititz, PA) were spaced 50 m apart and were placed on fallen trunks and against vertical tree trunks and lianas in proportion to their availability at each site (see Ribeiro et al., 2006). Traps set on vertical tree trunks were positioned between the tree base and 2 m above the ground. Thirty plastic-coated wire-mesh funnel traps (Double-sided Minnow Traps, Frabill®, Sydney, NE) were placed in each site, with one trap laid midway and flush with each arm of the drift fence of the 35-liter pitfall arrays (three traps per array).

We sampled each site for a total of 14 consecutive days for pitfall and funnel traps, and 12 consecutive days for glue traps, with a total effort of 2,100 35-liter pitfall-trap array nights (across all sites), 630 62-liter pitfall-trap array nights, 3,600 glue-trap nights, and 6,300 funnel-trap nights, shared equally between the three forest types. Traps were checked every morning by two observers.

In addition to the passive sampling, we undertook diurnal active samples (always between 0700 h and 1300 h) with 10 diurnal time-constrained searches (DTCS) at each site. Nocturnal samples were not possible because of the logistical constraints of working in such a large landscape (a necessary requirement for obtaining samples that are representative of the spatial heterogeneity within each habitat type). Active sampling was conducted along the first 500 m of each transect, for an average of one hour per sample (totaling 150 h of effort shared equally between the three forest types). Active searches were all conducted by one of two expert observers (the order of which was randomized between site visits). The observer searched intensively 2 m either side of the transect taking care to search the leaf litter, along rocks and logs, and under debris. We randomized the sample order of sites with respect to habitat type to avoid any systematic bias from seasonal effects. Sampling was always conducted across three sites during the same sampling session, and in nearly every session, we sampled sites from different forest types. Consequently, sampling in any given forest type (pooling across all sites) encompassed a wide range of environmental conditions and associated herpetofaunal activity patterns.

The average ($\pm$ standard deviation) rainfall and midday temperature for samples conducted in primary, secondary, and plantation forests (measured by an automatic data logger every 10 min in each site for an entire year; June 2004 to July 2005) was 169 $\pm$ 21.8 mm, 150 $\pm$ 28.8 mm, and 143.5 $\pm$ 28.1 mm, and 24.3 $\pm$ 0.41°C, 24.8 $\pm$ 0.5°C, and 25.7 $\pm$ 0.48°C, respectively. All captured individuals were identified, measured, and collected as voucher specimens and deposited in the Museu Paraense Emílio Goeldi, Belém, Brazil (catalog numbers available on request from the authors).

Data Analysis.—Differences in species richness among the sampling methods in each forest type were analyzed using individual-based rarefaction (Gotelli and Colwell, 2001), pooling data from across all sites for each forest type. In addition, we used sample-based rarefaction curves with the number of days as samples to compare the number of species captured by different methods following seven, 14, or 30 consecutive field days in each forest type. Rarefaction analyses were implemented in EstimateS v. 7.0 (R. K. Colwell, Statistical estimation of species richness and shared species from samples, User's guide and application published at: http://purl.oclc.org/estimates, 2004). Differences in species richness were evaluated by visual comparison of 95% confidence intervals (see Magurran, 2004).

To compare species-abundance patterns among sampling methods, we used standardized Whittaker plots, which compare species rank with the log of the relative abundance (Magurran, 2004). In addition, abundance ranks were compared between the methods, using nonparametric Spearman-rank correlations. All statistical tests were carried out using SPSS v.11.5 (SPSS, Chicago, IL, 2001).

To compare the cost effectiveness of the different sampling techniques, the cost (US$) per unit of effort for each method and the cost per individual captured were calculated. We included all labor costs and materials necessary for the deployment of pitfall traps in our calculations, as well as the price of funnel traps and glue traps. However, we did not include the costs associated with transportation because the cost of checking traps remained the same regardless of the number or the type of trap that was deployed.

Nonmetric Multidimensional Scaling (NMDS) was used to evaluate differences in perceived patterns of community structure as revealed by different sampling techniques. NMDS was preferred over other ordination techniques because it is an unconstrained method that does not impose limiting assumptions concerning the nature of species responses, making it the most appropriate ordination method for most community data (Clarke and Warwick, 2001; McCune and Grace, 2002). The similarity matrices for each method were based on the Bray-Curtis similarity index using square-root transformed and site standardized abundance data. Analysis of Similarity (ANOSIM, Clarke and Warwick, 2001) was used to compare differences in community structure between habitat types and sampling techniques. All multivariate analyses were conducted using Primer v. 5 (Clarke and Warwick, 2001).

The SVL (snout–vent length) and the tail length (for lizards) of each individual were measured to obtain a measure of total length. The average length of individuals collected by each method was then compared using parametric one-way ANOVAs to examine whether techniques differed in their selection of body size (total length; correcting for unequal variances where necessary). Pairwise post hoc comparisons were made using Tukey's subsets between each method for the different herpetofaunal groups (lizards and leaf litter amphibians). The maximum and minimum total lengths of the individuals captured per method were compared to estimate the variation in body size that each method could register for different species groups.

Results

Across all techniques we captured a total of 2,813 individuals, comprising a total of 67 species, including 1,535 lizards (29 species), 1,215 leaf litter amphibians (22 species), and 63 snakes (16 species; Table 1). Snakes were not included in the data analysis because of insufficient captures.

Differences in Species Richness among Sampling Techniques.—The funnel traps were excluded from all analyses of species richness and rank abundances because of insufficient captures, with the exception of lizards in *Eucalyptus* plantations (where we captured 63 specimens of three species, Table 1). However, funnel traps did register four species of reptiles that were not collected by the other methods (the lizard *Neusticurus bicarinatus* and the snakes *Drymoluber dichrous*, *Oxyrhopus melanogenys*, and *Xenopholis scalaris*). Glue traps failed to capture any amphibians, captured few lizards in *Eucalyptus* plantations, and, therefore, were analyzed only for lizards in primary and secondary forest. Regarding species caught only by a single sampling technique, pitfall traps (both sizes) registered 23 species, including six lizards, nine leaf litter amphibians and eight snakes, whereas glue traps caught two reptile species (one lizard and one snake), and DTCS caught five species, one lizard, two leaf litter amphibians, and two snakes (Table 1).

Rarefaction analyses showed that pitfall traps captured more species of lizard than both glue traps and DTCS in primary forest (Fig. 1a), whereas in secondary forest both pitfall traps and DTCS captured a similar number of lizard species (Fig. 1c). In *Eucalyptus* plantations there was no significant difference in species richness registered by the four methods (Fig. 1e). For leaf litter amphibians, the three methods analyzed (35-liter pitfall, 62-liter pitfall, and DTCS) registered a similar number of species in both primary and secondary forest (Fig. 1b,d), whereas in *Eucalyptus* plantations funnel traps and DTCS captured only a single species (*Adenomera* sp.). Rarefaction curves for 35-liter and 62-liter pitfall traps were almost indistinguishable in most forest types for both leaf litter amphibians and lizards.

Comparing sampling periods of different duration, the 35-liter pitfall traps and DTCS registered a similar number of species in primary forest for both lizards and leaf litter amphibians, after seven, 14 and 30 consecutive days of sampling (Fig. 2a,b). In secondary forest 35-liter pitfalls, 62-liter pitfalls and DTCS captured similar numbers of lizard species independent of the study period (Fig. 2c), whereas the 35-liter pitfall traps captured more species of leaf litter amphibians than all other methods, and the pattern was similar regardless of the duration of the study (Fig. 2d). In *Eucalyptus* plantations 35-liter pitfalls, 62-liter pitfalls, and DTCS captured a similar number of lizard species (Fig. 2e), whereas 35-liter and 62-liter pitfalls captured a similar number of leaf litter amphibian species following seven and 14 consecutive field days, but 35-liter pitfalls were more effective in longer studies (30 days; Fig. 2f). Funnel traps caught the lowest number of leaf litter amphibian and lizard species of any sampling technique, independent of the duration of the study, with the exception of lizards in *Eucalyptus* plantations (Fig. 2e).

TABLE 1. Species and number of individuals of leaf litter amphibians, lizards and snakes captured by different sampling methods in primary forest (PF), secondary forest (SF) and *Eucalyptus* plantations (E), in Jari, northeastern Brazilian Amazon. DTCS = diurnal time-constrained searches.

	35-L pitfalls			62-L pitfalls			Glue traps			Funnel traps			DTCS			
Species	PF	SF	E	PF	SF	E	PF	SF	E	PF	SF	E	PF	SF	E	Total
Bufo guttatus		2	2	1		2										7
Bufo margaritifer	3	27			3								1	1		35
Bufo marinus		5	4		7	3										19
Bufo sp.	35	20	3	14	20					1			13	2		108
Caecilia tentaculata	5															5
Allobates femoralis	14	2		6						3	3		1			29
Colostethus sp.	9												14	1		24
Dendrobates tinctorius	1												2			3
Epipedobates hahneli	13	2		4	3					3			30	1		56
Adenomera sp.	56	95	308	19	18	52				2	1	2	123	7	83	766
Eleutherodactylus chiastonotus													8			8
Eleutherodactylus marmoratus				1									1			2
Eleutherodactylus sp.		1											1			2
Leptodactylus knudseni		21														21
Leptodactylus mystaceus	4	23		1	2					1	1		1	3		36
Leptodactylus pentadactylus	1			1	1											3
Leptodactylus rhodomystax	2															2
Leptodactylus sp.		15			5											20
Leptodactylus stenodema	4			2												6
Lithodytes lineatus	1	52			6						2					61
Otophryne pyburni													1			1
Rhinatrema bivittatum	1															1
22 amphibian species	149	265	317	49	65	57	0	0	0	10	7	2	196	15	83	1,215
Coleodactylus amazonicus	56	66	19	11	8	6							61	80	22	329
Gonatodes humeralis	28	7	9	4	4	6	101	67	10				64	94	7	401
Gonatodes sp.	2			2									1			5
Lepidoblepharis heyerorum	1	8	1		12								1	1		24
Thecadactylus rapicauda	1						6						2			9
Alopoglossus angulatus			1													1
Arthrosaura kockii	2															2
Arthrosaura reticulata	2															2
Bachia flavescens	8		2	3	1									1		15
Cercosaura ocellata	3	4	45			10					2	4		1	11	80
Iphisa elegans	12	1		2						1			2			18
Leposoma guianense	29	1		6	1								5			42
Leposoma percarinatum			1	1		1							1			4
Neusticurus bicarinatus										1						1
Neusticurus rudis	1	1														2
Ptychoglossus brevifrontalis	2			1												3
Tretioscincus agilis	16			2			6			2			1			27
Anolis fuscoauratus	3			2			26	2					17	1		51
Anolis nitens	2												2			4
Anolis ortonii		1					1	1	4							7
Anolis punctatus							1									1
Iguana iguana						1										1
Mabuya nigropunctata							2						3			5
Ameiva ameiva	3	14	180			67				1	3	56	1	5	13	343
Cnemidophorus cryptus			28			20			2			3			40	93
Kentropyx calcarata	8	14		4	9		4			1	3		2	3		48
Tupinambis teguixin														2		2
Plica plica					1								1			2
Plica umbra	5	1		3			3						1			13
29 lizard species	184	118	286	41	36	111	150	70	16	6	8	63	165	188	93	1,535
Anilius scytale	1															1
Typhlophis squamosus	1		4			3										8
Apostolepis quinquelineata			1													1

TABLE 1. Continued.

Species	35-L pitfalls			62-L pitfalls			Glue traps			Funnel traps			DTCS			Total
	PF	SF	E	PF	SF	E	PF	SF	E	PF	SF	E	PF	SF	E	
Atractus snethlageae	1															1
Drymoluber dichrous										1						1
Leptodeira annulata															1	1
Liophis reginae			1													1
Oxyrhopus melanogenys										1	1	3				5
Pseudoboa neuwiedii			1									1			1	3
Siphlophis cervinus							1									1
Tantilla melanocephala			6			1										7
Xenopholis scalaris										1						1
Micrurus hemprichii				2						1	1					4
Micrurus lemniscatus	1															1
Typhlops reticulatus	1	4	13			6										24
Bothrops atrox													3			3
16 snake species	5	4	26	2	0	10	1	0	0	4	2	4	3	0	2	63
67 total species	338	387	629	92	101	178	151	70	16	20	17	69	364	203	178	2,813

When comparing patterns of cost effectiveness among different sampling techniques (pooling across all species), DTCS was the most cost effective with both the lowest cost per unit of effort and per individual sampled, independent of species (Table 2). In contrast, funnel traps had the highest cost and lowest benefit compared to the other methods, whereas 62-liter pitfall traps had a higher cost per unit of effort and individual captured compared with 35-liter buckets (Table 2). However, it should be noted that availability of trained observers capable of conducting reliable transect surveys is often one of the greatest limitations to effective active searches (e.g., DTCS).

Differences in Relative Abundance Distributions among Sampling Techniques.—Pitfall traps presented the most even species-relative abundance distribution for both leaf litter amphibians and lizards in all forest types (Fig. 3). Other techniques were particularly effective at capturing certain species and, therefore, revealed more uneven distributions. For example, *Gonatodes humeralis* was the most abundant lizard species in glue traps, comprising 67.4% of all captures in primary forest and 95.7% in secondary forest. Similarly, *Ameiva ameiva* represented 87% of all lizards captured by funnel traps in *Eucalyptus* plantations, whereas DTCS was particularly effective at capturing one amphibian morphospecies (*Adenomera* sp.—63% and 46.7% of all captures in primary and secondary forest, respectively—although this possibly represents more than one species) and two species of lizard (*G. humeralis* and *Coleodactylus amazonicus*, both comprising together 75.7% and 92.5% of all captures in primary and secondary forest, respectively). In *Eucalyptus* plantations, only one amphibian species was captured by funnel traps and DTCS (*Adenomera* sp.), and *Cnemidophorus cryptus* was the lizard most frequently sampled by DTCS (43% of all records).

The rank order of abundance of individual species trapped by 35-liter and 62-liter pitfalls was similar for both leaf litter amphibians (14 species) and lizards (20 species) in primary forest ($rs = 0.562$, $P = 0.012$; $rs = 0.787$, $P < 0.001$, respectively), for leaf litter amphibians in secondary forest ($rs = 0.625$, $P = 0.013$), and for lizards in *Eucalyptus* plantations ($rs = 0.981$, $P < 0.001$). The rank order of abundance was also similar for lizards sampled by 35-liter pitfalls and DTCS in primary forest ($rs = 0.459$, $P = 0.021$); in secondary forest by 62-liter pitfalls and DTCS ($rs = 0.533$, $P = 0.006$), glue traps and DTCS ($rs = 0.408$, $P = 0.043$), and 35-liter pitfalls and DTCS ($rs = 0.560$, $P = 0.020$); and in *Eucalyptus* by pitfall and funnel traps ($rs = 0.980$, $P < 0.001$; and $rs = 0.969$, $P < 0.001$ for 35-liter and 62-liter traps, respectively). There was no correlation between the rank order of abundance of leaf litter amphibians sampled by pitfalls and DTCS in primary or secondary forest ($rs < 0.389$ and $P > 0.1$).

Perceived Differences in Community Structure as Revealed by Different Sampling Techniques.—There were significant differences in the observed pattern of lizard community structure as perceived by each of the four sampling methods for all three forest types (ANOSIM: $R > 0.214$ and $P < 0.014$ in all cases, see Fig. 4). Pairwise comparisons showed that the perceived community structure was distinct for each method in both primary and secondary forest ($R > 0.24$, $P < 0.032$) except between 35-liter and 62-liter pitfalls ($R < 0.072$, $P > 0.317$). In the case of leaf litter amphibians, there was a difference in the pattern revealed by the three methods analyzed

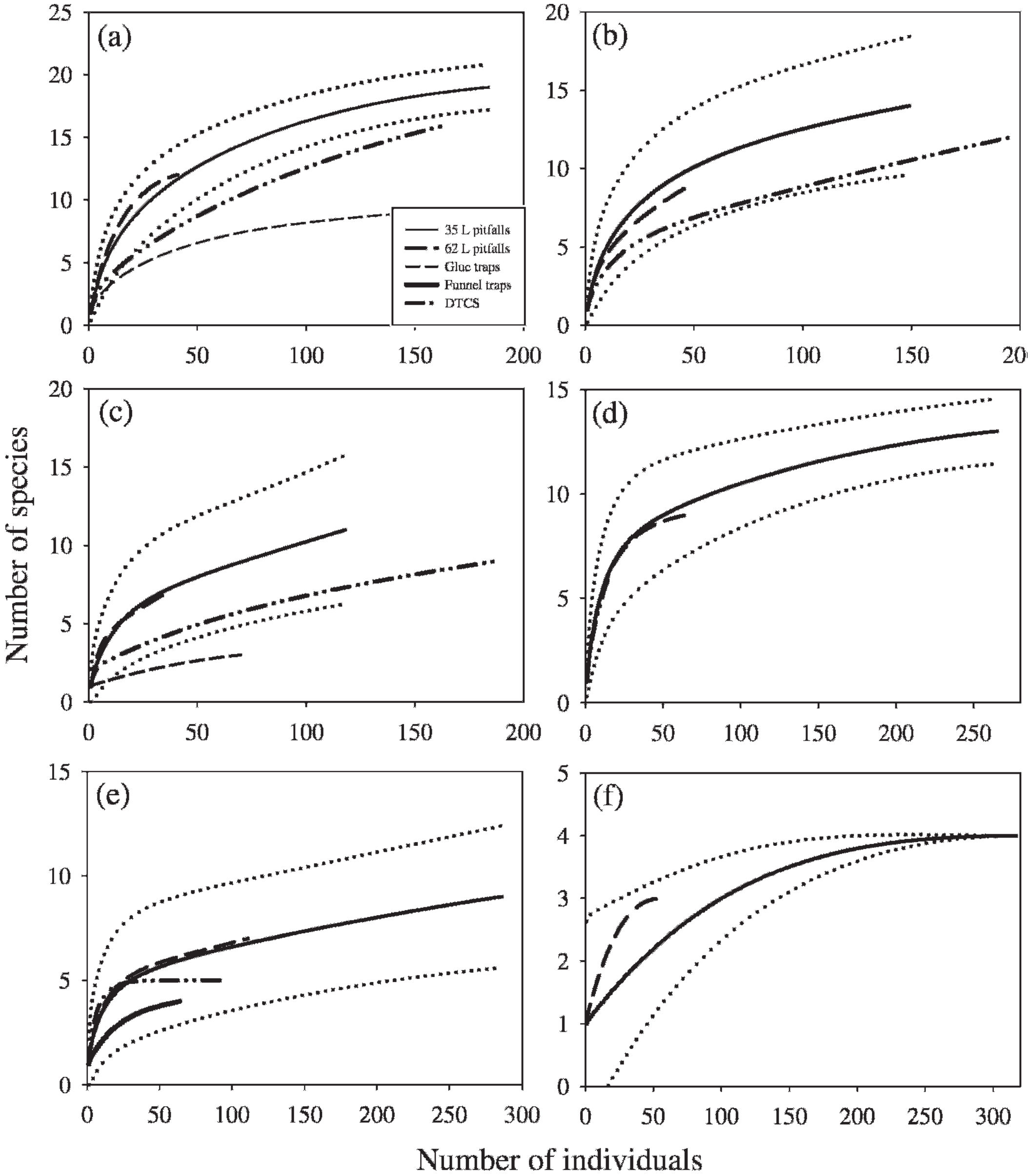

FIG. 1. Individual based rarefaction curves for lizards (a, c, e) and leaf litter amphibians (b, d, f) in primary forest (a, b), secondary forest (c, d), and *Eucalyptus* plantations (e, f), captured by different sampling methods (95% confidence limits shown only for 35-liter pitfall). DTCS = diurnal time-constrained survey. Funnel trap data (thick line) is only presented for lizards in plantation forest (e).

in secondary (Fig. 4d, $R = 0.26$, $P = 0.026$) but not primary forest (Fig. 4b, $R = -0.066$, $P = 0.72$). The difference in the perception of leaf litter amphibian community structure recorded in secondary forest was caused by a difference between 62-liter pitfalls and DTCS ($R = 0.48$, $P = 0.018$).

Differences in the Size of Species Captured among Sampling Techniques.—Different sampling techniques were effective at capturing different lizards of different lengths (ANOVA, $F = 55.881$; df = 4, 1015; $P < 0.001$), with funnel traps capturing larger animals on average than other methods, whereas both 62-liter and 35-liter pitfall arrays and glue traps and DTCS gave similar results (see Appendix 1). Nevertheless, in terms of maximum size, 35-liter pitfalls were capable of capturing the largest lizard (*A.*

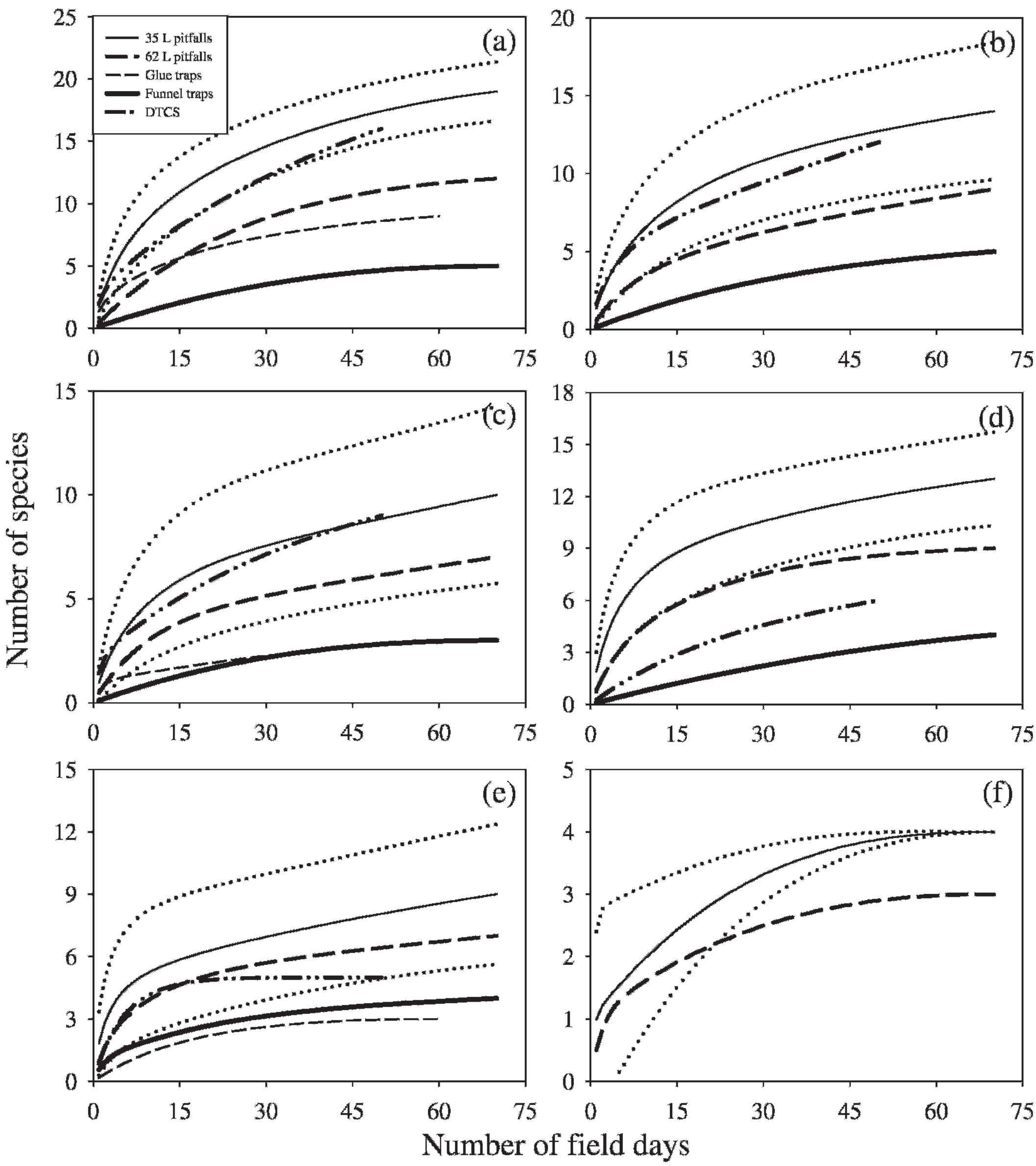

FIG. 2. Sample based rarefaction curves for lizards (a, c, e) and leaf litter amphibians (b, d, f) in primary forest (a, b), secondary forest (c, d), and *Eucalyptus* plantations (e, f), with the samples referring the consecutive field days of each method (95% confidence limits shown only for 35-liter pitfall). DTCS = diurnal time-constrained survey.

ameiva, 498 mm). For leaf litter amphibians, there was a significant difference in the average length of individuals captured by the four methods (F = 3.936; df = 3, 955; P = 0.008), with DTCS capturing smaller animals on average than all other methods. Similar to the case for lizards, 35-liter pitfall traps were capable of capturing both the largest (*Leptodactylus knudseni*, 143 mm) and smallest (*Adenomera* sp., 5 mm) species. We did not catch enough snakes to conduct a formal analysis, but our preliminary data indicate that 62-liter buckets failed to catch larger animals than smaller buckets and funnel traps.

DISCUSSION

Evaluating the Effectiveness of Different Techniques to Sample Leaf Litter Amphibians and Reptiles.—Pitfall trapping is considered by

TABLE 2. Total sample effort in primary forest, secondary forest, and *Eucalyptus* plantations by sampling method, the marginal cost (US$) of each method (excluding labor and transport cost), cost per unit of effort, number of individuals captured (leaf litter amphibians, lizards, and snakes), and the cost per individual registered (units of effort: 35-liter and 62-liter pitfall = trap stations, glue and funnel traps = traps nights; DTCS = human-hours). DTCS = diurnal time-constrained survey.

	35-L pitfall array	62-L pitfall array	Glue traps	Funnel traps	DTCS
Effort	2,100	630	3,600	6,300	150
Number of captures (individuals)	1,354	372	237	106	745
Total cost (US$)	2,317	964	320	810	0
Cost per unit of effort	1.10	1.53	0.08	0.12	0
Cost per individual captured	1.71	2.60	1.35	7.64	0

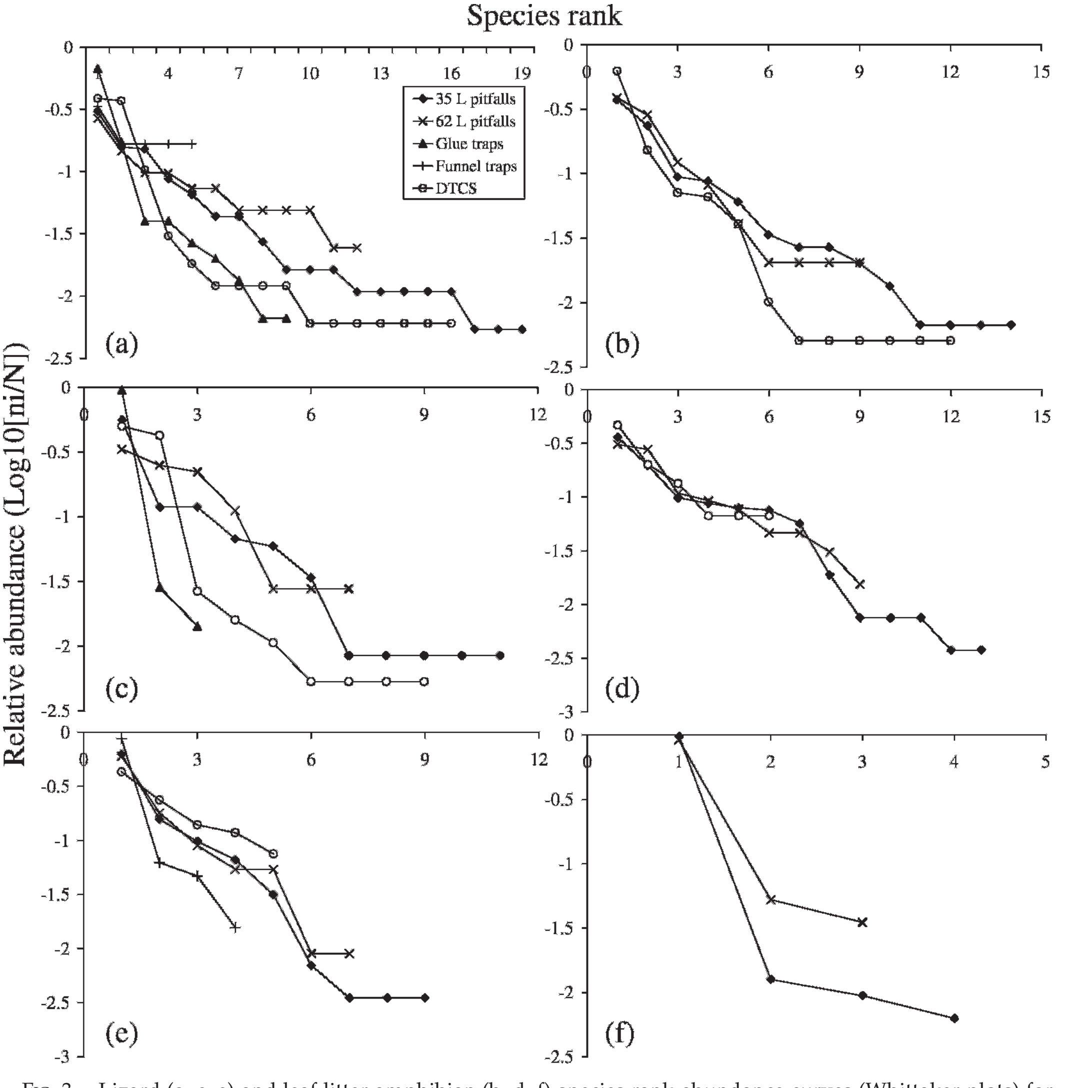

FIG. 3. Lizard (a, c, e) and leaf litter amphibian (b, d, f) species rank-abundance curves (Whittaker plots) for each method (a, b—primary forest; c, d—secondary forest; e, f—*Eucalyptus* plantations). DTCS = diurnal time-constrained survey.

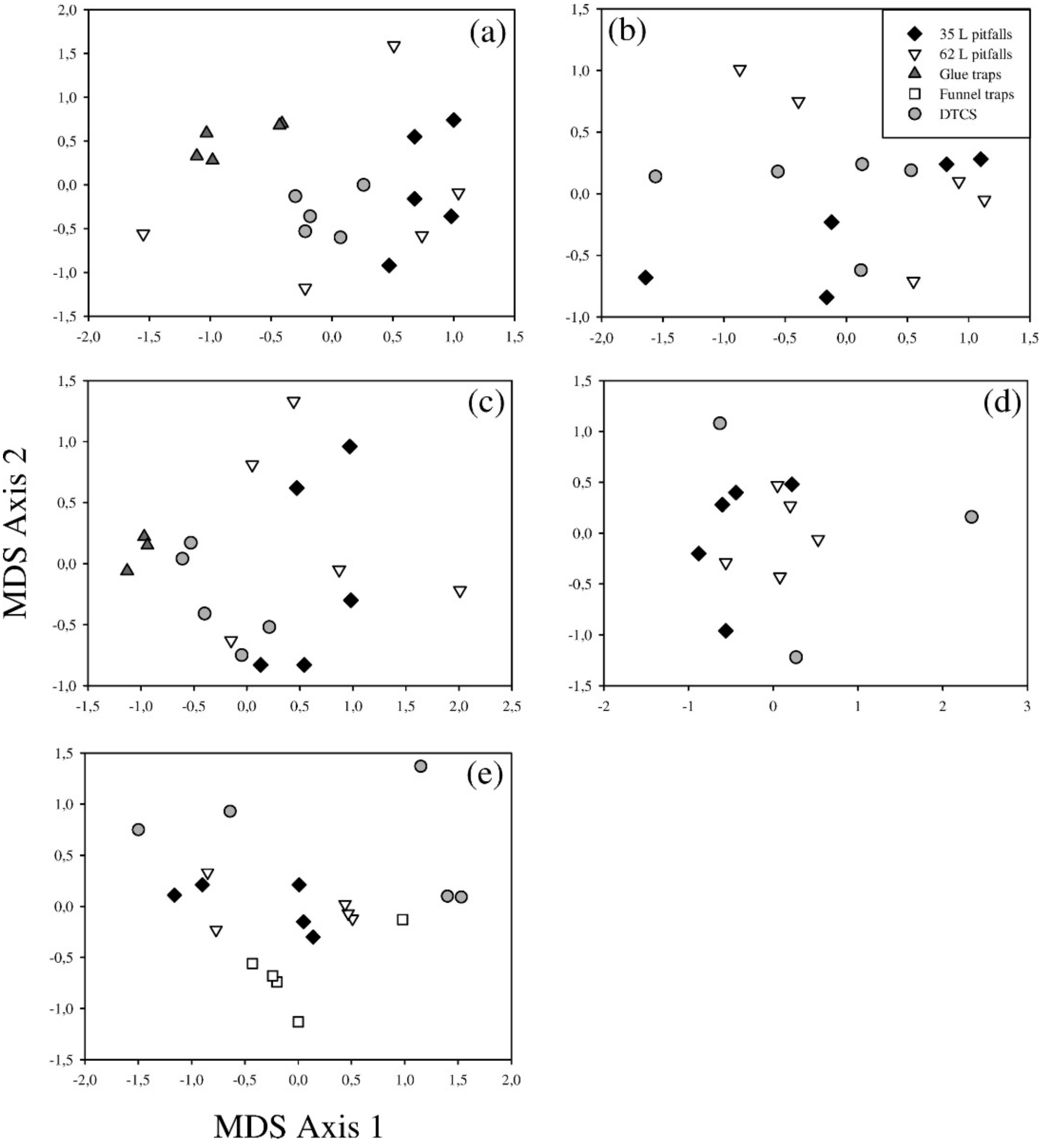

FIG. 4. Nonmetric Multidimensional scaling plot produced from the Bray-Curtis similarity matrix of species abundance by sampling methods for lizards (a, c, e) and leaf litter amphibians (b, d) in primary forest (a, b), secondary forest (c, d) and *Eucalyptus* plantations (e). Stress: (a) = 0.16; (b) = 0.12; (c) = 0.1; (d) = 0.08; (e) = 0.09. DTCS = diurnal time-constrained survey. Points clustered more closely together demonstrate that the same technique captures similar species independent of sample location.

many to be the most effective technique to sample leaf litter reptiles and amphibians (Campbell and Christman, 1982; Greenberg et al., 1994; Jorgensen et al., 1998; Crosswhite et al., 1999). However, in this study pitfall traps only registered significantly more species of lizard than other techniques in primary forest. They failed to catch significantly more species of lizards in secondary and plantation forest or amphibians in primary and secondary forest than diurnal time-constrained searches (DTCS). This finding is supported by Bury and Raphael (1983) and Rice et al. (1994), both of whom found similar levels of species richness for reptiles and amphibians using pitfall traps and DTCS. Rödel and Ernst (2004) found pitfall traps to be a poor method for sampling leaf-litter amphibians in West Africa. Rödel and Ernst's (2004) result may be the result of profound geographic differences between study regions, but it is difficult to make a direct comparison because they used significantly smaller buckets than we did in our study (less than 30 cm in depth). Nevertheless, pitfall traps (35-liter and 62-liter traps combined) registered nine leaf litter amphibian species that were not captured by the other methods, illustrating the importance of passive sampling in the study of terrestrial amphibians. In addition, six species of lizards and eight species of snakes were caught only by pitfall traps confirming the effectiveness of this method for sampling leaf litter or fossorial/semifossorial species in general (Bury and Corn, 1987; Greenberg et al., 1994; Enge, 2001). In contrast, DTCS exclusively sampled only one lizard, two leaf litter amphibians, and two snake species. Undoubtedly the number of species that can be captured by time-constrained surveys would increase with the addition of nocturnal searches (especially with acoustic sampling; e.g., Zimmerman and Rodrigues, 1990), although this is usually only possible for studies that have closely spaced sample sites and ready access to a research base to facilitate multiple night surveys.

In accordance with our results, a commonly cited limitation of pitfall arrays for the study of herpetofauna is that trap effectiveness differs widely among species (Gibbons and Semlitsch, 1981; Campbell and Christman, 1982; Bury and Corn, 1987) and that some species cannot be effectively sampled using pitfall traps (Gibbons and Bennett, 1974; Gibbons and Semlitsch, 1981; Jones, 1986; Dodd, 1991). Therefore, it is clear that no single method is adequate for sampling the entire leaf litter herpetofauna (Corn and Bury, 1990) and that pitfall trapping needs to be combined with active sampling such as time-constrained searches to maximize the chance of collecting a representative sample of the focal community.

Despite the fact that glue traps did not capture many species in our study, they were the only method that caught *Siphlophis cervinus* and *Anolis punctatus*. Bauer and Sadlier (1992), Glor et al. (2000), and Ribeiro-Júnior et al. (2006) have suggested that this technique is the most appropriate method for the study of arboreal/semiarboreal species and can be complementary to more traditional techniques like pitfall traps and DTCS. Although it is often difficult to select a single technique that is suitable for population studies (Paterson, 1998; Krysko, 2000), the fact that this method was so effective at sampling the semiarboreal lizard *G. humeralis* suggests that it may be useful for studying the autecology of this species (although the fact that it is a destructive technique carries obvious ethical issues and limits the type of ecological studies that may benefit from its use).

Funnel traps failed to provide meaningful abundance data for any species group in either primary or secondary forests. Greenberg et al. (1994) showed that funnel traps did not provide any additional value over pitfall traps and DTCS, and Jorgensen et al. (1998) did not find any species in funnel traps that were not also caught by pitfall traps. However, in our study, funnel traps exclusively captured four species of reptiles (one lizard and three snakes, see Table 1), and they were particularly efficient at capturing the large Teiid lizard, *A. ameiva*, in *Eucalyptus* plantations. Nevertheless, funnel traps consistently failed to capture more species of either amphibian or reptile in any forest type, and in contrast to the advice from researchers working in other ecosystems (e.g., Vogt and Hine, 1982; Enge, 2001), we do not recommend their use for herpetofaunal studies in Neotropical forests.

Multiple factors can affect the capture success of a particular sampling technique, including differences in animal body size (Crosswhite et al., 1999). Thompson et al. (2005) observed that small- to medium-sized lizards were more frequently captured in pitfalls (with 20-liter buckets) than in PVC tube traps (with 15 cm in diameter), whereas Friend et al. (1989) showed that the larger lizards were more likely to be caught in larger pitfalls (20-liter buckets) than smaller pits made of 16-cm diameter PVC piping. We observed a wide variability in body size of individuals captured by the different sampling techniques. Perhaps counter intuitively, DTCS consistently caught smaller leaf litter amphibians and lizards than other methods, although they were more successful at encountering large snakes. However, most important, and contrary to expectation, there was no significant difference in the average size of animals captured by the two sizes (35-liter and 62-liter) of pitfall trap, suggesting that larger buckets are not more effective at capturing larger species and individuals. Cechin and Martins (2000) compared the efficiency of pitfall traps composed of larger buckets (100–200 liter) with previous studies that employed more traditional sized traps (20–35 liter) and concluded that large traps are highly efficient for sampling herpetofaunal communities. However, interpretation of this conclusion is confounded by the fact that comparative studies were chosen from across different biomes (e.g., rain forest, grassland, and savannah) and in different seasons. Although we did not use traps greater than 62 liters, our study revealed no difference between smaller and larger pitfall traps in overall species richness, capture success, or community structure for either species group in any forest type. Allocation of limited financial and logistical resources in conservation must be made with considerable care (Sheil, 2001), and it is essential that studies concerned with sampling biodiversity undertake some form of cost-effectiveness analysis prior to selecting a particular technique (e.g., Garden et al., 2007). We recommend that 35-liter traps are preferable to 62-liter traps for sampling herpetofauna in the Brazilian Amazon because they are less expensive and easier to obtain, physically less challenging to install, yet return similar benefits.

Rapid Assessments and the Complementary Value of Alternative Sampling Techniques in Studies of Habitat Change.—Time-constrained surveys have been suggested as the most appropriate method for rapidly determining the species richness and species-relative-abundance structure for a specific area (e.g., rapid assessments; Sobrevila and Bath, 1992; Sayre et al., 2003). These same studies identified pitfall traps as a suitable method for reptiles, but necessitated long field periods for trap installation, therefore concluding that this technique was unviable for short-term studies. However, we found that pitfall traps registered a similar level of species richness as DTCS for lizard communities in all forest types studied, as well as for leaf litter amphibians in primary forest. Although we acknowledge that our active searches were limited to diurnal sampling and that we deployed a limited search effort, pitfall trapping exclusively captured a much greater number of species than any other technique (e.g., 23 species compared with five for DTCS for entire leaf litter herpetofauna combined), demonstrating the indispensability of this technique for sampling many cryptic leaf litter and semifossorial species. In support of their unique complementary value, Ryan et al. (2002) have also identified pitfall traps as an essential method for short-term surveys. Contrary to the belief that pitfall trapping imposes a substantial labor cost, with an efficient team of six people, we were able to install 10 trap stations of 35-liter pitfalls (40 buckets) and three trap stations of 62-liter pitfalls (12 buckets) in a single day.

One of the principle aims of a rapid assessment study is to efficiently identify rare, vulnerable, and endangered species, as well as to provide ecological information describing patterns of habitat use. Our data cast serious doubt about whether this is possible during a field campaign of less than 30 consecutive days, and we support Enge (1998, 2000) in recommending that representative samples of species-rich herpetofaunal assemblages require long-term (months or years) sampling programs that employ multiple sampling techniques. In presenting a cross-continental comparison of amphibian sampling in tropical forests Veith et al. (2004) recommend a minimum of 20 ''standardized visual transects'' to collect representative samples. However, this recommendation relies upon the availability of expert observers and only relates to sampling the subset of species that are susceptible to this technique. Data from rapid assessments should be analyzed with caution and in the context of a clear understanding of the level and type of sampling effort undertaken. This is especially important in the study of communities that have a highly uneven species-abundance distribution, noting that common species frequently dominate samples from short-term studies (thereby exaggerating the homogeneity of herptile assemblages among different sites).

Comparing the capture success across different methods for each forest type for all species combined, it was evident that one hour of transect searching captured more individuals of leaf litter amphibians and lizards per unit of cost than any other technique. Despite the additional costs associated with trap installation, comparisons of cost-per-unit effort or cost per individual can be misleading if a study is designed to simultaneously sample multiple sites across a large area (which is needed if researchers wish to collect representative samples from across all habitats in a given landscape). In this case, pitfall traps are often advantageous because a large number of trap arrays (high sampling effort) can be monitored very efficiently and (critically) without requiring skilled observers. For example, in our study, we were able to monitor all pitfall traps in a given site in less than one hour, the same amount of time necessary to conduct a single DTCS. Our ability to efficiently monitor large numbers of trap arrays allowed us to simultaneously sample three sites that were each spaced more than 30 km apart (i.e., each site was visited every day, therefore maximizing our ability to capture the variability in species assemblage composition within each habitat type; see Gardner et al., 2007a). Employing intensive active searches in each site, such as are typically recommended for rapid assessments, would greatly increase the amount of time needed in the field (thereby reducing the number of sites that can be surveyed within a given time period) and introduce potentially significant temporal effects.

Choice of sampling techniques requires consideration of the ecology and behavior of the species present in the study area (Gibbons and Semlistch, 1981; Crosswhite et al., 1999). Some species were captured in consistently high numbers by multiple sampling techniques (e.g., *Adenomera* sp. in all forest types, and *G. humeralis* and *C. amazonicus* in primary and secondary forest). However, when considering all species, perceived patterns of community structure among sites (of all habitats) were strongly dependent upon the choice of sampling method (see also Pearman et al., 1995), emphasizing the need for caution when drawing conclusions from sample data. Obviously, it would be ludicrous to recommend employing different techniques in different habitats if the objective is to collect comparative sample data. Instead, to ensure that samples of tropical forest lizards and leaf litter amphibians are representative of their respective parent communities, it is necessary (especially in studies of limited duration) wherever possible to employ multiple sampling techniques (e.g., Gardner et al., 2007a). The application of multiple techniques further strengthens the validity of such studies against criticisms of detection bias associated with particular methods, or method-habitat combinations (e.g., Schimdt, 2003) that would otherwise demand the use of mark-recapture techniques. The fact that our study revealed stronger methodological biases in sampling lizards than amphibians can be largely explained by the fact that our amphibian samples were restricted to leaf litter species.

Despite the recognized importance of understanding the consequences of habitat change for the conservation of many species of herpetofauna (e.g., Stuart et al., 2004), we currently have a very poor understanding of the value of many land-use options (e.g., plantations, secondary forest) for biodiversity (e.g., Barlow et al., 2007; Gardner et al., 2007a). It is possible that limitations of sampling design (including detection biases associated with the use of particular methods) have partly confounded attempts to provide robust evaluations of the value of converted and degraded forest land for biodiversity (Dunn, 2004; Barlow et al., 2007; Gardner et al., 2007b,c). Here, we have shown that comparisons of community structure among different habitat types are very sensitive to the choice of sampling method, with different techniques revealing different patterns.

Ecological survey data on patterns of species richness are essential both as an aid to conservation planning (Brooks et al., 2004) and to improve our understanding of the biodiversity value of human-dominated landscapes (Daily, 2001). Nowhere is the need for such data felt more urgently than in the case of tropical forests (Gardner et al., 2007c; Laurance, 2007). However, the severe limitation of financial resources available to conservation (James et al., 1999) demands that biodiversity studies are conducted in the most cost-effective fashion possible (Gardner et al., 2008). This includes the adoption of the most appropriate sampling techniques. We hope that the results presented here will be of assistance to tropical forest herpetologists concerned with improving the cost-effectiveness of their sampling methods and will help improve the quality of future studies that are urgently needed to improve our understanding of increasingly imperiled tropical forest landscapes.

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APPENDIX 1. Average total length and standard error (millimeters) for each herpetofaunal group (TL ± SE), specimens, forest type and maximum and minimum total length (millimeters) registered for each method, and the significance level of the pairwise Tukey post hoc comparisons. DTCS = diurnal time-constrained searches; PF = primary forest; SF = secondary forest; E = *Eucalyptus* plantation. Specimens: *AA* = *Ameiva ameiva*; *CA* = *Coleodactylus amazonicus*; *KC* = *Kentropyx calcarata*; *GH* = *Gonatodes humeralis*; *CO* = *Cercosaura ocellata*; *CC* = *Cnemidophorus cryptus*; *LK* = *Leptodactylus knudseni*; *A* = *Adenomera* sp.; *BG* = *Bufo gutattus*; *LM* = *Leptodactylus mystaceus*; *OP* = *Otophryne pyburni*.

	35-L pitfalls	62-L pitfalls	Glue traps	Funnel traps	DTCS
			Lizards		
TL ± SE	137.45 ± 4.77	151.47 ± 8.66	82.59 ± 3.95	248.03 ± 15.51	68.5 ± 2.68
Maximum TL	*AA* (SF) - 498	*AA* (E) - 400	*KC* (PF) - 330	*AA* (E) – 422	*CC* (E) - 214
Minimum TL	*CA* (SF- E) - 14	*CA* (SF) - 21	*GH* (PF) - 29	*CO* (SF) – 89	*CA* (SF) - 18
62-L pitfalls	$P = 0.450$				
Glue traps	$P < 0.001$	$P < 0.001$			
Funnel traps	$P < 0.001$	$P < 0.001$	$P < 0.001$		
TCS	$P < 0.001$	$P < 0.001$	$P = 0.485$	$P < 0.001$	
			Leaf litter amphibians		
TL ± SE	29.91 ± 1.67	31.6 ± 1.66		32.13 ± 2.66	18.75 ± 0.74
Maximum TL	*LK* (SF) - 143	*BG* (PF) - 141		*LM* (PF) – 56	*OP* (PF) - 55
Minimum TL	*A* (E) - 5	*A* (E) - 10		*A* (PF) – 17	*A* (PF) - 7
62-L pitfalls	$P = 0.958$				
Funnel traps	$P = 0.996$	$P = 1.000$			
TCS	$P = 0.007$	$P = 0.018$		$P = 0.047$	