Mammals of Iwokrama Forest

BURTON K. LIM, MARK D. ENGSTROM

Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada, M5S 2C6

ABSTRACT—As part of a larger project on biodiversity and conservation in Guyana, we documented 130 species of mammals from Iwokrama Forest. This included 7 marsupials, 4 xenarthrans, 86 bats, 5 primates, 8 carnivores, 1 perissodactyl, 4 artiodactyls, and 15 rodents. As is typical for most Neotropical sites, the 86 species of bats represent over half of the mammal diversity. Standardized collecting methods implemented in the 1997 faunal survey of Iwokrama Forest in central Guyana enabled us also to investigate species diversity and abundance resulting from the inventory of mammals. Four species of fruit-eating bats (*Artibeus lituratus*, *A. obscurus*, *A. planirostris*, and *Carollia perspicillata*) were the most abundant and accounted for 43% of the 2,097 total captures in mist nets and harp traps during 79 nights of sampling. For nonvolant mammals, terrestrial spiny rats (*Proechimys* spp.) represented over half (55%) of the 65 captures in primarily live box-style traps. We estimate that our inventory is approximately 70% complete with an additional 57 species of mammals expected to occur in Iwokrama Forest. More specialized field techniques are required to attain a complete inventory of mammals, and long-term monitoring should be established at several sites to study spatial and temporal variation.

INTRODUCTION

The mammals of Guyana are poorly known in comparison with neighbouring countries in northeastern South America. Species diversity and distributions in Guyana have largely been inferred (e.g., Eisenberg, 1989) from inventories of mammals in Venezuela (e.g., Handley, 1976) and Suriname (e.g., Husson, 1978). Since 1990, our surveys of the Iwokrama Forest region in central Guyana have given us the opportunity to provide the first taxonomically comprehensive inventory of mammals for any area in Guyana.

The first thorough documentation of mammalian diversity in Guyana was a checklist by Beebe (1919) wherein he recorded 119 mammal species. Subsequently, known species richness has gradually increased through accounts of new records for Guyana (e.g., Anthony, 1921a; Peterson, 1968; McCarthy & Handley, 1988), collections or updated lists for groups of mammals (e.g., Greenhall, 1959; Smith & Kerry, 1996), and checklists for circumscribed regions in the country (e.g., Anthony, 1921b; Parker et al., 1993). More recently, data on diversity and conservation of mammals in Guyana were summarized by Engstrom & Lim (2002) and there are 225 species of mammals currently documented in the country. This total includes 17 species collected for the first time in Iwokrama Forest and which represented new records for the country (Lim et al., 1999; Lim & Engstrom 2001a).

The objectives of the survey were to document diversity and abundance of species for Iwokrama Forest. The surveys also provide a basis for future biological monitoring programmes. The data collected fill significant gaps in our biological knowledge of mammals in the Guianas. In addition, the work provides a meaningful comparison of the diversity and composition of Guyana's mammalian fauna with that of other Neotropical regions.

METHODS

Study Sites

Iwokrama Forest is located in central Guyana and encompasses 3,600 square kilometers of predominately tropical lowland rainforest (Fig. 1). The northern and eastern limits are formed by the Siparuni and Essequibo Rivers, respectively, with tributaries and headwaters roughly delineating the remaining boundaries. An all-season laterite road bisects Iwokrama Forest in a northeast to southwest direction. The major topographic feature is Iwokrama Mountain in the southeast with an elevation under 1000 m. Our study is based on data accumulated from 13 sites in Iwokrama Forest (Fig. 1; Table 1). They are described in detail by Lim et al. (1999) and Lim & Engstrom (2001a; 2001b).

Methodology

We used a variety of methods to inventory mammals in Iwokrama Forest. These included mist nets, and harp traps to sample bats; snap, live, and pitfall traps to sample nonvolant mammals; and encounter

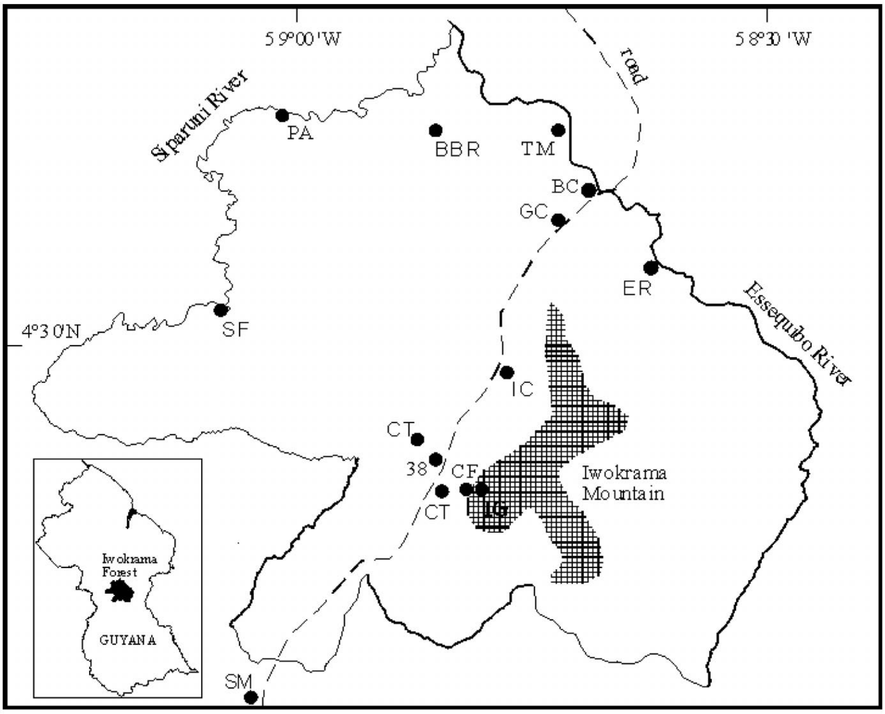

Fig. 1. Map of Iwokrama Forest with study sites as listed in Table 1.

surveys for large and nocturnal mammals. Primary fieldwork was conducted from 7 March to 13 April and 3 October to 21 November 1997 as part of the faunal surveys of Iwokrama Forest. Prior to these intensive surveys, collections had been made in the general vicinity of Iwokrama Forest by the Royal Ontario Museum (ROM) on three separate occasions in October 1990, July 1994, and July 1995 as part of a larger project designed to document the mammalian biodiversity of Guyana. Most of the localities are described in Lim et al. (1999) and Lim & Engstrom (2001a). In addition, a survey of bats of the Kurupukari area was done from 3 July to 8 September 1992 as part of an assessment of local biodiversity by the Open University in England (Smith & Kerry, 1996).

Small nonvolant mammals were trapped along transects at each of the survey sites using trapping stations placed approximately 5 m apart. Trapping stations consisted of either Victor snap-type rat-traps (8.7 cm by 17.5 cm) or collapsible box-type Sherman live traps (8 cm by 9 cm by 23 cm, and 12 cm by 14 cm by 35 cm). At each trapping station, one trap was placed on or secured above the ground (0.25 m to 3.0 m). Traps were preferentially situated near small mammal burrows and runways, and on vines or small branches. They were baited with sunflower seeds, bananas, peanut butter, or suet. Traps were checked daily and the following data were recorded from captured small mammals: reproductive condition, total length, tail length, hind foot length, ear length, and mass.

Wire Tomahawk traps were also used to target larger mammals, such as opossums. They were of two sizes measuring 60 cm by 24 cm by 24 cm, and 100 cm by 50 cm by 50 cm. Up to 10 Tomahawk traps were strategically set on the ground usually near large trees with vines leading up to the crowns to increase the chances of encountering animals. These traps were typically baited with sardines and fruit, when available.

At the Giaconda site we also used a series of plastic-sheet barriers (20–30 cm in height) partially buried in the ground to direct animals to 5-gallon bucket pitfall traps spaced approximately 10 m apart over a distance of 100 m. These traps sampled not only small terrestrial mammals, but also amphibians, reptiles and invertebrates (the latter were not collected as voucher specimens).

We used several types of nets and traps to sample the bat fauna. These included: understory mist nets set to a maximum height of 3 m above the ground with dimensions (length by height) of 12 m by 2.6 m, and 6 m by 2.6 m; large canopy mist nets set to a maximum height of 20 m above the ground and measuring 30.5 m by 9.1 m; and harp traps set to a maximum height of 3 m above the ground with dimensions 1.37 m by 1.70 m. The smaller ground-

Table 1. Localities surveyed in Iwokrama Forest and dates surveyed.

Symbol	Locality
CT	Cattle Trail, 30 to 40 km NE of Surama, 4°20′N 58°51′W to 4°23′N 58°52′W, 70 m; sampled for 6 days on 4–5 and 8–11 October 1990.
SM	Surama Sawmill, 5 km SE of Surama, 4°06′N 59°03′W, 80 m; sampled for 15 days from 17 to 31 July 1994.
IC	Iwokrama Cutline, 25 km SSW of Kurupukari, 4°28′N 58° 47′W; sampled for 9 days from 4 to 12 July 1995.
ER	Essequibo River, 10 km SSE of Kurupukari, 4°35′N 58°37′W; sampled for 6 days from 16 to 21 July 1995.
GC	Giaconda Camp and Three Mile Camp, 5 km SW of Kurupukari, 4°38′N 58°43′W, 75 m; sampled 11 days from 18 to 28 March 1997.
BBR	Burro-Burro River, 25 km WNW of Kurupukari, 4°44′N 58°51′W, 90 m; sampled for 13 days from 30 March to 11 April 1997.
38	38 miles by road from Surama, 35 km SW of Kurupukari, 4°22′N 58° 51′W, 70 m; sampled for 6 days from 3 to 8 October 1997.
CF	Cowfly Camp, 4.6 km on Iwokrama gorge cutline, 35 km SW of Kurupukari, 4°20′N 58° 49′W, 80 m; sampled for 11 days from 9 to 19 October 1997.
IG	Iwokrama Gorge Camp, base of Iwokrama Mt., 35 km SW of Kurupukari, 4°20′N 58°48′W, 150 m; sampled for 6 days from 20 to 25 October 1997.
TM	Turtle Mountain, 10 km NW of Kurupukari on the Essequibo River, 4°44′N 58° 43′W; sampled for 8 days from 30 October to 6 November 1997.
BC	Basecamp (Iwokrama Field Staton), 4°40′N 58°41′W, 70 m, and the vicinity of Kurupukari, 4°40′N 58°40′W, 70 m on the Essequibo R.; sampled by the ROM for 8 days from 19 to 20 October 1990, 13 to 15 July 1995, and 29 March, 12 April and 7 November 1997, and for 26 days between 3 July and 8 September 1992 by the Open University (Smith & Kerry, 1996).
SF	S Falls, 50 km WSW of Kurupukari on the Siparuni R., 4°32′N 59°05′W, 60 m; sampled for 7 days from 10 to 16 November 1997.
PA	Pakatau Falls, 42 km WNW Kurupukari on the Siparuni R., 4°45′N 59°01′W, 90 m; sampled for 14 days from 9 to 17 March and 17 to 21 November 1997.

level nets were set along bat fly-ways and were checked hourly. These nets were situated over small creeks, across trails, and in open areas that were frequented by bats. Two canopy mist nets were used to survey bats flying in the middle to upper canopy of the forest. Two harp traps were set across trails or streams with restricted or funneled fly-ways. Harp traps were used specifically to target bats that tend to avoid mist nets because of their high intensity echolocation calls. The following data were collected from captured bats: reproductive condition, total length, tail length, hind foot length, ear length, tragus length, forearm length, and mass.

During the day, tree hollows and foliage were opportunistically searched for roosting bats. We also carried out visual searches and listened for auditory cues of primates, cats, and other nocturnal and large mammals when in the forest setting or checking traps and nets.

Analyses

The number of species (species richness) is an unweighted measure of species diversity. Diversity indices have been used as a weighted measure for comparison between studies or sites. They incorporate species richness with measures of abundance (evenness or proportionality), and corrected for unequal sample sizes. Simpson's index of concentration or dominance is a commonly used measure of diversity and is a general case of Shannon's index, (Pielou, 1975). We used Simpson's index (SI), expressed as a negative logarithm that increases with the number of species (Simpson, 1949), as a measure of species diversity at the 13 localities sampled in Iwokrama Forest.

$SI = -\ln \Sigma ((n^2 - n)/(N^2 - N))$; where $n =$ the number of individuals for a species, and $N =$ the total number of individuals for all species.

Estimates of relative abundance for mammals in Iwokrama Forest are based on the two faunal survey trips in 1997 because standardized methods were used during these trips to record data, and because similar techniques and numbers of field workers were involved in each period. We present data from mist-netting and harp-trapping of bats, and from the trapping of small nonvolant mammals because these methods were the most quantifiable measures of relative abundance. We used capture and removal methods to collect voucher specimens for subsequent comparisons, ascertain which species are present in an area, and document relative abundance of different trophic guilds at individual localities. We estimated abundance by calculating catch-per-unit-effort (C/E). For nonvolant small mammals, unit-effort was recorded as the number of trap nights, defined as one trap set for one night. For bats, unit-effort was defined as the area (in square metres) of net and/or harp trap used per hour multiplied by 100, which was used as a constant to reduce the number of decimal places in calculations. The only major difference in netting strategies between the two field trips was the length of time the nets were left open. On the March 1997 trip, nets were typically closed by midnight because the first few hours after dusk usually were the times of highest bat activity. On the October 1997 trip, most nets were left open all night and closed at dawn to maximize the number of species caught. This, however, resulted in an increase in unit-effort at relatively non-productive hours (midnight to 0600 h) and a correlated decrease in catch-per-unit-effort.

There are several measures for estimating relative completeness of inventories and species richness (for a review, see Colwell & Coddington, 1994). A simple method is to calculate a species accumulation curve wherein the number of species is plotted against effort, such as the number of survey days. As the number of species recorded approaches the actual number that occurs in the area, the curve reaches an asymptote. Typically, species accumulate quickly in the initial discovery phase of the fieldwork and then are found at a slower rate, often by employing specialized methods of capture and observation.

For extrapolating species richness, Chao-1 is an abundance-based estimator (Chao, 1984) that uses the number of species documented only once (singletons) or twice (doubletons) during our entire study. The estimator assumes that in relatively incomplete inventories a large proportion of species will have been encountered only once or twice, whereas in inventories that approach the actual number of species occurring in the area, most species will have been captured repeatedly. Chao-2 is an incidence-based estimator (Chao, 1987) that uses the number of species documented in only one (uniques) or two (duplicates) of our 13 survey sites. The standard deviation of both estimators was calculated for S^* as originally formulated by Chao (1987) and not the formula in Colwell & Coddington (1994), which has typographical errors (Colwell, 1997). First-order jackknife is another incidence-based estimator that uses the number of species documented in only one sample (Burnham & Overton, 1978; 1979). These species richness extrapolations and associated standard deviations were implemented using the bias-corrected formulas in Estimate*S* version 6.0b1 (Colwell, 1997).

We compared the species of mammals found in Iwokrama Forest with 11 other well-surveyed sites in South and Central America (Fig. 2) to investigate patterns of biogeographic similarity. Our approach was a modification of analyses used by Simmons & Voss (1998), Lim & Engstrom (2001a), and Voss et al. (2002) wherein we combined sites that had complete data for bats and nonvolant mammals. Species by site presence or absence data were used to calculate a pair-wise matrix of Jaccard's similarity coefficients, which was then subjected to UPGMA cluster analysis using NTSYS-pc version 1.8 (Rohlf, 1993).

Specimen Preparation

Smaller species of mammals including bats, rodents, and marsupials comprise about 80% of the total mammal fauna in Guyana (Engstrom & Lim 2002) and many cannot be reliably identified to species without examination of cranial characteristics or comparisons with large series of museum specimens. Moreover, the systematic status of many groups is poorly understood and taxonomically unstable. The state of taxonomy of South American mammals, particularly for Amazonia, is similar to the rudimentary understanding of North American mammals at the turn of the last century wherein both overall biodiversity and degree of regional endemism were underestimated. Although there is not an equivalent to the U.S. Biological Survey which stimulated mammal studies throughout North America, great advances are being made nonetheless by collaboration between national and international researchers from most countries in South America. To obtain realistic estimates of mammalian biodiversity, there is an urgent need to build reference collections of voucher specimens and associated genetic materials for comparative analysis with others regions within the Guianas and South America. Resultant specimens from this project are deposited at the Royal Ontario Museum, University of Kansas, and Centre for the Study of Biological Diversity at the University of Guyana.

RESULTS

Species Richness

A total of 130 species of mammals was recorded from 13 general collecting sites in Iwokrama Forest, and they were represented by a total of 3,322 mammals captured or observed (Table 2; also see Smith & Kerry 1996). The taxonomic composition included 7 species of opossums, 2 anteaters, 2 arma-

Fig. 2. Neotropical lowland rainforest localities that have been extensively surveyed for mammals.

dillos, 86 bats, 5 monkeys, 8 carnivores, 1 tapir, 2 deer, 2 peccaries, and 15 rodents. One hundred and seventeen species of mammals are documented by voucher specimens whereas thirteen other species were observed but not collected.

Pakatau Falls had the highest number of mammal species recorded (64 species represented by 370 specimens) of the 13 collecting sites in Iwokrama Forest (Table 3). It was sampled for 14 days by 5 people (Table 1). The site with the lowest number of species (16 species; 53 specimens) was semi-inundated forest on the Essequibo River about 10 km upstream from Kurupukari. This site was sampled by only one person for six days.

Simpson's Index (SI) for Pakatau Falls was 2.762, which ranked fourth among the sites, whereas Essequibo River had the lowest value at 1.858. The Basecamp-Kurupukari locality had the highest SI at 2.996 and a species richness of 59. Interestingly, the Burro-Burro River Camp had 57 species but had the third lowest SI at 2.514. This locality had a high number of captures of two species of bats (*Artibeus lituratus* and *Pteronotus parnellii*; Table 2), which distorted the species evenness and lowered the SI. Cowfly Camp also had two species (*Artibeus planirostris* and *A. lituratus*) with a high number of captures, and this site had the second lowest SI at 1.993 although it was the sixth highest among the localities in richness (44 species).

Relative Abundance and Capture Rates

Based on the standardized results of the 1997 surveys at Iwokrama Forest, 2097 bats representing 73 species were captured in mist nets and harp traps (Table 2). These captures resulted from 495,136 square metre hours of effort over 79 sampling nights from the nine collecting sites. The number captured included bats that were kept as voucher specimens and those released. The four most abundant species (*Artibeus lituratus*, *A. obscurus*, *A. planirostris*, and *Carollia perspicillata*) were fruit-eating bats and also the only species, along with *Phyllostomus discolor*, *Trachops cirrhosus*, and *Chiroderma trinitatum*, that were caught at all nine localities. The four most abundant species accounted for 43% of the total catch. Twelve species of bats, all of which were insectivores with the exception of one carnivore (*Vam-*

Table 2. Number of individuals of each species (ranked within order) collected or observed at each of the survey sites in Iwokrama Forest, Guyana. See Table 1 for collecting site abbreviations.

Species	Collecting site													
	CT	SM	IC	ER	GC	BB	38	CF	IG	TM	BC	SF	PA	Total
ORDER DIDELPHIMORPHA (opossums)														
Philander opossum	6	3	1								2		3	15
Micoureus demerarae		2	1		1	2						1		7
Marmosa murina		3					1				2			6
Didelphis marsupialis										2			1	3
Monodelphis brevicaudata							1	1				1		3
Marmosa lepida					1								1	2
Marmosops pinheiroi										1				1
ORDER XENARTHRA (anteaters, armadillos, sloths)														
Myrmecophaga tridactyla													1	1
Tamandua tetradactyla										1				1
Dasypus kappleri						1				1			1	3
Priodontes maximus		1												1
ORDER CHIROPTERA (bats)														
Carollia perspicillata	26	47	18	7	56	33	15	22	25	7	54	7	39	356
Artibeus lituratus	1	18	7	1	27	96	8	80	21	20	20	11	39	349
Artibeus obscurus	6	40	7	19	25	61	12	27	3	21	26	15	19	281
Artibeus planirostris	14	39	1	3	7	14	16	118	14	4	10	3	10	253
Pteronotus parnellii		14	5	2	22	85		1		10	13		16	168
Rhinophylla pumilio	4	11	15	1	25	20	13	15	4		15	2	5	130
Ametrida centurio	3	12			3	10	1	4	10		4	9	64	120
Sturnira tildae	3	12	1		17	4		3	15	2	11		19	87
Artibeus gnomus	1	6	6		7	21	4	7	1	3	5	1		64
Artibeus concolor		20	4		10	18	1		3	1	3	1	1	62
Vampyressa bidens		2	4		10	12	1	13	5		3	2	9	61
Carollia brevicauda		2						21	7		27		9	61
Sturnira lilium		50						1	2					53
Lophostoma bidens		1		1	15	22	3			1	3		6	52
Phyllostomus discolor					3	2	1	1	2	2	3	28	4	46
Lophostoma silvicolum	2	3	4	5	6	3	1		1	2	9	2	7	45
Phyllostomus elongatus	6	4	2	2	2	5	1	2	2	4	3		9	42

Table 2. (*continued*)

Species	Collecting site													
	CT	SM	IC	ER	GC	BB	38	CF	IG	TM	BC	SF	PA	Total
Lonchophylla thomasi		5			9	3	2	2		3	9	6	3	42
Uroderma bilobatum	3	20			2	1	2	5	4	1	2			40
Trachops cirrhosus	6	1	4	2	2	6	1	6	1	2	1	1	4	37
Glossophaga soricina		3			4	10	1	3	1	1	8		6	37
Lionycteris spurrelli	1					19	1	4			5		5	35
Artibeus cinereus		31		1			1							33
Saccopteryx bilineata	1	6	2		4	2	4	5	1		5		1	31
Rhynchonycteris naso	1				2	3				9	1	8	6	30
Diclidurus isabellus						14				2		12		28
Chiroderma villosum		2			1	1			3	1	5	3	10	26
Chiroderma trinitatum					3	2	2	4	2	2	7	1	2	25
Vampyrodes caraccioli								20	4					24
Artibeus glaucus	1	7						7	1		5	1		23
Platyrrhinus helleri	1	3			1		1	5	3	2	3	1	3	23
Molossus molossus											20		2	22
Phyllostomus hastatus		4			5	2		1				4	6	22
Chrotopterus auritus	2	1		2	3	3	2	1		1	2	3	1	21
Noctilio albiventris											20			20
Myotis riparius	1	12				1					4			18
Molossus rufus		1			7		7					2		17
Choeroniscus minor		1				2	2				11			16
Mesophylla macconnelli		1			2	3		3			1		4	14
Micronycteris megalotis	1	2			1		1		3	2	1		2	13
Mimon crenulatum		1			3	2				3	1	1	1	12
Cormura brevirostris	4	3					3	1			1			12
Micronycteris minuta		1	4			2			1	1	1	1	1	12
Saccopteryx leptura		1						1		3	3		2	10
Trinycteris nicefori		3						1				2	3	9
Phylloderma stenops			2	1	1		1	1		1	1		1	9
Lophostoma carrikeri					2	5					2			9
Eumops hansae		2					2	1		1	1	1	1	9
Pteronotus personatus					1	1					2		5	9
Desmodus rotundus	1	1	1			3					1		1	8

Table 2. (*continued*)

Species	Collecting site													
	CT	SM	IC	ER	GC	BB	38	CF	IG	TM	BC	SF	PA	Total
Molossops neglectus							8							8
Myotis albescens	2												4	6
Vampyressa brocki					2			1	1		2			6
Anoura geoffroyi									1		5			6
Thyroptera tricolor	1	1						1			2			5
Macrophyllum macrophyllum			4											4
Peropteryx macrotis					1		1	1			1			4
Eumops auripendulus											4			4
Myotis nigricans	1				1								1	3
Micronycteris microtis					1	1					1			3
Centronycteris maximiliani						1							2	3
Cynomops paranus							2					1		3
Pteronotus gymnonotus														2
Saccopteryx canescens														2
Micronycteris brosseti					1									2
Glyphonycteris sylvestris														2
Vampyressa thyone					2	1		2			2	1	1	2
Eptesicus brasiliensis		2												2
Lasiurus atratus					1							1		2
Noctilio leporinus											1		1	2
Diclidurus albus						1								1
Diclidurus ingens						1								1
Peropteryx leucoptera											1			1
Saccopteryx gymnura		1												1
Lonchorhina aurita	1													1
Lampronycteris brachyotis													1	1
Glyphyonycteris daviesi								1						1
Micronycteris hirsuta										1				1
Lophostoma brasiliense						1								1
Lophostoma schulzi			1											1
Vampyrum spectrum						1								1
Diaemus youngi											1			1

Table 2. (*continued*)

Species	Collecting site													
	CT	SM	IC	ER	GC	BB	38	CF	IG	TM	BC	SF	PA	Total
Lasiurus blossevillii					1									1
Cynomops abrasus							1							1
Molossus sp.												1		1
Nyctinomops macrotis							1							1
ORDER PRIMATES (primates)														
Ateles paniscus		1		1	1	1			1	1		1	1	8
Alouatta macconnelli		1	1		1	1			1			1	1	7
Cebus olivaceus											1		1	2
Pithecia pithecia													1	1
Saimiri sciureus						1								1
ORDER CARNIVORA (carnivores)														
Potos flavus					1	6			2	2		1		12
Panthera onca					1		1					1		3
Puma concolor					1								1	2
Pteronura brasiliensis												1	1	2
Puma yagaroundi			1											1
Leopardus wiedii										1				1
Lontra longicaudus								1						1
Bassaricyon beddardi						1								1
ORDER PERISSODACTYLA (odd-toed ungulates)														
Tapirus terrestris	1	1	1			1						1		5
ORDER ARTIODACTYLA (even-toed ungulates)														
Mazama americana		1	1		1				1				1	5
Tayassu pecari						1		2					1	4
Mazama gouazoubira		1				1							1	3
Pecari tajacu									1					1
ORDER RODENTIA (rodents)														
Proechimys cuvieri	11	32	4	1	5	2	10	8	16	1	2	2	1	95
Cuniculus paca	1	1	3	4	1	9	1		1			1	5	27
Makalata didelphoides						17				1		4	3	25
Oryzomys megacephalus	5		1					1	6					13
Oecomys auyantepui		7					1	1					1	10
Oecomys bicolor		2				1						1	5	9

Table 2. (*continued*)

Species	CT	SM	IC	ER	GC	BB	38	CF	IG	TM	BC	SF	PA	Total
	Collecting site													
Dasyprocta leporina		1	1		1		1			1			2	7
Neacomys sp.								2	2					4
Oligoryzomys fulvescens		2									2			4
Proechimys guyannensis		3												3
Sciurus aestuans			1			1								2
Nectomys melanius	2													2
Oecomys rex	1													1
Hydrochoeris hydrochaeris													1	1
Mesomys hispidus		1												1
Totals	121	460	108	53	313	544	139	408	172	125	357	148	370	3322

pyrum spectrum) and one nectarivore (*Anoura geoffroyi*), were each caught only once during the study period (Table 2).

Spatial Variation

The catch-per-unit-effort (C/E) at the Iwokrama Field Station (2.252) near Kurupukari was over three times as high as the next highest value at Pakatau Falls (0.701; Table 3). Collecting at the Field Station, however, was opportunistic and the C/E appeared high because of one unusually productive evening of netting. For this reason, we have not included this locality in the comparison of relative abundance between sites. Because of the different netting strategies employed during the two field trips (nets left open all night during the second trip), the absolute C/E values are only comparable within each trip and each trip must be evaluated separately. During the first trip, the C/E ranged from 0.5036 at Burro-Burro River to 0.7645 at Pakatau Falls, a 50% difference. The C/E ranged from 0.1588 at Turtle Mountain to 0.6433 at Pakatau Falls during the second trip, a 400% difference. The relative abundance of bats among sites was much more variable for the second trip as compared to the first trip.

A total of 65 small nonvolant mammals (rodents and marsupials) representing 8 species were collected by Sherman live traps, Tomahawk live traps, and snap traps during 12,518 trap nights (Tables 2 and 3). The pitfall traps were only used at one site (Giaconda Camp) and did not capture any mammals. Turtle Mountain was the only site with no captures whereas no traps were set at the Iwokrama Field Station. Terrestrial spiny rats (*Proechimys* sp.) accounted for over half (55%) of the captures. The most successful site was Iwokrama Mountain Gorge, which accounted for just over one-third (22) of the total catch and a relative abundance (0.040) that was almost four times greater than the next highest value at 38-Mile Camp (0.011).

Temporal Variation

Our preliminary results for bats indicated that the C/E for the March 1997 trip (0.6127) was almost twice the value for October 1997 (0.3269). Although the nets were usually kept open all night in October to maximize number of species encountered, there were almost as many bats caught during 33 collecting nights in March (1026) as in 45 collecting nights in October (1071). Therefore, the abundance of bats in the March sample was probably higher than that in October and was not simply an artifact of the all-night netting strategy. Many factors may influence the capture rates of bats, such

Table 3. Statistics for the 13 collecting sites in the Iwokrama Forest area including unit effort for netting and trapping bats (square metre hours), catch per unit effort for bats (×100), unit effort for non-bats (trap nights), catch per unit effort for non-bats, number of mammal species collected, and Simpson's Index (-ln) of diversity. The last nine sites were sampled during the 1997 faunal surveys, and the collecting methods were standardized for calculating unit effort. See Table 1 for collecting site abbreviations.

	CT	SM	IC	ER	GC	BB	38	CF	IG	TM	BC	SF	PA	Total
Number of species of mammals	33	59	31	16	53	57	41	44	37	39	59	41	64	130
Simpson's index (-ln)	2.543	2.899	2.754	1.858	2.709	2.514	2.922	1.993	2.744	2.671	2.996	2.719	2.762	3.085
Unit effort for bats (sq m h)					45670	95116	39678	97746	29380	69263	4817	65794	47672	495136
Catch per unit effort for bats (×100)					0.6481	0.5036	0.2949	0.4000	0.4765	0.1588	2.252	0.1854	0.7006	0.4235
Unit effort for non-bats (trap nights)					2654	3507	814	1299	554	388	0	1461	1831	12518
Catch per unit effort for non-bats					0.0019	0.0011	0.0111	0.0100	0.0404	0	0	0.0027	0.0043	0.0052

as seasonality and lunar cycle. Within logistical limits, our methodology was aimed at reducing these effects. Both surveys were conducted during the dry season (Hawkes & Wall, 1993) and averaged 6 weeks in duration, which covered all moon phases.

Results for temporal variation in relative abundance were directly comparable at Pakatau Falls because it was the only site sampled on both trips. The relative abundances for bats at Pakatau Falls for March (0.7648) and November (0.6433) were similar. These data suggest that the apparent higher overall relative abundance in March might result from spatial rather than pronounced temporal variation. At Pakatau Falls in November, nets were left open all night only once, and only a few nets were set that night, so methodologically, relative abundance values were comparable between sampling periods. For individual species of bats, 27 of the 42 species had higher relative abundance values in March than November (Table 4). This shift in relative abundance of several species but similarity of overall abundance between trips is partly explained by the large number of *Ametrida centurio* (51) caught with nets over the Siparuni River in November, increasing the overall abundance value for this trip. Leaving nets open all night might artificially depress capture rates, however, capture rates at Pakatau Falls were noticeably higher than the adjacent camp of S Falls at the same time of year. These camps differed in that tree species diversity, height of canopy, and accessibility of trail systems (which increase the radius of the total area sampled) were all lower at S Falls, indicating that choice of site and variation among habitats also affects capture rates.

The temporal variation in the relative abundance for small nonvolant mammals indicated an opposite trend to that of bats, with values over five times higher for the October trip (0.011) than for the March trip (0.0019). Again this trend may be a sampling artifact because the Iwokrama Mountain Gorge site, where capture rates for small terrestrial mammals were relatively high (0.040), was sampled only in October.

Completeness of Survey

Using our records for all mammals, the Chao-1 estimate of species richness in Iwokrama Forest was 159 species (standard deviation, SD, of 15.6), suggesting that our survey is approximately 82% complete (130 species actually observed and 29 additional species expected). The estimate of Chao-2 was 171 species (SD of 18.7) and for Jackknife-1 was 167 (SD of 5.8). The Chao-1 formula provides a conservative point estimate of species richness and thus should be considered a lower bound (Colwell & Coddington, 1994; Simmons & Voss, 1998). Specifically for bats, the Chao-1 estimate was 99 species (SD of 10.6), suggesting that our bat survey is 87% complete (86 observed, 13 additional species expected). The estimate of Chao-2 was 111 species (SD of 15.8) and for Jackknife-1 was 108 (SD of 4.9). For non-volant mammals, the Chao-1 estimate was 57 species (SD of 11.7), suggesting that this survey is 77% complete (44 observed, 13 additional species). The estimate of Chao-2 for non-volant mammals was also 57 species (SD of 10.6) and for Jackknife-1 was 59 (SD of 4.1).

Another method of estimating total species richness and the completeness of this inventory is to compile a list of species that are likely to occur in Iwokrama Forest using known or inferred geographic distributions. Fifty-seven species known to occur in Guyana (Engstrom & Lim 2002) might also occur in Iwokrama Forest but have not yet been documented in this region (those species indicated by "?" in Table 5). Of these potential species, 24 are bats (for an expected total of 110 species of bats) and 33 are nonvolant mammals for a total of 187 species of mammals that might occur in Iwokrama Forest. These estimates provide a plausible upper bound for the number of species present in this area, and by these expected values the survey is approximately 78% complete for bats and 70% complete for mammals. These estimates are based on potential occurrences of mammals already known to exist in Guyana. The distributions of mammals in the Guianas in general, and in Guyana in particular, are not well understood. Species probably will be found in Iwokrama Forest that are not currently known from the country and this would extend the upper bound of our estimate above 187 species. For example, Lim et al. (1999) and Lim & Engstrom (2001a) recently reported 24 species of bats not previously known from Guyana. Thus, we believe that even the estimate of 187 species is conservative.

Biogeographic Similarity

Not surprisingly, based on a clustering of Jaccard's similarity coefficients for 12 well-surveyed Neotropical bat-collecting localities (Table 6), sites group by geographic proximity (Fig. 3). The sites in the northern Guianan region (Imataca, Iwokrama Forest, Paracou, and Arataye) are similar. Adjacent sites in southern Venezuela and northern Brazil form an eastern Amazonia cluster with the northern Guianan region. Balta, Manu, and Cuzco Amazonico in the western Amazon formed a distinct group subsequently allied with those in eastern Amazonia. Finally the Amazonian lowland sites form a divergent group relative to the bat faunas in Central America to the north (La Selva and Barro Colorado Island). Clearly Iwokrama Forest is representative of the Guianas region at the species level, and is highly diverse.

Table 4. Temporal variation based on number of bats captured and catch per unit effort (C/E: square metre × hour × 100) in mist nets and harp traps for each species during two collecting trips in 1997 to Pakatau Falls, Iwokrama Forest.

	March (33 species)		November (32 species)		Total (42 species)	
Species	#	C/E	#	C/E	Number	C/E
Ametrida centurio	13	0.058	51	0.203	64	0.134251
Artibeus lituratus	9	0.04	30	0.119	39	0.081809
Carollia perspicillata	29	0.129	10	0.04	39	0.081809
Artibeus obscurus	10	0.044	9	0.036	19	0.039856
Sturnira tildae	11	0.049	8	0.032	19	0.039856
Pteronotus parnellii	12	0.053	4	0.016	16	0.033563
Artibeus planirostris	9	0.04	1	0.004	10	0.020977
Chiroderma villosum	6	0.027	4	0.016	10	0.020977
Vampyressa bidens	1	0.004	8	0.032	9	0.018879
Carollia brevicauda	6	0.027	3	0.012	9	0.018879
Phyllostomus elongatus	3	0.013	6	0.024	9	0.018879
Lophostoma silvicolum	5	0.022	2	0.008	7	0.014684
Lophostoma bidens	5	0.022	1	0.004	6	0.012586
Glossophaga soricina	6	0.027		0	6	0.012586
Rhynchonycteris naso	4	0.018	2	0.008	6	0.012586
Phyllostomus hastatus	6	0.027		0	6	0.012586
Rhinophylla pumilio	2	0.009	3	0.012	5	0.010488
Lionycteris spurrelli	4	0.018	1	0.004	5	0.010488
Pteronotus personatus	4	0.018	1	0.004	5	0.010488
Phyllostomus discolor	2	0.009	2	0.008	4	0.008391
Trachops cirrhosus	3	0.013	1	0.004	4	0.008391
Mesophylla macconnelli	3	0.013	1	0.004	4	0.008391
Myotis albescens	4	0.018		0	4	0.008391
Lonchophylla thomasi	1	0.004	2	0.008	3	0.006293
Platyrrhinus helleri	2	0.009	1	0.004	3	0.006293
Trinycteris nicefori	3	0.013		0	3	0.006293
Molossus molossus	2	0.009		0	2	0.004195
Chiroderma trinitatum		0	2	0.008	2	0.004195
Saccopteryx leptura	1	0.004	1	0.004	2	0.004195
Centronycteris maximiliani	2	0.009		0	2	0.004195
Artibeus concolor		0	1	0.004	1	0.002098
Chrotopterus auritus	1	0.004		0	1	0.002098
Saccopteryx bilineata		0	1	0.004	1	0.002098
Mimon crenulatum		0	1	0.004	1	0.002098
Eumops hansae		0	1	0.004	1	0.002098
Micronycteris microtis		0	1	0.004	1	0.002098
Phylloderma stenops		0	1	0.004	1	0.002098
Micronycteris minuta	1	0.004		0	1	0.002098
Desmodus rotundus	1	0.004		0	1	0.002098
Myotis nigricans	1	0.004		0	1	0.002098
Pteronotus gymnonotus		0	1	0.004	1	0.002098
Lampronycteris brachyotis		0	1	0.004	1	0.002098
Totals	172	0.765	162	0.643	334	0.700624
Unit effort (square meters × hours)	22489		25183		47671.8	

Species Accounts of New Bat Records for Guyana

The combination of sustained fieldwork and use of different collecting techniques including large canopy nets, harp traps, and shooting resulted in the documentation of 17 new records of mammal species for Guyana from Iwokrama Forest (see Lim et al., 1999; Lim & Engstrom 2001a). All of these new records are bats, including *Centronycteris maximiliani*, *Diclidurus albus*, *D. ingens*, *D. isabellus*, *Peropteryx leucoptera*, *Saccopteryx gymnura*, *Lampronycteris*

Table 5. Species checklist of 225 mammals recorded from Guyana with 130 species documented from prior surveys (+), 57 potential occurences (?), and 38 species that are probably absent (−) from Iwokrama Forest. CITES appendix listings are indicated for endangered species.

Taxa	Iwokrama Forest	CITES Appendix
ORDER DIDELPHIMORPHA (Total = 16)		
FAMILY DIDELPHIDAE		
SUBFAMILY CALUROMYINAE		
Caluromys lanatus	−	
Caluromys philander	?	
SUBFAMILY DIDELPHINAE		
Chironectes minimus	?	
Didelphis imperfecta	?	
Didelphis marsupialis	+	
Gracilinanus emiliae	−	
Hyladelphys kalinowskii	?	
Lutreolina crassicaudata	−	
Marmosa lepida	+	
Marmosa murina	+	
Marmosops parvidens	?	
Marmosops pinheiroi	+	
Metachirus nudicaudatus	?	
Micoureus demerarae	+	
Monodelphis brevicaudata	+	
Philander opossum	+	
ORDER XENARTHRA (Total = 9)		
FAMILY BRADYPODIDAE		
Bradypus tridactylus	?	
FAMILY MEGALONYCHIDAE		
SUBFAMILY CHOLEOPINAE		
Choloepus didactylus	?	
FAMILY DASYPODIDAE		
SUBFAMILY DASYPODINAE		
Cabassous unicinctus	?	
Dasypus kappleri	+	
Dasypus novemcinctus	?	
Priodontes maximus	+	I
FAMILY MYRMECOPHAGIDAE		
Cyclopes didactylus	?	
Myrmecophaga tridactyla	+	II
Tamandua tetradactyla	+	
ORDER CHIROPTERA (Total = 122)		
FAMILY EMBALLONURIDAE		
Centronycteris maximiliani	+	
Cormura brevirostris	+	
Cyttarops alecto	?	
Diclidurus albus	+	
Diclidurus ingens	+	
Diclidurus isabellus	+	
Diclidurus scutatus	?	
Peropteryx kappleri	?	
Peropteryx leucoptera	+	
Peropteryx macrotis	+	
Rhynchonycteris naso	+	
Saccopteryx bilineata	+	

Table 5. (*continued*)

Taxa	Iwokrama Forest	CITES Appendix
FAMILY EMBALLONURIDAE		
Saccopteryx canescens	+	
Saccopteryx gymnura	+	
Saccopteryx leptura	+	
FAMILY NOCTILIONIDAE		
Noctilio albiventris	+	
Noctilio leporinus	+	
FAMILY MORMOOPIDAE		
Pteronotus gymnonotus	+	
Pteronotus parnellii	+	
Pteronotus personatus	+	
FAMILY PHYLLOSTOMIDAE		
SUBFAMLY PHYLLOSTOMINAE		
Chrotopterus auritus	+	
Glyphonycteris daviesi	+	
Glyphonycteris sylvestris	+	
Lampronycteris brachyotis	+	
Lonchorhina aurita	+	
Lophostoma brasiliense	+	
Lophostoma carrikeri	+	
Lophostoma schulzi	+	
Lophostoma silvicolum	+	
Macrophyllum macrophyllum	+	
Micronycteris brosseti	+	
Micronycteris hirsute	+	
Micronycteris homezi	?	
Micronycteris megalotis	+	
Micronycteris microtis	+	
Micronycteris minuta	+	
Mimon bennettii	–	
Mimon crenulatum	+	
Phylloderma stenops	+	
Phyllostomus discolor	+	
Phyllostomus elongatus	+	
Phyllostomus hastatus	+	
Phyllostomus latifolius	–	
Tonatia saurophila	+	
Trachops cirrhosus	+	
Trinycteris nicefori	+	
Vampyrum spectrum	+	
SUBFAMILY GLOSSOPHAGINAE		
Anoura caudifera	?	
Anoura geoffroyi	+	
Anoura latidens	–	
Choeroniscus godmani	?	
Choeroniscus minor	+	
Glossophaga longirostris	–	
Glossophaga soricina	+	
Lichonycteris obscura	?	
Lionycteris spurrelli	+	
Lonchophylla thomasi	+	
SUBFAMILY CAROLLIINAE		
Carollia brevicauda	+	
Carollia perspicillata	+	
Rhinophylla pumilio	+	

Table 5. (*continued*)

Taxa	Iwokrama Forest	CITES Appendix
SUBFAMILY STENODERMATINAE		
Ametrida centurio	+	
Artibeus amplus	–	
Artibeus cinereus	+	
Artibeus concolor	+	
Artibeus glaucus	+	
Artibeus gnomus	+	
Artibeus lituratus	+	
Artibeus obscurus	+	
Artibeus planirostris	+	
Chiroderma trinitatum	+	
Chiroderma villosum	+	
Mesophylla macconnelli	+	
Platyrrhinus aurarius	–	
Platyrrhinus brachycephalus	–	
Platyrrhinus helleri	+	
Sturnira lilium	+	
Sturnira tildae	+	
Uroderma bilobatum	+	
Uroderma magnirostrum	?	
Vampyressa bidens	+	
Vampyressa brocki	+	
Vampyressa thyone	+	
Vampyrodes caraccioli	+	
SUBFAMILY DESMODONTINAE		
SUBFAMILY VESPERTILIONINAE		
Desmodus rotundus	+	
Diaemus youngi	+	
FAMILY NATALIDAE		
Natalus tumidirostris	?	
FAMILY FURIPTERIDAE		
Furipterus horrens	?	
FAMILY THYROPTERIDAE		
Thyroptera discifera	?	
Thyroptera tricolor	+	
FAMILY VESPERTILIONIDAE		
SUBFAMILY VESPERTILIONINAE		
Eptesicus andinus	?	
Eptesicus brasiliensis	+	
Eptesicus chiriquinus	–	
Eptesicus furinalis	?	
Lasiurus atratus	+	
Lasiurus blossevillii	+	
Lasiurus ega	?	
Myotis albescens	+	
Myotis nigricans	+	
Myotis riparius	+	
Rhogeessa io	?	
FAMILY MOLOSSIDAE		
Cynomops abrasus	+	
Cynomops paranus	+	
Cynomops planirostris	?	
Eumops auripendulus	+	
Eumops bonariensis	?	

Table 5. (*continued*)

Taxa	Iwokrama Forest	CITES Appendix
FAMILY MOLOSSIDAE		
Eumops glaucinus	?	
Eumops hansae	+	
Eumops maurus	?	
Eumops trumbulli	?	
Molossops neglectus	+	
Molossops temminckii	?	
Molossus coibensis	?	
Molossus molossus	+	
Molossus pretiosus	−	
Molossus rufus	+	
Molossus sinaloae	−	
Molossus sp.	+	
Neoplatymops mattogrossensis	−	
Nyctinomops laticaudatus	?	
Nyctinomops macrotis	+	
Promops centralis	−	
Promops nasutus	?	
ORDER PRIMATES (Total = 8)		
FAMILY CALLITRICHIDAE		
Saguinus midas	?	II
FAMILY CEBIDAE		
SUBFAMILY ALOUATTINAE		
Alouatta macconnelli	+	II
SUBFAMILY ATELINAE		
Ateles paniscus	+	II
SUBFAMILY CEBINAE		
Cebus apella	?	II
Cebus olivaceus	+	II
Saimiri sciureus	+	II
SUBFAMILY PITHECIINAE		
Chiropotes satanas	−	II
Pithecia pithecia	+	II
ORDER CARNIVORA (Total = 17)		
FAMILY CANIDAE		
Cerdocyon thous	−	II
Speothos venaticus	?	II
FAMILY FELIDAE		
SUBFAMILY FELINAE		
Puma yaguarondi	+	II
Leopardus pardalis	?	I
Leopardus tigrinus	−	I
Leopardus wiedii	+	I
Puma concolor	+	I
SUBFAMILY PANTHERINAE		
Panthera onca	+	I
FAMILY HERPESTIDAE		
SUBFAMILY HERPESTINAE		
Herpestes javanicus	−	

Table 5. (*continued*)

Taxa	Iwokrama Forest	CITES Appendix
FAMILY MUSTELIDAE		
SUBFAMILY LUTRINAE		
Lontra longicaudis	+	I
Pteronura brasiliensis	+	I
SUBFAMILY MUSTELINAE		
Eira barbara	?	
Galictis vittata	?	
FAMILY PROCYONIDAE		
SUBFAMILY POTOSINAE		
Bassaricyon beddardi	+	
Potos flavus	+	
SUBFAMILY PROCYONINAE		
Nasua nasua	?	
Procyon cancrivorus	?	
ORDER CETACEA (Total = 5)		
FAMILY BALAENIDAE		
Eubalaena australis	–	I
FAMILY DELPHINIDAE		
Delphinus delphis	–	
Globicephala macrorhynchus	–	II
Sotalia fluviatilis	–	I
FAMILY PLATANISTIDAE		
Inia geoffrensis	–	II
ORDER SIRENIA (Total = 2)		
FAMILY TRICHECHIDAE		
Trichechus inunguis	–	I
Trichechus manatus	–	I
ORDER PERISSODACTYLA (Total = 1)		
FAMILY TAPIRIDAE		
Tapirus terrestris	+	II
ORDER ARTIODACTYLA (Total = 5)		
FAMILY TAYASSUIDAE		
Pecari tajacu	+	II
Tayassu pecari	+	II
FAMILY CERVIDAE		
SUBFAMILY CERVINAE		
Mazama americana	+	
Mazama gouazoubira	+	
Odocoileus cariacou	–	
ORDER RODENTIA (Total = 41)		
FAMILY SCIURIDAE		
SUBFAMLY SCIURINAE		
Sciurillus pusillus	?	
Sciurus aestuans	+	
FAMILY MURIDAE		
SUBFAMILY MURINAE		
Mus musculus	–	
Rattus norvegicus	–	
Rattus rattus	–	

Table 5. (*continued*)

Taxa	Iwokrama Forest	CITES Appendix
SUBFAMILY SIGMODONTINAE		
Holochilus sciureus	?	
Neacomys guianae	?	
Neacomys paracou	+	
Nectomys melanius	+	
Neusticomys venezuelae	?	
Oecomy auyantepui	+	
Oecomys bicolor	+	
Oecomys rex	+	
Oecomys roberti	?	
Oecomys rutilus	?	
Oecomys trinitatis	?	
Oligoryzomys fulvescens	+	
Oryzomys macconnelli	?	
Oryzomys megacephalus	+	
Oryzomys yunganus	?	
Podoxymys roraimae	–	
Rhipidomys macconnelli	–	
Rhipidomys nitela	?	
Rhipidomys leucodactylus	?	
Sigmodon alstoni	–	
Zygodontomys brevicauda	–	
FAMILY ERETHIZONTIDAE		
Coendou melanurus	–	
Coendou prehensilis	?	
FAMILY CAVIIDAE		
SUBFAMILY CAVIINAE		
Cavia aperea	–	
FAMILY HYDROCHAERIDAE		
Hydrochoeris hydrochaeris	+	
FAMILY DASYPROCTIDAE		
Dasyprocta leporina	+	
Myoprocta acouchy	?	
FAMILY CUNICULIDAE		
Cuniculus paca	+	
FAMILY ECHIMYIDAE		
SUBFAMILY ECHIMYINAE		
Echimys chrysurus	?	
Isothrix sinnamariensis	–	
Makalata didelphoides	+	
SUBFAMILY EUMYSOPINAE		
Mesomys hispidus	+	
Proechimys cuvieri	+	
Proechimys guyannensis	+	
Proechimys hoplomyoides	–	

brachyotis, *Micronycteris brosseti*, *M. microtis*, *Lophostoma carrikeri*, *Vampyressa thyone*, *Vampyrodes caraccioli*, *Lasiurus atratus*, *Myotis riparius*, *Cynomops paranus*, *Molossops neglectus*, and *Molossus* sp. The following are brief observations and distributional notes on the 17 species recorded for the first time in Guyana during the Iwokrama Forest study.

Two *Centronycteris maximiliani* were netted at approximately 2100 hr on 13 March 1997. They were caught side-by-side about 10 m above the ground

Table 6. Species of mammals reported from 12 Neotropical sites and used in the faunal similarity analysis: (1) La Selva, Costa Rica (n = 117); (2) Barro Colorado Island, Panama (n = 112); (3) Imataca, Venezuela (n = 130); (4) Paracou, French Guiana (n = 141); (5) Arataye, French Guiana (n = 129); (6) Cunucunuma, Venezuela (n = 93); (7) Manaus, Brazil (n = 106); (8) Rio Xingu, Brazil (n = 95); (9) Balta, Peru (n = 130); (10) Manu, Peru (n = 159); (11) Cuzco Amazonico, Peru (n = 103); and (12) Iwokrama Forest, Guyana (n = 130). Modified from Simmons & Voss, 1998; Lim & Engstrom 2001a, and Voss et al. 2001. See Fig. 3 for resultant UPGMA clustering of Jaccard's similarity coefficients.

	Locality											
Species	1	2	3	4	5	6	7	8	9	10	11	12
Caluromys derbianus	1	1	0	0	0	0	0	0	0	0	0	0
Caluromys lanatus	0	0	0	0	0	1	1	0	1	1	1	0
Caluromys philander	0	0	0	1	1	1	1	1	0	0	0	0
Caluromysiops irrupta	0	0	0	0	0	0	0	0	0	1	0	0
Chironectes minimus	1	1	0	1	1	1	0	0	1	0	0	0
Didelphis imperfecta	0	0	1	0	1	0	0	0	0	0	0	0
Didelphis marsupialis	1	1	1	1	1	1	1	1	1	1	1	1
Glironia venusta	0	0	0	0	0	0	0	0	0	1	0	0
Gracilinanus agilis	0	0	0	0	0	0	0	0	1	1	0	0
Gracilinanus emiliae	0	0	0	1	0	0	0	0	0	0	0	0
Hyladelphys kalinowskii	0	0	0	1	0	0	0	0	0	0	0	0
Marmosa lepida	0	0	0	0	1	0	0	0	0	0	0	1
Marmosa mexicana	1	0	0	0	0	0	0	0	0	0	0	0
Marmosa murina	0	0	1	1	1	1	1	1	1	1	1	1
Marmosa robinsoni	0	1	0	0	0	0	0	0	0	0	0	0
Marmosops noctivagus	0	0	0	0	0	0	0	0	1	1	1	0
Marmosops parvidens	0	0	0	1	1	0	1	1	1	1	1	0
Marmosops pinheiroi	0	0	0	0	0	0	0	0	0	0	0	1
Metachirus nudicaudatus	0	1	1	1	1	0	1	1	1	1	1	0
Micoureus demerarae	0	0	1	1	1	1	1	1	0	0	0	1
Micoureus regina	0	0	0	0	0	0	0	0	1	1	1	0
Monodelphis adusta	0	0	0	0	0	0	0	0	0	0	1	0
Monodelphis brevicaudata	0	0	1	1	1	1	1	1	0	0	0	1
Monodelphis glirina	0	0	0	0	0	0	0	0	0	1	0	0
Philander andersoni	0	0	0	0	0	1	0	0	0	0	0	0
Philander mcilhennyi	0	0	0	0	0	0	0	0	1	0	0	0
Philander opossum	1	1	1	1	1	0	1	1	1	1	1	1
Bradypus tridactylus	0	0	1	1	1	0	1	0	0	0	0	0
Bradypus variegatus	1	1	0	0	0	0	0	1	1	1	1	0
Choloepus didactylus	0	0	1	1	1	1	1	1	0	0	0	0
Choloepus hoffmanni	1	1	0	0	0	0	0	0	1	1	1	0
Cabassous centralis	1	1	0	0	0	0	0	0	0	0	0	0
Cabassous unicinctus	0	0	1	1	0	0	0	0	1	0	0	0
Dasypus kappleri	0	0	1	1	1	1	1	0	1	0	0	1
Dasypus novemcinctus	1	1	1	1	1	1	1	1	1	1	1	0
Priodontes maximus	0	0	1	1	1	1	1	0	1	1	0	1
Cyclopes didactylus	1	1	0	1	1	1	1	0	1	1	0	0
Myrmecophaga tridactyla	1	0	1	1	1	1	1	0	1	1	1	1
Tamandua mexicana	1	1	0	0	0	0	0	0	0	0	0	0
Tamandua tetradactyla	0	0	1	1	1	1	1	1	1	1	1	1
Centronycteris centralis	1	1	0	0	0	0	0	0	0	0	0	0
Centronycteris maximiliani	0	0	0	1	0	0	1	0	0	0	0	1
Cormura brevirostris	1	1	1	1	1	1	1	0	0	1	0	1
Cyttarops alecto	1	0	0	0	0	0	0	0	0	0	0	0
Diclidurus albus	1	1	1	0	0	0	1	0	0	0	0	1
Diclidurus ingens	0	0	0	0	0	0	0	0	0	0	0	1
Diclidurus isabellus	0	0	0	0	0	0	0	0	0	0	0	1
Diclidurus scutatus	0	0	1	1	1	0	0	0	0	0	0	0
Peropteryx kappleri	1	0	1	1	0	0	0	0	0	1	0	0
Peropteryx leucoptera	0	0	0	1	0	0	1	0	0	0	1	1

Table 6. (*continued*)

	Locality											
Species	1	2	3	4	5	6	7	8	9	10	11	12
Peropteryx macrotis	0	0	1	1	1	1	1	1	0	0	0	1
Rhynchonycteris naso	1	1	1	1	1	1	1	1	1	1	1	1
Saccopteryx bilineata	1	1	1	1	1	1	1	1	1	1	1	1
Saccopteryx canescens	0	0	1	0	0	0	0	1	0	0	0	1
Saccopteryx gymnura	0	0	0	1	0	0	0	0	0	0	0	1
Saccopteryx leptura	1	1	1	1	1	1	1	1	1	1	1	1
Noctilio albiventris	1	1	1	1	0	0	1	1	1	1	1	1
Noctilio leporinus	1	1	1	1	0	1	1	0	0	1	0	1
Mormoops megalophylla	0	0	0	1	0	0	0	0	0	0	0	0
Pteronotus davyi	1	0	0	0	0	0	0	0	0	0	0	0
Pteronotus gymnonotus	0	1	0	0	0	0	0	0	0	0	0	1
Pteronotus parnellii	1	1	1	1	1	1	1	1	0	0	0	1
Pteronotus personatus	0	0	0	0	0	0	0	0	0	0	0	1
Chrotopterus auritus	1	1	1	1	1	1	0	1	0	1	1	1
Glyphonycteris daviesi	1	0	1	1	0	0	0	1	0	0	0	1
Glyphonycteris sylvestris	0	0	0	1	1	0	0	1	0	0	0	1
Lampronycteris brachyotis	1	1	0	0	0	0	0	0	0	1	0	1
Lonchorhina aurita	0	0	0	0	0	0	0	0	0	0	0	1
Lonchorhina sp. nov.	0	0	1	0	1	1	0	0	0	0	0	0
Lophostoma brasiliense	1	1	1	1	0	0	0	1	1	1	0	1
Lophostoma carrikeri	0	0	0	1	0	0	0	0	1	0	0	1
Lophostoma schulzi	0	0	0	1	1	0	0	0	0	0	0	1
Lophostoma silvicolum	1	1	1	1	1	1	1	1	1	1	1	1
Macrophyllum macrophyllum	1	1	1	1	1	1	1	1	1	1	0	1
Micronycteris brosseti	0	0	0	1	0	0	0	0	0	0	0	1
Micronycteris hirsuta	1	1	0	1	0	0	0	0	0	1	0	1
Micronycteris homezi	0	0	0	1	0	0	0	0	0	0	0	0
Micronycteris megalotis	0	0	1	1	1	1	1	1	1	1	1	1
Micronycteris microtis	1	1	1	1	1	1	0	0	0	0	0	1
Micronycteris minuta	1	0	1	1	0	0	0	0	0	1	1	1
Micronycteris schmidtorum	1	1	0	1	0	1	0	0	0	1	0	0
Mimon bennettii	0	0	0	1	1	0	0	0	0	0	0	0
Mimon cozumelae	1	0	0	0	0	0	0	0	0	0	0	0
Mimon crenulatum	1	1	1	1	1	0	1	0	1	1	1	1
Phylloderma stenops	1	1	1	1	1	1	0	0	0	1	0	1
Phyllostomus discolor	1	1	1	1	1	0	1	1	0	0	0	1
Phyllostomus elongatus	0	0	1	1	1	1	1	1	1	1	1	1
Phyllostomus hastatus	1	1	1	1	1	1	1	1	1	1	1	1
Phyllostomus latifolius	0	0	0	0	1	0	0	0	0	0	0	0
Tonatia saurophila	1	1	1	1	1	0	1	1	1	1	0	1
Trachops cirrhosis	1	1	1	1	1	0	1	1	1	1	1	1
Trinycteris nicefori	1	1	1	1	1	0	1	1	1	0	0	1
Vampyrum spectrum	1	1	1	1	1	0	1	0	0	1	1	1
Anoura caudifera	0	0	0	1	1	1	1	1	1	1	0	0
Anoura cultrata	0	0	0	0	0	0	0	0	0	1	0	0
Anoura geoffroyi	0	0	1	0	1	0	0	0	1	1	0	1
Anoura latidens	0	0	1	0	0	0	0	0	0	0	0	0
Anoura sp. nov.	0	0	0	0	0	0	0	0	0	1	0	0
Choeroniscus godmani	1	0	1	0	0	0	0	0	0	1	0	0
Choeroniscus minor	0	0	1	1	1	0	1	1	1	1	1	1
Glossophaga commissarisi	1	1	0	0	0	0	0	0	0	1	0	0
Glossophaga soricina	1	1	1	1	1	1	1	1	1	1	1	1
Hylonycteris underwoodi	1	0	0	0	0	0	0	0	0	0	0	0
Lichonycteris obscura	1	0	1	1	1	0	1	0	0	0	0	0
Lionycteris spurrelli	0	0	1	0	1	1	0	0	0	1	0	1

Table 6. (*continued*)

Species	Locality											
	1	2	3	4	5	6	7	8	9	10	11	12
Lonchophylla robusta	1	1	0	0	0	0	0	0	0	0	0	0
Lonchophylla thomasi	0	0	1	1	1	0	1	1	1	1	1	1
Scleronycteris ega	0	0	0	0	0	1	0	0	0	0	0	0
Carollia brevicauda	1	1	1	0	1	1	1	0	1	1	1	1
Carollia castanea	1	1	0	0	0	0	0	0	1	1	1	0
Carollia perspicillata	1	1	1	1	1	1	1	1	1	1	1	1
Carollia sp. nov.	0	0	0	0	0	0	0	0	0	0	1	0
Rhinophylla fischerae	0	0	0	0	0	0	0	1	0	0	0	0
Rhinophylla pumilio	0	0	1	1	1	1	1	1	1	1	1	1
Ametrida centurio	0	1	1	1	1	1	1	0	0	0	0	1
Artibeus amplus	0	0	0	0	0	1	0	0	0	0	0	0
Artibeus anderseni	0	0	0	0	0	0	0	0	1	1	1	0
Artibeus cinereus	0	0	1	1	0	0	1	1	1	1	1	1
Artibeus concolor	0	0	1	1	1	1	1	1	1	0	0	1
Artibeus glaucus	0	0	1	0	0	1	0	0	0	1	0	1
Artibeus gnomus	0	0	1	1	1	1	0	1	0	1	0	1
Artibeus jamaicensis	1	1	0	0	0	0	0	0	0	0	0	0
Artibeus lituratus	1	1	1	1	1	1	1	1	1	1	1	1
Artibeus obscurus	0	0	1	1	1	1	0	1	1	1	1	1
Artibeus phaeotis	1	1	0	0	0	0	0	0	0	0	0	0
Artibeus planirostris	0	0	1	1	1	1	1	1	1	1	1	1
Artibeus watsoni	1	1	0	0	0	0	0	0	0	0	0	0
Centurio senex	0	1	0	0	0	0	0	0	0	0	0	0
Chiroderma salvini	0	0	0	0	0	0	0	0	0	1	1	0
Chiroderma trinitatum	0	0	1	1	1	1	1	0	1	1	0	1
Chiroderma villosum	1	1	1	1	1	1	0	1	1	1	1	1
Ectophylla alba	1	0	0	0	0	0	0	0	0	0	0	0
Enchisthenes hartii	0	1	0	0	0	0	0	0	0	1	0	0
Mesophylla macconnelli	0	1	1	1	1	1	1	1	1	1	1	1
Platyrrhinus brachycephalus	0	0	1	0	0	0	0	0	1	1	0	0
Platyrrhinus dorsalis	0	0	0	0	0	0	0	0	0	1	0	0
Platyrrhinus helleri	1	1	1	1	1	1	1	1	1	1	1	1
Platyrrhinus infuscus	0	0	0	0	0	0	0	0	1	1	1	0
Platyrrhinus lineatus	0	0	0	0	0	0	0	0	0	1	0	0
Sphaeronycteris toxophyllum	0	0	0	0	0	0	0	0	0	1	0	0
Sturnira erythromos	0	0	0	0	0	0	0	0	0	1	0	0
Sturnira lilium	1	0	1	1	1	1	1	1	1	1	1	1
Sturnira ludovici	1	0	0	0	0	0	0	0	0	0	0	0
Sturnira luisi	0	1	0	0	0	0	0	0	0	0	0	0
Sturnira magna	0	0	0	0	0	0	0	0	0	1	0	0
Sturnira oporaphilum	0	0	0	0	0	0	0	0	0	1	0	0
Sturnira tildae	0	0	1	1	1	1	0	1	1	1	1	1
Uroderma bilobatum	1	1	1	1	1	1	1	1	1	1	1	1
Uroderma magnirostrum	0	1	1	0	0	0	1	1	1	1	1	0
Vampyressa bidens	0	0	1	0	0	1	0	0	1	1	0	1
Vampyressa brocki	0	0	0	1	1	0	0	1	0	0	0	1
Vampyressa melissa	0	0	0	0	0	0	0	0	0	1	0	0
Vampyressa nymphaea	1	1	0	0	0	0	0	0	0	0	0	0
Vampyress thyone	1	1	1	0	0	0	0	0	1	1	1	1
Vampyrodes caraccioli	1	1	1	0	0	1	0	0	1	1	0	1
Desmodus rotundus	1	1	1	1	1	1	1	1	1	1	1	1
Diaemus youngi	0	0	0	1	0	0	0	0	0	0	0	1
Diphylla ecaudata	0	0	0	0	0	0	0	1	0	1	0	0
Natalus stramineus	0	1	0	0	0	0	0	0	0	0	0	0
Furipterus horrens	1	0	0	1	0	1	0	1	0	1	0	0

Table 6. (*continued*)

	Locality											
Species	1	2	3	4	5	6	7	8	9	10	11	12
Thyroptera discifera	0	1	0	0	0	0	0	0	0	0	0	0
Thyroptera tricolor	1	1	1	1	1	1	1	0	1	1	1	1
Eptesicus brasiliensis	0	0	1	0	0	1	1	0	1	1	1	1
Eptesicus chiriquinus	1	0	1	1	0	0	0	0	0	0	0	0
Eptesicus furinalis	1	1	1	1	0	0	0	0	1	1	0	0
Eptesicus melanopterus	0	0	0	0	0	0	1	0	0	0	0	0
Lasiurus atratus	0	0	1	0	0	0	0	0	0	0	0	1
Lasiurus blossevillii	0	0	0	1	0	0	1	0	1	0	0	1
Lasiurus ega	0	0	0	0	0	0	0	0	1	1	1	0
Myotis albescens	1	1	0	0	0	1	1	1	1	1	1	1
Myotis elegans	1	0	0	0	0	0	0	0	0	0	0	0
Myotis keaysi	0	0	0	0	0	0	0	0	0	1	0	0
Myotis nigricans	1	1	1	1	1	1	1	0	1	1	1	1
Myotis riparius	1	1	1	1	1	0	0	1	1	1	1	1
Myotis simus	0	0	0	0	0	0	0	0	1	1	0	0
Rhogeessa io	1	1	0	0	0	0	0	0	0	0	0	0
Cynomops abrasus	0	0	1	1	0	0	1	0	1	0	0	1
Cynomops greenhalli	0	0	1	0	1	0	0	0	1	0	0	0
Cynomops paranus	0	0	1	1	1	0	0	0	0	0	0	1
Cynomops planirostris	0	0	0	0	1	0	0	0	0	0	0	0
Eumops auripendulus	0	1	1	1	0	0	0	0	0	0	0	1
Eumops hansae	0	0	1	1	1	0	0	0	0	0	0	1
Eumops trumbulli	0	0	0	0	0	0	1	0	0	0	0	0
Molossops neglectus	0	0	1	0	0	0	0	0	0	0	0	1
Molossus barnesi	0	0	0	1	0	0	0	0	0	0	0	0
Molossus bondae	1	1	0	0	0	0	0	0	0	0	0	0
Molossus coibensis	0	1	0	0	0	0	0	0	0	0	0	0
Molossus molossus	0	1	1	1	1	1	1	0	1	1	1	1
Molossus rufus	0	0	1	1	1	1	1	0	0	0	0	1
Molossus sinaloae	1	1	0	1	0	0	0	0	0	0	0	0
Molossus sp.	0	0	0	0	0	0	0	0	0	0	0	1
Neoplatymops mattogrossensis	0	0	0	0	0	0	0	1	0	0	0	0
Nyctinomops laticaudatus	0	1	1	0	1	1	0	0	0	1	0	0
Nyctinomops macrotis	0	0	0	0	0	0	0	0	0	0	0	1
Promops centralis	0	0	0	1	0	0	0	0	0	0	0	0
Callimico goeldii	0	0	0	0	0	0	0	0	0	1	0	0
Callitrix pygmaea	0	0	0	0	0	0	0	0	0	1	0	0
Saguinus fuscicollis	0	0	0	0	0	0	0	0	0	1	1	0
Saguinus imperator	0	0	0	0	0	0	0	0	1	1	0	0
Saguinus midas	0	0	0	1	1	0	1	0	0	0	0	0
Saguinus niger	0	0	0	0	0	0	0	1	0	0	0	0
Saguinus oedipus	0	1	0	0	0	0	0	0	0	0	0	0
Alouatta belzebul	0	0	0	0	0	0	0	1	0	0	0	0
Alouatta macconnelli	0	0	1	1	1	1	1	0	1	1	1	1
Alouatta palliata	1	1	0	0	0	0	0	0	0	0	0	0
Aotus infulatus	0	0	0	0	0	0	0	1	0	0	0	0
Aotus lemurinus	1	1	0	0	0	0	0	0	0	0	0	0
Aotus nigriceps	0	0	0	0	0	0	0	0	1	1	1	0
Aotus trivirgatus	0	0	0	0	0	1	0	0	0	0	0	0
Ateles chamek	0	0	0	0	0	0	0	0	1	1	0	0
Ateles geoffroyi	1	0	0	0	0	0	0	0	0	0	0	0
Ateles paniscus	0	0	0	1	1	0	1	0	0	0	0	1
Callicebus brunneus	0	0	0	0	0	0	0	0	0	1	0	0
Callicebus cupreus	0	0	0	0	0	0	0	0	1	0	0	0
Callicebus moloch	0	0	0	0	0	0	0	1	0	0	0	0

Table 6. (*continued*)

Species	Locality											
	1	2	3	4	5	6	7	8	9	10	11	12
Callicebus torquatus	0	0	0	0	0	1	0	0	0	0	0	0
Cebus albifrons	0	0	0	0	0	0	0	0	1	1	1	0
Cebus apella	0	0	0	1	1	0	1	1	1	1	1	0
Cebus capucinus	1	1	0	0	0	0	0	0	0	0	0	0
Cebus olivaceus	0	0	1	0	1	1	0	0	0	0	0	1
Chiropotes satanas	0	0	0	0	0	1	1	1	0	0	0	0
Lagothrix lagotricha	0	0	0	0	0	0	0	0	1	1	1	0
Pithecia irrorata	0	0	0	0	0	0	0	0	0	1	0	0
Pithecia monachus	0	0	0	0	0	0	0	0	1	0	0	0
Pithecia pithecia	0	0	1	1	1	1	1	0	0	0	0	1
Saimiri boliviensis	0	0	0	0	0	0	0	0	1	1	1	0
Saimiri sciureus	0	0	0	1	1	1	0	1	0	0	0	1
Atelocynus microtis	0	0	0	0	0	0	0	0	1	1	1	0
Speothos venaticus	0	0	1	1	1	0	1	0	1	0	0	0
Herpailurus yaguarondi	1	1	1	1	1	0	0	0	1	1	1	1
Leopardus pardalis	1	1	1	1	1	1	1	0	1	1	1	0
Leopardus tigrinus	0	0	1	0	1	0	0	0	0	0	0	0
Leopardus wiedii	1	1	1	1	1	1	0	0	1	1	0	1
Panthera onca	1	1	1	1	1	0	1	0	1	1	1	1
Puma concolor	1	1	1	1	1	0	1	0	1	1	1	1
Conepatus semistriatus	1	0	0	0	0	0	0	0	0	0	0	0
Eira barbara	1	1	1	1	1	1	1	0	1	1	1	0
Galictis vittata	1	1	0	1	1	0	0	0	1	1	1	0
Lontra longicaudis	1	1	1	0	1	1	1	0	1	1	1	1
Mustela spp.	1	0	0	0	0	0	0	0	0	0	1	0
Pteronura brasiliensis	0	0	1	0	1	0	0	0	1	1	1	1
Bassaricyon beddardi	0	0	0	0	0	0	0	0	0	0	0	1
Bassaricyon gabbii	1	1	0	0	0	0	0	0	1	1	0	0
Bassariscus sumichrasti	0	1	0	0	0	0	0	0	0	0	0	0
Nasua narica	1	1	0	0	0	0	0	0	0	0	0	0
Nasua nasua	0	0	1	1	1	1	1	1	1	1	0	0
Potos flavus	1	1	1	1	1	1	1	1	1	1	1	1
Procyon cancrivorus	0	1	0	0	0	0	0	0	1	1	0	0
Procyon lotor	1	0	0	0	0	0	0	0	0	0	0	0
Tapirus bairdii	1	1	0	0	0	0	0	0	0	0	0	0
Tapirus terrestris	0	0	1	1	1	1	1	1	1	1	1	1
Pecari tajacu	1	1	1	1	1	0	1	1	1	1	1	1
Tayassu pecari	1	1	1	1	1	1	1	0	1	1	1	1
Mazama americana	1	1	1	1	1	1	1	1	1	1	1	1
Mazama gouazoubira	0	0	0	1	1	0	1	0	0	1	0	1
Odocoileus cariacou	1	1	0	0	0	0	0	0	0	0	0	0
Microsciurus alfari	1	1	0	0	0	0	0	0	0	0	0	0
Microsciurus flaviventer	0	0	0	0	0	0	0	0	0	1	0	0
Sciurillus pusillus	0	0	0	1	1	0	0	0	0	0	0	0
Sciurus aestuans	0	0	1	1	1	0	0	0	0	0	0	1
Sciurus gilvigularis	0	0	0	0	0	0	1	1	0	0	0	0
Sciurus granatensis	1	1	0	0	0	0	0	0	0	0	0	0
Sciurus ignitus	0	0	0	0	0	0	0	0	1	1	1	0
Sciurus igniventris	0	0	0	0	0	1	0	0	0	0	0	0
Sciurus spadiceus	0	0	0	0	0	0	0	0	1	1	1	0
Sciurus variegatoides	1	0	0	0	0	0	0	0	0	0	0	0
Orthogeomys cherrei	1	0	0	0	0	0	0	0	0	0	0	0
Heteromys desmarestianus	1	1	0	0	0	0	0	0	0	0	0	0
Melanomys caliginosus	1	0	0	0	0	0	0	0	0	0	0	0
Neacomys spp.	0	0	1	1	1	1	1	1	1	1	1	1

Table 6. (*continued*)

	Locality											
Species	1	2	3	4	5	6	7	8	9	10	11	12
Nectomys spp.	0	0	1	1	1	1	1	1	1	1	1	1
Neusticomys oyapocki	0	0	0	1	0	0	0	0	0	0	0	0
Neusticomys peruviensis	0	0	0	0	0	0	0	0	1	1	0	0
Nyctomys sumichrasti	1	0	0	0	0	0	0	0	0	0	0	0
Oecomys auyantepui	0	0	1	1	1	0	1	0	0	0	0	1
Oecomys bicolor	0	1	1	0	1	1	1	1	1	1	1	1
Oecomys concolor	0	0	0	0	0	1	0	0	0	0	0	0
Oecomys paricola	0	0	0	0	0	0	0	1	0	0	0	0
Oecomys superans	0	0	0	0	0	0	0	0	1	1	1	0
Oecomys rex	0	0	1	0	1	0	1	0	0	0	0	1
Oecomys roberti	0	0	0	0	0	0	0	1	0	0	1	0
Oecomys rutilus	0	0	0	1	1	0	0	0	0	0	0	0
Oecomys trinitatis	0	1	0	0	0	0	0	1	0	0	0	0
Oligoryzomys spp.	1	1	1	1	1	0	0	0	1	1	1	1
Oryzomys bolivaris	1	0	0	0	0	0	0	0	0	0	0	0
Oryzomys emmonsae	0	0	0	0	0	0	0	1	0	0	0	0
Oryzomys macconnelli	0	0	1	1	1	0	1	0	1	1	0	0
Oryzomys megacephalus	0	0	1	1	1	0	1	1	0	0	0	1
Oryzomys nitidus	0	0	0	0	0	0	0	0	1	1	1	0
Oryzomys perenensis	0	0	0	0	0	0	0	0	1	1	1	0
Oryzomys talamancae	0	1	0	0	0	0	0	0	0	0	0	0
Oryzomys yunganus	0	0	0	1	1	0	0	0	1	0	1	0
Oxymycterus spp.	0	0	0	0	0	0	0	1	0	1	0	0
Rhipidomys gardneri	0	0	0	0	0	0	0	0	0	1	1	0
Rhipidomys leucodactylus	0	0	0	0	1	1	0	0	0	0	0	0
Rhipidomys nitela	0	0	1	1	1	0	1	1	0	0	0	0
Sigmodontomys alfari	1	0	0	0	0	0	0	0	0	0	0	0
Tylomys panamensis	0	1	0	0	0	0	0	0	0	0	0	0
Tylomys watsoni	1	0	0	0	0	0	0	0	0	0	0	0
Coendou bicolor	0	0	0	0	0	0	0	0	1	1	1	0
Coendou melanurus	0	0	1	1	0	0	0	0	0	0	0	0
Coendou mexicanus	1	0	0	0	0	0	0	0	0	0	0	0
Coendou prehensilis	0	0	1	1	1	1	1	1	0	0	0	0
Coendou rothschildi	0	1	0	0	0	0	0	0	0	0	0	0
Hydrochoeris hydrochaeris	0	1	1	0	1	0	0	1	1	1	0	1
Dinomys branickii	0	0	0	0	0	0	0	0	1	1	0	0
Dasyprocta fuliginosa	0	0	0	0	0	1	0	0	0	0	0	0
Dasyprocta leporina	0	0	1	1	1	0	1	1	0	0	0	1
Dasyprocta punctata	1	1	0	0	0	0	0	0	0	0	0	0
Dasyprocta variegata	0	0	0	0	0	0	0	0	1	1	1	0
Myoprocta acouchy	0	0	0	1	1	0	1	1	0	0	0	0
Myoprocta pratti	0	0	0	0	0	1	0	0	1	1	1	0
Cuniculus paca	1	1	1	1	1	1	1	1	1	1	1	1
Dactylomys spp.	0	0	0	0	0	0	0	1	1	1	0	0
Diplomys labilis	0	1	0	0	0	0	0	0	0	0	0	0
Echimys chrysurus	0	0	0	0	1	0	1	1	0	0	0	0
Hoplomys gymnurus	1	0	0	0	0	0	0	0	0	0	0	0
Isothrix bistriata	0	0	0	0	0	0	0	0	0	0	1	0
Isothrix pagurus	0	0	0	0	0	0	1	0	0	0	0	0
Makalata didelphoides	0	0	1	1	1	0	0	1	0	0	0	1
Makalata occasius	0	0	0	0	0	0	0	0	0	1	0	0
Mesomys spp.	0	0	0	1	1	1	1	1	1	1	1	1
Proechimys brevicauda	0	0	0	0	0	0	0	0	1	1	1	0
Proechimys cuvieri	0	0	0	1	1	0	1	1	0	0	0	1
Proechimys goeldii	0	0	0	0	0	0	0	1	0	0	0	0

Table 6. (*continued*)

Species	Locality 1	2	3	4	5	6	7	8	9	10	11	12
Proechimys guyannensis	0	0	1	1	1	1	1	0	0	0	0	1
Proechimys oris	0	0	0	0	0	0	0	1	0	0	0	0
Proechimys pattoni	0	0	0	0	0	0	0	0	1	1	0	0
Proechimys semispinosus	1	1	0	0	0	0	0	0	0	0	0	0
Proechimys simonsi	0	0	0	0	0	0	0	0	1	1	1	0
Proechimys steerei	0	0	0	0	0	0	0	0	1	1	1	0
Sylvilagus brasiliensis	1	1	1	0	0	0	0	1	1	1	1	0

in a large canopy net set in the forest near Pakatau Falls. A third individual was shot while flying over a small valley in the forest near the Burro-Burro River Camp at 1700 hr on 1 April 1997. These bats were found flying in the middle canopy in semi-open forested areas near large rivers. This species seems to be uncommon but probably is present throughout the forested areas of Iwokrama. It is widely distributed but uncommon in northern South America. In the Guianas, *C. maximiliani* has

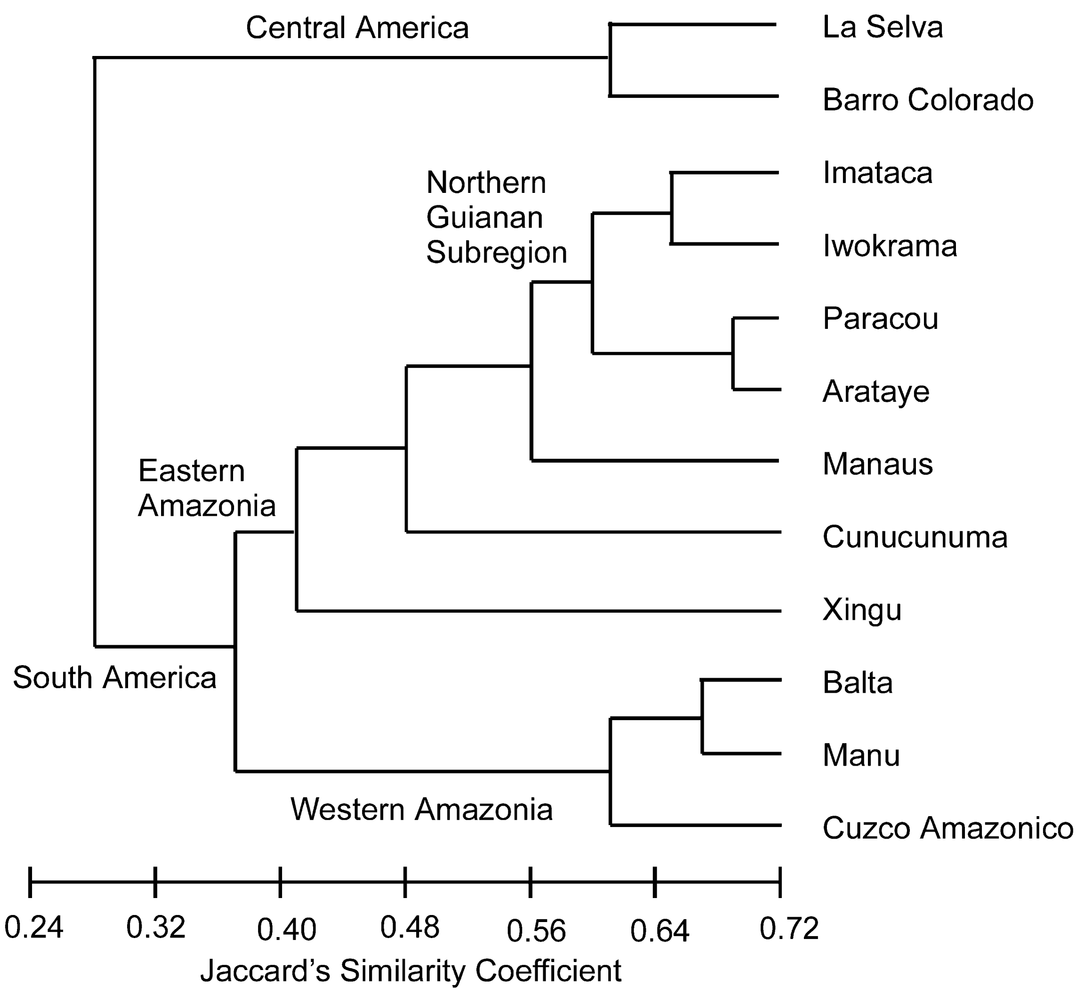

Fig. 3. Phenogram derived from UPGMA cluster analysis of Jaccard's similarity coefficients among Neotropical lowland rainforest localities that have been well-surveyed for mammals.

been previously reported from a few localities across Venezuela, Suriname, and French Guiana (see Lim et al., 1999 for more detail).

Diclidurus albus and *D. ingens* were shot while flying high over the river near the Burro-Burro River Camp after midnight, early on 10 April 1997. Four *D. isabellus* were also shot during the same evening flying lower over the river and often near the surface of the water. An additional nine *D. isabellus* were shot over the same general vicinity of the Burro-Burro River during the evenings of 4, 5, and 6 April 1997. Two *D. isabellus* were shot while flying over the Essequibo River near Turtle Mountain on 1 November 1997 and 12 more were shot while flying over the Siparuni River near S Falls on the evenings of 10, 11, 12, and 13 November 1997. No individuals of *Diclidurus* were caught in mist nets or harp traps set over water or land. *D. isabellus* seems locally common over large open rivers throughout Iwokrama Forest whereas *D. albus* and *D. ingens* should be considered rare. Only eight specimens of *D. ingens* were known previously and all were from southeastern Colombia and Venezuela; *D. albus* is more widely distributed in the Neotropics and has been reported from Venezuela and Suriname; and *D. isabellus* was previously known only from Amazonian Brazil and Venezuela.

Peropteryx leucoptera was caught in a mist net set across a trail in the understory of secondarily disturbed forest near the access road to the Iwokrama Field Station at approximately 2000 hr on 12 April 1997. This species is rare but should be found in any of the forested areas of Iwokrama. This record from Guyana means that *P. leucoptera* is now documented in all countries of northern South America. Based on additional specimens caught subsequently south of Georgetown (Lim, Engstrom, and Jafferally, unpublished data), we anticipate that *P. leucoptera* is broadly distributed but uncommon in lowland forest in Guyana.

Saccopteryx gymnura was netted near a thatched roof building in the clearing at the old Surama Sawmill at about 1900 hr on 19 July 1994. Until recently, the only confirmed record of this species was the holotype collected over 100 years ago at Santarém on the Amazon River, Brazil. Subsequently, three specimens collected in Guyana over 20 years ago have been identified as *S. gymnura*, two specimens have been recently collected in French Guiana, and three more were reported from Brazil (Simmons & Voss, 1998). *Saccopteryx gymnura* is very rare and one of the least known bats of South America. Its occurrence in the Iwokrama Forest area is an important addition to the fauna of the region.

Lampronycteris brachyotis was caught in an understory net set over a stream in terra firme forest at Pakatau Falls on 17 November 1997. This species is widely distributed from southern Mexico to northeastern Brazil and can be locally abundant, especially with suitable cave habitats. It is probably rare but present throughout Iwokrama Forest, particularly in relatively dry forest. *Lampronycteris brachyotis* has been reported from Venezuela and Suriname.

Two *Micronycteris brosseti* were caught in a mist net set in terra firme forest at Three Mile (Giaconda) Camp on 24 March 1997. It was recently described as a new species from French Guiana (Simmons & Voss, 1998). This is the smallest species of *Micronycteris* in Guyana and is easily confused with *M. minuta* in the hand. Distinguishing features of *M. brosseti* include a combination of pale grey ventral fur, short hairs on the ears, and a calcar longer than the hindfoot (Lim et al., 1999).

Seven specimens from Iwokrama Forest were tentatively identified as *Micronycteris microtis* (Lim et al., 1999). This species has only recently been separated from *M. megalotis* based on subtle morphological differences (Simmons, 1996). This example of cryptic diversity highlights the need to collect series of specimens for each species to avoid underestimating biodiversity and emphasizes the difficulties of identifying some bats at the site of capture. The collecting sites in Iwokrama Forest for *M. microtis* include Burro-Burro River Camp, Giaconda Camp, Kurupukari, Pakatau Falls, 30 km SE of Surama, and Surama Sawmill. Only one *M. microtis* was netted at each site except Surama Sawmill where we caught two of these bats. The bat from Giaconda Camp was caught in a canopy net set within terra firme forest and the remaining bats were netted in the forest understory. This species seems to be widespread throughout Iwokrama Forest but uncommon. *Micronycteris microtis* is widely distributed from southern Mexico to Amazonian Brazil including reports from Venezuela and Suriname.

Two *Lophostoma carrikeri* were caught in a canopy net set within terra firme forest at Giaconda Camp on 24 March 1997, five were netted in high nets or in ground-level nets set over small streams at Burro-Burro River Camp on 31 March, 2, 6, and 8 April 1997, and two were netted in a high net set at the edge of disturbed forest near the Iwokrama Field Station on 12 April 1997. This species may appear locally abundant especially if nets are set close to their roosts but more typically they seem to be uncommon in forested areas. *Lophostoma carrikeri* is found in northern South America including Venezuela and Suriname.

Two *Vampyressa thyone* were collected at Cowfly Camp on 12 and 13 October 1997 with one captured in a canopy net set down the middle of a 20 m wide river and the other in an understory net set within mixed forest on undulating terrain. This species appears to be uncommon in Iwokrama Forest. It is distributed from southern Mexico to Bolivia and considered distinct from *V. pusilla*, which occurs in Paraguay and southeastern Brazil (Lim et al. 2003). In the Guianas, *V. thyone* has been previously reported from Venezuela but not from Suriname although it has been found in French Guiana.

Twenty *Vampyrodes caraccioli* were captured in canopy nets at Cowfly Camp on consecutive evenings from 10 to 17 October 1997. Four more were caught higher in elevation at Iwokrama Gorge Camp on 20, 21, and 23 October 1997, where two were captured in a canopy net and two in understory nets. This species may be locally common within the remote forested areas of Iwokrama Forest perhaps in regions higher in elevation. It had been previously reported from Venezuela and Suriname.

One *Lasiurus atratus* was caught about 15 m above the main road at Giaconda Camp in a canopy net on 27 March 1997. Another was caught in an understory net set over the Siparuni River at S Falls on 15 November 1997. This species was recently described based on eight specimens from southern Venezuela, Suriname, and French Guiana (Handley, 1996). *Lasiurus atratus* is one of two endemic bats of the Guiana Shield (*Lophostoma schulzi* the other) and is rare (Lim et al. 2004).

One *Myotis riparius* was caught in a ground-level mist net set in forest 30 km NE of Surama on 11 October 1990. Twelve individuals were found roosting in a small crack and hollow in a branch of a 15 cm diameter tree felled by local inhabitants near Surama Sawmill on 25 July 1994. One was also caught at Burro-Burro River (Clearwater) Camp in a mist net on 31 March 1997. This species has been reported from Venezuela and French Guiana, and only recently documented in Suriname (Lim & Engstrom, unpublished data).

Eight *Molossops neglectus* were caught in a canopy net about 15 m above the main road at 38-Mile Camp on 5, 6, and 8 October 1997. Until recently, only 11 specimens of this species were recorded, all from Suriname, Peru, and Brazil (Ascorra et al., 1991). More recently, it has been reported from Venezuela (Ochoa et al., 1993), Colombia (Lim & Engstrom 2001a), extreme northeastern Argentina (Barques et al., 1993), and southeastern Brazil (Gregorin et al. 2003). Previously, no more than two individuals of this species were caught at any one place and these were all caught while flying high over the ground. Our use of a large canopy net for prolonged periods of time demonstrates the biases associated with the conventional methods of capturing bats with understory nets to estimate species diversity and abundance. Many species of bats, especially aerial insectivores go undetected although they may be present in high numbers but are difficult to capture because of their ability to detect nets or pattern of foraging high in the canopy.

Two *Cynomops paranus* were collected at 38-Mile Camp on 7 October 1997 about 15 m above the main road in a canopy net. Another was collected at S Falls on 14 November 1997 in an understory net set across a river. This bat is rare and is usually found flying in open areas over rivers or roads. These specimens were included in a recent systematic study of the genus (Peters et al. 2002). *Cynomops paranus* has been previously reported from Venezuela and Suriname.

One specimen of *Molossus* sp. was collected in a mist net across a river at S Falls on 14 November 1997. This specimen is smaller than any other currently recognized species of *Molossus* in the Guianas (see Lim & Engstrom 2001a). Before any taxonomic conclusions are made, a systematic revision of the genus is needed because the species limits within this widespread genus are poorly understood.

Besides the 17 species of bats documented from Iwokrama Forest and recorded for the first time in Guyana, one of the more surprising discoveries was Beddard's olingo (*Bassaricyon beddardi*). It was found with two kinkajous (*Potos flavus*) on the evening of 5 April 1997 in trees along the shore of the Burro-Burro River. Other species of olingos can be locally common and it is not unusual to find them foraging together with the more common kinkajous (Emmons, 1997). The subtle external distinctions between these two nocturnal mammals has probably led both species in Guyana to be referred to as 'night monkeys' by the Amerindians. This local name has caused added confusion because this is the same common name as the proper night monkey, *Aotus* spp., which has not been reported from Guyana. This is the first record of Beddard's olingo since a description of the anatomy of the holotype in 1900 (Pocock, 1921) although we were told that it also occurred along the main road to Lethem. This species should be regarded as present but with unknown status because of its confusion with kinkajous.

DISCUSSION

General Features of the Iwokrama Mammal Fauna

Iwokrama Forest is one of the largest and most pristine tracts of intact lowland rainforest in the world. At present, it is an excellent example of robust, relatively undisturbed lowland tropical forest with large populations of game mammals such as labba or paca (*Cuniculus paca*), wild hog or peccari (Tayassuidae), bush cow or tapir (*Tapirus terrestris*), deer (*Mazama* spp.), and endangered large to medium sized mammals such as jaguar (*Panthera onca*), several species of monkeys (Cebidae), giant armadillo (*Priodontes maximus*), and giant otter (*Pteronura brasiliensis*) that usually are rare or absent in disturbed forests. The diversity of mammals in Iwokrama Forest is also high, especially for bats. Bats, however, are relatively difficult to sample and inventory accurately. Nonetheless, bats typically comprise 50% or more of the total number of mammal species in Neotropical lowland forests, and are important not only in terms of total biodiversity but also ecology. For example, bats are primary seed dispersers and flower pollinators for many plants.

Diversity Indices and Species Richness

Because it is usually impractical to do a complete inventory to enumerate all species (species richness), diversity indices have been used to estimate the species diversity based on relative abundance. In general, many diversity indices presume an equal probability of capture for all species (e.g., Wilson et al., 1996). If this assumption is violated, the index will underestimate diversity because of species unevenness and not necessarily because of actual low diversity. For example, nets set near a roosting site or fruiting tree (e.g., *Ficus*) used by *Artibeus* will capture a disproportionate number of these fruit-eating bats and fewer of other species that do not roost in large groups or congregate at feeding sites.. Another problem with diversity indices is that as the actual number of species is approached, increased sampling lowers the index. Complete sampling would negate the need for diversity indices because the number of species would represent actual total diversity. Ideally, the best estimates of diversity would be made through regular and ongoing surveys at fixed sites until the species accumulation curves level off at or near the number of species expected.

From our surveys in Iwokrama Forest, a few localities with distinct species compositions and/or high species richness should be resampled to determine whether they merit special attention from a conservation standpoint. For example, Pakatau Falls had high species richness and several unusual species were present, including the rare bats *Centronycteris maximiliani*, *Lampronycteris brachyotis*, *Diclidurus isabellus*, as well as a large local population of *Ametrida centurio*. Likewise Burro-Burro River Camp included the bats *Centronycteris maximiliani*, *Diclidurus isabellus*, *D. albus*, *D. ingens*, *Lophostoma brasiliense*, *Vampyrum spectrum* and the olingo *Bassaricyon beddardi*. We caution, however, that most of the mammals caught only at these localities were uncommon, and eventually might prove to be widely distributed throughout Iwokrama Forest. Cowfly and Iwokrama Gorge camps had relatively high densities of rodents, including *Neacomys* sp. and bats that might be more characteristic of localities at slightly higher elevations in this region (e.g., *Vampyrodes caraccioloi* and *Anoura geoffroyi*). Surama Sawmill bordering Iwokrama Forest at the edge of savannah also had high species richness and some unusual species, perhaps due in part to its location at the ecotone of two major habitat types. Even Iwokrama Field Station located in disturbed forest on the banks of the Essequibo River had several interesting species, including the bats *Noctilio albiventris* and *Peropteryx leucoptera*. Clearly, additional sampling is required to determine areas of special conservation concern and priority for preservation of biodiversity in Iwokrama Forest. However, in particular, we recommend that the area around the Iwokrama Mountains be protected as one of the more unusual physiographic features in Iwokrama Forest and one supporting high diversity and abundance of terrestrial mammals.

Relative Abundance and Capture Rates

Capture rates during the 1997 faunal surveys in Iwokrama Forest were considerably lower than for a published study from Paracou, French Guiana (Simmons & Voss, 1998) wherein they caught 2,748 bats in 27,679 net metre hours for an overall capture rate (bats per net metre hrs × 100) of 9.9. Converted to net square metre hours (9.9/2.6–the height of nets used in their survey), their capture rate of 3.8 is nearly a ten-fold increase above our mean value of 0.424. Rather than actual differences in abundances of bats, this discrepancy probably stems from differences in methodology. Because we had the advantage of extra personnel to assist in trapping and netting, our strategy was to set 30–40 nets within the first 3–4 days at a camp and then reset approximately 10 nets on subsequent days. On the November 1997 trip, nets were left open all night at several localities. Although the large canopy net (with a surface area equivalent to 18 short nets) was very successful in capturing species not readily caught in standard ground-level nets (e.g., *Centronycteris maximiliani*, *Lophostoma carrikeri*, *Vampyrodes caraccioloi*, *Molossops neglectus*; see Lim & Engstrom 2001b) capture rates per square metre are lower than for smaller nets (often half or less). Frequent use of these nets depresses the overall capture rate. Nonetheless, this sampling strategy was the best way for us to take advantage of the extra personnel at several camps. Quantitatively these circumstances resulted in lower capture rates but increased overall sampling of species.

Perhaps more telling is the rate of capture per day of sampling. In total, over 79 sampling days we caught 2,097 bats, whereas Voss and Simmons

(1998) caught 2,748 bats in about 175 days at Paracou, indicating that our increased level of capture effort (number of net hours, relative to attention and movement of individual nets) yielded more bats per day, but fewer numbers of bats per net. Nonetheless, actual density of bats are likely similar between Iwokrama and Paracou. Our methodological approach also was taken because the inventory schedule allowed only two field seasons of 6–8 weeks, necessitating intensive sampling over relatively short periods at several camps. In contrast to our strategy, Simmons & Voss (1998) set relatively few nets per night, monitored the nets constantly, usually closed them after peak bat activity passed, and moved the nets every day, over a longer survey. All of these practices increase capture rates, at the expense of setting large numbers of nets. As noted by Simmons & Voss (1998:190), "comparisons of species richness among Neotropical rainforest bat inventories are complicated by problems related to methods, ecological scope, and intensity of faunal sampling at different sites", to which we would add size of area surveyed.

For nonvolant small mammals, the overall relative abundance reported from Cuzco Amazónica in Peru (Woodman et al., 1996) was higher by a factor of 10 (0.053) compared with our results from Iwokrama Forest (0.0052). Relatively low abundances of rodents elsewhere in Guyana (Kanuku Mountains) were also reported by Parker et al. (1993) and have been observed by us at other localities (see Lim & Norman 2002). This probably reflects real differences in relative abundances of small mammals between sites in eastern and western Amazonia. Because of generally low abundance of both terrestrial and arboreal mammals in Iwokrama Forest, these groups would be impractical to survey for detailing significant changes in relative abundance over time, although changes in species diversity could be examined.

Methodological Considerations

We were unable to adequately assess patterns of seasonal variation in relative abundances based on two trips during dry seasons to different sites. Ideally, seasonal changes in abundance should be assessed by a monitoring programme established at selected sites and conducted at four standardized times including two wet and two dry season samples per year, over at least two years. Bats would be the best exemplar for mammals and could be obtained in sufficient numbers to determine significant trends in relative abundances with geographic, local, seasonal, and habitat alterations. We recommend that monitoring transects of 10 to 20 nets each be established at three to four sites in Iwokrama Forest, where adequate trail systems are available to move nets. The sites should be sampled over a six or eight-day period, and the nets moved every two days (bats quickly learn the location of nets, and avoid them). Initially, these sites should be resampled four times each year: if seasonal variation proves minimal, they could then be sampled bi-annually or annually as part of a long-term monitoring programme.

No single method can be used to estimate the relative abundance of mammals because of the disparity in techniques needed to survey different groups and their differing probabilities of being detected. Observational methods that are useful for surveying primates and other large mammals during the day will not work for bats because they are small and volant. Most bats cannot be identified in flight (if indeed they can be observed at all) and must be captured to document their presence. Even within a group such as bats, standard ground-level mist netting will miss most of the trophic guild of aerial insectivores, so other approaches must be used such as canopy netting (Lim & Engstrom 2001b).

For purposes of comparison among sites or long-term monitoring, abiotic factors that influence the variability of abundance must be held to a minimum or they can result in misleading conclusions. Keeping factors such as climatic and trapping conditions constant is very difficult especially for large-scale projects such as that in Iwokrama Forest. The unpredictability of weather, and the training of students and other personnel in the field are examples of variables that can affect the estimation of relative abundance. We assume that weather patterns and the different learning curves of people average out over the duration of a field trip to give us some degree of constancy or control over these potential sources of variation. Nonetheless, to obtain more precise estimates of relative abundances sites should be sampled at different seasons over at least a 2-year span.

Completeness of the Survey.—Prior to 1990, little was known biologically about the mammals in Iwokrama Forest beyond that inferred from Amerindian hunters working in the area. The Site Resource Survey of Iwokrama Forest listed 52 species "known or expected to occur within the Reserve" (Hawkes & Wall, 1993:151). Our current total is 130 species based on voucher specimens and confirmed observation with an additional 57 species of mammals expected to occur in Iwokrama Forest (Table 5). In addition to our recent work (Lim et al., 1999; Lim & Engstrom 2001a, b), the only other publication on mammal species from Iwokrama Forest is the study of bat diversity by Smith & Kerry (1996). Our survey period was relatively short (79 field days in one year) which is less than other previous, well-documented inventories (Voss & Em-

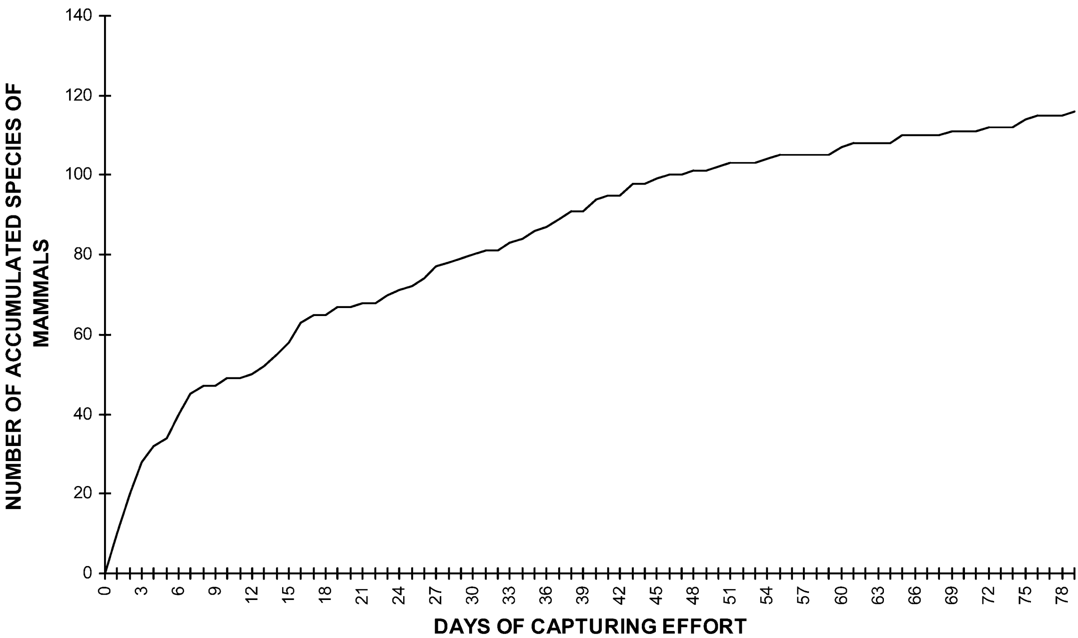

Fig. 4. Species accumulation curve of mammals recorded during the 1997 Iwokrama Forest faunal survey.

mons, 1996). Nonetheless, when combined with previous records in Iwokrama Forest, our survey includes a relatively large proportion of the species likely to occur here.

Our estimates of mammalian diversity in Iwokrama Forest ranged from 159 to 187 species based on species richness estimators and inferred distribution. These figures contrast with the prediction of Voss & Emmons (1996) that only about 150 species might be sympatric at any rainforest site in the Guianas. This underestimate is most obvious for bats where Iwokrama Forest potentially may have 110 species instead of the predicted maximum of 90. This discrepancy underscores both the gaps in our knowledge of the diversity of mammal communities in Guyana and the critical need for additional survey work. Documenting every species of mammal that occurs in Iwokrama Forest is not a practical goal but Simmons & Voss (1998) suggested, and we agree, that surveys should be at least 90% complete to provide enough data for meaningful comparisons among Neotropical communities. Our one-year survey approaches that goal (estimates to approximately 70% complete for mammals and 79% complete for bats) but additional survey work or employment of other methods (e.g., detailed community surveys in Amerindian communities) clearly is necessary to define species richness and relative abundance of mammals from Iwokrama Forest. It is axiomatic that one cannot set realistic conservation priorities for protected areas without having a detailed knowledge of the organisms contained within them.

Although the species accumulation curve for Iwokrama Forest is still slowly rising (Fig. 4), more specialized and directed methods should now be used to record those species that have eluded detection. In this regard, a review of rarely encountered species in the initial survey (those for which only one or two observations or captures were made), and the species predicted to occur in the area but which have not yet been recorded, is informative. Of the 24 species of bats caught only once or twice in Iwokrama Forest (Table 2), 20 are insectivores and the majority of these catch insects on the wing. Likewise, of the 24 additional, undocumented bat species predicted to occur in Iwokrama Forest, 19 are aerial insectivores (Table 5). Three other potential species are nectarivores. A similar proportion in trophic guild representation for predicted but undocumented bat species was found at Manu in Peru (Patterson et al., 1996). Both aerial insectivores and nectarivores often fly in openings (over streams, in tree falls, etc.), high in the subcanopy or canopy level, or above the canopy. Thus these bats are difficult to catch in ground-level nets and must be sampled by specialized techniques, such as setting large canopy-level nets or using ultra-sonic detectors to listen for echolocation calls. The latter technique has the disadvantage that the characteristics of the echolocation calls of each species within a community must be known in advance, information which is not available for most Neotropical bats or communities.

For the 23 species of rarely observed, non volant mammals found in Iwokrama Forest (Table 2), 11 of the species are arboreal, 4 are aquatic, and 8 are terrestrial. All of the terrestrial species are large. Similarly, of the 33 additional, undocumented nonvolant species that might occur in Iwokrama Forest (Table 5), 16 are arboreal, 3 are aquatic, and 14 are terrestrial. Eleven of the potential terrestrial species are of medium or large body size. These comments suggest that future inventory efforts should be directed at searching in trees for arboreal species, walking transects in the day and night to search for medium to large sized terrestrial species (which are usually uncommon and difficult to observe), and setting traps in or near streams for small aquatic species. For terrestrial species, some effort should also be expended searching for mammal signs (tracks and scats) although some species can be difficult to identify by sign alone. Thus for further inventory work, we recommend using infra-red trigger cameras set along trails to record carnivores or in front of burrows for armadillos, intensive transect surveys for sloths and monkeys, intensified canopy netting for aerial insectivorous bats, and increased canopy trapping for arboreal mammals. Likewise, visits to unsurveyed field camps should also be planned, as we were unable to visit all potential sites in the short period available for the survey. Visiting new sites often results in encountering additional species.

Iwokrama Mammal Fauna in a Broader Context

In our survey of mammals, some groups are better represented in the inventories than others. In particular, because bats comprise such a large proportion of total diversity they were intensively surveyed. In the following comparison of Iwokrama Forest and other Neotropical sites, we first discuss all mammals, and then focus on the pattern for bats.

In Iwokrama Forest, bats comprise the largest proportion of the fauna (66%), followed by rodents (12%), carnivores (6%), marsupials (5%), and then primates, ungulates, and xenarthrans (each comprising less than 4% of the total fauna). There are 25 species of mammals endemic to the Guiana Shield (Lim et al. 2004). We have documented eight Guianan endemics in Iwokrama Forest including the short-tailed opossum (*Monodelphis brevicaudata*), Schulz's round-eared bat (*Lophostoma schulzi*), red bat (*Lasiurus atratus*), black spider monkey (*Ateles paniscus*), Guianan saki (*Pithecia pithecia*), Paracou spiny mouse (*Neacomys paracou*), Auyan-tepui arboreal rice rat (*Oecomys auyantepui*), and royal arboreal rice rat (*O. rex*).

Among the Neotropical sites that have been well surveyed (Figs. 2 and 3), species composition in Iwokrama Forest is most similar to localities in the northern Guianas (Paracou and Arataye, French Guiana; Imataca, Venezuela). These in turn cluster with localities in eastern Amazonia (Cunucunuma, Venezuela; Manaus and Rio Xingu, Brazil). Eastern Amazonia is allied to localities in western Amazonia (Cuzco Amazonico, Balta, and Manu, Peru), which are most distinct from localities in Central America (La Selva, Costa Rica; Barro Colorado Island, Panama).

A point of interest in the species composition is the apparently depauperate primate fauna of Iwokrama Forest. We recorded only five species of primates in Iwokrama Forest (Tables 2 and 5) and from conversations with local hunters these taxa may comprise the total primate fauna. Three other species are known east of the Essequibo River, all of which we have observed at the former Tropenbos field station in the Demerara Timbers Limited forest concession south of Mabura Hill and approximately 40 km northeast of Iwokrama Forest. The number of primate species is much lower than that observed at sites in western Amazonia (e.g., Yasuni National Park, Ecuador, Engstrom et al. unpubl. data; Balta and Manu, Peru–summarized in Voss & Emmons, 1996), where 10 species or more often co-occur (see Table 7). We are confounded to explain this distribution but a low species richness of primates has been noted at Kartabo, Guyana (Anthony, 1921b; Beebe, 1925) and eastern Guianan primate faunas generally appear to contain relatively few species in general (Voss & Emmons, 1996).

Likewise, Iwokrama Forest appears to contain fewer rodent species than other Amazonian localities, particularly those to the west (Table 7). We believe that the low species richness of rodents results, in part, from an incomplete inventory of this group in Iwokrama Forest, which in turn is a result of low capture rates and relative abundance. One future methodological emphasis should be a systematic survey of the canopy fauna for arboreal species.

Most remarkable is the high diversity of bats found in Iwokrama Forest. Our total of 86 species of bats exceeds that of most other inventories in the Neotropics (see Table 7), and we estimate that another 16–24 species (or more) may occur in Iwokrama Forest. The list of bats is particularly rich in representation of aerial insectivores, the majority of which are in the upper canopy. Clearly, the bat fauna in Iwokrama Forest is diverse, however, the relatively high species richness recorded can also be attributed to intensive sampling using a variety of methods. Several species of sheath-tailed bats (Emballonuridae) were collected only by shooting over water, and several other species of Emballonuridae and Molossidae (free-tailed bats) were taken in large

Table 7. Comparison among 12 Neotropical sites for numbers of species in each of the mammalian Orders (modified from Voss & Emmons 1996; Simmons & Voss, 1998; Lim & Engstrom 2001a; and Voss et al. 2001).

	Mammal Order								
Locality	Didelphimorpha	Xenarthra	Chiroptera	Primates	Carnivora	Ungulata	Rodentia	Lagomorpha	Total
La Selva	5	7	65	4	14	5	16	1	117
Barro Colorado	6	6	63	4	13	5	14	1	113
Imataca	7	8	78	3	12	4	17	1	130
Paracou	11	9	79	6	10	5	21	0	141
Arataye	11	8	61	7	13	5	24	0	129
Cunucunuma	8	7	50	7	6	3	12	0	93
Manaus	9	8	52	6	8	5	18	0	106
Rio Xingu	8	4	47	7	2	3	23	1	95
Balta	11	9	56	10	15	4	24	1	130
Manu	12	7	80	13	14	5	27	1	159
Cuzco	9	5	45	7	11	4	21	1	103
Iwokrama	7	4	86	5	8	5	15	0	130

canopy nets set well above ground level. The high diversity of phyllostomine and stenodermatine bats results mainly from standard netting at ground level. However, intensive surveys using a similar array of methods in other parts of Amazonia, in particular the western Amazon basin of Ecuador and Peru, should yield even higher diversity estimates.

Bat Diversity.—The bat diversity of Iwokrama Forest and Guyana was recently summarized by Smith & Kerry (1996) as comprising 45 and 96 species, respectively. Our work (Lim et al., 1999; Lim & Engstrom 2001a) based on vouchered specimen collections, has increased the number of bat species in Iwokrama Forest to 86 and in Guyana to 122 (Table 5; Engstrom & Lim 2002). At present, Iwokrama Forest has the highest reported bat species diversity of any protected area or general locality in the world, surpassing the 85 reported from the nearby Kanuku Mountains region in southwestern Guyana (Parker et al., 1993). This region includes both forest and savanna, and is approximately four times the area of Iwokrama Forest. Protected area status and exact boundaries for the Kanuku Mountains region are still to be determined but there is potential for the total to reach 89 species of bats based on a recent survey (Lim & Norman 2002).

Other areas with high reported bat species diversity include Manu Biosphere Reserve in Peru with 80 (Pacheo et al., 1993; Patterson et al., 1996), Paracou in French Guiana with 79 (Simmons & Voss, 1998), Imataca Forest Reserve in Venezuela with 79 (Ochoa G., 1995), and the general vicinity of San Juan de Manapiare in Venezuela with 72 (Handley, 1976; Findley, 1993–incorrectly reported this number as 78). Based on more recent inventory work, the unpublished species-level diversity at Manu is currently 94 species of bats (B. D. Patterson, pers. comm.). Manu encompasses an area of 18,812 km^2 and an elevational range from 380 to 3,450 m including a broad range of habitats from wet lowland forest to alpine puna grassland. However, only two main river courses have been surveyed (Pacheco et al., 1993). This is compared with the smaller area (3,600 km^2), restricted range of elevations (70 to 1000 m), and forest types in Iwokrama. As summarized in this study, there are only 13 localities surveyed. At the other end of the scale, the Paracou site yielded a remarkable 78 species of bats from one locality representing a comparatively small area (3 km radius) in lowland rainforest. This site is one of the first to be intensively surveyed with the main objective being as complete an inventory of mammals as possible (Simmons & Voss, 1998). The relative sizes of Paracou, Iwokrama, and Manu highlight the difficulty of making direct comparisons among inventories where geographic coverage may be governed more by exigency and opportunity than researcher driven design. Comparisons of absolute diversity are compromised by effects such as differences in altitudinal and habitat diversity, physical extent, and access. Thus our emphasis is on the fact that our estimates of actual species diversity in Iwokrama Forest are near the upper limits of predicted diversity for a relatively homogeneous tract of lowland forest in the Guianas, and are high relative to what we would have predicted at the onset of the inventory. Moreover Iwokrama Forest contains a large percentage of the fauna known to occur anywhere within Guyana, emphasizing its importance as an area for conservation of mammals.

Specimen Collecting

For poorly known regions, the first step of a faunal survey is a gross assessment of biodiversity. Many organisms including small mammals, however, can only be reliably inventoried by capturing techniques and even then many are difficult to identify in the hand. Consequently, inventories that have not included extensive voucher collections have proven inaccurate or are unverifiable (see reviews in Voss & Emmons, 1996; Simmons & Voss, 1998) and/or are superficial, resulting in gross underestimates of the actual species-level diversity (e.g., Robinson, 1998). For example, the only previous detailed survey of nonvolant mammals from anywhere in Guyana that can now be used in detailed assessments of biodiversity is based on a collection amassed by Beebe (1919; 1925) and others near Kartabo and Bartica in the 1920s (see Voss & Emmons, 1996). Because this inventory (which focused on mammals other than bats) was documented using voucher specimens (deposited at the American Museum of Natural History), it has been possible to reaffirm the identifications based on current taxonomy, and separate species in those collections now known to be distinct.

Subsequent monitoring programmes will be meaningful only if compared to the reference of a well-documented, thorough inventory of species richness. An accurate assessment of species richness requires a firm understanding of alpha-level taxonomy (description and definition of the species present) for which specimens serve as the basis of reference. Therefore, it is imperative that professionally collected and curated voucher specimens are available for study, particularly for small mammals (e.g., marsupials, rodents, bats). Specimens serve to unambiguously document the presence of species and their relative abundances, are used in the determination of taxonomic status of populations, and in the estimation of evolutionary and geographic relationships of the species in the area to those in other geographic regions.

During the course of our work we have documented numerous species in Iwokrama Forest (especially of bats) that have been described or recognized only recently (e.g. *Lasiurus atratus*, *Micronycteris microtis*, *Lophostoma schulzi*, *Artibeus gnomus*) or that are cryptic and can only be confirmed based on specimens (e.g. *Saccopteryx gymnura*, *Vampyressa brocki*, *Oecomys rex*). We have also used specimens collected to study the taxonomy and systematics of some groups which were in doubt, for example: *Carollia* spp. (Lim & Engstrom 1998; Wright et al. 1999); *Artibeus planirostris* (Lim & Wilson 1993; Lim 1997; Lim et al. 2004); *Tonatia saurophila* (Williams et al. 1995); *Cynomops* (Peters et al. 2002); and *Vampyressa thyone* (Lim et al. 2003). Similar studies are ongoing on the sheath-tailed bat family Emballonuridae, fruit-eating bats (*Artibeus*), big-eared bats (*Tonatia*), common opossums (*Didelphis*) and spiny mice (*Neacomys*). These studies will result in a more accurate assessment of levels of mammalian diversity and the collections on which they are based are available for subsequent research.

Suggestions for Monitoring

Long-term monitoring of changes in species richness and abundance for mammals can often be difficult. However, with a reasonable level of training and funding, the benefits in terms of tracking the health and status of Iwokrama Forest will be worth the effort and expense. For large mammals, observational transects can be established in different habitats throughout Iwokrama Forest and sampled on a regular basis, either once a month or twice per year. This technique would work well for larger mammals observable during the daytime such as primates, peccaries, and deer. The field guide to Neotropical rainforest mammals by Emmons (1997) or the guide developed for Iwokrama (Engstrom et al., 1999) would serve as sources for identification. Field workers would record direct sightings, indirect observations such as tracks or scats, and vocalizations. Observational transects can also be done at night for nocturnal mammals but a higher level of skill is required to identify species with headlamps and/or flashlights.

Larger mammals, however, comprise only 20% of the known species of mammals in Guyana (Engstrom & Lim 2002). Bats represent over half of the species diversity with the remainder being rodents and marsupials. To adequately monitor these smaller nocturnal mammals requires capturing with mist nets and live traps. Transects or grids can be established in different habitats throughout Iwokrama Forest and sampled in a similar routine to those employed in the observational transects. One major problem will be identification, which can be difficult for many species. Identification keys based on external characters (e.g., Lim & Engstrom 2001a) work well for some species but some groups require examination of cranial material. Identification of smaller mammals in the field by local biologists will require an extensive training programme.

An example of a group of small mammals that would be suited to further monitoring work is leaf-nosed bats of the subfamily Phyllostominae. Using voucher collections assembled in the initial survey, we have now documented 24 species of phyllostomine bats in Iwokrama Forest. This species richness is in line with recent inventories at Paracou in French Guiana (Simmons & Voss, 1998), Les Nouragues in French Guiana (Feer & Charles-Dominique 2001), and MCSE Reserves north of Manaus in Brazil (Sampaio et al. 2003). Phyllostomines are typically insectivores or carnivores that glean insects and small vertebrates off the ground, leaves, branches, or surfaces of water. These gleaning bats are particularly important to monitoring programmes for wet lowland forests because the species are sensitive to environmental disturbance and many species become uncommon or absent in disturbed forest (Fenton et al., 1992). This level of diversity is high compared to other areas in Central and South America and is attributable to the current pristine state of Iwokrama Forest. The continued presence, diversity and relative abundance of this group would serve as an important indicator of the health of Iwokrama Forest over time. In contrast, a few species of frugivorous (fruit-eating) bats are most common in secondary forests or clearings (e.g., *Sturnira lilium* and *Carollia perspicillata*) and we would expect their relative abundance and absolute numbers to increase in disturbed areas.

Potential for Commerce

The larger species of mammals, such as diurnal monkeys, agouti, deer, peccaries, tapir, and otters, are a potential draw for ecotourism in Iwokrama Forest. In addition, night- spotting can be an intriguing experience for ecotourists and species of interest for observation include labba, marsupials, armadillos, kinkajous, and olingos. Because many species are territorial, the probability of encountering them is higher if their behavioural patterns are investigated beforehand.

Bat demonstrations could also be used as a night-time component of ecotours. This would require that guides be trained in setting up mist nets in appropriate places, removing bats without harming them, correctly identifying them (at least to genus), and learning their natural history. For most eco-tourists, the chance to see a fruit-eating or nectar-feeding bat up close is fascinating and the exact identification of the species may be ancillary. The important role of bats in the ecosystem as seed dispersers, flower pollinators, and controllers of insect populations can be highlighted as the different bats are captured.

Although populations of some game animals may seem high in Iwokrama Forest (e.g., labba), we doubt there is any capacity for commercial harvesting beyond subsistence hunting as a dietary supplement for protein. We strongly recommend that no plan for commercial harvest of mammals in Iwokrama Forest be implemented. In other areas of the Neotropics, over-hunting has lead to extirpation or reduction to such low numbers that observation becomes happenchance.

Potential Threats

Conservation concerns include the potential for increasing colonization by people from the coast or from Brazil using the road that bisects Iwokrama Forest, encroachment on the periphery by surface miners working along the rivers with associated pollution and altered aquatic environments, and excessive hunting pressures on large mammals. Subsistence hunting should be regulated to ensure a sustainable harvest.

Of the 29 species of mammals in Guyana listed as endangered under CITES (Appendix I and II), 16 have been documented in Iwokrama Forest and an additional four species are expected to occur there (Table 5). A high proportion (31%) of the nonvolant (nonflying) mammals in Iwokrama are recognized as endangered worldwide because there are no mainland bats in the Neotropics that are included on the CITES lists. Thus Iwokrama Forest is one of the important and relatively well-studied reservoirs of Neotropical fauna in the eastern Guianas and should be integral in conservation initiatives in South America.

At present, it is difficult to predict the effects of forest use on the distribution and abundance of mammals in Iwokrama Forest. However, the Burro-Burro River Camp (Clearwater), which was the only site located within the Sustainable Utilization Zone (Hawkes & Wall, 1993), had one of the highest observed levels of species richness (57 species) among the 13 localities so far surveyed in Iwokrama. This site also yielded 7 of the 17 new species records for the country and had 4 of the 16 species that were documented only at one location (Table 2). The tall mixed forest in the Burro-Burro River plain provides not only diverse roosting habitats for many species of bats but also the best commercial forest in Iwokrama (Hawkes & Wall, 1993). Although more survey work needs to be done, we also believe that the higher altitude areas such as those near

Iwokrama Mountain may contain a diverse mammal fauna and one of the few areas where small terrestrial mammals are abundant.

Conclusions and Recommendations

Although the survey of mammals was in general highly successful, we believe the survey period was too short to provide a comprehensive assessment of total biodiversity and relative abundance. Moreover, we were unable to satisfactorily assess seasonal variation in distributions and abundances within Iwokrama Forest or to confidently document variation in occurrences of mammals among sites. Indeed we did not have enough time to visit all field camps or major sections of Iwokrama Forest, our time in most other camps was short, and we usually were able to obtain only one seasonal sample. Examination of the species accumulation curves (Fig. 4) and our estimates of actual species richness in Iwokrama, indicate that we are short of a goal of documenting 90 % of the overall fauna as suggested for robust, quantitative comparisons with other Neotropical sites (see Voss & Emmons, 1996). We estimated our survey to be approximately 70–80% complete, and that the total number of mammal species in Iwokrama falls between 162–187 species.

We recommend that inventories be continued to: (1) better document overall species richness in Iwokrama Forest; (2) accurately assess local variation in species richness and abundances of different groups of mammals among areas of Iwokrama Forest; and, (3) document seasonal variation among a few selected camps (including at least Burro-Burro River, Pakatau Falls, and one of the camps near Iwokrama Mountain).

These data would serve to provide a more thorough baseline for monitoring subsequent faunal changes, help set conservation priorities, and accurately document the unanticipated high species-level diversity in Iwokrama Forest. With additional fieldwork, Iwokrama Forest would become one of the two most completely inventoried sites for mammals in the Guianas (the other being Paracou, French Guiana) and as an exemplar, would serve as one of the most accurate indicators of species composition and richness in eastern Amazonia. From a more pragmatic perspective, the information gathered will provide an accurate basis for mapping wildlife populations in Iwokrama Forest, setting regional conservation priorities in northern South America, and stressing the critical importance of conserving large tracts of forest.

We recommend that the baseline survey of mammals be extended for two more years, consisting of two, 6–8 week survey periods per year (i.e., a total of four more field trips). These trips should be designed to: (1) extend the initial survey to all field camps, regions, and major habitat associations within Iwokrama Forest; (2) revisit 3–4 selected sites within Iwokrama Forest on each trip to assess seasonal and annual fluctuations in species richness and abundance; (3) thoroughly survey base sites to be used in subsequent monitoring studies; and (4) focus on designing methods and techniques designed to sample mammals missed in initial inventories, particularly in sites already well surveyed (e.g., Pakatau Falls).

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