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Sampling amphibians and reptiles in the Iwokrama Forest ecosystem

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ABSTRACT—We compared species richness estimates for eight camps sampled in 1997 to inventory the herpetofauna of the Iwokrama Forest. Regression analyses and Coleman curves documented that species richness was lowest in the camp at the highest elevation. We also found that the four standard sampling methods we used in 1997 differed significantly in detecting species. All methods were necessary to generate a complete species list of 141 species, but visual encounter surveys and opportunistic collecting discovered the largest number of species in Iwokrama. Our results show that meaningful comparisons of species diversity are only possible when effort has been standardized.

INTRODUCTION

Donnelly et al. (in press) describe how the Iwokrama Forest herpetofauna compares to other faunas in South America. Based on their analysis, the Iwokrama herpetofauna resembles those from Suriname and French Guiana more than it does the Venezuelan herpetofauna. While Duellman (1999) claims that the Amazon Basin + Guianan lowlands contain a single fauna, others have suggested that the fauna of the Guianan region may be distinct from that of the Amazon Basin (Donnelly et al. 2005; Hoogmoed 1979a). Most species known from Iwokrama are “rare”, and only a few are common across the Reserve (Donnelly et al. 2005). In this paper, we update the report by Donnelly et al. (2005) to include information obtained during a ranger training course conducted in 2002 and during our work in Surama savannas in 2002. We provide information on species distributions across the Iwokrama forest, on how animals were captured, and when they were captured.

Collections of amphibians and reptiles from the Iwokrama Forest provide information on the composition of a rainforest herpetofauna from central Guyana. Our studies in the region fill a gap between studies done in Venezuela and studies done in Eastern Guayana. Central Guyana is home to “frontier forest” that had not been explored prior to the Ver-

tebrate Survey conducted by the Academy of Natural Sciences. We hope our description of the Iwokrama herpetofauna stimulates additional research. We are expanding our studies of the forest herpetofauna to include the fauna found in the Rupununi savanna, and we provide preliminary information for savanna species in this paper.

Surveys of herpetofaunal assemblages in northern South America have focused on the entire region (Duellman 1999; Duellman & Hoogmoed 1992; Hoogmoed 1979a, b) or concentrated on Venezuela (Duellman 1997; Gorzula & Señaris 1999) French Guiana (Chippaux 1986; Gasc & Rodrigues 1980; Hoogmoed 1982; Hoogmoed & Avila Pires 1991; Hoogmoed & Lescure 1975; Lescure 1976, 1986; Lescure & Marty 2001 [2000]) or Suriname (Goin 1971; Hoogmoed 1979b, 1980, 1982). Few surveys have been done in Guyana and most of the information for amphibians and reptiles stems from work done by Beebe and Boulenger. Beebe made collections in the Kartabo region of Guyana (Beebe 1915, 1919, 1925, 1944a, b, 1945, 1946) and generated a list, but the lack of voucher material for Beebe’s collection complicates use of his list. Beebe’s identifications were not always correct (e.g., he used the name *Neusticurus rudis* [Beebe 1945] for a specimen of *N. bicarinatus*—MAD pers. obs.). Boulenger published research on amphibians and reptiles collected near table-top mountains in Guyana (Boulen-

ger 1895a, b, 1900a, b; McDiarmid & Donnelly, 2005). As herpetological research continues in Guyana, new species will be discovered because the region is poorly known (e.g., Duellman & Yospa 1996; MacCulloch & Lathrop 2001, 2002; Noonan & Harvey 2000).

The herpetology research we have done in Iwokrama shows how research and conservation intersect through capacity building, and the research-conservation link is important for developing countries (see Bickford 2005). While "scientific progress" is made more slowly when it is associated with training, we believe that the long-term benefits for conservation are enhanced with training activities. This enhancement occurs when people living near the forest gain benefits derived from the conserved ecosystem. Our research and training efforts span a five-year period. During the 1997 herpetological survey in Iwokrama, capacity was enhanced for professionals, university students, Amerindian rangers, and Amerindian parabiologists. During the 1999 ranger training course capacity was enhanced for the ranger trainees, three Guyanese post-graduates, and three of the ranger trainees that were participants in the 1997 surveys. The experienced trainees extended their training in 1999 as they worked with their peers. During the 2002 ranger training course, an alumna from the 1999 course helped teach the course to ranger trainees and one University of Guyana student. The University student extended her experience in 2002 by helping ranger trainees acquire particular skills. Ranger trainees that complete the program gain employment with Iwokrama, but in some cases, trained rangers have left Iwokrama for other job opportunities that required the skill set developed during the training course.

Collections of amphibians and reptiles were made during the Iwokrama Vertebrate Survey (1997–1998), and during Amerindian Ranger Training Courses (in 1999 and 2002). We also report on a small collection made in the savanna near the Amerindian village of Surama. These specimens were collected in 2002 with members of local wildlife clubs.

To generate a complete species list for any site, a combination of sampling methods is needed to sample all amphibians and reptiles because species vary ecologically (e.g., from being fossorial to canopy-dwelling). Animal activity patterns are diurnal, crepuscular, or nocturnal, so diurnal and nocturnal sampling is required. While use of all possible methods is best, limited financial resources typically require researchers to select among sampling methods (see Heyer et al. 1994, 2001).

Campbell & Christman (1982) compared sampling methods in Florida (drift fence arrays using pitfall and funnel traps, quadrats, time-constrained

searches, road-cruising, and opportunistic collecting) across several sites. The number of species detected varied among methods; drift fence arrays and time constrained searches resulted in the greatest number of species (29 species with arrays and 24 species with time-constrained searches). Quadrat sampling captured few species (6–9 species) but did not vary across habitat types. Road-cruising and opportunistic collecting obtained species not collected in other ways (Campbell & Christman, 1982). Unfortunately, Campbell & Christman did not standardize effort across sites or methods.

Pearman et al. (1995) compared the efficiencies of four sampling methods in a tropical forest site in Ecuador and found differences among methods, but the methods were compared without standardizing effort. Pearman et al. (1995) detected the greatest number of species with visual encounter surveys. We extend the analysis of Pearman et al. (1995) by comparing among methods with standardized effort. We used a rarefaction approach to determine how sites and methods varied (Sanders 1968; Simberloff 1979). We compare these estimates of species richness with estimates obtained from a simulation approach (Colwell 1997; Colwell & Coddington 1994).

METHODS

The Vertebrate Survey of the Iwokrama forest began in 1997. All specimens collected prior to the herpetological survey were collected opportunistically (Collection One). The herpetological component of the survey took place during the 1997 rainy season (Table 1). Eight sites were sampled using four standard methods during the herpetological survey (nocturnal visual encounter surveys, diurnal visual encounter surveys, litter plots, and opportunistic collecting; see Heyer et al. 1994). The standard methods used are described in detail in Donnelly et al. (2005) and will be summarized here. We worked out of eight field camps established as part of the vertebrate survey (Table 1). Site selection depended on river or road access. At each camp we established trails and scouted rivers and creeks for visual encounter surveys. Surveys were conducted during the day and night along trails or from boats. Leaf litter plots (5 × 5 m and 8 × 8 m) were haphazardly selected in forest sites and sampled during the day. All animals observed or captured with other sampling methods were collected opportunistically. Pitfall traps associated with drift fence arrays were used at the Three Mile Camp only. The amount of time spent in each camp was not equal nor was sampling intensity (Table 1, Table 2). The specimens collected during the herpetological survey were placed in Collection Two. Additional observations of amphibians

Table 1. Collection sites visited during the Vertebrate Survey of the Iwokrama Forest. Abbreviations: m asl—meters above sea level; NA—not available.

Camp	Collection dates	Elevation (m asl)	Latitude, longitude
Maipuri	pre-May 1997	NA	4°45.25 N, 58°35.28 W
Tiger Creek	pre-May 1997	NA	4°31.47 N, 58°33.62 W
Muri Scrub	9–14 May 1997	80	4°25.20 N, 58°50.96 W
Cowfly	14–20 May 1997	120	4°20.00 N, 58°49.00 W
Third Camp	20–27 May 1997	224	4°20.00 N, 58°48.00 W
Three Mile	28 May–8 June 1997	102	4°37.98 N, 58°42.87 W
Burro-Burro	9–20 June 1997	83	4°43.86 N, 58°51.04 W
Kabocali	24 June–3 July 1997	101	4°17.10 N, 58°44.85 W
Cutline	5–11 June 1997	70	4°35.00 N, 58°44.85 W
Pakatau	13–24 July 1997	85	4°45.00 N, 59°01.00 W
Kurupukari	1997, 1999, 2002	70	4°43.91 N, 58°59.00 W
Surama	2002	NA	4°13.58 N, 59°06.96 W

and reptiles were made by GGW during subsequent fieldwork in the forest.

In 1999 and 2002, Amerindian ranger training courses were held at the Kurupukari Base Camp. Collections of amphibians and reptiles were made in the area of the base camp, along rivers and creeks near the base camp, and at Three-Mile camp (in 1999 only) as part of course activities. We used visual encounter surveys (day and night) and litter plot samples to collect during the ranger training. Specimens were also collected opportunistically during both training sessions.

In 2002, we collected amphibians and reptiles near Surama with Amerindian wildlife club members. We collected amphibians opportunistically, during time-constrained visual encounter surveys, and during distance-constrained visual encounter surveys. We also collected a few reptiles during amphibian sampling. In summary, Collection One was made during early 1997 (Jan.–Apr.), Collection Two

was made during the 1997 herpetological survey (May–July), Collection Three was made during the 1999 ranger training course (Aug.), Collection Four was made during the 2002 ranger training course (Aug.), and Collection Five was made in Surama in 2002 (Aug.). Specimens were obtained during the five collecting efforts. Animals were killed in the field, fixed in 10% formalin, and stored in 70% ethanol. Tissues (liver and muscle) were extracted from some specimens prior to formalin fixation and stored in 95% ethanol. Representative specimens have been deposited in the Centre for Biodiversity, University of Guyana, Georgetown, Guyana; the American Museum of Natural History, New York; the United States National Museum of Natural History, Washington D.C.; and the Herpetology Collection at Florida International University.

We plotted the number of species obtained as a function of the number of individuals sampled to describe the pattern of species accumulation for all

Table 2. Collection efforts during the herpetological survey measured as the number of samples taken with each method. The camps are abbreviated as follows: MURI = Muri Scrub, COW = Cowfly, TC = Third Camp, MILE = Three Mile, BURRO = Burro-Burro, KABO = Kabocali, CUT = Cutline, and PAK = Pakatau. The methods are abbreviated as follows: DVES = daytime visual encounter surveys, PLOTS = litter plots, NVES = night-time visual encounter surveys, OP = opportunistic collecting.

Camp	Days in camp	Sampling method				Total samples
		DVES	PLOTS	NVES	OP	
MURI	5	2	25	11	6	44
COW	6	2	28	8	6	44
TC	7	6	20	4	8	38
MILE	11	17	36	25	11	89
BURRO	11	14	50	26	9	99
KABO	9	21	36	27	8	92
CUT	6	14	20	11	3	48
PAK	11	22	40	24	9	97

data. We used regression analysis to examine the relationship between the number of individuals (N) and species richness (S). We used log transformations to normalize the data. We compared the slopes of regression lines with analysis of covariance and post-hoc multiple comparisons tests (Zar 1984). The minimum number of individuals collected using all methods at any camp was 50, and we used regression equations to estimate species richness for each camp based on a fixed N of 50.

Linear regression was used to compare how well different methods sampled species. The raw data were transformed to examine the relationship between the log of the number of individuals (N) and the log of species richness (S). We used analysis of covariance to compare slopes and nonparametric multiple comparisons tests to determine how methods differed. We used regression equations to estimate species richness at a fixed N of 16 (the lowest number of individuals obtained by litter plots). We also compared the methods using the number of person hours as a measure of effort instead of the number of individuals collected.

We used EstimateS (Colwell 1997) to generate Coleman curves for our data set. Coleman curves were used to estimate the number of species at each of the eight camps and estimate the number of species detected by the four methods. The number of species per sample was averaged over 100 randomizations to remove the effect of sample order and differences due to the number of individuals collected.

RESULTS

A total of 59 amphibians and 82 reptiles are known from the Iwokrama ecosystem (Appendix). Eight reptile species (4 turtles, 2 lizards, and 1 snake, and the Black Caiman) are known only from observations (i.e., specimens were not taken). Many amphibian species were found at a single camp (> 30% of the total number of species), but 21% of the amphibian species were widespread through the Reserve (Fig. 1). The majority of amphibian species were collected with one or two methods (Fig. 1). Four amphibian species were collected using four or five methods (two bufonids and two leptodactylids). Almost half of the amphibian species were represented in one of the five collections (Fig. 1). *Bufo marinus* and *Leptodactylus bolivianus* were represented in all collections (Appendix).

Most of the reptile species (i.e., snakes) were only found in one camp and were captured with a single method (Fig. 1). Most of the captures were opportunistic (62% of the species captured with a single method were captured opportunistically; Donnelly et al. 2005).

During the herpetological survey (Collection Two), the number of species accumulated increased rapidly through the first 500 individuals. The rate of increase of species addition then slowed considerably, but was still increasing (with over 3000 individual observations; Fig. 2A). In three camps (Burro-Burro, Kabocali and Three Mile, the accumulation curve flattened (data not shown). In the other five camps, the accumulation curve did not flatten (data not shown).

There was a significant positive relationship between the log of the number of individuals and the log of the number of species (Table 3). The slopes of the regression lines varied significantly and four types of lines (high richness [Pakatau, Burro-Burro and Muri Scrub], moderately high richness [Kabocali], moderately low richness [Three Mile and Cutline], and low richness [Cowfly and Third Camp]) were detected by the multiple comparisons analysis. (Table 3).

There was a significant positive relationship between the number of species and the number of individuals for each method. The slopes of the four regression lines vary significantly (Table 4) suggesting that the methods accumulate species at different rates. We also compared method efficiency by plotting the relationship between the number of person hours expended and the number of species obtained by the methods. Relationships between numbers of species obtained by the four methods and numbers of person hours expended for each method were each positive and significant (Table 5). The slopes obtained by litter plots and daytime visual encounter surveys were not different from each other but they differed from the other two methods (Table 5).

We used the entire data set (all individuals observed during the 1997 herpetological survey) to estimate species richness, and the resulting Coleman curve is shown in Fig. 2B. Its shape is different from the raw data (compare panels in Fig. 2). The estimated number of species in the different camps ranges from 16 (in Third camp) to almost 30 (in Pakatau) based on sampling 100 individuals (Fig. 3). The Coleman curves estimated higher species richness based on opportunistic collecting and nocturnal visual encounter surveys than the other two methods for a fixed N of 83 (Fig. 4).

Training activities in 2002 resulted in the addition of two species (*Hamptophryne boliviana* and *Polychrus marmoratus*) to the list of Iwokrama Forest (Appendix). We observed little overlap between the savanna anuran fauna and the forest anuran fauna (Appendix).

DISCUSSION

A total of 141 species are known from the greater Iwokrama ecosystem that includes nine sites in the

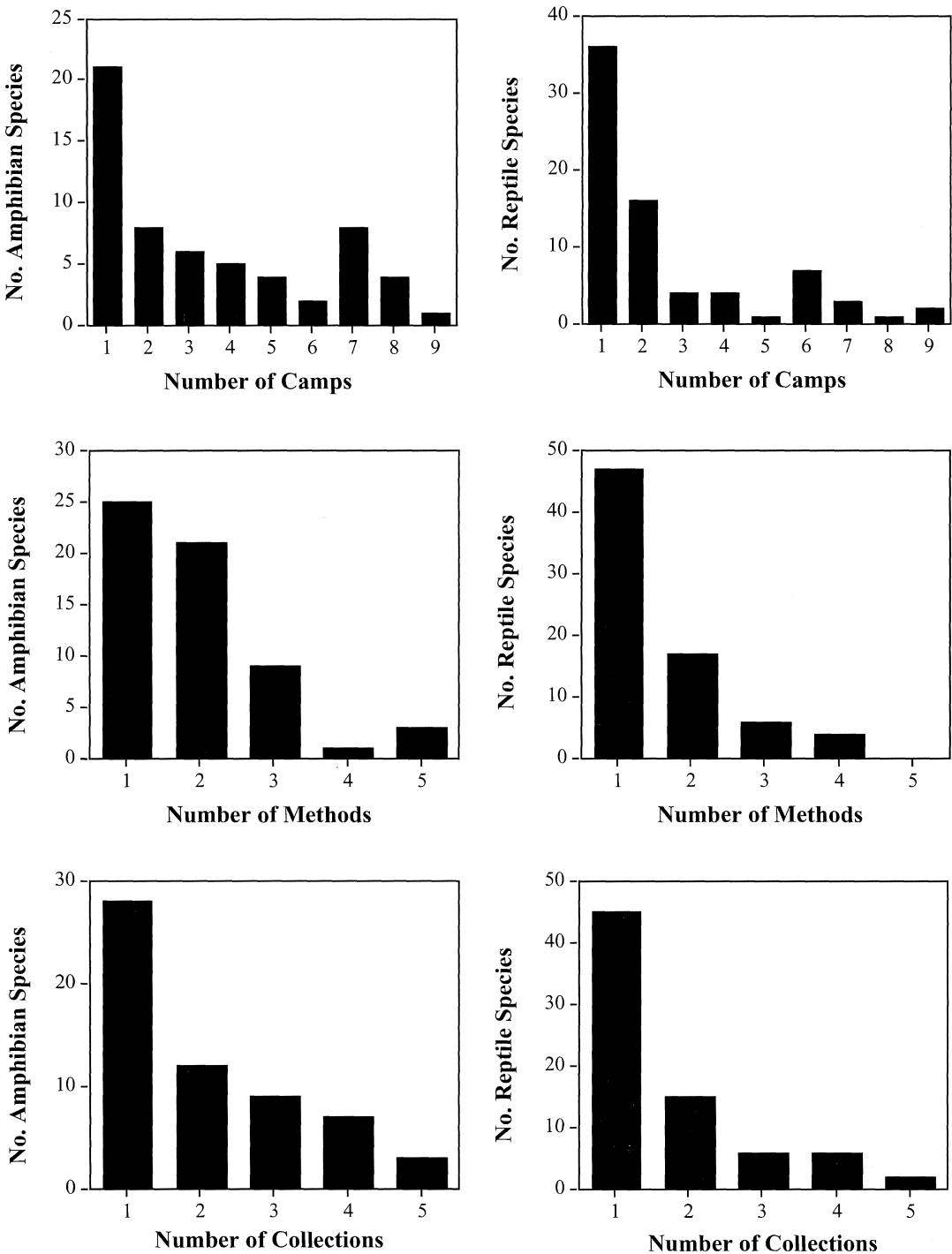


Fig. 1. The number of amphibian and reptile species detected in camps, by methods, and in collections. See text for explanation.

forest and a Rupununi wetland. The composition of the Iwokrama herpetofauna includes widespread species as well as those that are only known from the Guianan region of South America (Donnelly et al. 2005; Hoogmoed 1979a). We have not yet ex-

plored the richness of the canopy herpetofauna and we are certain that the species list for the region will continue to increase with additional research in the region.

Comparisons of species richness across sites and

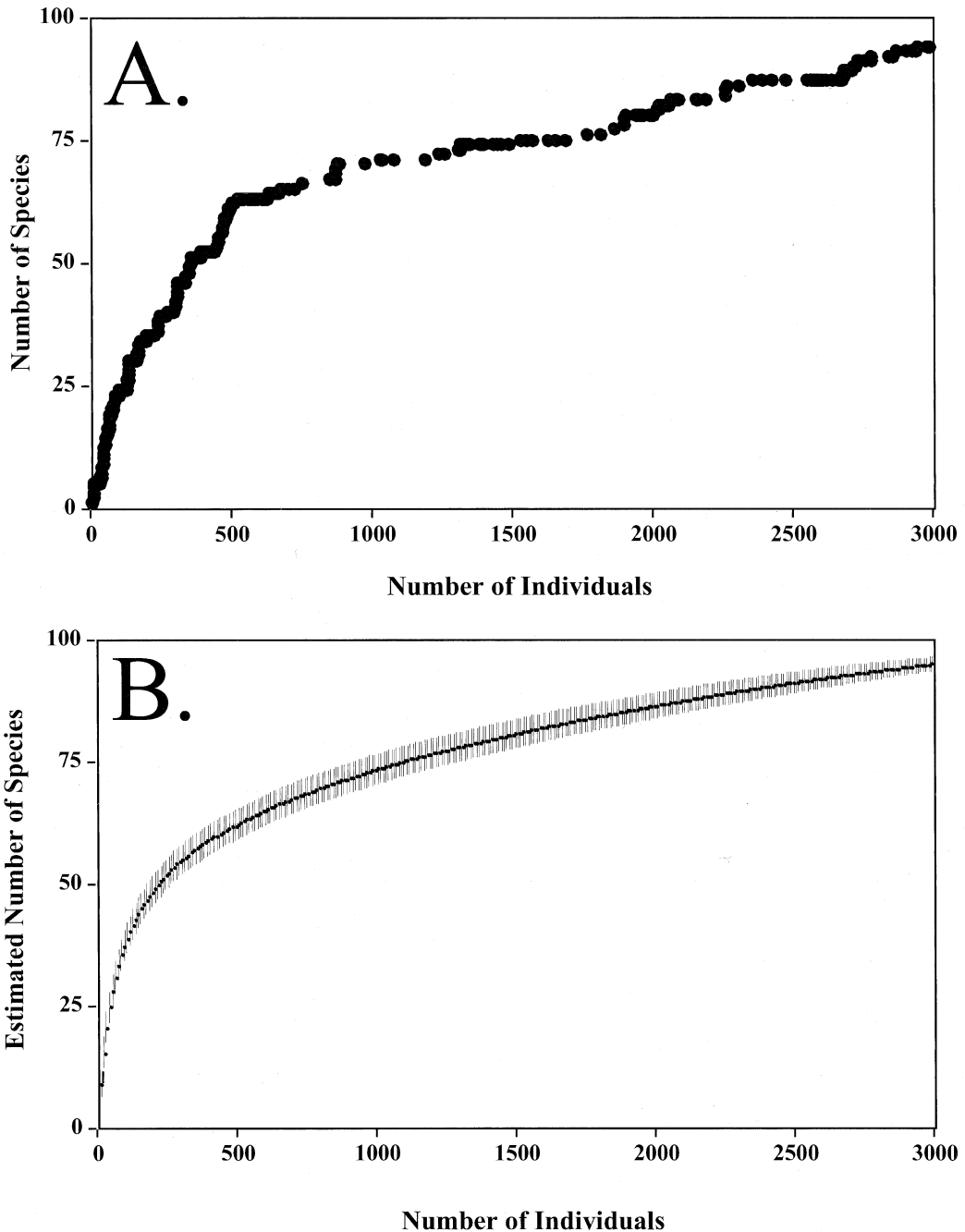


Fig. 2A (above). Species accumulation curve for the 1997 herpetological survey data. All methods and all camps are represented in the data set. Figure 2B (below). Coleman curve for the Iwokrama Forest with data from all camps and sampling methods pooled. Species (\pm one standard deviation) occurrence is averaged over 100 randomizations of the samples from the 1997 herpetological survey. The Coleman curve is an estimate of the expected number of species that would be sampled at a given level of effort (number of individuals).

studies are hampered by a lack of standardization in sampling. Differences in sampling intensity directly affect the number of individuals collected, and therefore can affect the number of taxa detected

(Simberloff 1972). Observed differences in species richness may be the result of either real differences in species richness or sampling artifact (Magurran 1988; Sanders 1968; Simberloff 1972, 1979, Turner

Table 3. Comparison of the relationship between the log of the number of individuals and the log of the number of species among camps. *Italic letters indicate slopes that were significantly different from each other based on nonparametric multiple comparisons tests.* The abbreviation DF = degrees of freedom. The camps are indicated by the following abbreviations: PAK = Pakatau, BUR = Burro-Burro, MURI = Muri Scrub, KABO = Kabocali, MILE = Three Mile, CUT = Cutline, COW = Cowfly, TC = Third Camp.

Camp	Equation	r ²	DF	F	p
PAK	<i>a</i> log(y) = log(0.93) + 0.81*log(x)	0.973	1,19	658.78	<0.01
BUR	<i>a</i> log(y) = log(1.16) + 0.78*log(x)	0.992	1,23	2804.19	<0.01
MURI	<i>a</i> log(y) = log(0.96) + 0.77*log(x)	0.984	1,18	1070.23	<0.01
KABO	<i>b</i> log(y) = log(1.06) + 0.71*log(x)	0.975	1,17	622.55	<0.01
MILE	<i>c</i> log(y) = log(1.31) + 0.67*log(x)	0.987	1,18	1313.77	<0.01
CUT	<i>c</i> log(y) = log(1.91) + 0.62*log(x)	0.988	1,17	1287.05	<0.01
COW	<i>d</i> log(y) = log(1.70) + 0.58*log(x)	0.970	1,17	509.98	<0.01
TC	<i>d</i> log(y) = log(1.69) + 0.54*log(x)	0.969	1,12	344.78	<0.01

and Trexler 1997). While the rate of species accumulation in Iwokrama slowed after the first 500 individuals were collected, the curves suggest that we have not yet discovered all the species of the Iwokrama forest (see Fig. 2).

Species diversity differed across camps based on the 1997 herpetological survey collections. The simulations to generate Coleman curves showed that the species richness patterns across camps did not differ substantially but Third Camp had significantly fewer species than the other seven camps (Fig. 3). Both analyses (regression and simulation) show that Third Camp species richness is lower than it is in the other camps. Scott (1976) describes high diversity at mid-elevation sites but we did not observe this at Third Camp.

We found that the methods differed significantly from each other in accumulating species. Litter plots in the Iwokrama forest were not productive in terms of the number of species discovered. This result agrees with that obtained by Allmon (1994) in Brazilian Amazonia. While this method has been used successfully by herpetologists in Central America (Heinen 1992; Scott 1976; Watling and Donnelly 2002), it is inefficient in some South American sites.

There were species captured in litter plots that were not captured using other methods (Donnelly et al. 2005) so the method should be included when one needs to compile a complete species list. Pearman et al. (1995) suggested that nighttime nocturnal visual encounter surveys provided the most accurate estimate of species richness for an area. We obtained results that suggest nighttime nocturnal visual encounter surveys and opportunistic collecting are efficient in obtaining species, but both methods are biased by observer skills. We recommend that field teams use visual encounter surveys during the day and at night because they are cost effective (in terms of equipment and supplies) and flexible. We also recommend that survey leaders balance field teams according to observer skill and experience.

Our results show that meaningful comparisons of species diversity are only made when effort is standardized. Use of simulation models (Coleman curves) support our observations of differences among methods. Species richness varies across the Iwokrama landscape and ideally, sampling at a site should continue until the species accumulation curve flattens. Simulation studies may be useful in targeting appropriate "stop rules" for designing sur-

Table 4. Comparison of the relationship between the log of the number of individuals and the log of the number of species among methods. *Italic letters indicate slopes that were significantly different from each other based on nonparametric multiple comparisons tests.* The methods are abbreviated as follows: OC = opportunistic collecting, LP = litter plots (quadrat sampling), DVES = daytime visual encounter surveys, NVES = nighttime visual encounter surveys.

Method	Equation	r ²	DF	F	p
OC	<i>a</i> log(y) = log(0.37) + 1.97*log(x)	0.981	1,26	1275.52	<0.01
LP	<i>b</i> log(y) = log(0.79) + 0.87*log(x)	0.987	1,8	520.21	<0.01
DVES	<i>c</i> log(y) = log(1.63) + 0.65*log(x)	0.990	1,19	1763.87	<0.01
NVES	<i>d</i> log(y) = log(2.19) + 0.52*log(x)	0.993	1,41	5804.20	<0.01

Table 5. Comparison of the relationship between the log of the number of individuals and the log of the number of species using the number of person hours. *Italic letters indicate slopes that were significantly different from each other based on nonparametric multiple comparisons tests. The methods are abbreviated as in Table 4.*

Method	Equation	r^2	DF	F	p
OC	<i>a</i> $\log(y) = \log(0.40) + 0.86*\log(x)$	0.941	1,12	340.54	<0.01
LP	<i>a</i> $\log(y) = \log(0.74) + 0.73*\log(x)$	0.950	1,10	172.67	<0.01
DVES	<i>b</i> $\log(y) = \log(2.02) + 0.60*\log(x)$	0.972	1,44	1506.65	<0.01
NVES	<i>b</i> $\log(y) = \log(2.18) + 0.56*\log(x)$	0.964	1,48	1253.36	<0.01

vey protocols. Our results indicate that 11 days is probably not enough time to adequately sample amphibian and reptile diversity in complex tropical forests, therefore care should be made when making conservation recommendations with limited sampling effort.

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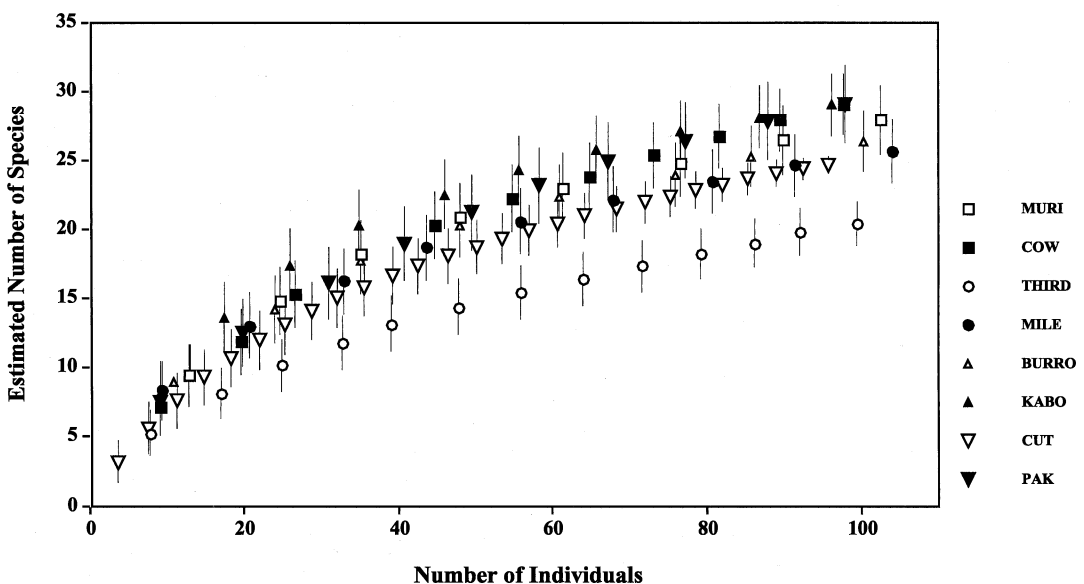


Fig. 3. Coleman curves for localities sampled in the Iwokrama Forest during the 1997 herpetological survey. Species (\pm one standard deviation) occurrence is averaged over 100 randomizations of the samples. The camps are indicated by the following abbreviations: MURI = Muri Scrub, COW = Cowfly, THIRD = Third Camp, MILE = Three Mile, BURRO = Burro-Burro, KABO = Kabocali, CUT = Cutline, and PAK = Pakatau.

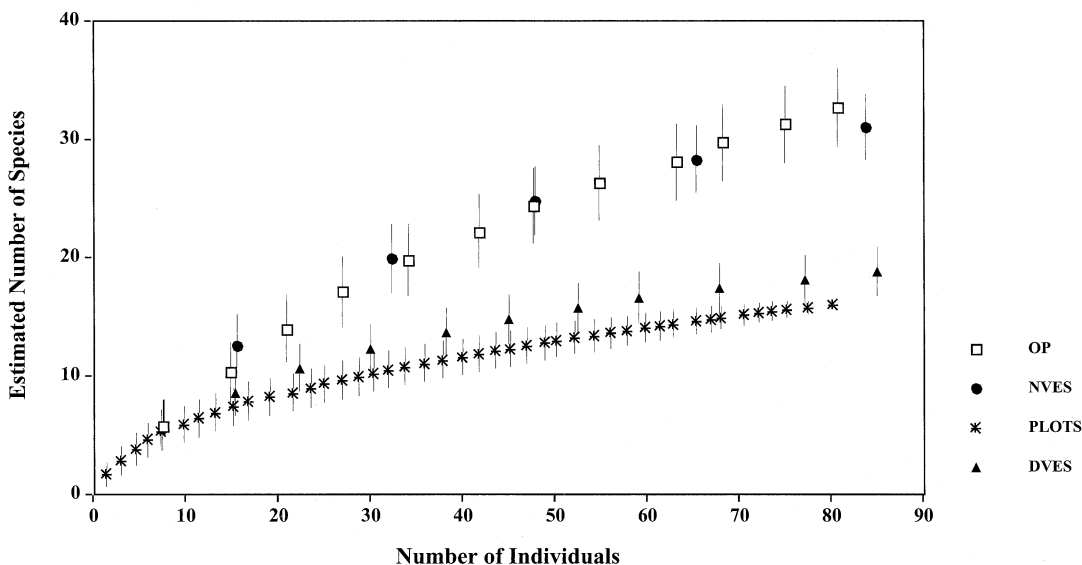


Fig. 4. Coleman curves for methods used to sample the Iwokrama herpetofauna during the 1997 survey. The average species (\pm one standard deviation) occurrence is averaged over 100 randomizations of the samples from the 1997 herpetological survey. The methods are indicated by the following abbreviations: OP = opportunistic collecting, NVES = nighttime visual encounter surveys, PLOTS = litter plots, and DVES = daytime visual encounter surveys.

on the manuscript. This is contribution 81 to the program in Tropical Biology at Florida International University.

LITERATURE CITED

- Allmon, W. D. 1994. A plot study of forest floor litter frogs, Central Amazon, Brazil. *Journal of Tropical Ecology* 7:503–522.
- Beebe, W. 1915. Lizards of the genus *Ameiva* in Bartica District. Notes on their color and pattern variation. *Bulletin of the Museum of Comparative Zoology Harvard* 59:417–479.
- Beebe, W. 1919. The higher vertebrates of British Guiana, Amphibia, Reptilia and Mammalia. *Zoologica* 2:205–227.
- Beebe, W. 1925. Studies of a tropical jungle. One quarter of a square mile of jungle at Kartabo, British Guiana. *Zoologica*, 6:1–193.
- Beebe, W. 1944a. Field notes on the lizards of Kartabo, British Guiana, and Caripito, Venezuela. Part 1. Gekkonidae. *Zoologica* 29:145–159.
- Beebe, W. 1944b. Field notes on the lizards of Kartabo, British Guiana, and Caripito, Venezuela. Part 2. Iguanidae. *Zoologica* 29:195–215.
- Beebe, W. 1945. Field notes on the lizards of Kartabo, British Guiana, and Caripito, Venezuela. Part 3. Teiidae, Amphisbaenidae and Scincidae. *Zoologica* 30:7–32.
- Beebe, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. *Zoologica* 31:11–52.
- Bickford, D. P. 2005. Long-term frog monitoring by local people in Papua New Guinea and the 1997–98 El Niño southern oscillation. In: M. A. Donnelly, B. I. Crother, C. Guyer, M. H. Wake, and M. E. White (eds), *Ecology and evolution in the tropics: a herpetological perspective*. University of Chicago Press, Chicago, IL.
- Boulenger, G. A. 1895a. Description of a new batrachian (*Oreophryne Quelchii*) discovered by Messrs. J. J. Quelch and F. McConnell on the summit of Mount Roraima. *Annals and Magazine of Natural History*, ser. 6,15:521–522.
- Boulenger, G. A. 1895b. Correction to p. 521 ('Annals,' June 1895). *Annals and Magazine of Natural History*, ser. 6,16:125.
- Boulenger, G. A. 1900a. Reptiles, Pages 53–54 + pl. 5 in E. R. Lankester (communicator), Report on a collection made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana. *Transactions of the Linnean Society of London*, 2nd series, *Zoology* 8:51–76.
- Boulenger, G. A. 1900b. Batrachians. Pages 55–56, pl. 5, in E. R. Lankester (communicator), Report on a collection made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana. *Transactions of the Linnean Society of London*, 2nd series, *Zoology*, 8:51–76.
- Campbell, H. W. and S. P. Christman. 1982. Field techniques for herpetofaunal community analysis. In: N.J. Scott, Jr. (ed.). *Herpetological communities*, pp. 193–200. United States Department of the Interior, Fish and Wildlife Service, Wildlife Research Report 13, Washington D.C.
- Chippaux, J-P. 1986. Les serpents de la Guyane française. *Collection Faune Tropicale Paris* 27:1–93.
- Colwell, R. K. 1997. EstimateS. Statistical estimation of species richness and shared species from samples. Version 5.0 (<http://viceroy.eeb.uconn.edu/estimates>).
- Colwell, R. K. and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society London B* 349:1–10.

- sophical Transactions of the Royal Society (Series B) 345:101–118.
- Donnelly, M. A., M. H. Chen, and G. G. Watkins. 2005. The Iwokrama herpetofauna: an exploration of diversity in a Guyanan rainforest. In: M.A. Donnelly, B.I. Crother, C. Guyer, M.H. Wake, and M.E. White (eds), *Ecology and evolution in the tropics: a herpetological perspective*. University of Chicago Press, Chicago, IL.
- Duellman, W. E. 1997. Amphibians of La Escalera region, Southeastern Venezuela: taxonomy, ecology, and biogeography. *Scientific Papers Natural History Museum University of Kansas* 2:1–52.
- Duellman, W. E. 1999. Distribution patterns of amphibians in South America. In: W.E. Duellman (ed.), *Patterns of distribution of amphibians: a global perspective*, pp. 255–328. Johns Hopkins University Press, Baltimore.
- Duellman, W. E. and M. S. Hoogmoed. 1992. Some hylid frogs from the Guiana highlands, northeastern South America: new species, distributional records, and a generic reallocation. *Occasional Papers of the Museum of Natural History University of Kansas*. 147:1–21.
- Duellman, W. E. and M. Yoshpa. 1996. A new species of *Tepuibhyla* (Anura: Hylidae) from Guyana. *Herpetologica* 52:275–281.
- Gasc, J. P. and M. T. Rodrigues. 1980. Liste préliminaire des serpents de la Guyane française. *Bulletin Museum natural Historie Paris*, 4e sér., 2, section A, no 2: 559–598.
- Goin, C. J. 1971. A synopsis of the tree frogs of Suriname. *Annals of the Carnegie Museum* 43:1–23.
- Gorzula, S. and J. C. Señaris. 1999. Contribution to the herpetofauna of the Venezuelan Guayana. I. A data base. *Scientia Guaianae* 8:1–269+129 photographs.
- Heinen, J. T. 1992. Comparisons of the leaf litter herpetofauna in abandoned cacao plantations and primary rain forest in Costa Rica: some implications for faunal restoration. *Biotropica* 24:431–439.
- Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds). 1994. *Measuring and monitoring biological diversity: standard methods for amphibians*. Smithsonian Institution Press, Washington D.C.
- Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds). 2001. *Medición y monitoreo de la diversidad biológica: métodos estandarizados para anfibios*. Smithsonian Institution Press and Editorial Universitaria de la Patagonia, Washington D.C. and Buenos Aires.
- Hoogmoed, M. S. 1979a. The herpetofauna of the Guianan Region. In: W. E. Duellman (ed.), *The South American herpetofauna: its origin, evolution, and dispersal*, pp. 241–279. Monograph of the Museum of Natural History, University of Kansas, Lawrence.
- Hoogmoed, M. S. 1979b. Resurrection of *Hyla ornatissima* Noble (Amphibia, Hylidae) and remarks on related species of green tree frogs from the Guiana Area. Notes on the Herpetofauna of Surinam VI. *Zool. Verhandelingen*. 172:1–46.
- Hoogmoed, M. S. 1980. Revision of the genus *Atractus* in Surinam, with the resurrection of two species (Colubridae, Reptilia). Notes on the Herpetofauna of Surinam VII. *Zoologische Verhandelingen* 175:1–47.
- Hoogmoed, M. S. 1982. Snakes of the Guianan region. *Memorias do Instituto Butantan* 46:219–254.
- Hoogmoed M. S. and T. C. S. Avila-Pires. 1991. Annotated checklist of the herpetofauna of Petit Saut, Sinnamary River, French Guiana. *Zoologische Mededelingen Leiden* 65:63–88.
- Hoogmoed, M. S. and J. Lescure. 1975. An annotated checklist of the lizards of French Guiana, mainly based on two recent collections. *Zoologische Mededelingen Leiden* 49:141–171.
- Lescure, J. 1976. Contribution à l'étude des Amphibiens de Guyane française. VI. Liste préliminaire des Anoures. *Bulletin du Muséum National D'Histoire Naturelle* 3e série, number 377 *Zoologie*:476–524.
- Lescure, J. 1986. Les amphibiens anoures de la forêt Guyanaise (Région de Trois Sauts, Guyane Française). *Mémoires du Muséum National d'Histoire Naturelle. Nouv. Sér.* 132:43–52.
- Lescure, J. and C. Marty. 2001 [2000]. Atlas des amphibiens de Guyana. *Patrimoines Naturels*, 45:388 pp.
- MacCulloch, R. D. and A. Lathrop. 2001. A new species of *Arthrosaura* (Sauria: Teiidae) from the highlands of Guyana. *Caribbean Journal of Science* 37:174–181.
- MacCulloch, R. D. and A. Lathrop. 2002. Exceptional diversity of *Stefania* (Anura: Hylidae) on Mount Ayanagana, Guyana: three new species and new distribution records. *Herpetologica* 58:327–346.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, N.J.
- McDiarmid, R. W. and M. A. Donnelly. 2005. The herpetofauna of the Guayana Highlands: Amphibians and reptiles of the Lost World. In: M.A. Donnelly, B.I. Crother, C. Guyer, M.H. Wake, and M.E. White (eds.), *Ecology and evolution in the tropics: a herpetological perspective*. The University of Chicago Press, Chicago, IL.
- Noonan, B. P. and M. B. Harvey. 2000. A new species of glass frog (Anura: Centrolenidae) from the highlands of Guyana. *Herpetologica* 56:294–302.
- Pearman, P. B., A. M. Velasco, and A. López. 1995. Tropical amphibian monitoring: a comparison of methods for detecting inter-site variation in species' composition. *Herpetologica* 51:325–337.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* 102:243–282.
- Scott, N. J., Jr. 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* 8:41–58.
- Simberloff, D. 1972. Properties of the rarefaction diversity measurement. *American Naturalist* 106:414–418.
- Simberloff, D. 1979. Rarefaction as a distribution-free method of expression and estimating diversity. In: J.F. Grassle, G.P. Patil, W.K. Smith, and C. Taille (eds), *Ecological diversity in theory and practice* pp. 159–176. International Cooperative Publishing House, Fairland.
- Turner, A. M. and J. C. Trexler. 1997. Sampling aquatic invertebrates from marshes: evaluating the options. *Journal of the North American Benthological Society* 16:694–709.
- Watling J. I. and M. A. Donnelly. 2002. Seasonality in reproduction and community composition of leaf litter frogs in a Central American rainforest. *Journal of Zoology (London)* 258:269–276.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice Hall, Englewood Cliffs, N.J.

Appendix (continued)

Taxon	Camps													Methods						Collecting period									
	MS	CF	TC	TM	BB	KA	CL	PA	BC	SUR	TIG	MP	UNK	OP	DVES	NVES	LL	PF	COLL	COLL	1	2	1999	02	BC	O2	SUR		
Frogs & Toads (continued)																													
<i>Phyllomedusa tomopterna</i>																													
<i>Phyllomedusa vaillanti</i>																													
<i>Scinax boesemani</i>																													
<i>Scinax proboscidea</i>																													
<i>Scinax rubra</i>																													
<i>Scinax</i> sp. 1																													
<i>Scinax</i> sp. 2																													
<i>Scinax nebulosa</i>																													
<i>Stefania evansi</i>																													
<i>Adenomera andreae</i>																													
<i>Ceratophrys cornuta</i>																													
<i>Leptodactylus bolivianus</i>																													
<i>Leptodactylus fuscus</i>																													
<i>Leptodactylus knudseni</i>																													
<i>Leptodactylus mystaceus</i>																													
<i>Leptodactylus palliandrostris</i>																													
<i>Leptodactylus petersi</i>																													
<i>Leptodactylus rhodomystax</i>																													
<i>Leptodactylus</i> sp. 1																													
<i>Leptodactylus</i> sp. 2																													
<i>Physalaemus</i> sp.																													
<i>Chiasmocleis</i> sp.																													
<i>Elachistocleis ovalis</i>																													
<i>Haemiphrone boliviana</i>																													
<i>Pipa pipa</i>																													
<i>Rana palmipes</i>																													
Turtles																													
<i>Chelus fimbriatus</i> *																													
<i>Geochelone carbonaria</i> *																													
<i>Geochelone denticulata</i>																													
<i>Platemys platycephala</i>																													
<i>Podocnemis expansa</i> *																													
<i>Podocnemis unifilis</i> *																													
<i>Rhinoclemmys punctularia</i>																													

Appendix (continued)

Taxon	Camps													Methods					Collecting period					
	MS	CF	TC	TM	BB	KA	CL	PA	BC	SUR	TIG	MP	UNK	OP	DVES	NVES	LL	PF	COLL 1	COLL 2	1999	02 BC	O2 SUR	
Lizards																								
<i>Anolis fuscocaudatus</i>																								
<i>Anolis nitens</i>																								
<i>Anolis orthonii</i>																								
<i>Anolis</i> sp. 1																								
<i>Anolis</i> sp. 2																								
<i>Anolis trachyderma</i>																								
<i>Plica umbra</i>																								
<i>Polychrus marmoratus</i>																								
<i>Tropidurus bispidus</i> *																								
<i>Uranoscodon superciliosus</i>																								
<i>Iguana iguana</i> *																								
<i>Colodactylus septentrionalis</i>																								
<i>Gonatodes humeralis</i>																								
<i>Gonatodes</i> sp																								
<i>Pseudogonatodes guianensis</i>																								
<i>Thecadactylus rapicauda</i>																								
<i>Mabuya nigropunctata</i>																								
<i>Ameiva ameiva</i>																								
<i>Bachia flavescens</i>																								
<i>Cercosaura ocellata</i>																								
<i>Cnemidophorus lemniscatus</i>																								
<i>Iphisa elegans</i>																								
<i>Kentropyx calcarata</i>																								
<i>Kentropyx striatus</i>																								
<i>Leposoma guianense</i>																								
<i>Leposoma percarinatum</i>																								
<i>Neusticurus rudis</i>																								
<i>Tupinambis teguixin</i>																								
Amphisbaenian																								
<i>Amphisbaena fuliginosa</i>																								

Appendix (continued)

Taxon	Camps													Methods					Collecting period						
	MS	CF	TC	TM	BB	KA	CL	PA	BC	SUR	TIG	MP	UNK	OP	DVES	NVES	LL	PF	COLL	COLL	2	1999	02 BC	O2 SUR	
Snakes																									
<i>Typhlops reticulatus</i>																									
<i>Anilius scytale</i>																									
<i>Boa constrictor</i>																									
<i>Corallus caninus*</i>																									
<i>Corallus hortulana</i>																									
<i>Epicraterus cenchria</i>																									
<i>Eunectes murinus</i>																									
<i>Atractus flammeigerus</i>																									
<i>Chironomus</i> sp																									
<i>Chironomus fuscus</i>																									
<i>Chironomus scurrulus</i>																									
<i>Dipsas catesbyi</i>																									
<i>Dipsas pavonina</i>																									
<i>Dipsas variegata</i>																									
<i>Drymoluber dichrous</i>																									
<i>Erythrolamprus aesculapii</i>																									
<i>Eunectes murinus</i>																									
<i>Helicops angularis</i>																									
<i>Hydrops mairii callostictus</i>																									
<i>Hydrops triangularis</i>																									
<i>Imantodes cenchoa</i>																									
<i>Leptodeira annulata</i>																									
<i>Leptophis abaelulla</i>																									
<i>Liophis reginae</i>																									
<i>Liophis typhlus</i>																									
<i>Oxybelis aeneus</i>																									
<i>Oxybelis fulgidus</i>																									
<i>Oxyrhopus petola</i>																									
<i>Oxyrhopus trigeminus</i>																									
<i>Pseudoboa coronata</i>																									
<i>Pseudoboa neuwiedi</i>																									
<i>Pseustes poecilonotus</i>																									
<i>Pseustes sulphureus</i>																									
<i>Tantilla melanocephala</i>																									
<i>Tripanurgos compressus</i>																									

Appendix (continued)

Taxon	Camps												Methods					Collecting period					
	MS	CF	TC	TM	BB	KA	CL	PA	BC	SUR	TIG	MP	UNK	OP	DVES	NVES	LL	PF	COLL		1999	02 BC	O2 SUR
													1	2									
Snakes (continued)																							
<i>Bothriopsis bilineata</i>																							
<i>Bothrops atrox</i>	+	+	+	+	+	+	+	+	+	+				+	+	+	+	+	+	+	+	+	+
<i>Lachesis muta</i>																							
<i>Micrurus circumalis</i>					+																		
<i>Micrurus hemprichii</i>					+																		
<i>Micrurus lemniscatus</i>				+																			
<i>Micrurus psυχes</i>					+																		
Crocodiles																							
<i>Caiman crocodilus</i>																							
<i>Palaosuchus palpebrosus</i>																							
<i>Palaosuchus</i> sp.																							
<i>Melanosuchus niger*</i>																							

Species with a * sign after the name were observed but not collected. All other species are represented by observations and specimens (data available from MAD). The camps are indicated by the following abbreviations: MS = Muri Scrub, CF = Cowfly, TC = Third Camp, TM = Three Mile, BB = Burro-Burro, KA = Kabocai, CL = Cutline, PA = Pakatau, BC = Kurupukari Base Camp, SUR = Surama, TIG = Tiger Creek, MP = Maipuri, UNK = unknown. The methods are indicated by the following abbreviations: OP = opportunistic collecting, DVES = daytime visual encounter survey, NVES = nighttime visual encounter survey, LL = leaf litter plots, PF = pitfall traps. Collecting periods are abbreviated as follows: COLL 1 = animals collected in Iwokrama prior to the herpetological surveys (Jan.-Apr., 1997), COLL 2 = animals collected during the herpetological survey (May-July 1997), COLL 3 = animals collected during the 1999 ranger training course, COLL 4 = animals collected during the 2002 ranger training course, and COLL 5 = animals collected in the savannas near Surama.