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Estimates of forest floor litter frog communities: A comparison of two methods

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Abstract Estimates of forest leaf litter frog density, mass, richness and diversity given by the widely used 8 m × 8 m large plot method (LPM) were compared with estimates obtained by a newly proposed method (small 2 m × 1 m plots with leaf removal; SPLR). The study site was an undisturbed area of the Atlantic Rainforest of Ilha Grande, an island located in the south of Rio de Janeiro State, Brazil. Twenty-four LPM (totalling 1536 m^2 of forest floor) and 90 SPLR (totalling 180 m^2 of forest floor) were performed. The estimates obtained by the two methods differed markedly, indicating that even using a much smaller sampling area (11.7% of that of LPM), SPLR gave frog density estimates six times higher, and frog mass estimates approximately 2.5 times higher than estimates provided by LPM. The species richness and diversity obtained by the two methods were similar, despite the fact that the total area sampled with SPLR was much smaller. These data suggest that LPM may underestimate the abundance and biomass of leaf litter frogs in a given area.

Key words: Atlantic Rainforest, Brazil, community, comparison of methods, density estimate, litter frogs, monitoring, tropical forest.

INTRODUCTION

Most estimates of litter frog density and diversity in tropical forest areas have been based on data gathered using plot methods (e.g. Allmon 1991; Jaeger & Inger 1994; Giaretta *et al.* 1997). A quadrat of a given size (usually 1–64 m^2) on the forest floor is carefully searched for frogs by a fixed number of participants (Scott 1976, 1982; Allmon 1991). Many different plot sizes have been used in such studies (e.g. 1 m × 1 m, 5 m × 5 m plots (Fauth *et al.* 1989; Allmon 1991; Gascon 1996); 6 m × 6 m plots (Toft 1980a,b; Toft *et al.* 1982); and 8 m × 8 m plots (Lloyd *et al.* 1968; Scott 1976, 1982; Lieberman 1986; Giaretta *et al.* 1997)). However, it was recommended that 8 m × 8 m plots be used because many previous studies with litter frogs have used plots of that (or similar) size (Jaeger & Inger 1994). Many estimates of litter frog densities on different continents have been obtained in tropical forest areas using large quadrats, and these have indicated significant between-site differences in abundance and diversity of litter frogs (e.g. Brown & Alcala 1961; Lloyd *et al.* 1968; Scott 1976, 1982; Inger 1980a,b; Allmon 1991). A different quadrat method uses a small plot of 1 m × 1 m (point sampling), where one person drops a frame on the forest floor and then removes all stones, pieces of wood and leaves from within the area to count frogs (Jaeger & Inger 1994). However, due to the lack of comparative studies on the relative efficacy of frog sampling methods (Pearman *et al.* 1995), we have no information regarding the extent to which plot methods may differ in accuracy in the estimation of abundance and diversity of litter frog communities.

During a litter frog project, carried out by CFDR and MVS in an Atlantic forest area using a modified point-sampling method (2 m × 1 m quadrants with all leaf litter removed), we obtained an estimate of the density of litter frogs (approximately 41 frogs per 100 m^2, $n = 104$ plots), which was much higher than any previous estimates of litter frog abundance in other lowland tropical rainforest areas (see reviews in Allmon 1991; Gascon 1996; Giaretta *et al.* 1997). This led us to consider that our relatively high estimate might result from one or both of two possibilities: (i) the method that we developed might give more accurate estimates of the densities of litter frogs; and/or (ii) the density of the litter frog community in the area we studied is higher than in any other rainforest area previously reported.

In the present study, we compared the estimates of some frog community parameters obtained by the large plot method (using the recommended 8 m × 8 m quadrat; hereafter referred to as LPM) with those given by the 2 m × 1 m small plot method with leaf litter removal (hereafter referred to as SPLR). Specifically, we addressed the following questions:

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1. Which method gives higher estimates of density, species richness, diversity and biomass of litter frogs living on the forest floor?
2. Are there differences between the methods in terms of the body size of the frogs sampled?
3. Does diurnal or nocturnal sampling affect the results?

METHODS

Study area

The study was carried out in a remnant patch of undisturbed Atlantic Rainforest near Vila Dois Rios (23°11′S, 44°12′W), Ilha Grande, an island in the south of Rio de Janeiro State, in south-eastern Brazil. The Atlantic Rainforest biome (now reduced to less than 10% of its original area) consists of a strip of evergreen tropical rainforest that extends along the Atlantic coast of Brazil from north-east to south (for more details see Eiten (1992)). Ilha Grande is covered by Atlantic Rainforest with different levels of regeneration due to disturbances caused by human activities throughout the previous centuries. It was an important area for coffee, corn and sugar production in the past, but such activities ceased after the area became a State Park (Araújo & Oliveira 1988). Remnants of undisturbed forest exist in the less accessible central areas of the island. Annual rainfall in the area is about 1700 mm with a mean annual temperature of about 23°C (Araújo & Oliveira 1988). The study area is located 220–230 m above sea level.

Comparison of methods

Field work was carried out in an area of approximately 14 ha of undisturbed Atlantic Rainforest, during four months (January–May) of the rainy season in 1997. We sampled the frogs using both methods on each day during four consecutive days of each month. Methods were used in alternate periods each day, to minimize between-method variations in weather conditions on successive days. For each method we sampled the same number of plots in the morning (07.00–11.50 hours), in the afternoon (12.10–17.30 hours) and at night (19.00–23.00 hours). No area of forest floor was sampled more than once.

We carried out the following procedures for each method:

1. Large plot method. We established randomly 24 quadrats of 8 m × 8 m (64 m^2) over 14 ha of study area, with each quadrat located at least 100 m from any other. We marked the corners of the plots with wooden stakes and the plots were completely enclosed by a flexible plastic fence 35 cm high. The lower edge of the plastic was attached to the ground with string when relief irregularities, fallen tree trunks or large boulders impeded burial of it. After erecting the fence, all five authors moved through the entire plot on hands and knees, side-by-side, carefully searching for frogs, with the aid of hand rakes. All leaves, logs, pieces of wood, fallen branches and stones inside the plot were overturned to bare soil, and rock crevices and spaces between tree roots were also checked for frogs. Each plot was searched for about 1 h giving an effort measurement of 5 person-hours. Using this method, we sampled two plots monthly during each period of the day (morning, afternoon and night), for a total of six plots per month.
2. Small plot with litter removal method. In the same general area of the forest, we established SPLR plots. To minimize between-method variations in relief, soil conditions and amount of litter of the areas sampled, SPLR plots were always established between two LPM plots. Each SPLR plot was located at least 20 m away from adjacent SPLR and LPM plots. During SPLR sampling, we rapidly marked a 2 m × 1 m area of forest floor using a previously prepared 2 m × 1 m cotton string having at each of its vertices small bamboo sticks with coloured flags to facilitate visualization of the plot limits. After inserting the bamboo sticks in the ground, we checked for the presence of frogs on the leaf litter surface within the plot. All leaf litter inside the plot was systematically removed by compressing portions of the leaf litter between the hands and rapidly transferring them into a 100 L plastic bag; this process usually took about 1 min. After all the leaf litter was removed, we carefully checked the ground within the plot for any remaining frogs. SPLR sampling was usually carried out by two persons, although in some cases it was feasible for a single person to collect the litter. After moving to a clearing in the forest, all material inside each plastic bag was transferred, piece by piece, to a white plastic tray, and carefully checked for the presence of frogs. Each sack was sorted by one person, who took approximately 1 h to complete the searching process. Each of the five people checked approximately the same number of SPLR sacks. We sampled 30 SPLR plots during each period of the day (morning, afternoon and night), for a total of 90 plots.

In the field, frogs were killed with ether and preserved in vials of 70% alcohol, then transported to the laboratory. In the laboratory, each frog was identified to species, had its snout–vent length (SVL) measured with a Vernier caliper (to the nearest 0.1 mm) and was weighed (to the nearest 0.001 g) on an electronic

Mettler balance (Mettler–Toledo, Greifennsee, Switzerland). Prior to performing each statistical analysis, we tested the assumption of normality of data distribution and used non-parametric tests when the data did not fit a normal distribution. Differences in mean SVL and body mass of the frogs sampled by each method were tested by the Kruskal–Wallis test (Zar 1984). To test for between-method differences in abundance distributions of frogs by species and by size, we used χ^2 tests (Zar 1984), amalgamating the rarer species and the poorly represented size categories, respectively, into an 'others' category in order to maintain reasonable expected cell frequencies. Frog species diversity was estimated for each method by using the Shannon–Wiener diversity index (Magurran 1988). Differences between diversity values were tested using a *t*-test (Magurran 1988).

We also compared the two methods in terms of the proportions of frogs collected during each period of the day, to assess if the results of the sampling methods were independent of frog activity. To make the abundance and biomass of frogs statistically comparable between the two methods, we standardized the total frog abundance and biomass found per plot to frogs per m^2 and g ha^{-1}, respectively, for both methods. As an index of the relative efficiency of each method in sampling all frogs discovered within a given plot by a particular observer, we calculated the percentage of frogs seen during sampling and effectively captured by the observers (seen and captured; SC).

Table 1. Total number of individuals sampled and estimated density (frogs per 100 m^2; in parentheses) of each frog species of the litter frog community in the Atlantic Rainforest of Ilha Grande, for each of the sampling methods

Frog species	LPM	SPLR
Brachycephalidae		
Psyllophryne didactyla	8 (0.52)	32 (17.78)
Bufonidae		
Dendrophryniscus brevipollicatus	3 (0.20)	1 (0.56)
Leptodactylidae		
Adenomera marmorata	10 (0.65)	1 (0.56)
Eleutherodactylus binotatus	5 (0.33)	3 (1.67)
Eleutherodactylus guentheri	0	1 (0.56)
Eleutherodactylus cf. *octavioi*	2 (0.13)	0
Eleutherodactylus parvus	32 (2.08)	13 (7.22)
Proceratophrys appendiculata	3 (0.20)	0
Zachaenus parvulus	22 (1.43)	20 (11.11)
Microhylidae		
Chiasmocleis sp.	6 (0.39)	2 (1.11)

LPM, large plot method; SPLR, small plot with litter removal.

RESULTS

Species abundance and density

We recorded nine frog species using LPM and eight species using SPLR (Table 1). We found a total of 91 frogs using LPM and 73 using SPLM, although the total area sampled was much larger for LPM (1536 m^2) compared to that of SPLR (180 m^2). The number of frogs per plot found by LPM ranged from 0 to 14, whereas using SPLR the number ranged from 0 to 6 frogs (Fig. 1). No frogs were found in 16.7% of the LPM plots and in 56.7% of the SPLR plots (Fig. 1).

The pooled frog density estimated by LPM was 5.9 frogs per 100 m^2, whereas that estimated by the SPLR was 40.6 frogs per 100 m^2. The density estimated by SPLR was 6.86 times larger than that estimated by

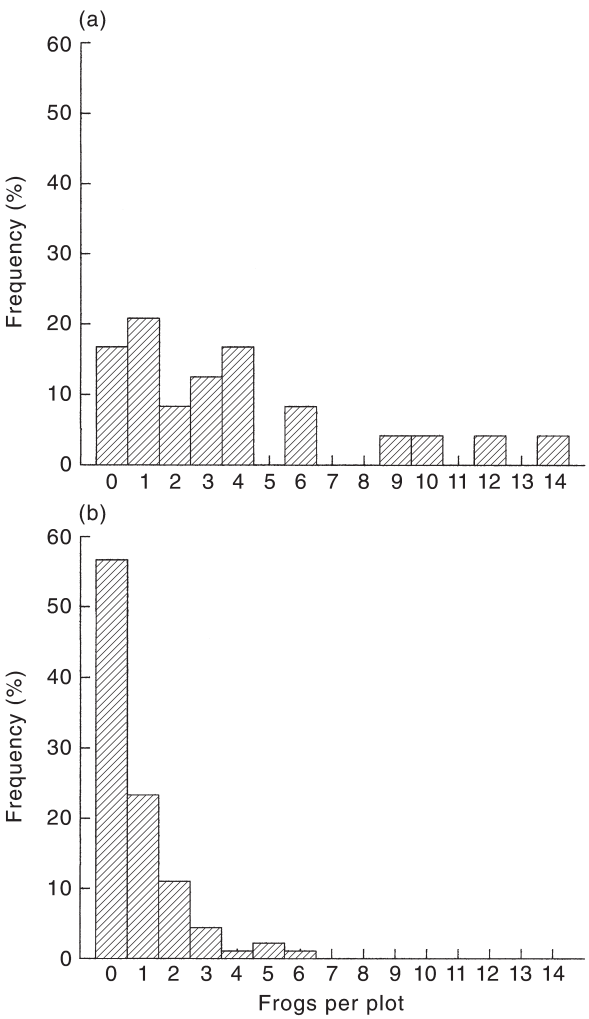


Fig. 1. Frequency distributions of plots containing different numbers of frogs sampled by (a) the large plot method (LPM) and (b) the small plot with litter removal (SPLR) method.

LPM. Separate densities estimated by SPLR were two or more times higher than those of LPM sampling for each frog species, except for *Proceratophrys appendiculata* and *Eleutherodactylus* cf. *octavioi*, which were not recorded in SPLR plots, and for *Adenomera marmorata*, which had a similar density using both methods (Table 1). Frog species diversity (H′) did not differ significantly between methods (H′(LPM) = 1.81; H′(SPLR) = 1.43; $t = 0.59$; d.f. = 15; $P = 0.564$).

The distribution of abundances of frog species in the community differed between methods ($\chi^2 = 34.42$; d.f. = 6; $P < 0.0001$) (Fig. 2). The most abundant species of frog found in LPM samples was *E. parvus* (35.2% of all frogs found), whereas *Psyllophryne didactyla* was the most abundant (43.8% of all frogs found) in SPRL samples (Fig. 2). Although the smallest species of the local frog community, *P. didactyla*, was relatively uncommon in LPM samples, the SPLR method indicated that it was the most common frog species in the same community. *Zachaenus parvulus* was equally well represented in the samples of both methods (Fig. 2).

Frog size and mass

The SVL of frogs sampled by SPLR (mean ± SD, 13.4 ± 1.16 mm; $n = 72$) was significantly smaller than that of frogs sampled by LPM (18.2 ± 1.03 mm;

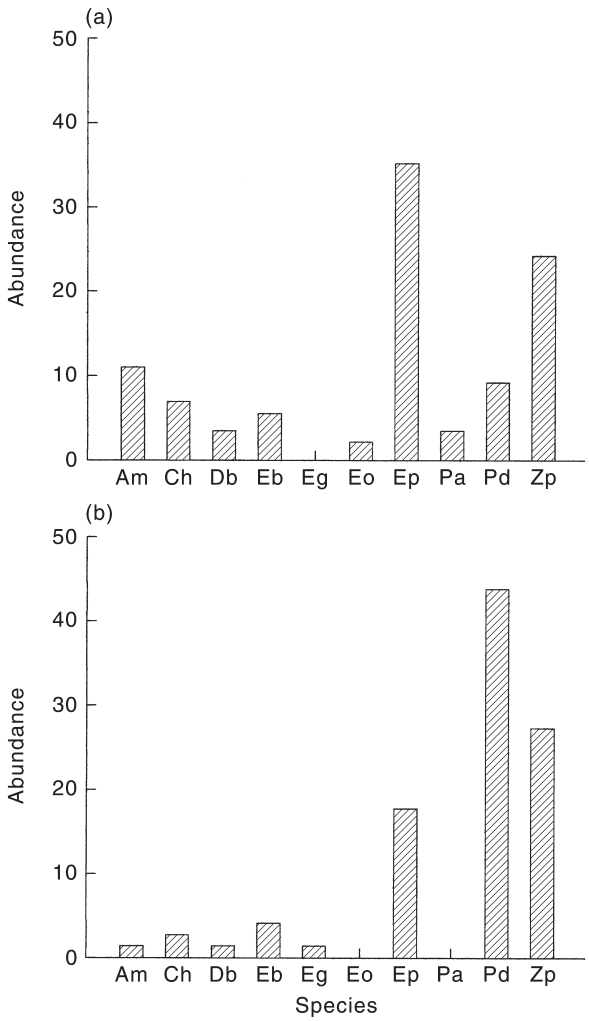


Fig. 2. Distribution of abundance of each frog species at the Ilha Grande community as sampled by (a) the large plot method (LPM; $n = 91$ frogs) and (b) the small plot with leaf litter removal (SPLR; $n = 73$) method. Ep, *Eleutherodactylus parvus*; Eb, *Eleutherodactylus binotatus*; E, *Eleutherodactylus* cf., *octavioi*; Eg, *Eleutherodactylus guentheri*; Am, *Adenomera marmorata*; Zp, *Zachaenus parvulus*; Pa, *Proceratophrys appendiculata*; Db, *Dendrophryniscus brevipollicatus*; Ch, *Chiasmocleis* sp.; Pd, *Psillophryne didactyla*.

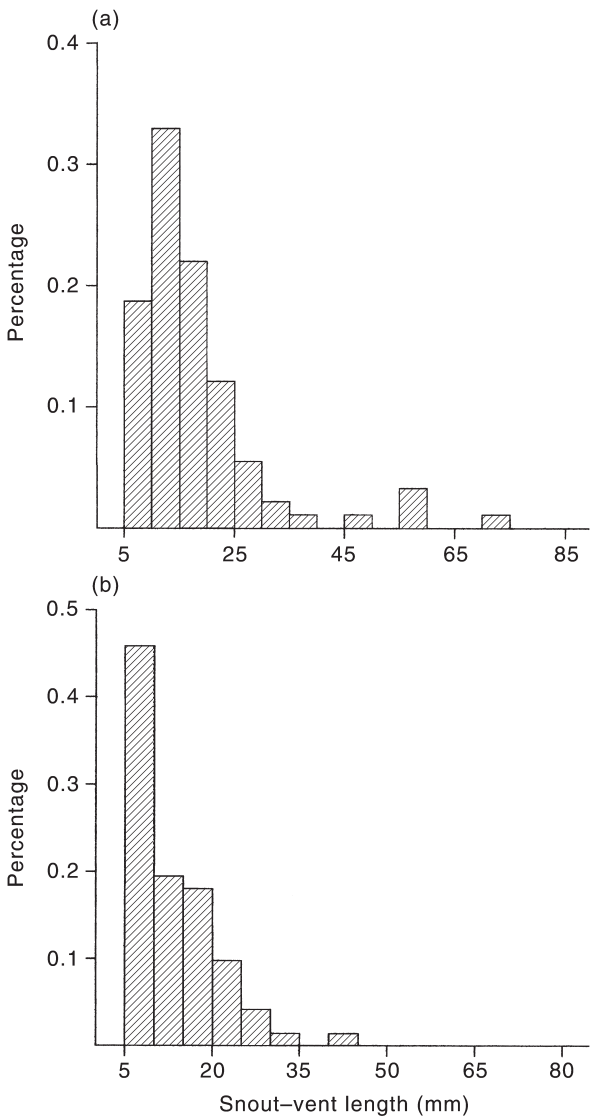


Fig. 3. Distribution of abundance of different sized frogs sampled by (a) the large plot method (LPM; $n = 91$ frogs) and (b) the small plot with leaf litter removal (SPLR; $n = 73$ frogs) method.

$n = 91$; H = 11.71; $P < 0.0001$). Figure 3 compares frog size and frog abundance for both methods. The two methods differed significantly in the distribution of abundance of frog sizes ($\chi^2 = 14.83$; d.f. = 5; $P = 0.011$). Similarly, average body mass of the frogs sampled was significantly lower for SPLR (0.658 ± 0.564 g; $n = 72$) than for LPM (2.049 ± 0.501 g; $n = 91$; H = 9.57; $P < 0.005$). The largest species found during the study (*P. appendiculata*) was not found in SPLR sampling (Table 1).

However, the estimate of total litter frog biomass per hectare was lower for LPM (1150 g ha^{-1}) than for SPLR (2630 g ha^{-1}) and both methods differed significantly in the estimates of frog mass per ha (H = 4.06; $P < 0.05$).

Sampling period

With LPM, most frogs (71.4% of the total) were captured during nocturnal samplings. With SPLR the temporal differences were reduced, with most frogs collected during afternoon samplings (43.8%) (Table 2). The two methods differed in the proportion of frogs found during the three sampling periods ($\chi^2 = 28.947$; d.f. = 2; $P < 0.0001$). Twelve frogs were seen but escaped (averaging 0.5 frogs lost per plot) during LPM sampling, whereas none of the frogs that were seen were lost during SPLR sampling. Hence, the percentage of frogs seen and captured was 86.8% when using LPM and 100% when SPLR was used. Of the frogs lost in LPM, 7% (2/28) were lost during diurnal sampling and 13% (10/75) were lost during nocturnal sampling.

In short, SPLR samples gave higher estimates of frog density and biomass, smaller average frog size and different proportions of frog species compared to LPM samples.

DISCUSSION

The present study indicates that the estimates obtained by the two sampling methods differ consistently for most parameters tested, with generally higher values across parameters for SPLR. Most of the differences may be attributed to differences in efficiency in sampling leaf litter frogs. When comparing frog density and biomass, the two methods differed markedly, and SPLR seemed to give more accurate estimates than LPM. While LPM data produced an estimated pooled density of about six frogs per 100 m^2, the SPLR method indicated a pooled frog density nearly seven times higher (more than 40 frogs per 100 m^2) on the forest floor at Ilha Grande. Similarly, the total litter frog biomass per unit of forest floor estimated by SPLR was approximately 2.3 times greater than that estimated by LPM, indicating that the latter method considerably underestimates the biomass of frogs actually living on the forest floor.

Despite the considerable differences in total area sampled (the total forest floor area sampled by SPLR was only 11.7% of that sampled by LPM) the number of species and diversity obtained by the two methods were similar. This indicates that the use of SPLR may provide a similar estimate of species richness and diversity of leaf litter frogs by sampling a much smaller area.

The differences in the distribution of abundance of the frog species obtained by each method suggest that LPM underestimates small-sized frogs, being more efficient in finding larger individuals. Conversely, the use of SPLR found small and comparatively large frogs (e.g. adults of *E. binotatus* and large adult *Z. parvulus*). It may be argued that SPLR may be inefficient at sampling some comparatively large-bodied frogs, such as *P. appendiculata*, which was the largest species sampled in the study and was found only in LPM samples. However, the data from LPM (which seems to be efficient in sampling larger frog species) indicated that there was a density of one *P. appendiculata* for each 500 m^2 of forest floor. As the total area sampled in the SPLR during the study was only 180 m^2, the absence of *P. appendiculata* in the SPLR sampling may reflect the low probability of finding one individual of this species, given the small area of forest floor surveyed. The difference between methods in finding different frog sizes also suggests that the choice of method may produce bias in ecological analysis of frog communities.

In spite of being a species of relatively large size in the leaf litter community, *Z. parvulus* had a lower density per area estimated by LPM than it did estimated by SPLR. Part of this difference may be explained by the defensive behaviour of this species. The main defence of *Z. parvulus* appears to be camouflage, because its colouration is quite variable and usually similar to that of dead leaves. When disturbed, *Z. parvulus* extends the hind and forelegs, and assumes a shape similar to a dead leaf (Sazima 1978; Rocha *et al.* 1998). It is possible that individuals in that condition would be less easily detected during

Table 2. Absolute numbers and proportions of frogs sampled using each of the sampling methods, in the morning, afternoon and night in the Atlantic Rainforest of Ilha Grande

Period of day	LPM (24 plots; $n = 91$ frogs)	SPLR (90 plots; $n = 73$ frogs)
Morning	15 (16.5%)	18 (24.7%)
Afternoon	11 (12.1%)	32 (43.8%)
Night	65 (71.4%)	23 (31.5%)

LPM, large plot method; SPLR, small plot with litter removal.

sampling on the forest floor (LPM) than during the sorting of SPLR (which is done on a tray with a white bottom). Alternatively, the between-method differences in sampling of *Z. parvulus* could be due to greater disturbance caused by the observer while performing LPM, resulting in flight of the frogs before the observer reached their initial locations.

Observer reduction of frog escape from plots prior to detection is presumably greater in SPLR than in LPM because of smaller plot sizes, and because the fence that encloses LPM plots has limited efficiency in preventing frog escape. Although, in the LPM method, the fence is established along the edges of the plot to prevent frog escape (Inger 1980b; Allmon 1991), our experience was that it is difficult (due to irregularities of the terrain, fallen trunks and boulders) to maintain effective attachment of the fence to the ground along plot edges. As a result, depending on the frequency of these microhabitat characteristics in each plot, the plastic fence does not come into contact with the ground at many points along each edge, reducing its effectiveness in preventing frogs from escaping. As a whole, SPLR plots can be checked for the presence of frogs and because all material is rapidly removed in a plastic bag, a lower rate of frog escape should occur using this method.

High rates of frog escape from LPM plots (13.2%) is consistent with other leaf litter frog studies (e.g. Allmon 1991) and results from the fact that, after a frog escapes onto the forest floor, it is not easy for the observer to recapture it, due to the poor illumination within the forest and frog defensive characteristics (e.g. concealing colouration and/or flight to inaccessible shelter). Conversely, with the SPLR method, the leaf litter is sorted more carefully, in stronger light and in a tray with a border that reduces the chance of frog escape (none of the frogs seen were lost in 90 SPLR plots).

A between-method comparison considering the number of frogs sampled in each period of the day suggests that the LPM method may be efficient for sampling at night, but yields the least number of frogs in the afternoon period. Conversely, the afternoon period yielded the largest number of SPRL samples. This probably results from the greater difficulty in finding litter frogs during the afternoon, when light is low. On the other hand, the use of head lanterns compensated for the lack of natural lighting, which may partly explain the greater efficiency of LPM in nocturnal sampling compared to morning and afternoon samplings (Rocha *et al.* 2000).

One additional limitation of the LPM relative to the SPLR is the fact that the former requires a team of two to six people, depending on the plot area used. Such a crew may not be available and can be expensive. Also, in studies that have used LPM in different areas of the world, the wide variance in sampling effort that can result from differences in crew size may be significant. Moreover, differential efficiency of frog detection and capture among crew members may introduce further variation. However, the effects of such variance on estimates have not been evaluated. Conversely, SPLR can be easily performed even by a single person (a researcher or a well-trained technician). This may be especially advantageous in monitoring programmes that need regular sampling efforts, because it would lead to a smaller variance due to sampling effort between areas (or between different periods of the day), thus keeping the data comparable.

One problem associated with plot sampling is the considerable level of disturbance it causes to frog microhabitats and to the many other species living in the leaf litter of the forest floor. The overturning of the leaf litter, digging of the soil surface, and displacement of logs and rocks caused by researchers during LPM sampling may cause important structural and microclimatological alterations of the microhabitats in the areas surveyed, although there is no information on the effects of such disturbance on the leaf litter community. Although digging of the soil surface with a hoe, as was originally done in some plot studies (Brown & Alcala 1961; Lloyd *et al.* 1968), was abandoned in later studies because it did not improve the sampling (Scott 1976; Fauth *et al.* 1989), many other procedures used by researchers during LPM samplings could still have a considerable impact over a large proportion of forest floor. The disturbance caused by SPLR sampling, on the other hand, should cause a considerably smaller impact on the forest floor (and, consequently, on the leaf litter fauna community), at least when considering each individual 2 m^2 plot. It should be pointed out, however, that if the litter removed during SPLR sampling is not returned to the forest floor where it was removed, it is possible that the structural impact on the forest floor habitat caused by this method could be even greater in the long run than that caused by LPM on an equivalent area. The effect of SPLR litter removal may be minimized because the total area disturbed is not continuous as is the case with LPM. The question of which method causes the greatest impact is quite complex, and we have no concise data to assess it properly. Finally, it should be pointed out that the SPLR method allows the gathering of data on some microhabitat conditions that could affect frog densities and frequencies of occurrence, such as the relative proportions (by mass) of leaf litter, stones and wooden matter on each plot, which is only possible through removal of all material within the plot for weighing (and is therefore not feasible using the LPM method).

In conclusion, SPLR has at least eight advantages relative to LPM: (i) it provides similar estimates of species richness and diversity after sampling a smaller forest floor area; (ii) it gives more accurate estimates of frog abundance and biomass per unit of forest floor;

(iii) it can be performed by a single person; (iv) it seems to be less sensitive to biases caused by different frog observation abilities and by variation of frog activity among daily periods, allowing more reliable estimates; (v) it is more efficient in minimizing rates of frog escape from observers; (vi) it should produce more comparable estimates in monitoring programmes in different areas (or at the same area) by reducing the variance introduced by the unequal numbers of observers performing the plot samplings in different areas; (vii) it may allow gathering of some data on structural microhabitat (e.g. relative percentage of leaves, wood and stones per plot) that requires litter removal and which may have influence on some frog community parameters; and (viii) it may cause less disturbance to the forest floor microhabitat, as a smaller area of leaf litter is disturbed per plot. However, we suggest some care must be taken to set up the following:

1. The plots sampled should be randomly placed to avoid sampling only in areas with abundant leaf litter, which may overestimate frog abundance.
2. Leaf litter removal must be conducted as fast as possible to avoid frog movements in and out of the plots.
3. Leaf litter should be returned to the forest floor where it was removed.

Development of rapid, accurate and sensitive methods for biodiversity monitoring have an increasing importance in ecological research, conservation and management, particularly in the case of the current world frog decline. The estimates obtained in the present study by the SPLR method indicate that the Atlantic Rainforest of Ilha Grande has the highest abundance of forest litter frogs surveyed so far. However, the large plot methods may underestimate the abundance and mass of leaf litter frogs of a given area and this suggests to us that, for most of the areas in which such methods have been used, the local leaf litter frog abundance and biomass could be considerably higher than the estimates presented (see review in Allmon 1991).

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REFERENCES

Allmon W. D. (1991) A plot study of forest floor litter frogs, Central Amazon, Brazil. *J. Trop. Ecol.* **7,** 503–22.

Araújo D. S. D. & Oliveira R. R. (1988) Reseva Biológica Estadual da Praia do Sul (Ilha Grande, Estado do Rio de Janeiro): lista preliminar da flora. *Acta Bot. Bras.* **1,** 83–94.

Brown W. C. & Alcala A. C. (1961) Populations of amphibians and reptiles in the submontane and montane forests of Cuernos de Negros, Phillipines islands. *Ecology* **42,** 628–36.

Eiten G. (1992) Natural Brazilian vegetation types and their causes. *An. Acad. Bras. Ciênc.* **64**(Suppl. 1)**,** 35–65.

Fauth J. E., Crother B. I. & Slowinski J. B. (1989) Elevational patterns of species richness, eveness and abundance of the Costa Rican leaf-litter herpetofauna. *Biotropica* **21,** 178–85.

Gascon C. (1996) Amphibian litter fauna and river barriers in flooded and non-flooded Amazonian rainforests. *Biotropica* **28,** 136–40.

Giaretta A. A., Sawaya R. J., Machado G. *et al.* Diversity and abundance of litter frogs at altitudinal sites at Serra do Japi, Southeastern Brazil. *Rev. Bras. Zool.* **14,** 341–6.

Inger R. F. (1980a) Relative abundances of frogs and lizards in forests of Southeast Asia. *Biotropica* **12,** 14–22.

Inger R. F. (1980b) Densities of floor-dwelling frogs and lizards in lowland forests of Southeast Asia and Central America. *Am. Nat.* **115,** 761–70.

Jaeger R. & Inger R. F. (1994) Standard techniques for inventory and monitoring: Quadrat sampling. In: *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians* (eds W. R. Heyer, M. A. Donnely, R. W. McDiarmid, L. C. Hayek & M. S. Foster) pp. 97–102. Smithsonian Institution Press, Washington DC.

Lieberman S. S. (1986) Ecology of the leaf litter herpetofauna of a Neotropical rainforest: La Selva, Costa Rica. *Acta Zool. Mex.* **15,** 1–71.

Lloyd M., Inger R. F. & King W. (1968) On the diversity of reptile and amphibian species in a Bornean rainforest. *Am. Nat.* **102,** 497–515.

Magurran A. E. (1988) *Ecological Diversity and its Measurement.* Cambridge University Press, Cambridge.

Pearman P. B., Velasco A. M. & López A. (1995) Tropical amphibian monitoring: a comparison of methods for

detecting inter-site variation in species composition. *Herpetologica* **51,** 325–37.

Rocha C. F. D., Van Sluys M., Alves M. A. S., Bergallo H. G. & Vrcibradic D. (2000) Activity of leaf-litter frogs: When should frogs be sampled? *J. Herpetol.* **34,** 285–7.

Rocha C. F. D., Van Sluys M., Bergallo H. G., Alves M. A. S. & Vrcibradic D. (1998) *Zachaenus parvulus* (Leaf Frog): Defensive behaviour and color pattern. *Herpetol. Rev.* **29,** 232–4.

Sazima I. (1978) Convergent defensive behavior of two leaf-litter frogs of southeastern Brazil. *Biotropica* **10,** 158.

Scott Jr N. J. (1976) The abundance and diversity of the herpetofauna of tropical forest litter. *Biotropica* **8,** 41–58.

Scott Jr N. J. (1982) The herpetofauna of forest litter plots from Cameroon, Africa. *US Fish Wildl. Res. Report* **13,** 145–50.

Toft C. (1980a) Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* **45,** 131–41.

Toft C. (1980b) Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. *Oecologia* **47,** 34–8.

Toft C., Rand A. S. & Clarke M. (1982) Population dynamics and seasonal recruitment of *Bufo typhonius* and *Colosthetus rubicola* (Anura) on Barro Colorado Island. In: *Seasonal Rhythms of Tropical Forest, Barro Colorado Island* (ed. E. G. Leigh) pp. 397–403. Smithsonian Institution Press, Washington DC.

Zar J. H. (1984) *Biostatistical Analysis*. Prentice Hall, Englewood Cliffs, New Jersey.