

Utah State University

DigitalCommons@USU

---

All Graduate Theses and Dissertations

Graduate Studies

---

5-2009

## Terrestrial Small Mammals from the Gamba Complex in Gabon: Distribution Patterns and Landscape Influences

Carrie J. O'Brien  
*Utah State University*

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>



Part of the [Other Life Sciences Commons](#)

---

### Recommended Citation

O'Brien, Carrie J., "Terrestrial Small Mammals from the Gamba Complex in Gabon: Distribution Patterns and Landscape Influences" (2009). *All Graduate Theses and Dissertations*. 353.

<https://digitalcommons.usu.edu/etd/353>

This Thesis is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact [digitalcommons@usu.edu](mailto:digitalcommons@usu.edu).



TERRESTRIAL SMALL MAMMALS FROM THE GAMBA COMPLEX IN GABON:  
DISTRIBUTION PATTERNS AND LANDSCAPE INFLUENCES

by

Carrie J. O'Brien

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology  
(Wildlife Ecology)

Approved:

---

John A. Bissonette, Ph.D.  
Major Professor

---

William J. McShea, Ph.D.  
Committee Member

---

Douglas Ramsey, Ph.D.  
Committee Member

---

Byron Burnham, Ed.D.  
Dean of Graduate Studies

UTAH STATE UNIVERSITY  
Logan, Utah

2009

Copyright © Carrie J. O'Brien 2009

All Rights Reserved

## ABSTRACT

Terrestrial Small Mammals from the Gamba Complex in Gabon:  
Distribution Patterns and Landscape Influences

by

Carrie J. O'Brien, Master of Science

Utah State University, 2009

Major Professor: Dr. John A. Bissonette  
Department: Wildland Resources

The small mammal communities of central Africa are not well understood, and the southwestern section of Gabon has not been previously surveyed except for some recent work in Monts Doudou. At five sites within the Gamba Complex we set out to 1) document the species of terrestrial rodents (Muridae) and shrews (Soricidae) weighing less than 100 g, 2) compare the community composition between inland and coastal sites, and 3) evaluate our sampling protocols. Using a combination of pitfall lines, Sherman live traps, and snap traps we captured 721 individuals of 12 rodent and 10 shrew species in 15,792 trap-nights. The rodent community was dominated by *Hylomyscus stella* and the shrew community by *Sylvisorex johnstoni*, in agreement with nearby studies. The coastal sites were less diverse with 3 rodent species and 1 shrew species only found at inland sites. The inland Rabi site had the most diverse small mammal community due to 2 species captured in secondary forests and fields near the oil facility. Our use of pitfalls

was essential to our capture of shrews, and our protocol of switching from live to snap traps midway through the trapping period resulted in more species than expected.

The ecological factors influencing distribution patterns of small mammals in central Africa is not well understood. We evaluated the role of disturbance at paired inland and coastal sites using landscape variables generated from satellite imagery. Regression analyses revealed that while the amount of forest present at a site was strongly correlated with rodent richness ( $F = 16.437$ ;  $df = 1$ ;  $p = 0.001$ ), shrew richness was negatively correlated with the amount of roads (partial  $F = 12.232$ ;  $df = 1$ ;  $p = 0.007$ ) and rainfall (partial  $F = 6.035$ ;  $df = 1$ ;  $p = 0.036$ ) and positively with elevation (partial  $F = 6.832$ ;  $df = 1$ ;  $p = 0.028$ ). Our results suggest that while disturbance at Rabi has created additional habitats for rodents, the loss of specialist rodents from coastal sites reflects their inability to tolerate the edge-affected, fragmented, and less diverse forests in that region.

(70 pages)

## DEDICATION

To my parents, who nurtured my love of science from an early age.

## ACKNOWLEDGMENTS

I would like to thank the Smithsonian Institution Monitoring and Assessment of Biodiversity Program, Shell Foundation, Shell Gabon, and Utah State University for the funding and support provided to me throughout this study. I would also like to thank Dr. Patrick Barrière and Dr. Michael Carleton, who generously offered their time and expertise to identify my specimens. I am grateful to all of the Gabonese who helped in the field and the lab, especially Sylvain Guimondou. My thanks to Marius Burger and Olivier S.G. Pauwels, with whom I joined forces in the pitfall effort, and to Brian Schmidt and Christina Gebhard, who gave me tips and assisted me in my voucher specimen collection. I am also thankful to Melissa Songer for all of her hard work during the first trip. I am extremely grateful that Dr. Bill McShea gave me the opportunity to go to Gabon and then tirelessly offered his advice on this work. I also want to thank my committee member Dr. Douglas Ramsey for his time and helpful suggestions. My sincere gratitude goes to Dr. John A. Bissonette, my major professor, for always believing in me. His support and encouragement made all of the difference, and I couldn't have done this without him. I want to thank Sarah, who knew this was possible but did not see the end result. Most of all, I would like to thank my mother and sister for their loving support which kept me moving forward.

Carrie O'Brien

## CONTENTS

	Page
ABSTRACT .....	iii
DEDICATION .....	v
ACKNOWLEDGMENTS .....	vi
LIST OF TABLES .....	viii
LIST OF FIGURES .....	ix
CHAPTER	
1 INTRODUCTION .....	1
2 DISTRIBUTION PATTERNS AND EVALUATION OF SAMPLING TECHNIQUES .....	7
Introduction.....	7
Study Area .....	8
Materials and Methods.....	10
Results.....	12
Discussion.....	20
3 SPECIES RICHNESS AND LANDSCAPE INFLUENCES .....	26
Introduction.....	26
Materials and Methods.....	28
Results.....	38
Discussion.....	43
4 CONCLUSION.....	47
LITERATURE CITED .....	54

## LIST OF TABLES

Table		Page
2-1	Details of each survey location within the Gamba Complex, Gabon.....	13
2-2	List of insectivores (Soricidae) and rodents (Muridae) captured in the Gamba Complex, Gabon (February 2002 – April 2003).....	14
2-3	A comparison of species composition and relative abundance (percent) for insectivores captured in this study and in other regions of the Congo basin.....	16
2-4	A comparison of species composition and relative abundance (percent) for terrestrial rodent species captured in this study and in other regions of the Congo basin.....	17
3-1	Results of backwards stepwise logistic regression with six site variables and individual species presence or absence with bootstrapping.....	43

## LIST OF FIGURES

Figure	Page
2-1	Study locations in the Gamba Complex of southwestern Gabon, Africa.....9
2-2	Species accumulation curves for the four study locations.....19
2-3	Species accumulation curves for combined inland and coastal locations.....19
2-4	Mean number of individuals captured per 100 trap nights, grouped by Muridae and Soricidae, using pitfalls or a combination of live and snap traps.....20
2-5	Mean number of new species captured for each day during a 6-day period from rodent traps.....21
3-1	Study locations in the Gamba Complex of southwestern Gabon, Africa.....28
3-2	Average monthly rainfall, from 1985 – 2002, recorded by Shell at Rabi and Gamba .....29
3-3	Landcover classification map of Rabi with study sites surrounded by buffers .....34
3-4	Elevation layer for the Gamba Complex, with study locations in yellow.....36
3-5	Results of linear regression for rodent species richness and the amount of upland forest within the 500 m buffers.....39
3-6	Results of linear regression for rodent species richness and the amount of forest within the 500 m buffers.....39
3-7	Results of linear regression with shrew species richness and the amount of rainfall during the sampling period.....40
3-8	Results of linear regression for shrew species richness and the amount of roads within the 200 m buffers.....41
3-9	Results of linear regression for shrew species richness and elevation.....41

## CHAPTER 1

### INTRODUCTION

Disturbance in tropical forests leads to inter-correlated changes in vegetation structure. Human-initiated disturbance, often caused by logging operations or roads, is of growing concern worldwide. The resulting canopy destruction is associated with increased understory density, increased ground vegetation, and reduced sapling density in the road margin (Malcolm and Ray 2000). Treefall gaps, a natural disturbance, leads to similar changes. Disturbance, natural or unnatural, causes increased heterogeneity in forest structure. Gabon is known for its natural heterogeneity in habitat, with areas of savannas interspersed with strips of gallery forest and forest islands often in close proximity to continuous forest (Tutin et al. 1997). In Gabon, a patch of tropical rainforest can be extremely complex by having diverse vertical strata (August 1983), but very homogenous, i.e., low horizontal variation. Woodland savanna are less complex but very patchy.

Disturbance can lead to distinct changes in the small mammal community. Delany (1971) reported that local forest degradation led to an increase in rodent richness without necessarily losing species. Malcolm and Ray (2000) saw higher rodent abundances with increased understory density in the Central African Republic. The increase in rodent abundance in disturbed habitats was especially evident among forest species typically associated with treefall gaps and other secondary habitats (Malcolm and Ray 2000). Neotropical small mammals are also known to increase in abundance and species richness after disturbances such as fragmentation and logging (Lambert et al. 2006).

Community studies conducted along a gradient of disturbance suggested that the highest species diversity occurs in habitats with intermediate levels of disturbance frequency and intensity (Conde and Rocha 2006; Connell 1978).

Malcolm and Ray (2000) found that the ratio of *Hylomyscus* to *Praomys* within a small mammal community may provide a measure of regional forest degradation. They found that *Hylomyscus* occurs in relatively high proportions in interior primary forest and lower proportions in degraded areas, whereas *Praomys* is known to occur in secondary habitats. A threshold may be apparent where low disturbance leads to higher abundances, but as degradation increases, *Hylomyscus* declines (Malcolm and Ray 2000). This suggests forest small mammal communities vary as function of the degree of disturbance in the surrounding landscape.

Possible explanations for these community effects include changes in species-specific predation pressure, increased competition, and species-specific changes in resource abundance. In the Amazon, Lambert et al. (2006) found that insect biomass was highest in disturbed or edge-affected areas. Beck et al. (2004) quantified resource availability in treefall gaps in the Amazon. Many plants in gaps produce more fruits than when in the understory (Bullock 1980; Denslow et al. 1986; Levey 1990). Examination of fauna in treefall gaps have found a greater richness of birds (Levey 1988; Schemske and Brokaw 1981). In Africa, several terrestrial rodents were found to have higher densities in treefall gaps while others had higher densities in the understory (Lwanga 1994; Struhsaker 1998). Beck et al. (2004) found no difference in resource density between gaps and the understory. One rodent species had higher survival and per capita recruitment in understory than in gaps, while the reverse was true for another rodent

species. These results suggest that small mammals have species – specific resource and habitat requirements (Lambert et al. 2006; Beck et al. 2004).

Small mammals may be selecting habitats with increased heterogeneity because of a variety of different resources and a reduction in interspecific competition. Regardless, this appears to result in the coexistence of a larger number of ecologically similar species (Conde and Rocha 2006). Williams et al. (2002) found that vegetation complexity had a strong effect on the composition of a small mammal communities present at a sampling point, whereas vegetation heterogeneity best explained patterns of species richness. In Lopé, Gabon, a diverse assemblage of large mammals was found using the the patches of forest that were located in open grassland. This is surprising since the species are associated with forest habitats (Tutin et al. 1997). It appears that the large mammals were willing to travel across open grassland to visit the forest fragments. In central Amazonia, the richness of small mammals increased in forest fragments, with few if any species lost when compared to continuous forest (Gascon et al. 1999). Some species associated with the matrix (grassland) occasionally invaded the fragments (forests), contributing to the increase in richness. Animal communities that were able to use the matrix tended to increase or remain stable in forest fragments, whereas those that avoided the matrix (i.e. forest specialists) often declined or disappeared (Gascon et al. 1999). Therefore, differences in habitat preferences among species appears to account for which species are able to take advantage of increased habitat heterogeneity.

Other than disturbance, small mammal community composition in tropical ecosystems may change according to gradients in elevation and rainfall. While some surveys in African montane zones show an increase in species richness and endemism

with elevation (Yalden 1988), others (Austin et al. 1992; Kasangaki et al. 2003; Misonne 1963) found decreasing small mammal richness with altitude. Goodman and Hutterer (2004) surveyed three elevation zones on Monts Doudou in the Gamba Complex, Gabon and found the highest richness and capture rates of insectivores in the lowest zone. However, this study did not represent a large elevation change (110 m to 625 m, summit 650 m) compared to other studies with elevation gradients that both start and end at higher altitudes. In a review of the literature, McCain (2005) found that 49% of studies involving elevation gradients showed the highest richness of fauna at mid-elevations. Small mammals may be responding to climatic factors directly (i.e., by tracking temperatures) or indirectly by tracking vegetative traits that respond to climate (McCain 2005). Other recent studies in Costa Rica (McCain 2004) and Madagascar (Goodman and Rasolonandrasana 2001) have found mid-elevation peaks in richness for small mammals.

Tropical forests in central Africa show seasonal variability in rainfall, relative humidity, leaf and fruit fall, and leaf litter depth. Because many small mammals show seasonal variations in abundance and breeding activity, community composition and structure differs seasonally (Dieterlen 1986; Duplantier 1989; Nicolas et al. 2005; Nicolas and Colyn 2003). Studies on insectivores suggest that trap success of shrews is at a minimum during the dry season (Barrière et al. 2000; Lasso et al. 1996). A recent study of insectivores in Moukalaba – Doudou National Park, Gabon found that trap success was minimal during the long dry season (July), and at a maximum during the short rainy season (March – May; Nicolas et al. 2005). While some insectivores showed more seasonality than others, the four most abundant shrew species were captured in nearly all months and *Sylvisorex johnstoni* remained dominant throughout the year (Nicolas et al.

2005). A different pattern emerged for rodents, with abundances peaking around the dry season (Nicolas and Colyn 2003; Ray 1998). In contrast with the insectivores, Nicolas and Colyn (2003) found that the dominant rodent species in Moukalaba - Doudou varied seasonally, with *Hylomyscus stella* dominant or co-dominant in the short rainy or long dry season and *Hybomys univittatus* dominant or co-dominant in the long rainy or short dry seasons. Trap success of shrews may be at minimum during the dry season because they enter torpor as a means of coping with scarce resources. Rodents may be more vulnerable to being trapped during the dry season because of their increased movement activity in search of limited resources.

### **Goals and Objectives**

My main objective in this thesis is to address whether differing levels of disturbance can explain patterns of small mammal community composition across the Gamba Complex, or whether abiotic factors like elevation and rainfall can better explain these patterns. The Gamba Complex is a good place to explore this question because there is a diverse assemblage of small mammals present and the study locations had varying degrees of disturbance. Of the three inland locations, there is one site with old but continuous disturbance (Rabi), one site with new disturbance (Toucan), and one site with little to no human disturbance (Moukalaba-Doudou). While the two coastal sites both had natural fragmentation, one site was highly disturbed (Gamba) and the other had little to no disturbance (Loango).

In 2000, the Smithsonian Institution's Monitoring and Assessment of Biodiversity Program (SIMAB), with support from Shell Foundation and Shell Gabon, began to

design a biological survey of the Gamba Complex in collaboration with local stakeholders, government, and industry. An inventory and monitoring program was developed with the goal of encouraging environmentally friendly resource extraction while promoting the conservation of biodiversity. As part of a team of biologists conducting the biological assessment, I conducted five small mammal surveys in the Gamba Complex in 2002 – 2003. The results of my work are reported in this thesis. In chapter 2, I discuss the results of the small mammal trapping, evaluate the success of the trapping methodologies, and compare the results to other small mammal studies in central Africa. In chapter 3, I used satellite imagery to generate habitat variables at the study locations to investigate whether patterns of small mammal richness across the Gamba Complex can be explained by differing levels of disturbance or by abiotic factors such as elevation and rainfall. Chapter 1 is an introduction to the issues that I address in chapters 2 and 3 and chapter 4 summarizes the results of my research.

## CHAPTER 2

### DISTRIBUTION PATTERNS AND EVALUATION OF SAMPLING TECHNIQUES

#### Introduction

The Guineo-Congolian region encompasses 2.8 million km<sup>2</sup> of lowland rainforest stretching from the coastal regions of West Africa to the eastern part of the Democratic Republic of Congo (White 2001). The region is renowned for both its plant and animal diversity, with 8000 species of plants (80% endemic) and 270 species of lowland mammals belonging to 120 genera (Grubb 2001; White 2001). Gabon, in the heart of the Guineo-Congolian region, has over 88% of its original tropical moist forest remaining, which is the highest of all West, Central, and East African rainforest countries (Naughton-Treves and Weber 2001).

While there have been repeated surveys of large mammals in the region (Boddicker et al. 2006; Happold 1996; Hart 2001; Lahm et al. 2006; Muchaal and Ngandjui 1999; Ray 2001; Turkalo and Fay 2001; White 1994; Whitesides et al. 1988), only in recent years have terrestrial small mammal communities received the same attention. Surveys in northeastern Gabon (Brosset 1988; Duplantier 1982; Duplantier 1989; Goodman et al. 2001), central Gabon (Barrière and Colyn 1997; Nicolas and Colyn 1999), the Central African Republic (Barrière et al. 2000; Malcolm and Ray 2000; Morvan et al. 1999; Ray and Hutterer 1995), the Democratic Republic of Congo (Barrière and Colyn 1997; Dieterlen 1986; Dudu et al. 2005; Gubista 1999; Nicolas and Colyn 1999), Cameroon (Barrière and Colyn 1997; Nicolas and Colyn 1999) and Equatorial Guinea (Lasso et al. 1996) have demonstrated a diverse small mammal community. The

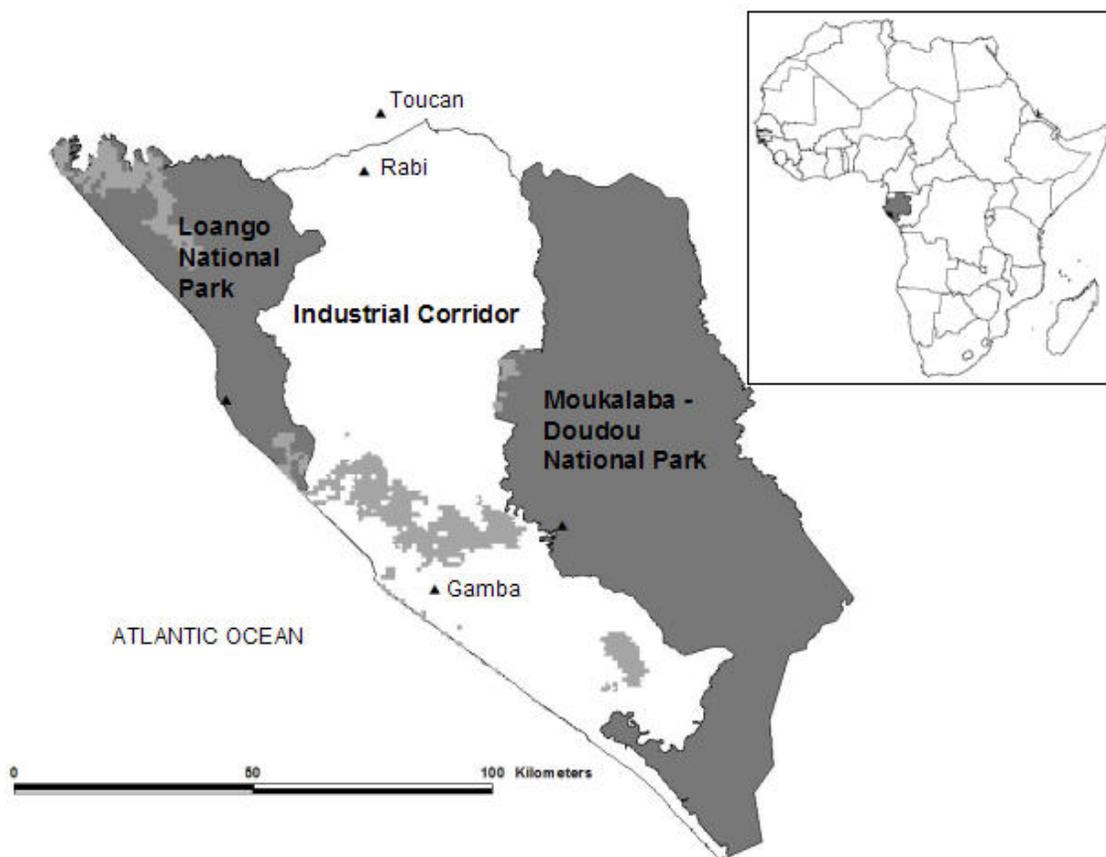
southern section of Gabon, including the Gamba Protected Areas Complex, has not been comprehensively surveyed, except for some recent work in the Monts Doudou area (Goodman and Hutterer 2004; Nicolas and Barrière 2001; Nicolas et al. 2004).

In this paper, we document species of terrestrial insectivores (Soricidae) and rodents (Muridae) weighing less than 100 g that occur in the Gamba Complex, compare faunal composition between coastal and inland sites, and test the success of different sampling protocols. In addition, we discuss our findings in the context of other mammal surveys conducted in lowland rainforests of Central Africa.

### Study Area

The Gamba Complex in southern Gabon is comprised of the Ndogo lagoon and its drainages and encompasses over 11,000 km<sup>2</sup> of coastal and inland rainforest. The altitude is less than 1000 m except for a few higher peaks, and the rainfall averages 1600-2000 mm per year. The major habitat types within the complex include coastal scrub forest, mangrove forest, savannah, seasonally flooded forest, and upland forest. The complex is the focus of conservation efforts due to its abundance of large mammal species including elephant (*Loxodonta africana cyclotis*), buffalo (*Syncerus caffer nanus*), hippopotamus (*Hippopotamus amphibius*), gorilla (*Gorilla gorilla gorilla*), and chimpanzee (*Pan troglodytes troglodytes*).

All small mammal trapping was centered around five focal areas: two recently-named national parks (Loango and Moukalaba – Doudou), the township of Gamba, and the Shell Gabon oil concessions in Rabi and Toucan (Fig. 2-1). Both the Loango and Gamba sampling areas were within five km of the coast, while the remaining sites were



**FIG. 2-1.**—Study locations in the Gamba Complex of southwestern Gabon, Africa

greater than 20 km from the coast. Each of these locations was sampled during 2002-2003 (Table 2-1). Most of the sampling was conducted in forest; forested sites comprised more than 90% of the trapping effort. The trapping effort was relatively similar among sites, with the exception of surveys near Gamba which were  $2/3$  that of the other sites. The Rabi, Toucan, and Gamba areas had a system of roads that was used to access study sites. The location of all survey sites was marked with a GPS and each survey line was placed into one of the habitat classes discussed above.

## Materials and Methods

### **Trapping protocol and voucher specimens**

Pitfall traps were used to document insectivores or animals rarely trapped in live traps using a protocol similar to other projects in Gabon (Goodman et al. 2001; Goodman and Hutterer 2004; Nicolas and Colyn 2006) and in other tropical regions (Hice and Schmidly 2002; Laurance 1992; Lyra-Jorge and Pivello 2001). The pitfall traps consisted of 20-liter plastic buckets sunk so that their rims were flush with the ground. The buckets measured 355 mm deep, 295 mm diameter at the rim and 255 mm diameter at the base. Small drainage holes were punched in the base of the buckets. We created a 100 m pitfall line by placing 11 buckets 10 meters apart. A 0.5 m high drift fence was erected vertically across the tops of the buckets by stapling plastic sheeting onto wooden stakes. The base of the fence was covered with soil and leaf litter to encourage animals to travel along the fence (instead of under it) and towards the buckets. Three lines of pitfall traps were positioned at each site. The pitfall lines were operated for a period of seven nights, for a total of 231 trap-nights (11 buckets x 3 lines = 33; 33 buckets x 7 nights = 231) and were checked each morning.

Additionally, 26 Sherman live traps spaced approximately 5 m apart were placed in lines, with 3 lines at each site. The traps measured 10 x 6 x 6 cm and were baited with a mixture of peanut butter and oats. After three nights the Sherman traps were replaced with snap traps (an equal number of museum specials and Victor rat traps) baited with peanut butter. The traps at each site were run for 6 nights, for a total of 468 trap-nights (26 traps x 3 lines = 78; 78 traps x 6 nights = 468). The traps were checked each morning

and re-baited as necessary. Twenty-four sites were surveyed in the Gamba Complex, and 16 of those sites contained pitfall lines.

All animals found dead in the traps and the first captures of each potentially new species at a site were prepared as voucher specimens. All other animals were released. Specimens were prepared either as standard museum skins with associated skulls and skeletons, as fluid-preserved specimens, or as full skeletons. Tissue samples were collected from all specimens and are housed at the Natural Science Resource Laboratory at Texas Tech University in Lubbock, TX. The specimens are deposited at the Smithsonian National Museum of Natural History (USNM) in Washington, DC and with the Gamba Biodiversity Program in Gamba, Gabon. Species identification for insectivores was determined by Patrick Barriere at the University of Rennes 1 in Paimpont, France; rodents were identified by Michael Carleton at USNM.

### **Taxonomical conventions**

Taxonomy of small mammals in the region is challenging due to the limited number of specimens and the existence of phenotypically similar species. Recent work with the shrews (Family Soricidae) has led to taxonomical revisions (Qu  rouil et al. 2001; Qu  rouil et al. 2006) and the naming of new species (Hutterer et al. 2001). Of particular concern are the three following Crocidura complexes: *hildegardeae* (composed of *C. hildegardeae*, *C. denti*, and *C. attila*), *poensis* (composed of *C. poensis*, *C. batesi*, and *C. nigrofusca*), and *olivieri* (composed of *C. olivieri*, *C. goliath*, and *C. mutesae*), which are in urgent need of revision (Qu  rouil et al. 2006).

The rodent species found within the Guineo-Congolian region have the same challenges with recent revisions of *Praomys* (Lecomte et al. 2002; Volobouev et al. 2002) and *Hylomyscus* (Quérrouil 2001). There is much work to be done to clarify this diverse assemblage of species that overlap in distribution. An inventory within the Gamba Complex would provide needed information for additional taxonomic study and contribute toward a clearer geographical understanding of these species complexes.

I adopted several conventions in listing certain species names in the text and tables. The designation "cf." (as in *Crocidura cf. denti*) suggests that the specimen(s) best fit within the morphological variation described for the named species, but could, under further examination, represent a different species. "*Crocidura poensis* complex" (Table 2-3) is used to represent *C. cf. poensis* and *C. batesi*, while "*Praomys tullbergi* group" (Table 2-4) suggests the potential presence of both *P. tullbergi* and the recently-described *P. petteri* (Lecomte et al. 2001; Nicolas and Colyn 2003; Van der Straeten et al. 2003).

Incidental captures included *Chlorotalpa leucorhina* (1), *Graphiurus* sp. (3), *Potamogale velox* (1), and *Cricetomys emini* (2).

## Results

A total of 721 individuals of 12 rodent and 10 insectivore species were captured in 15,792 trap-nights (Tables 2-1 and 2-2).

### **Comparison of species composition between coastal and inland sites**

While several species were found in all five study locations, four species were missing from the coastal sites. Three rodent species (*Deomys ferrugineus*, *Hybomys*

**TABLE 2-1.**—Survey locations within the Gamba Complex, Gabon.

Site	Location	Elevation Range (m)	Dates Surveyed	Trap Nights	Number of Rodent Species (Muridae) <sup>1</sup>	Number of Insectivore Species (Soricidae) <sup>1</sup>
Rabi	inland	51 - 92	2/19 – 3/14/02	3666	12	9
Toucan	inland	35 - 86	5/29 – 6/13/02 <sup>2</sup>	3484	10	8
Loango	coastal	9 - 33	10/25 – 11/9/02 <sup>3</sup>	3501	5	6
Gamba	coastal	14 - 38	11/13 – 11/28/02	2097	4	4
Moukalaba-Doudou	inland	25 - 173	3/27 – 4/16/03	3033	10	8
<b>TOTAL</b>				<b>15792</b>	<b>12</b>	<b>10</b>

<sup>1</sup>does not include incidental captures, i.e. *Chlorotalpa*, *Potamogale*, *Graphiurus* or the large murid *Cricetomys*

<sup>2</sup> one site surveyed 2/28 – 3/6/02

<sup>3</sup> first pitfall surveyed 9/27 – 10/3/02

*univittatus*, and *Lophuromys nudicaudus*) and one insectivore (*Paracrocidura schoutedeni*) were only captured at inland locations (Table 2-2, shaded columns). We did not find any small mammal species unique to the coastal region. The 2 coastal locations were each dominated by a different rodent species; in Loango, *Praomys tullbergi* while in Gamba, *Malacomys longipes*. Both *P. tullbergi* and *M. longipes* were minor components of the rodent community elsewhere in the Gamba Complex. Overall, the most common rodent species was *Hylomyscus stella* and the most common shrew species was *Sylvisorex johnstoni*. The most diverse small mammal community was found at Rabi, primarily because of two species captured in secondary forests and fields around the oil facility. Two individuals of *Stochomys longicaudatus* were captured in the secondary growth surrounding oil production at Rabi, and *Mus minutoides* was present around human camps and development at Rabi and Gamba. Our sole capture of *Sylvisorex konganensis*, a recently-named species (Ray and Hutterer 1995), was high on a slope in

**TABLE 2-2.**—Insectivores (Soricidae) and rodents (Muridae) captured in the Gamba Complex, Gabon (February 2002 – April 2003). Shaded locations are inland sites. Individuals captured during other times are listed as incidental (I).

Scientific Name	Common Name	Mean Adult Weight (g)	Total No. Captured	No. Captured per Location				
				Rabi	Toucan	Loango	Gamba	Moukalaba - Doudou
<b>Soricidae<sup>1</sup></b>								
<i>Crocidura batesi</i>	Bates' shrew	10.5	10	5	2	2	I	1
<i>Crocidura crenata</i>	Jumping white-toothed shrew	8.2	38	11	17	2	I	8
<i>Crocidura dolichura</i>	Long-tailed musk shrew	7.0	10	2	8		I	
<i>Crocidura goliath</i>	Giant forest shrew	50.8	20	4	3	5	6	2
<i>Crocidura grassei</i>	Grasse's forest shrew	10.2	6	1		1		4
<i>Paracrocidura schoutedeni</i>	Lesser large-headed shrew	9.3	10	6	1			3
<i>Suncus remyi</i>	Remy's pygmy shrew	1.8	5	2	2		1	
<i>Sylvisorex johnstoni</i>	Pygmy forest musk shrew	2.9	98	24	33	11	23	7
<i>Sylvisorex c.f. konganensis</i>	unknown – recently discovered	5.0	1					1
<i>Sylvisorex ollula</i>	Greater forest musk shrew	13.6	34	4	20	2	3	5
<b>Muridae<sup>1</sup></b>								
<i>Deomys ferrugineus</i>	Congo forest mouse	50.8	23	2	7			14
<i>Grammomys rutilans</i>	Shining thicket rat	54.4	6	2	3		I	1
<i>Heimyscus fumosus</i>	African smoky mouse	20.8	33	3	7	7		16
<i>Hybomys univittatus</i>	Peter's striped mouse	51.9	43	14	13			16
<i>Hylomyscus aeta</i>	Beaded wood mouse	22.8	11	3	6	1		1
<i>Hylomyscus parvus</i>	Little wood mouse	13.2	33	3	11	8	4	7
<i>Hylomyscus stella</i>	Stella wood mouse	17.4	172	13	80	33	8	38
<i>Lophuromys nudicaudus</i>	Fire-bellied brush-furred rat	32.1	9	6	1			2
<i>Malacomys longipes</i>	Long-footed rat	80.8	32	3	6	I	17	6
<i>Mus minutoides</i>	Pygmy mouse	7.8	28	28			I	
<i>Praomys tullbergi</i>	Tullberg's soft-furred rat	31.7	93	2	2	74	2	13
<i>Stochomys longicaudatus</i>	Target rat	71.1	2	2				
<b>TOTAL</b>			<b>717</b>					

<sup>1</sup> does not include incidental species, i.e. *Chlorotalpa*, *Potamogale*, *Graphiurus*, or the large murid *Cricetomys*

Moukalaba - Doudou. The site had an elevation of 173 m, while the average elevation of sampled sites excluding Moukalaba - Doudou was 41.5 m.

The Soricidae captured in the Gamba Complex ranged in size from the tiny *Suncus remyi* (1.8 g) to the large *Crocidura goliath* (50.8 g). The *Crocidura* are the most successful group of African shrews, and also the most widespread (Delany and Happold 1979). However, of the four Soricidae genera we observed in the complex (viz., *Crocidura*, *Paracrocidura*, *Sylvisorex*, and *Suncus*), the diminutive *Sylvisorex johnstoni* dominated the shrew community at each study location. *Sylvisorex johnstoni* comprised 42% of all shrew captures, followed by *S. ollula* and *Crocidura crenata* (both about 15%) (Table 2-3).

The Muridae is the largest family of rodents, with approximately 1,335 species (Nowak 1999). The murid rodents *Hylomyscus stella* and *Praomys tullbergi* comprised the majority of captures overall (35 and 19%, respectively) and were found at each study location (Table 2-2, Table 2-4). The Muridae are typically frugivorous or omnivorous. An exception is the link rat, *Deomys ferrugineus*, the only insectivorous rodent captured (Happold 1996). The majority of the Muridae are terrestrial, with the exception of the arboreal *Grammomys rutilans* and the three species of *Hylomyscus* captured in this study (Happold 1996). While the *Hylomyscus* are considered arboreal, *H. stella* in particular makes frequent use of the forest floor (Happold 1996).

**TABLE 2-3.**— A comparison of species composition and relative abundance (percent) of insectivores captured in this study and in other regions of the Congo basin. Studies are listed in order of their spatial proximity to the Gamba Complex. The total number of individuals captured is listed at the bottom of each column. For species where abundances were not given, we have indicated their presence with an “X”.

Species	This study	Monts Doudou, Gabon <sup>1</sup>	Monts Doudou, Gabon <sup>2</sup>	Minkebe, Gabon <sup>3</sup>	Makoukou, Gabon <sup>4</sup>	Equatorial Guinea <sup>5</sup>	Ngotto Forest, CAR <sup>6</sup>
<i>Sylvisorex ollula</i>	14.6	10.1	9.7	17.2	5.1	11.6	9.3
<i>Sylvisorex johnstoni</i>	42.1	30.4	41.0	6.9	15.2	30.8	25.0
<i>Crocidura poensis</i> complex	4.7	10.1	10.9	3.5	50.0	3.8	13.3
<i>Paracrocidura schoutedeni</i>	4.3	X	13.5	13.8		15.4	17.6
<i>Crocidura goliath</i>	8.6	1.3	5.0	17.2	1.9	3.8	0.08
<i>Crocidura crenata</i>	16.3	16.4	6.2	10.3	7.6		8.1
<i>Crocidura dolichura</i>	4.3	2.5	3.6	3.5	8.9	3.8	8.4
<i>Crocidura grassei</i>	2.6	X	9.1	6.9	3.1	3.8	0.08
<i>Suncus remyi</i>	2.1	1.3	1.0	3.5	5.1		3.6
<i>Crocidura</i> cf. <i>mutusae</i>							0.3
<i>Crocidura</i> cf. <i>nigrofusca</i>							0.08
<i>Crocidura</i> cf. <i>denti</i>							0.9
<i>Crocidura hildegardae</i>							0.08
<i>Crocidura ludia</i>							0.6
<i>Congosorex verheyeni</i>							1.8
<i>Crocidura olivieri</i>				13.8	3.1	27.0	9.4
<i>Crocidura maurisca</i>				3.5			
<i>Sylvisorex konganensis</i>	0.4						0.8
<b>Total Captured</b>	233	79	503	29	158	26	1350

<sup>1</sup>Goodman and Hutterer 2004, <sup>2</sup>Nicolas *et al.* 2004, <sup>3</sup>Goodman *et al.* 2001, <sup>4</sup>Brosset 1988, <sup>5</sup>Lasso *et al.* 1996, <sup>6</sup>Barrière *et al.* 2000

**TABLE 2-4.**— A comparison of species composition and relative abundance (percent) of terrestrial rodent species captured in this study and in other regions of the Congo basin. Studies are listed in order of their spatial proximity to the Gamba Complex. The total number of individuals captured is listed at the bottom of each column. Our incidental captures of *Cricetomys* are included in Table 2-4 because the species was reported in Malcom and Ray's (2000) study.

Species	This study	Monts Doudou, Gabon <sup>1</sup>	Makoukou, Gabon <sup>2</sup>	Central African Republic <sup>3</sup>	Democratic Republic of Congo <sup>4</sup>	Democratic Republic of Congo <sup>5</sup>
<i>Cricetomys emini</i>	0.4			2.2		
<i>Deomys ferrugineus</i>	4.7	2.7	11.1	3.9	6.8	4.4
<i>Grammomys rutilans</i>	1.4	0.2	0.4	2.8	0.4	
<i>Heimyscus fumosus</i>	6.7	10.6	11.5	3.5		
<i>Hybomys univittatus</i>	9.0	17.6	3.1	10.0		21.1
<i>Hylomyscus aeta</i>	2.2	0.5		9.7		
<i>Hylomyscus parvus</i>	6.7	0.3	2.6			
<i>Hylomyscus alleni</i> – <i>stella</i> group	35.1	40.2	58.1	33.3	14.5	40.0
<i>Lophuromys nudicaudus</i>	1.8	0.9		0.4		
<i>Praomys tullbergi</i> group	19.2	21.5	12.0	32.6		
<i>Stochomys longicaudatus</i>	0.4	0.1	0.5	1.6	4.9	
<i>Malacomys longipes</i>	6.5	5.4			13.0	1.1
<i>Mus minutoides</i>	5.7				0.9	5.6
<i>Lemniscomys striatus</i>					1.2	
<i>Oenomys hypoxanthus</i>					2.1	2.2
<i>Lophuromys flavopunctatus</i>					7.8	2.3
<i>Praomys jacksoni</i>					22.2	23.3
<i>Lophuromys sikapusi</i>			0.7			
<i>Hybomys lunaris</i>					24.9	
<i>Lophuromys luteogaster</i>					0.9	
<i>Colomys goslingi</i>					0.4	
<b>Total Captured</b>	490	1155	549	1163	3541	90

<sup>1</sup>Nicolas *et al.* 2004, <sup>2</sup>Duplantier 1989, <sup>3</sup>Malcolm and Ray 2000, <sup>4</sup>Dieterlen 1986, <sup>5</sup>Gubista 1999

## Evaluation of sampling protocols

Examination of the species accumulation curves for each location indicates that sampling intensity was sufficient to characterize the small mammal community (Fig. 2-2). When the species accumulation curves were grouped into inland and coastal categories, the cumulative number of new species reached its peak around 5,000 trap-nights in each category (Fig. 2-3).

Pitfall lines and traps did not equally sample the small mammal community (Fig. 2-4). Although there was no significant difference for rodents, there were significantly more insectivores captured in pitfalls than Sherman or snap traps. This difference might be partially due to the smaller size range of insectivores, but a general linear model of capture rates showed weight was not a significant determinant (partial  $F = 1.83$ , d.f. = 1,  $P = 0.18$ ). Trap type (partial  $F = 9.78$ , d.f. = 1,  $P = 0.002$ ) and the interaction between trap type and animal taxonomy (partial  $F = 28.07$ , d.f. = 1,  $P < 0.001$ ) explained the greatest amount of variability in capture frequency (multiple  $r^2=0.212$ ).

A closer examination of the role of pitfalls in influencing rodent species richness estimates suggested that species-specific differences in capture rates may be important. At the 15 sites containing both pitfalls and live and snap traps, for 6 out of the 10 rodent species present the pitfall captures can be excluded without causing a loss in species richness. Two relatively uncommon rodent species (*Heimyscus fumosus*, present at 6 of 15 sites; *Hylomyscus aeta*, present at 5 of 15 sites) were missing from one site each if pitfall captures were excluded, and one rare rodent species (*Lophuromys nudicaudus*, present at 4 of 15 sites) was captured exclusively in pitfalls. Pitfalls seem to be of

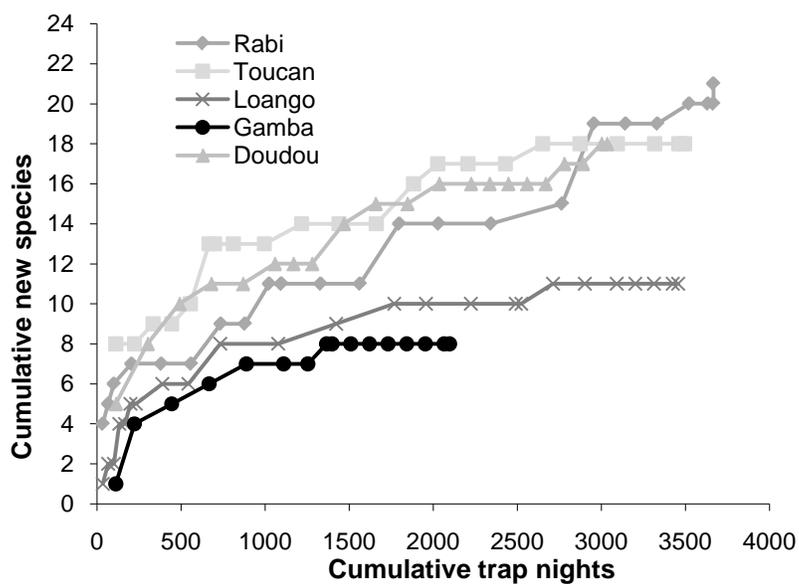


FIG. 2-2.—Species accumulation curves for the five study locations.

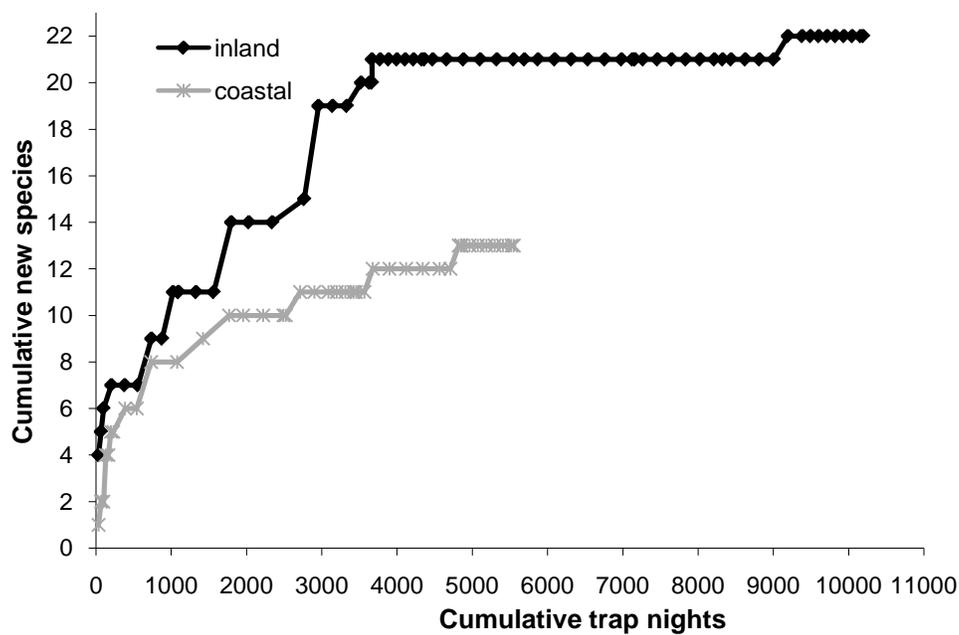
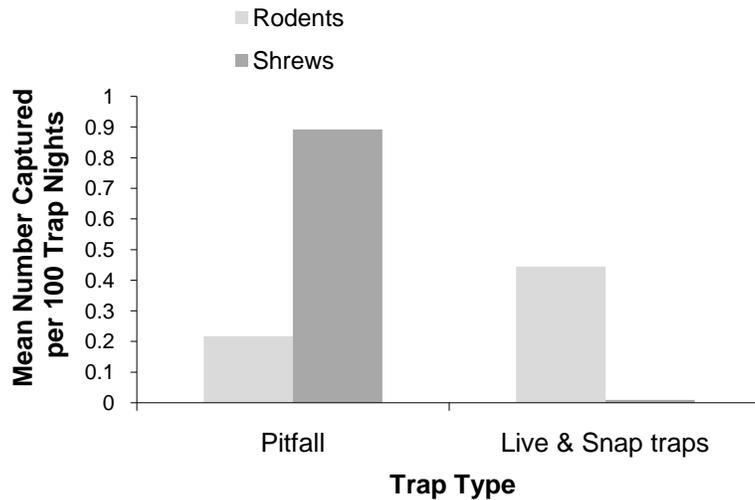


FIG. 2-3.—Species accumulation curves for combined inland and coastal locations.



**FIG. 2-4.**—Mean number of individuals captured per 100 trap nights, grouped by Muridae and Soricidae, using pitfalls or a combination of live and snap traps.

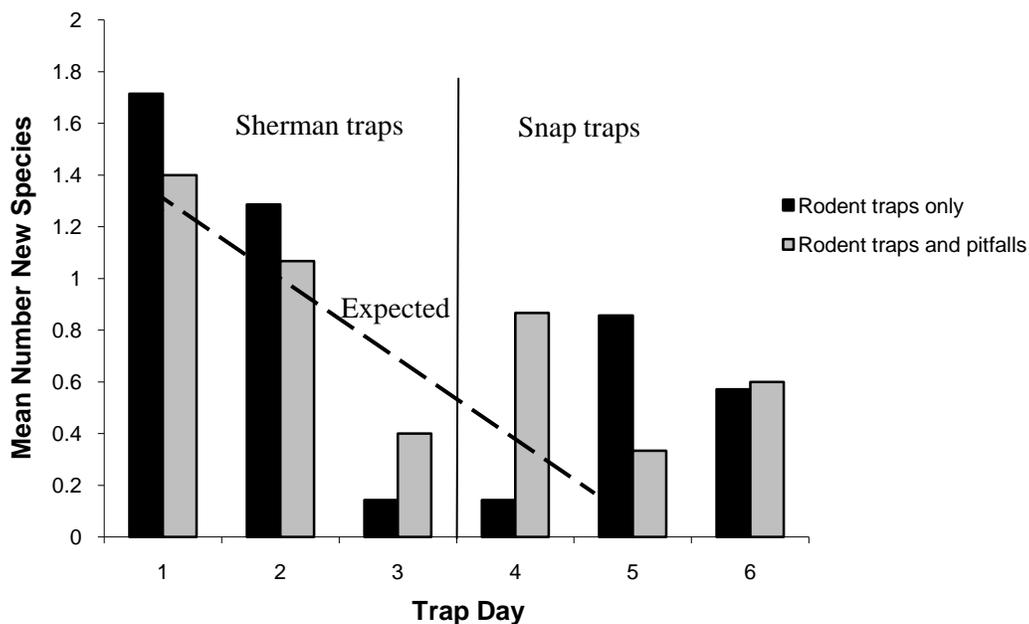
particular importance to one rodent species (*Hylomyscus parvus*, present at 11 of 15 sites), which was missing from 4 sites when pitfall captures were excluded.

The trapping protocol called for three days of live-traps followed by 3 days of snap-traps. We used this protocol at sites that contained pitfalls (Fig. 2-5, gray bars) and at sites with only traps (Fig. 2-5, black bars). In both sets of trapping sites, the number of new species captured increased with the transfer from live to snap-traps, contrary to expectations.

## Discussion

### Distribution and diversity

The distribution of mammals is not consistent across the Congo basin, with obvious concentrations in mammal species richness that are not due to obvious physical



**FIG. 2-5.**—Mean number of new species captured for each day during a 6-day period from rodent traps. For the first 3 days, Sherman live-traps were used. During the remaining 3 days, the live-traps were replaced with snap-traps. The dashed line represents the expected pattern of a gradual drop-off in new species captured during the trapping period, assuming that Sherman and Snap traps have equivalent effectiveness.

or landscape barriers (Happold 1996). Two main theories have been used to explain the distribution of mammalian species richness within the Guineo-Congolian region. First, the current distribution of mammals in the region may be due to contractions and expansions of the rainforest zone over evolutionary time. Glaciations in the northern hemisphere led to dry conditions in the tropics, so rainforests contracted to a few isolated refugia (Happold 1996). Interglacial periods led to expansions of the forest outwards from the refugia, and fauna from previously isolated refugia could become sympatric. This pattern of contraction and expansion may have assisted in speciation (Happold 1996) and several areas within the region have been identified as potential refugia for high species richness. Apart from scattered montane refuges, some argue for the

existence of a major fluvial refuge in the Congo Basin (Colyn et al. 1991; Colyn and Deleporte 2002; Grubb 2001). Rivers are often barriers to ranges or mark vicariance (fragmentation of the environment) of taxa within forest zones, especially for primates.

A second theory is that the high mammalian diversity in the Guineo-Congolian region reflects high plant species diversity (Campbell et al. 2006). One hectare plots in the region can contain more than 100 tree species (Delany and Happold 1979).

Additionally, the abundance and diversity of vegetation, along with the vertical stratification of the forest, results in the creation of “niches” by the many forest mammal species in the area (Delany and Happold 1979). Different species within a taxon use different strata of the rainforest or spend a different proportion of their time in each strata. The Makokou area in northeastern Gabon recorded 124 species of mammals, with rodents composing about 25% of the total species (Happold 1996). Mammal species richness in the Guineo-Congolian rainforest is similar to that of rainforests in other parts of the world; for example Wilson (1983) recorded 137 mammal species for a rainforest in Costa Rica.

### **Comparison of trapping protocols**

Small mammal surveys in the Gamba Complex were conducted using pitfalls, Sherman live-traps, and snap-traps. Pitfalls are an effective method of sampling terrestrial small mammals, especially shrews that are rarely taken in conventional traps (Williams and Braun 1983). The size of the pitfall bucket is critical in the capture of African soricids, with larger pitfall buckets being more effective at capturing and retaining a wider variety of shrews (Goodman et al. 2001; Goodman and Hutterer 2004). An

examination of the mean number of rodents and shrews captured per 100 trap nights in either traps or pitfalls found distinct differences based on taxonomy. While more rodents were captured in traps than in pitfalls, the difference was not significant. Shrews were much more effectively sampled using a pitfall design, and the effect did not seem to depend on weight. Perhaps their limited vision and their feeding habits (i.e., attraction to insects in the litter and perhaps the ones that have fallen into the buckets) make them more susceptible to capture in pitfalls.

A second component of our protocol was to replace live-traps with snap traps after three days at a location. This change increased the number of species captured. While we expected that the number of new species captured in live traps should gradually decrease over the six days of trapping at a location, there was an increase in new species in days 4 through 6. Switching to snap traps resulted in more species than we would expect if we used live-traps alone.

The species accumulation curves for our four survey locations revealed that our technique was effective for sampling the small mammal community. The most striking pattern was that the inland sites had a higher average richness than coastal sites. The lower species richness in the coastal sites was mostly due to the absence of the rodents typical of inland forest communities, i.e., *Hybomys*, *Deomys*, and *Lophuromys*. We did not find any rodents typical of the savanna, including *Lemniscomys striatus*, *Mastomys* sp., *Pelomys* sp., or *Lophuromys sikapusi*. Likewise we did not find any shrews that inhabit the savanna or disturbed forest, for example *Crocidura olivieri* and *C. cf. denti*. We were surprised to find a low species richness considering the diversity of habitats found in the coastal region (i.e., savannah, scrub forest, mangrove forest, and gallery

forest). However, coastal forests in Gabon are known to be poor in terms of the diversity and abundance of fruiting plant species (Lahm, pers. comm.). Therefore the carrying capacity of the environment for frugivorous murid rodents may be lower than in inland forests. Some lowland forests were populated by crabs that could compete with small mammals for insects and other resources. It is interesting to note that the common rodent species in the coastal region (i.e. *Praomys*, *Hylomyscus*, and *Malacomys*) are considered omnivorous (Kingdon 1997; Nowak 1999).

Overall, 10 species of shrews and 12 species of rodents were found during our surveys in the Gamba Complex. Our results are comparable to other nearby studies (Brosset 1988; Duplantier 1989; Goodman et al. 2001; Goodman and Hutterer 2004; Lasso et al. 1996; Malcolm and Ray 2000; Nicolas et al. 2004). Studies conducted further from the Gamba Complex revealed increasingly different species lists and abundances (Dieterlen 1986; Gubista 1999; Barrière et al. 2000). The insectivore species recorded in our survey were very similar to those reported in other areas of Gabon, with the exception of our single capture of *Sylvisorex* c.f. *konganensis* in Moukalaba – Doudou. This species has not been recorded in Gabon before, but it is known to occur in the Central African Republic (Barrière et al. 2000). It is surprising that 2 recent studies in the Moukalaba-Doudou region, including one that captured more than 500 insectivores, did not record this species (Goodman and Hutterer 2004; Nicolas et al. 2004). Insectivore surveys in the Central African Republic revealed 16 species in the Dzanga-Sangha forest (Ray and Hutterer 1995) and 18 species in the Ngotto forest (Barrière et al. 2000), and may represent a localized region for high insectivore diversity. However, we recorded an equal or greater number of rodent species than any of the other reported studies. There

was high agreement with nearby communities, with other surveys in Gabon also being dominated by *Hylomyscus stella*.

The Gamba Complex has a rich small mammal fauna that is comparable to other areas of the Guineo-Congolian region. The diversity of habitat types near the coastal sites was not correlated with increased small mammal species richness. Further studies are needed to determine if resources within coastal forests tend to be lower than those of inland forests. This is a hypothesis that seems to be supported by the plant community composition and structure (Campbell et al. 2006). At this time, we argue that the lack of specialist rodents from coastal forests is indicative of fewer resources being available within this seasonally flooded habitat.

## CHAPTER 3

### SPECIES RICHNESS AND LANDSCAPE INFLUENCES

#### Introduction

The Guineo-Congolian region encompasses 2.8 million km<sup>2</sup> of lowland rainforest stretching from the coastal regions of West Africa to eastern Democratic Republic of Congo (White 2001). The region is renowned for both its plant and animal diversity, with 8000 species of plants (80% endemic) and 270 species of lowland mammals belonging to 120 genera (Grubb 2001; White 2001). Gabon, in the heart of the Guineo-Congolian region, has over 88% of its original tropical moist forest remaining, which is the highest of all West, Central, and East African rainforest countries (Naughton-Treves and Weber 2001).

While there have been repeated surveys of large mammals in the region (Boddicker et al. 2006; Happold 1996; Hart 2001; Lahm et al. 2006; Muchaal and Ngandjui 1999; Ray 2001; Turkalo and Fay 2001; White 1994; Whitesides et al. 1988), only in recent years have terrestrial small mammal communities received the same attention. Surveys in northeastern Gabon (Brosset 1988; Duplantier 1982; Duplantier 1989; Goodman et al. 2001), central Gabon (Barrière and Colyn 1997; Nicolas and Colyn 1999), the Central African Republic (Barrière et al. 2000; Malcolm and Ray 2000; Morvan et al. 1999; Ray and Hutterer 1995), the Democratic Republic of Congo (Barrière and Colyn 1997; Dieterlen 1986; Dudu et al. 2005; Gubista 1999; Nicolas and Colyn 1999), Cameroon (Barrière and Colyn 1997; Nicolas and Colyn 1999) and Equatorial Guinea (Lasso et al. 1996) have demonstrated a diverse small mammal community. The

southern section of Gabon, including the Gamba Protected Areas Complex, has not been comprehensively surveyed, except for some recent work in the Monts Doudou area (Goodman and Hutterer 2004; Nicolas and Barrière 2001; Nicolas et al. 2004).

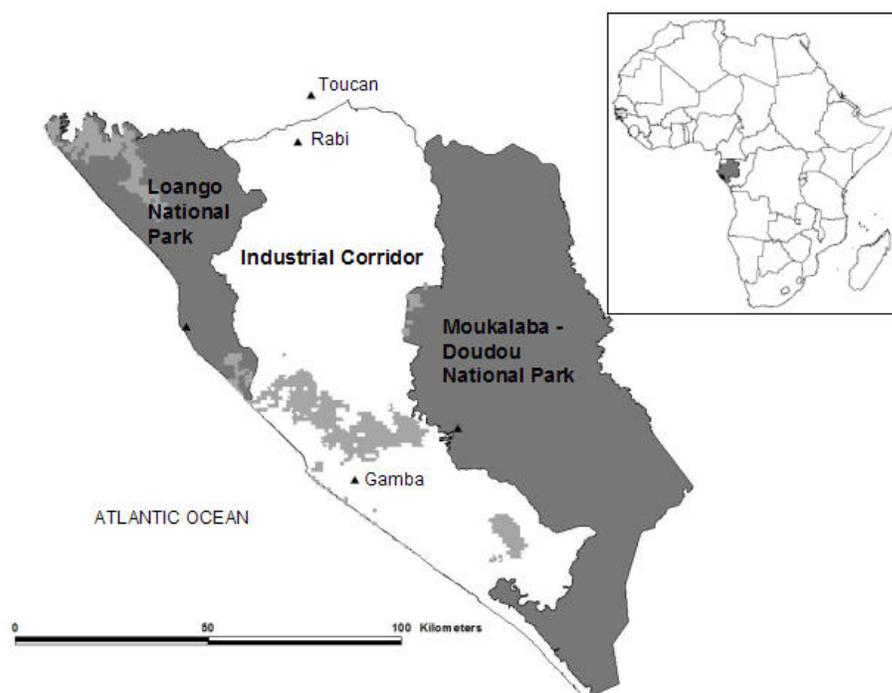
Further work into the small mammal communities of the Guineo-Congolian region have looked at population structure (i.e. age classes, sex ratios, reproduction; Barrière et al. 2000; Dieterlen 1986; Duplantier 1989; Nicolas et al. 2003; Nicolas et al. 2004;), phylogeny and evolution (Quéroil et al. 2001, Quéroil et al. 2003), and seasonal variability (Nicolas et al. 2005), but few studies have examined community composition as a function of differing levels of disturbance in the surrounding habitat. Malcolm and Ray (2000) examined the effects of logging disturbance on small mammal communities in the Central African Republic, and suggest that African rodents can be ecological indicators of forest change. In this study, I report on 3 inland and 2 coastal small mammal communities with differing levels of disturbance. Using satellite imagery, I investigated whether rodent and shrew communities in the Gamba Complex vary as a function of forest quantity or disturbance, or whether the variation can be explained by abiotic factors such as elevation or rainfall. In addition, I performed the same investigation into individual species within the small mammal community.

## Materials and Methods

### Study area and sites

#### Gamba Complex

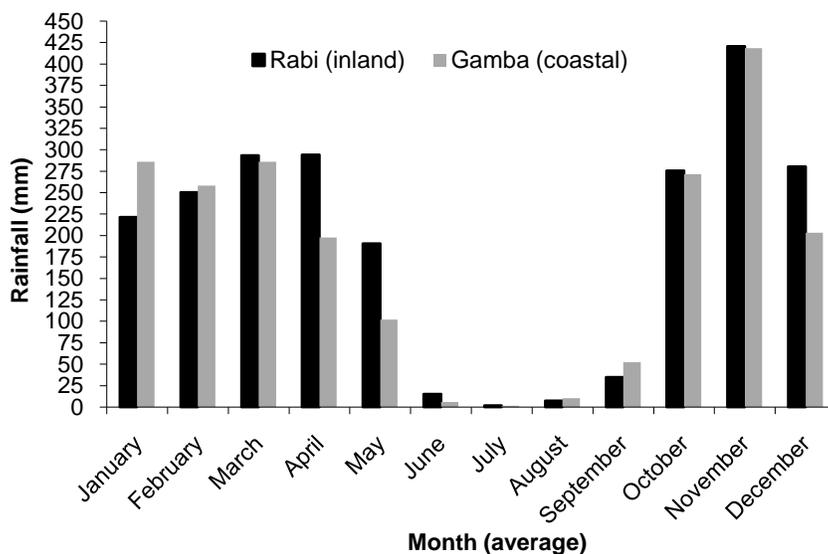
Located in southwestern Gabon, the Gamba Complex is the country's largest protected area, totaling 11,320 km<sup>2</sup>, and is home to a diverse mix of habitats (Fig. 3-1). The coastal regions are a mosaic containing littoral, mangrove, coastal scrub, lowland seasonally-flooded, and upland non-flooded forests, as well as open grasslands (Campbell et al. 2006). Inland, there are large expanses of upland non-flooded forest with lowland seasonally-flooded forest along the streams and rivers. The mean temperature is between 24-28° C and the mean annual rainfall is approximately 2,300 mm inland and 2,093 mm



**FIG. 3-1.**—Study locations in the Gamba Complex of southwestern Gabon, Africa

near the coast (Shell Gabon unpublished data). There is often a short dry season in January and a longer dry season from June to September (Fig. 3-2).

Difficult access to most of the complex may account for the significant populations of African forest elephant (*Loxodonta cyclotis*), African forest buffalo (*Syncerus caffer nana*), western lowland gorilla (*Gorilla gorilla gorilla*), chimpanzee (*Pan troglodytes troglodytes*), hippopotamus (*Hippopotamus amphibius*) present in the area. The complex was a mix of faunal reserves and hunting areas for trophy sport hunting until 2002 when the Gabonese government created two national parks in the Gamba Complex; Loango (1,550 km<sup>2</sup>) and Moukalaba - Doudou (4,500 km<sup>2</sup>). Between the two parks is the Rabi - Ndogo industrial corridor (3,585 km<sup>2</sup>), which contains oil and logging concessions and associated towns and villages.



**FIG. 3-2.**—Average monthly rainfall, from 1985-2002, recorded by Shell at Rabi and Gamba.

I conducted surveys for small mammals at five locations in the Gamba Complex: three within the industrial corridor (Rabi, Toucan, and Gamba) and one location in each of the national parks (Loango and Moukalaba - Doudou).

*Rabi.* This inland site, in the northern part of the industrial corridor, is a Shell Gabon oil concession that has been in operation since 1985. Rabi is a 17 x 8 km block of land containing wellheads, infrastructure, and a laterite road network. Access to the area is highly restricted and vehicle speed limits are strictly enforced. The Shell Oil Company permits no hunting; any employee caught hunting or transporting wildlife products is dismissed. Prior to being an oil field, Rabi was selectively logged. In the development of the oil field, Shell minimized forest clearing, and approximately 90% of the original forest cover has been maintained. The Rabi area has undulating terrain comprised of upland and lowland forest. The region around Rabi is sparsely populated ( $<0.2$  inhabitants/km<sup>2</sup>) with few villages or logging camps within 30 km (Laurance et al. 2006).

*Toucan.* Toucan adjoins Rabi along the northern border of the industrial complex. The area was under active oil exploration and development by Shell at the time of this study. In 2001 a 12 km road was constructed connecting Rabi and Toucan, and during our study a 5 km extension was added to the north. The forest at Toucan is similar to Rabi, and some of our sites were near the road development and logging operations that were occurring in the area.

*Gamba.* Gamba, with approximately 7,000 people in the town and surrounding villages, is the population center of the complex. An oil pipeline runs from the Rabi oil fields to the Gamba oil facility. This coastal site in the southern part of the industrial corridor also contains the Ndogo lagoon, the largest freshwater lagoon system in Africa.

The vegetation cover is mostly a grassland - forest mosaic on white sands, containing secondary forests in various stages of succession. The grasslands are maintained by annual burning. Hunting is officially prohibited by Shell, but unlike at Rabi, the rule is not strongly enforced. Access to the area was easy due to the extensive road network and tracks through the grasslands.

*Loango.* The Loango park, along the coast, is 45 km northwest of Gamba. The site is characterized by coastal and mangrove forests along the beach, progressing from a grassland - forest mosaic to solid blocks of forest further inland. The forest appears undisturbed with little evidence of logging or settlements. No roads were present in the area and access to sites was by foot.

*Moukalaba – Doudou.* This park contains a forested mountain range (Monts Doudou) with grassland savannas in the east. The southwest corner of the park was selected for this study, and was accessed by the Ndogo lagoon. The camp was at the base of Monts Doudou between the mountain and the lagoon. Due to our proximity to the mountain, we were able to survey at higher elevations than at the other study locations. The forest resembled that of Rabi and Toucan with upland forest and seasonally flooded forest along waterways and the lagoon. There was no evidence of logging, hunting, or settlements. Access to sites at Moukalaba - Doudou was on foot and all trails had to be constructed.

### **Vegetation Measurements**

I used the vegetation data obtained by a team surveying these same locations (except Gamba) during the same time as our small mammal surveys. The team sampled

75 plots 0.1 ha in size and collected data on all trees > 5 cm diameter at breast height (dbh). Their results revealed a gradient from low tree species diversity and high habitat diversity along the coast to high tree species diversity and lower habitat diversity inland (Campbell et al. 2006). The Rabi - Toucan forests had the highest tree species richness, with 203 species recorded at Rabi (21 plots) and 180 at Toucan (19 plots). Loango (27 plots) had a mix of habitats and contained 95 species. Moukalaba - Doudou had very high species composition (137 species), with less sampling effort (8 plots), and appeared similar to the Rabi - Toucan forests in structure and richness.

The survey locations each had 2+ forest types (i.e., upland, lowland), however each type was unique to the location. Rabi upland forest was different in species composition from Toucan upland forest even though their overall structure and richness were similar. The vegetation team concluded that habitat types can't be defined by the presence of key species, but rather by broad types defined by environmental conditions and similarities in structure and richness.

## **Data analysis**

### Image Acquisition and Classification

I obtained three post-2000 images that covered my study areas and are as cloud-free as possible. For the Rabi/Toucan region I used an ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) image taken 7/31/01, for Loango an ASTER image taken 3/18/01, and for Gamba/Doudou a Landsat 7 ETM+ (Enhanced Thematic Mapper Plus) image taken 2/4/03. There are differences between ASTER images and Landsat images. The ASTER images cover a small area (60 km x 60 km

scene) and the first three visible and near infrared spectral bands (VNIR) have a spatial resolution of 15 m, while the Landsat 7 ETM+ images have a swath width of 185 km, and contain 8 spectral bands, 6 of which have a 28.5 m resolution.

The EarthSat Geocover orthorectified dataset contains images with high positional accuracy that can be used as a reference for other imagery (Tucker et al. 2004). I aligned each image to the corresponding EarthSat image using image-to-image registration in ERDAS Imagine. I collected ground control points in both images until I reached an RMS error of less than one pixel. Resampling using nearest neighbor was used to create the new image, and I confirmed proper alignment visually.

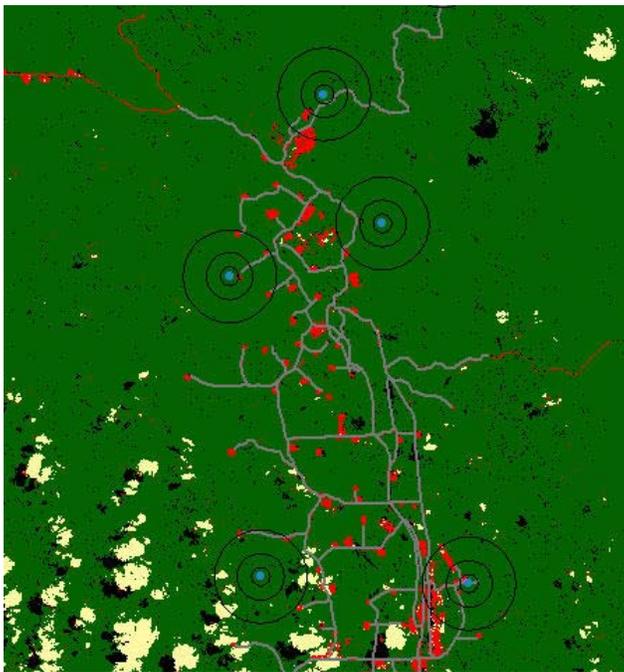
Because the ASTER and Landsat images have different spatial resolutions, I used the panchromatic band of the Landsat image to sharpen the resolution of the other spectral bands of the image to 15 m within ERDAS Imagine. Therefore the ASTER and Landsat images have the same effective resolution of 15 m.

An unsupervised classification was performed on a subset of the three images using ERDAS Imagine. I created 256 classes and assigned each to one of five landcover categories: forest, open, water, clouds, and shadow/no data. The image was then recoded so the new image contained those five classes. I had some mixed pixels, which occurs when two or more different features on the ground have such a similar reflectance that they are grouped into the same class. When the number of pixels involved was minor, I classified the mixed pixels as “no data.” When more pixels were involved, I made a new subset of the image and ran the classification again. The only image that required a second reclassification was the Loango ASTER, where clouds in the beach zone were classified as open areas. I separated the clouds and sand by visually delineating the sandy

areas using on-screen digitizing. I used ArcView's Map Calculator to subtract the digitized sandy areas from the mixed class, which resulted in a separate cloud class. I merged the cloud and open classes back into the previous land cover classification. After classification, I exported the images as grids for use in ArcView.

### Variable generation

Using the GPS locations collected in the field, I designated the center of each study site and created 2 buffers (200 and 500 m). I used ArcView Spatial Analyst extension to calculate the amount of each landcover class within the buffers (Fig. 3-3). The amount of forested and open habitat was recorded in both km<sup>2</sup> and percent. When



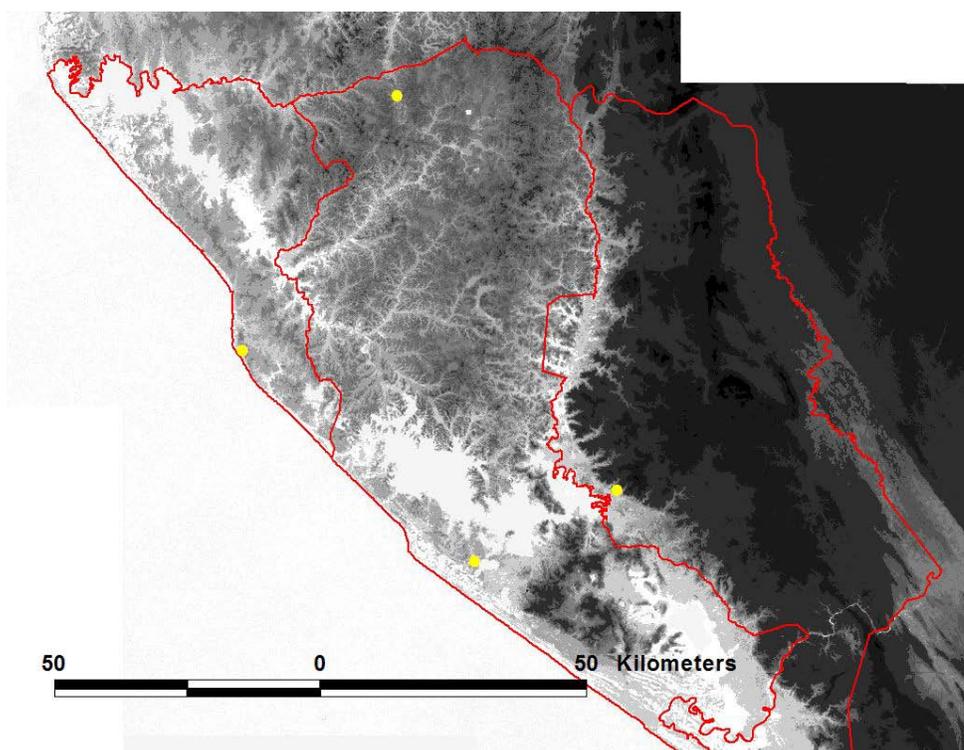
**FIG. 3-3.**—Landcover classification map of Rabi with study sites (blue) surrounded by buffers. The red areas are forest openings for oil platforms and buildings, and the grey areas are roads. Clouds and their shadows are evident.

calculating the percent of forest or open habitat, I subtracted the amount of cloud and shadow from the total available habitat in the buffer. If the clouds and shadow were > 40% of the buffer area, the site was excluded.

I made a road layer by digitizing the roads in and around each study site. After clipping the road layer to the buffers, I calculated the total length of roads within each buffer. Roads were only present in the Rabi, Toucan, and Gamba locations (Fig. 3-3).

Daily rainfall data has been collected by Shell at both the Rabi and Gamba locations for more than 20 years. For this analysis I used the total rainfall (mm) during the week of the trapping at a site. I used an average of the Rabi and Gamba rainfall amounts for all Loango and Moukalaba - Doudou locations since direct measurements were not available.

I created an elevation layer using the SRTM (Shuttle Radar Topography Mission) data from 2000 (Fig. 3-4). SRTM images correspond to LandSat tiles and are at a 90 m resolution. After converting the SRTM images to grids, I used ArcView's Get Grid Value extension to extract the elevation at the center of each study site. Using both the original imagery and the SRTM layer, I delineated upland and lowland forest and created both a lowland and upland binary grid. A forest binary grid was made as well, and using logical multiplication, was multiplied by the lowland and upland binary grids using ArcView's Map Calculator to result in upland and lowland forest layers. These new layers were kept separate from the landcover classification grid since they are based on the 90 m resolution elevation layer. I used ArcView's Spatial Analyst to calculate the amount of lowland and upland forest within each buffer.



**FIG. 3-4.**—Elevation layer for the Gamba Complex, with study locations in yellow.

#### Variable preparation and analysis

I used regression analyses to examine which landscape factors might explain the observed differences in small mammal richness across the Gamba Complex. I considered rodents and shrews separately; shrew richness can only be calculated for sites containing pitfall traps, while rodent richness can be determined from all sites. I used linear regression for analyses involving rodent or shrew richness and logistic regression for analyses using the presence/absence of individual species.

The list of possible independent variables for analysis included: amount forest (200 and 500m buffers), amount open (200, 500), % forest (200, 500), % open (200, 500), amount lowland forest (200, 500), amount upland forest (200, 500), amount roads (200, 500), elevation, and rainfall during the trapping week. Each variable was checked

for normality and examined in a correlation matrix. Rainfall and lowland/upland forest were the only variables that were normally distributed; the remaining variables required transformations. As expected, the amount forest, amount open, % forest, and % open variables were highly correlated with each other. I examined how each of these variables predicted richness using the nonparametric Kruskal-Wallis test, which does not have any assumptions of normality but less power. The amount forest variable performed better, so I used that variable in the analyses and eliminated the other three correlated variables. Therefore, six variables were used for the regression analyses - amount forest, lowland forest, upland forest, elevation, rainfall and roads. I used the 500 m buffer for the rodents and the 200 m buffer for the shrews. I selected the 200 m buffer for the shrews due to their smaller body size and tendency to have smaller home ranges in comparison to rodents.

Using Systat 11, I ran a backwards stepwise linear regression with the above six variables (with the 500 m buffer) and the dependent variable "rodent richness." The alpha to enter and remove was 0.1, there were 23 potential cases with 1 removed (due to no data which was caused by having a cloud cover greater than 40%). There were no outliers. Following stepwise procedures, I ran a complete linear regression on the significant variables. I used bootstrapping because of the small sample size. The decision rule was that a variable needed to stay significant ( $p < 0.05$ ) > 80% of the time.

I repeated the same process for the shrews, using the six variables at the buffer size of 200 and the dependent variable "shrew richness." There were 16 potential cases and 2 were removed because they were outliers.

I examined the relationship of individual species captured at 3 or more sites to the same six variables using backwards stepwise logistic regression. Each species was coded as present (1) or absent (0) for each site. I performed bootstrapping with complete logistic regression for those species with significant variables.

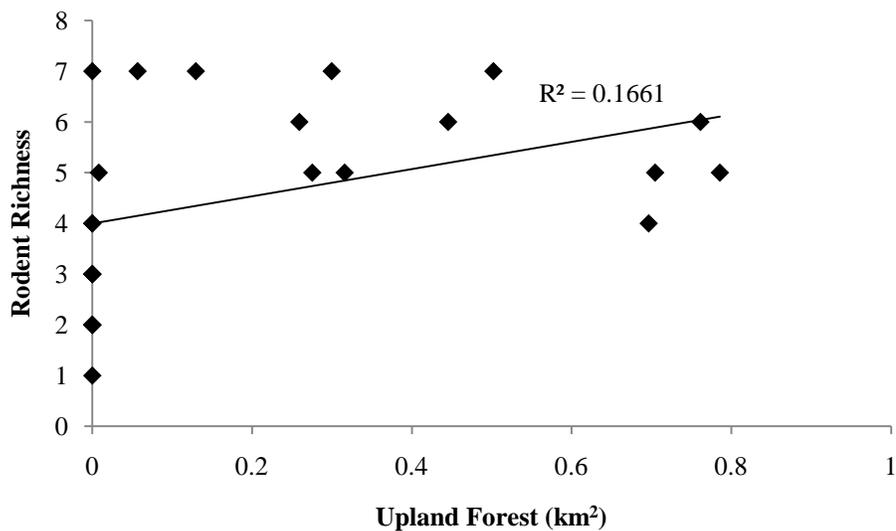
## Results

### Regression analyses

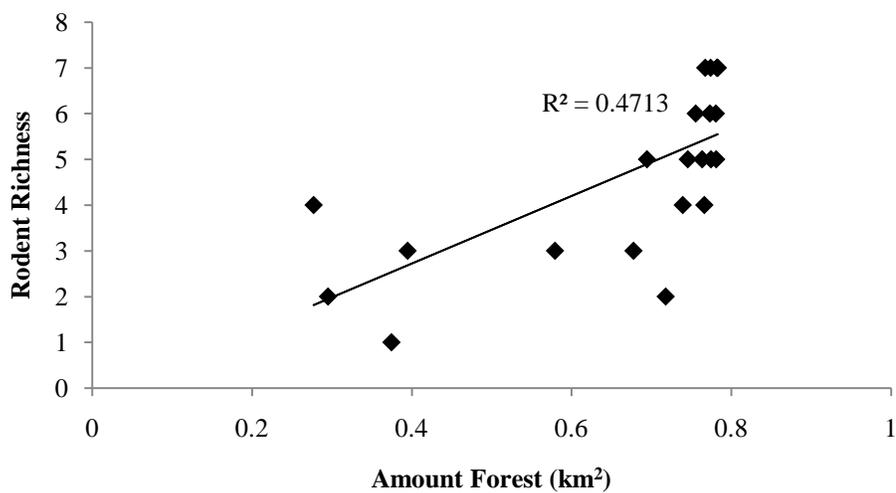
#### Species richness

The rodent backwards stepwise regression analysis identified three significant variables: lowland forest (partial  $F = 6.973$ ;  $df = 1$ ;  $p = 0.017$ ), upland forest (partial  $F = 7.140$ ;  $df = 1$ ;  $p = 0.016$ ), and amount of forest (partial  $F = 5.287$ ;  $df = 1$ ;  $p = 0.034$ ). I performed a complete linear regression with each of these variables to clarify the relationship and to determine the coefficients. Lowland forest ( $F = 0.088$ ;  $df = 1$ ;  $p = 0.770$ ) did not have a clear relationship with rodent richness. While upland forest ( $F = 4.169$ ;  $df = 1$ ;  $p = 0.054$ ; Fig. 3-5) was positively correlated with rodent richness, the amount of forest ( $F = 16.437$ ;  $df = 1$ ;  $p = 0.001$ ) had the strongest positive relationship with rodent richness (Fig. 3-6).

The shrew backwards stepwise regression analysis also identified three significant variables: elevation (partial  $F = 6.832$ ;  $df = 1$ ;  $p = 0.028$ ), rainfall (partial  $F = 6.035$ ;  $df = 1$ ;  $p = 0.036$ ) and roads (partial  $F = 12.232$ ;  $df = 1$ ;  $p = 0.007$ ). As with the rodent analysis, I performed a complete linear regression with each of these variables to clarify



**FIG. 3-5.**—Results of linear regression for rodent species richness and the amount of upland forest within the 500 m buffers.

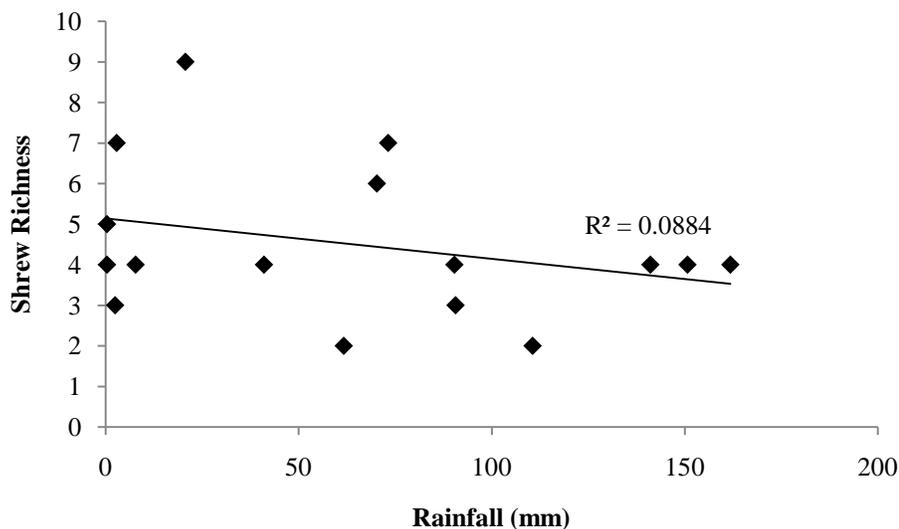


**FIG. 3-6.**—Results of linear regression for rodent species richness and the amount of forest within the 500 m buffers.

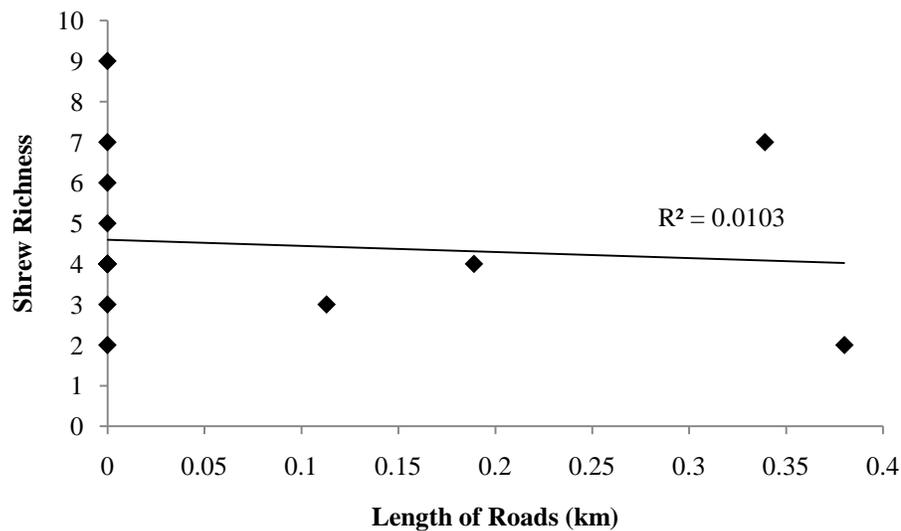
the relationship and to determine the coefficients. When examined individually, rainfall ( $F = 1.357$ ;  $df = 1$ ;  $p = 0.264$ ; Fig. 3-7), roads ( $F = 0.313$ ;  $df = 1$ ;  $p = 0.585$ ; Fig. 3-8), and elevation ( $F = 2.916$ ;  $df = 1$ ;  $p = 0.110$ ; Fig. 3-9) were only weakly correlated with shrew richness, which suggests that the interaction among the three variables could be important. I also examined the relationship between shrew richness and the amount of forest, since it was important for understanding species richness in rodents. For shrews, however, the amount of forest was only weakly associated with species richness ( $F = 1.575$ ;  $df = 1$ ;  $p = 0.232$ ).

#### Individual species

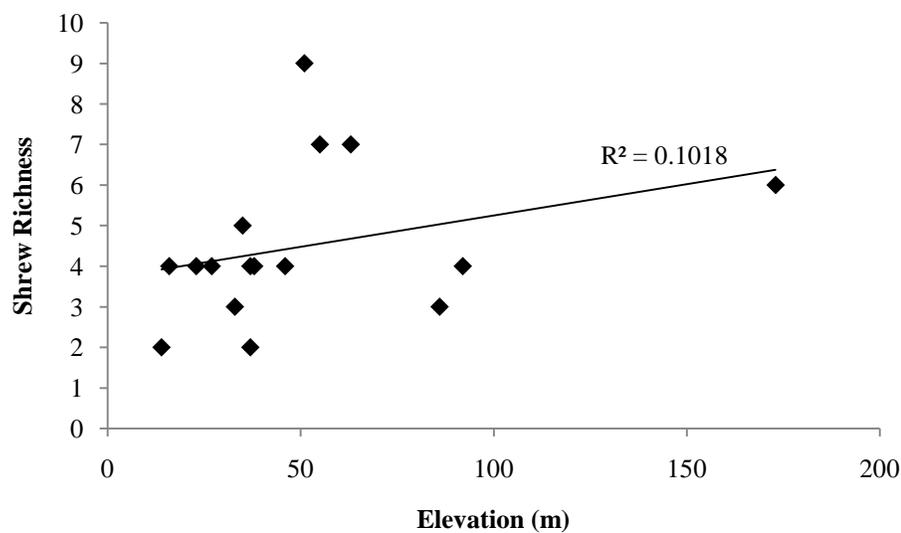
Three rodent species (*Hylomyscus parvus*, *Lophuromys nudicaudus*, *Malacomys longipes*) had similar results to the rodent analyses described in the previous section,



**FIG. 3-7.**—Results of linear regression with shrew species richness and the amount of rainfall during the sampling period.



**FIG. 3-8.**—Results of linear regression for shrew species richness and the amount of roads within the 200 m buffers.



**FIG. 3-9.**—Results of linear regression for shrew species richness and elevation.

with lowland forest, upland forest, and the amount of forest contributing significantly to linear regression. I used logistic regression to examine the relationship of each of these variables with the three rodent species mentioned above. *H. parvus* and *M. longipes* had the strongest relationship with lowland forest, while *L. nudicaudus* was associated with upland forest (Table 3-1). The result for *M. longipes* was significant (lowland forest; LL = 4.633; df = 1; p = 0.031) and nearly so for *H. parvus* (lowland forest; LL = 2.794; df = 1; p = 0.095) and *L. nudicaudus* (upland forest; LL = 3.524; df = 1; p = 0.060), however all three species failed the bootstrapping.

Overall, five of eight rodent species with significant results were associated with forest variables (Table 3-1). *Praomys tullbergi* was negatively associated with roads (LL = 4.851; p = 0.028) and was more common in the roadless study locations, especially Loango. Nearly half (46%) of the captures of *H. stella* were from one study location (Toucan), which was sampled during the dry season, which could explain why this species had a negative association with rainfall (LL = 4.665; df = 1; p = 0.031). One shrew species, *Crocidura crenata*, was positively associated with the amount of forest (LL = 8.67; df = 1; p = 0.003), and this species was more common in the inland study locations. Inland shrew species *P. schoutedeni* was positively associated with elevation (LL = 11.216; p = 0.001), in agreement with the linear regression results for shrew richness. *Crocidura goliath* contradicted the shrew richness model and was positively associated with roads and negatively with upland forest (LL = 9.856; df = 2; p = 0.007). *C. goliath* was more abundant in Gamba, even with the lower trapping effort at that site.

**TABLE 3-1.**— Results of backwards stepwise logistic regression with six site variables and individual species presence or absence with bootstrapping. Only those species found at 3 or more trapping sites (but not every site) were included.

Species	No. of Sites Present	Significant Variables	LL <sup>3</sup>	df	P
<b>Soricidae</b>					
<i>Crocidura batesi</i>	5/15	none			
<i>Crocidura crenata</i>	11/15	Amt forest (+)	8.67	1	0.003
<i>Crocidura dolichura</i>	5/15	rainfall (-)	7.547	1	0.006
<i>Crocidura goliath</i> <sup>1</sup>	11/22	roads (+), upland (-)	9.856	2	0.007
<i>Crocidura grassei</i>	3/15	none			
<i>Paracrocidura schoutedeni</i>	4/15	elevation (+)	11.216	1	0.001
<i>Suncus remyi</i>	4/15	none			
<i>Sylvisorex ollula</i>	10/15	none			
<b>Muridae</b>					
<i>Deomys ferrugineus</i>	11/22	Amt forest (+)	17.378	1	<0.001
<i>Grammomys rutilans</i>	5/22	elevation (+)	5.545	1	0.019
<i>Heimyscus fumosus</i>	9/22	none			
<i>Hybomys univittatus</i>	12/22	upland (+)	10.602	1	0.001
<i>Hylomyscus aeta</i>	7/22	none			
<i>Hylomyscus parvus</i> <sup>2</sup>	12/22	lowland (+)	2.794	1	0.095
<i>Hylomyscus stella</i>	18/22	rainfall (-)	4.665	1	0.031
<i>Lophuromys nudicaudus</i> <sup>2</sup>	6/22	upland (+)	3.524	1	0.060
<i>Malacomys longipes</i> <sup>2</sup>	10/22	lowland (+)	4.633	1	0.031
<i>Praomys tullbergi</i>	13/22	roads (-)	4.851	1	0.028

<sup>1</sup> Used all sites because this species is often caught in sherman and snap traps

<sup>2</sup> Results from complete logistic regression. Failed bootstrapping.

<sup>3</sup> Log likelihood

## Discussion

My findings provide an initial examination of which landscape factors are important in explaining the distribution of small mammals in the Gamba Complex of Gabon. Shrew richness was correlated with abiotic factors: elevation, rainfall, and roads. Rodent richness was correlated with the amount of forested habitat available.

Generally, the forests of Loango harbored less tree species diversity than the inland forests of Rabi, Toucan, and Moukalaba-Doudou (Campbell et al. 2006). Coastal regions had less diversity and abundance of fruiting plant species (Lahm, pers. comm). It is of interest that the rodents that dominated in our coastal locations (*Praomys* and

*Malacomys*) are known to be abundant in secondary forest growth and to have an omnivorous diet (Kingdon 1997; Nowak 1999).

When Malcolm and Ray (2000) surveyed small mammals in unlogged forest and along logging extraction routes in southwestern Central African Republic, they found increased rodent abundance and diversity along the borders of logging roads, a zone characterized by a dense understory, low tree diversity and low sapling density. Unlogged forest sites had an increase in rodent abundance with increasing understory density, with high understory density occurring where there were gaps in the canopy. They suggested that rodents can act as indicators of forest disturbance, and proposed that the ratio of captures of *Hylomyscus* to *Praomys* could provide a measure of the amount of regional forest degradation. High proportions of *Hylomyscus* relative to *Praomys* were found in interior primary forest and lower proportions were found in degraded areas. *Praomys* by preference dwells in secondary habitats and degraded areas (Rosevear 1969), while *Hylomyscus* is rare in forest remnants or forests degraded by logging or agricultural activities. In our study, *Hylomyscus* dominated the rodent community at Rabi, Toucan and Moukalaba - Doudou while *Praomys* dominated in the forest patches of Loango. Forest cover was more patchy at Gamba than Loango and had correspondingly lower abundance of both *Praomys* and *Hylomyscus*.

Malcolm and Ray (2000) suggest there may be a threshold effect, in that low levels of disturbance lead to increases in abundance, but as degradation increases, *Hylomyscus* will decline. I found that in Toucan, where disturbance was recent and expanding, there was a high abundance of *Hylomyscus*. Highly degraded forest is dominated by *Mus* and other species known to inhabit savannas and agricultural areas,

such as *Lemniscomys striatus*, *Mastomys* sp., *Pelomys* sp., or *Lophuromys sikapusi*.

*Lophuromys nudicaudus* is known to prefer cleared areas and secondary growth due to its dependence on grass (Rosevear 1969), however we did not capture this species in Loango or Gamba. Certainly, additional work is needed to determine if the loss of rodent species from coastal forests was due to 1) less abundant resources (fruits, seeds, vegetable matter) and/or 2) forest structure or microhabitat differences, i.e., canopy cover, understory composition and density, or differences in litter layer.

### **Conclusions and Recommendations**

The disturbance and edge habitats created by oil production may explain why Rabi had the highest small mammal diversity in the Gamba Complex. *Mus* and *Stochomys* were able to take advantage of these specialized habitats that were not found elsewhere. This increase in diversity may be temporary or short-term and increased disturbance due to logging could lead to a decline in species richness. I suggest that the patchiness of the forest as well as fewer resources in coastal areas has led to dominance of the rodent community by generalist species.

The study results for shrews at higher elevations are ambiguous. Goodman and Hutterer's (2004) study in Moukalaba - Doudou showed the highest richness and abundance of shrews at the lowest elevation, while my work on the other side of the mountain range found the opposite pattern. My study is in agreement with others that found increasing species richness and endemism with increasing elevation (Heim de Balsac 1968; Hutterer et al. 1987), although the elevation range in the trapping locations in Moukalaba-Doudou was quite small. The capture of *Sylvisorex konganensis* was a first

for Gabon. It is possible that the region may be a refugium for shrews. I suggest that additional work is needed to assess the level of fragmentation and possible mitigation strategies for future development in the Rabi area. An investigation into the resources available to small mammals in both inland and coastal forests would help put in perspective the seemingly contradictory results for shrews at different elevations.

## CHAPTER 4

### CONCLUSION

Small mammal trapping at five locations in the Gamba Complex revealed a diverse assemblage of species. A total of 12 rodent and 10 insectivore species were recorded, which is similar to results obtained by nearby studies. The sampling methodology was found to be effective for small terrestrial mammals. Pitfall lines with large buckets were critical to our capture of insectivores, which are often missed in live and snap traps (Goodman et al. 2001; Goodman and Hutterer 2004; Nicolas and Colyn 2006; Williams and Braun 1983). Another key component of the methodology was a switch from live traps to snap traps on day three (the midpoint) of trapping at a site. This change was critical because it resulted in an increase of new species captured. The extensive sampling in a variety of habitats at both inland and coastal locations provided important information to aid in resolving taxonomic issues. Due to the existence of phenotypically similar species, collection of specimens was essential to gaining accurate species identifications. I was fortunate to work with two experts, M. Carleton and P. Barrière, who are at the forefront of defining phylogenetic relationships in African small mammal communities. The 16s rRNA sequences of several of my insectivore specimens were examined to confirm their identification. This work led to the surprising identification of a single specimen of *Sylvisorex konganensis*, a species not previously recorded in Gabon. My results can also serve as a baseline for further monitoring in the Gamba Complex, an area without secure protection from increasing resource extraction.

The regression analyses I conducted suggest that the rodent and insectivore communities in the Gamba Complex have different habitat requirements. Rodent communities were positively associated with forest (lowland and upland) while insectivore communities were positively associated with elevation and negatively with roads and rainfall. I suspect that while the rodents in this survey may be tied to certain resources contained within the forest, the insectivores in general may be less particular during the search for their prey as long as certain abiotic factors are met.

The individual species regression analyses provided a more detailed look into the community and was especially interesting for those species which did not follow the pattern mentioned above. The rodents found only at inland locations (i.e., *Deomys ferrugineus*, *Hybomys univittatus*, *Lophuromys nudicaudus*) were all positively associated with forest variables. The two most dominant members of the rodent community did not conform to the rodent model with *Hylomyscus stella* negatively associated with rainfall and *Praomys tullbergi* negatively associated with roads. The result for *H. stella* can be attributed to the higher number of captures in Toucan during the dry season. *P. tullbergi* was a minor component of the rodent community in most locations but dominated at Loango, where there were no roads. The insectivore *Crocidura goliath* was positively associated with roads and negatively with upland forest, suggesting it was tolerant of disturbance and of lowland, seasonally flooded forest. *Crocidura crenata*, a relatively common member of the insectivore community at inland but not coastal locations, was positively associated with the amount of forest. The inland-only insectivore *Paracrocidura schoutedeni* was positively associated with elevation, with all three

captures of the species at Moukalaba – Doudou occurring at the high elevation site (173m).

Monts Doudou within Moukalaba – Doudou National Park has been the focus of other recent small mammal surveys because it is suspected to be montane refuge for small mammals (Goodman and Hutterer 2004; Nicolas et al. 2004). Distinct vegetation communities similar to other montane flora of the Congo Basin occur near its summit (Goodman and Hutterer 2004). The two small mammal studies conducted on the other side of Monts Doudou (Goodman and Hutterer 2004; Nicolas et al. 2004) did not find any small mammals unique to montane zones in other regions of the Congo Basin. My study did find one unique species to the Moukalaba – Doudou survey, *Sylvisorex konganensis*, a recently described species from the Central African Republic (Ray and Hutterer 1995). It appears to be a rare member of the insectivore community and has been captured in lowland forest (Barriere et al. 2000; Ray and Hutterer 1995). Therefore, while it is an exciting discovery for Gabon, this species is not a relic in other montane zones and its capture high on a slope in this survey is likely a result of little being known about its distribution. The elevation range in Moukalaba – Doudou is quite narrow and may explain why montane species have not been reported. Although elevation was significant in the insectivore regression model, it may be due to the inability of some species to tolerate lowland, flooded forest.

A long-term study of small mammals at a lowland site in Moukalaba – Doudou had a strikingly similar species list to that of our study (Nicolas and Colyn 2003; Nicolas et al. 2005). The exceptions were their single capture of *Crocidura cf. nigrofusca* and their division of the genus *Praomys* into separate species. If I assume the same divisions

in my captures of *Praomys*, this study had a higher richness due to the captures of *Mus* and *Stochomys* at Rabi. Therefore our rapid inventory of sites appears successful in determining the richness of the small mammal community. While the long-term study was able to document seasonal variations in abundance and shifts in community composition, the dominant rodent (*Hylomyscus stella*) and insectivore (*Sylvisorex johnstoni*) were identical to this study (Nicolas and Colyn 2003; Nicolas et al. 2005). My results do confirm their findings of increased *H. stella* abundance during the dry season (Nicolas and Colyn 2003). However, I did not find a lower abundance of insectivores during the dry season. This could be due to the higher pitfall effort at Toucan (dry season) relative to all other survey locations.

While the Toucan and Moukalaba-Doudou locations had high species richness (18 species), additional species were found at Rabi due to the creation of additional habitats through disturbance. The increase in richness was primarily from species associated with treefall gaps and secondary habitats, i.e., *Stochomys longicaudatus* and *Mus minutoides*. The vegetation team reported that treefall gaps were quite common in both the Rabi and Toucan forests (Campbell et al. 2006). Lianas were also abundant and are often considered indicators of disturbance (Laurance et al. 2001). Campbell et al. (2006) suggested that the disturbance appeared to stem mostly from natural causes (i.e. treefall gaps). The Rabi and Toucan forests also had evidence of old, selective logging scattered throughout at a low intensity (Campbell et al. 2006). At Moukalaba – Doudou, the vegetation team found very rich forests with fewer lianas than Rabi-Toucan and little evidence of selective logging, suggesting a less disturbed environment (Campbell et al. 2006).

Forests in the coastal locations were less rich than those of the inland locations (Campbell et al. 2006), and the small mammal community had a similar drop in richness. The decrease in small mammal richness can be primarily attributed to the loss of specialist rodents. *Deomys ferrugineus* is a termite specialist, *Hybomys univittatus* is a gap specialist, and *Lophuromys nudicaudus* is a grass specialist (Malcolm and Ray 2000; Rosevear 1969). It is surprising that *L. nudicaudus* was not found in the coastal locations where grass was present. Gamba differed from Loango in that the rodent community in Gamba was dominated by *Malacomys longipes*, a stream-side specialist (Malcolm and Ray 2000; Rosevear 1969). However, due to the extensive savannas present in Gamba, our survey was conducted in gallery forests that are often associated with streams (Tutin et al. 1997). Gamba was different from Loango is that the diversity of habitats was lower and did not appear to contain dry forest islands or continuous blocks of forest. Additional study is needed to determine if the dominance of different rodent species in the two coastal locations was caused by the lower survey effort there.

The differential ability of species to use and tolerate the savanna matrix may explain the loss of specialists in the coastal locations. *Praomys tullbergi* is a generalist found in disturbed and secondary habitats and appears to be able to use the savanna to move among forest fragments in Loango. *Hylomyscus stella* appears less tolerant of disturbance and did not dominate the community in Loango as it did at the inland locations. These results are congruent with the findings of Malcolm and Ray (2000). The insectivore *Crocidura goliath* may also be tolerant of disturbance, as is noted for its close relative *C. olivieri*. No other insectivore in this study was more abundant in the coastal locations. The differing habitat requirements of members of the small mammal

community may explain which species are able to take advantage of disturbed and secondary habitats and which disappear. The disturbance in the Rabi area has led to an increase in species richness by the creation of additional habitats. In coastal locations, certain specialist rodents appear unable to use the savanna. They require continuous forest nearby to meet their needs. Like Malcolm and Ray's (2000) study, the small mammal community of the Gamba Complex was dominated by rainforest species. I conclude that these species differ in their ability to use edge-affected, fragmented, or disturbed habitats which has led to the loss of species in coastal locations.

### **Recommendations**

The Rabi – Toucan area in the Industrial Corridor of the Gamba Complex provides an important link to adjacent Loango and Moukalaba- Doudou National Parks. Currently, the Rabi area is better protected than the national parks in Gabon as a result of Shell's strict policies. However, villages are proliferating along the oil and logging roads in the Toucan area, just to the north of Rabi. Oil production at Rabi has fallen sharply and Shell is expected to abandon its operation there. Shell's departure could lead to a dramatic increase in hunting and logging in the region. In addition to ensuring the protection of Loango and Moukalaba – Doudou, my data suggest that the future of the critical wildlife habitat of Rabi is in peril and requires protection and security before the Shell Oil Company leaves. From a small mammal perspective, the Rabi – Toucan area appear to be at an intermediate level of disturbance. Additional disturbance could lead to a loss of species, beginning with a shift in dominance from *Hylomyscus stella* to *Praomys*

*tullbergi*. In order to prevent the loss of biodiversity it is important to protect this delicately balanced ecosystem from further threats.

## LITERATURE CITED

- AUGUST, P.V. 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 64(6):1495-1507.
- AUSTIN, P.K., W.T. STANLEY, J.C. KERBIS PETERHANS, AND R.L. KITYO. 1992. Preliminary results of a small mammal survey along an elevational gradient in the Rwenzori mountains, Uganda. American Society of Mammalogists Annual Meeting, Salt Lake City, UT.
- BARRIÈRE, P., AND M. COLYN. 1997. *Ecologie des Peuplements de Soricidae Forestiers d'Afrique Centrale: Considérations Nouvelles sur Base de la Méthode de Piégeage Pitfall*. Report to Université de Rennes 1, Rennes France.
- BARRIÈRE, P., V. NICOLAS, R.K. MARO, G. YANGOUNDJARA, AND M. COLYN. 2000. *Ecologie et Structuration des Peuplements de Micromammifères Musaraignes et Rongeurs*. Report to ECOFAC-CEE, Libreville, Gabon.
- BECK, H., M.S. GAINES, J.E. HINES, AND J.D. NICHOLS. 2004. Comparative dynamics of small mammal populations in treefall gaps and surrounding understorey within Amazonian rainforest. *Oikos* 106:27-38.
- BODDICKER, M. L., S. MBOUMBA, R. NGANGUI, AND S. GUIMONDOU. 2006. The occurrence and relative abundance of large mammals encountered in the Gamba Complex of Gabon. Pp. 417-423 in *Gamba, Gabon: Biodiversity of an Equatorial African Rainforest* (A. Alonso, M.E. Lee, P. Campbell, O.S.G. Pauwels, and F. Dallmeier, eds.). *Bulletin of the Biological Society of Washington*, No. 12.
- BROSSET, A. 1988. Le peuplement de mammifères insectivores des forêts du nord-est du Gabon. *Revue d'Ecologie (Terre et Vie)* 43:23-46.
- BULLOCK, S.H. 1980. Demography of an under-growth palm in littoral Cameroon. *Biotropica* 12:247-255.
- CAMPBELL, P., P. RIVERA, D. THOMAS, H. BOUROBOU-BOUROBOU, T. NZABI, A. ALONSO, AND F. DALLMEIER. 2006. Floristic structure, composition, and diversity of an equatorial forest in Gabon. Pp. 253-273 in *Gamba, Gabon: Biodiversity of an Equatorial African Rainforest* (A. Alonso, M.E. Lee, P. Campbell, O.S.G. Pauwels, and F. Dallmeier, eds.). *Bulletin of the Biological Society of Washington*, No. 12.
- COLYN, M., AND P. DELEPORTE. 2002. Biogeographic analysis of central African forest Guenons. Pp. 61-78 in *The Guenons: Diversity and Adaptation in African Monkeys* (M.E. Glenn, and M. Cords, eds.). Kluwer Academic /Plenum Publishers, New York.

- COLYN, M., A. GAUTHIER-HION, AND W. VERHEYEN. 1991. A re-appraisal of the paleoenvironment history in Central Africa: Evidence for a major fluvial refuge in the Zaire basin. *Journal of Biogeography* 18:403-407.
- CONDE, V.Y., AND C.F. ROCHA. 2006. Habitat disturbance and small mammal richness and diversity in an Atlantic rainforest area in southeastern Brazil. *Brazilian Journal of Biology* 66(4):983-990.
- CONNELL, J.H. 1978. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a nonequilibrium state. *Science* 199:1302-1310.
- DELANY, M.J. 1971. The biology of small rodents in Mayanja forest, Uganda. *Journal of Zoology* 165:85-129.
- DELANY, M.J., AND D.C.D. HAPPOLD. 1979. *Ecology of African mammals*. Longman Publishing Group, New York.
- DENSLOW, J.S., T.C. MOERMOND, AND D.J. LEVEY. 1986. Spatial components of fruit display in understory trees and shrubs. Pp. 37-45 in *Frugivores and seed dispersal* (A. Estrada, and T.H. Fleming, eds.). W. Junk Publishers, The Netherlands.
- DIETERLEN, F. 1986. Seasonal reproduction and population dynamics in rodents of an African lowland rain forest. *Cimbebasia* 8(A):1-8.
- DUDU, A., S. CHURCHFIELD, AND R. HUTTERER. 2005. Community structure and food niche relationships of coexisting rain-forest shrews in the Masako Forest, north-eastern Congo. Pp. 229-239 in *Advances in the Biology of Shrews II* (J.F. Merritt, S. Churchfield, R. Hutterer, and B.I. Sheftel, eds.). Special Publication of the International Society of Shrew Biologists No. 1, New York.
- DUPLANTIER, J. 1982. Les rongeurs myomorphes forestiers du nord-est du Gabon: peuplements, utilisation de l'espace et des ressources alimentaires, rôle dans la dispersion et la germination des graines. Ph.D. thesis, Université des Sciences et Techniques du Languedoc, France.
- DUPLANTIER, J. 1989. Les rongeurs myomorphes forestiers du nord-est du Gabon: structure du peuplement, démographie, domaines vitaux. *Revue d'Ecologie (Terre et Vie)* 44:329-346.
- GASCON, C., T.E. LOVEJOY, R.O. BIERREGAARD JR., J.R. MALCOLM, P.C. STOUFFER, H.L. VASCONCELOS, W.F. LAURANCE, B. ZIMMERMAN, M. TOCHER, AND S. BORGES. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91:223-229.
- GOODMAN, S.M., AND R. HUTTERER. 2004. A report on the shrews (Mammalia: Soricidae) of Mts Doudou, Gabon: Elevational distribution and preliminary insights

- into their ecology. Pp. 93-106 in *Monts Doudou, Gabon: A floral and faunal inventory, with reference to elevational variation* (B. Fisher, ed.). *Memoirs of the California Academy of Sciences* No. 28, San Francisco.
- GOODMAN, S.M., AND B.P.N. RASOLONANDRASANA. 2001. Elevational zonation of birds, insectivores, rodents and primates on the slopes of the Andringitra Massif, Madagascar. *Journal of Natural History* 35:285-305.
- GOODMAN, S.M., R. HUTTERER, AND P.R. NGNEGUEU. 2001. A report on the community of shrews (Mammalia: Soricidae) occurring in the Minkebe Forest, north-eastern Gabon. *Mammalian Biology* 66:22-34.
- GRUBB, P. 2001. Endemism in African rain forest mammals. Pp. 88-100 in *African Rain Forest Ecology and Conservation: An Interdisciplinary Perspective* (W. Weber, L.J.T. White, A. Vedder, and L. Naughton-Treves, eds.). Yale University Press, New Haven.
- GUBISTA, K.R. 1999. Small mammals of the Ituri Forest, Zaire: diversity and abundance in ecologically distinct habitats. *Journal of Mammalogy* 80:252-262.
- HAPPOLD, D.C.D. 1996. Mammals of the Guinea-Congo rain forest. *Proceedings of the Royal Society of Edinburgh* 104B:243-284.
- HART, J.A. 2001. Diversity and abundance in an African forest ungulate community and implications for their conservation. Pp. 183-206 in *African Rain Forest Ecology and Conservation: An Interdisciplinary Perspective* (W. Weber, L.J.T. White, A. Vedder, and L. Naughton-Treves, eds.). Yale University Press, New Haven.
- HEIM DE BALSAC, H. 1968. Considerations préliminaires sur le peuplement des montagnes africaines par les Soricidae. *Biologia Gabonica* 4:299-323.
- HICE, C.L., AND D.J. SCHMIDLY. 2002. The effectiveness of pitfall traps for sampling small mammals in the Amazon basin. *Mastozoología Neotropical* 9:85-89.
- HUTTERER, R., P. BARRIÈRE, AND M. COLYN. 2001. A new myosoricine shrew from the Congo Basin referable to the forgotten genus *Congosorex* (Mammalia: Soricidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 71(suppl.):7-16.
- HUTTERER, R., E. VAN DER STRAETEN, AND W. VERHEYEN. 1987. A checklist of the shrews of Rwanda and biogeographical considerations on African Soricidae. *Bonner zoologische Beiträge* 38:155-172.
- KASANGAKI, A., R. KITYO, AND J. KERBIS. 2003. Diversity of rodents and shrews along an elevational gradient in Bwindi Impenetrable National Park, southwestern Uganda. *African Journal of Ecology* 41:115 – 123.

- KINGDON, J. 1997. Kingdon field guide to African mammals. Academic Press, London.
- LAHM, S. A., AND J.P. TEZI. 2006. Assessment of the communities of medium-sized and large arboreal and terrestrial mammals in the Rabi/Toucan region of the Ngové-Ndogo hunting domain and southwestern Loango National Park. Pp. 383-416 in Gamba, Gabon: Biodiversity of an Equatorial African Rainforest (A. Alonso, M.E. Lee, P. Campbell, O.S.G. Pauwels, and F. Dallmeier, eds.). Bulletin of the Biological Society of Washington, No. 12.
- LAMBERT, T.D., J.R. MALCOLM, AND B.L. ZIMMERMAN. 2006. Amazonian small mammal abundances in relation to habitat structure and resource abundance. *Journal of Mammalogy* 87(4):766-776.
- LASSO, C., R. HUTTERER, AND A. RIAL. 1996. Records of shrews (Soricidae) from Equatorial Guinea, especially from Monte Alen National Park. *Mammalia* 60:69-76.
- LAURANCE, W.F. 1992. Abundance estimates of small mammals in Australian tropical rainforest: a comparison of four trapping methods. *Wildlife Research* 19:651-655.
- LAURANCE, W.F., B.M. CROES, L. TCHIGNOUMBA, S.A. LAHM, A. ALONSO, M.E. LEE, P. CAMPBELL, AND C. ONDZEANO. 2006. Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology* 20(4):1251-1261.
- LAURANCE, W.F., S.D. PEREZ, P. DELAMONICA, P.M. FEARNSIDE, S. D'ANGELO, A. JEROZOLINSKI, L. POHL, AND T.E. LOVEJOY. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82(1):105-116.
- LECOMPTE, E., C. DENYS, AND L. GRANJON. 2001. An identification key for species within the genus *Praomys* (Rodentia: Muridae). Pp. 127-139 in African Small Mammals (C. Denys, L. Granjon, and A. Poulet, eds.). Collection Colloques et Séminaires, Paris.
- LECOMPTE, E., L. GRANJON, AND C. DENYS. 2002. The phylogeny of the *Praomys* complex (Rodentia: Muridae) and its phylogeographic implications. *Journal of Zoological Systematics and Evolutionary Research* 40:8-25.
- LEVEY, D.J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69:1076-1089.
- LEVEY, D.J. 1990. Habitat-dependent fruiting behavior of an understory tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* 6:409-420.

- LWANGA, J.L. 1994. The role of seed and seedling predators and browsers in the regeneration of two forest canopy species (*Mimusops bagshawei* and *Strombosia scheffleri*) in Kibale Forest Reserve, Uganda. Ph.D. thesis, University of Florida, Gainesville.
- LYRA-JORGE, M.C., AND V.R. PIVELLO. 2001. Combining live trap and pitfall to survey terrestrial small mammals in savanna and forest habitats, Brazil. *Mammalia* 65:524-530.
- MALCOLM, J.R., AND J.C. RAY. 2000. Influence of timber extraction routes on central African small-mammal communities, forest structure, and tree diversity. *Conservation Biology* 14:1623-1638.
- MCCAIN, C.M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography* 31:19-31.
- MCCAIN, C.M. 2005. Elevational gradients in diversity of small mammals. *Ecology* 86(2):366-372.
- MISONNE, X. 1963. Les rongeurs de Rwenzori et des régions voisines. *Explor. Parc. Natn. Albert* ser 14:1 – 164.
- MORVAN, J., V. DEUBEL, P. GOUNON, E. NAKOUNE, P. BARRIÈRE, S. MURRI, O. PERPETE, B. SELEKON, D. COUDRIER, V. VOLCHKOV, A. GAUTHIER-HION, AND M. COLYN. 1999. Identification of Ebola virus sequences present as RNA or DNA in organs of different species of terrestrial small mammals of Central African Republic. *Microbes and Infection* 1(14):1193-1201.
- MUCHAAL, P.K., AND G. NGANDJUI. 1999. Impact of village hunting on wildlife populations in the Western Dja Reserve, Cameroon. *Conservation Biology* 13:385-396.
- NAUGHTON-TREVES, L., AND W. WEBER. 2001. Human dimensions of the African rain forest. Pp. 30-43 in *African Rain Forest Ecology and Conservation: An Interdisciplinary Perspective* (W. Weber, L.J.T. White, A. Vedder, and L. Naughton-Treves, eds.). Yale University Press, New Haven.
- NICOLAS, V., AND M. COLYN. 2006. Relative efficiency of three types of small mammal traps in an African rainforest. *Belgian Journal of Zoology* 136:107-111.
- NICOLAS, V., AND M. COLYN. 1999. Les Muridae Forestiers d'Afrique Tropicale: Distinction des Espèces du Genre *Praomys* et Caractérisation Préliminaire des Communautés. Report to Université de Rennes 1, Rennes, France.
- NICOLAS, V., AND P. BARRIÈRE. 2001. Rapport d'expertise sur le Volet Biodiversité, Biogéographie et Ecologie de la Conservation des Monts Doudou: Modèles

- Fauniques et Dynamique Evolutive. Programme WWF de Diversité Biologique du Refuge Forestier Pléistocène des Monts Doudou (Gabon), rapport n° 3.
- NICOLAS, V., P. BARRIÈRE, AND M. COLYN. 2005. Seasonal variation in population and community structure of shrews in a tropical forest of Gabon. *Journal of Tropical Ecology* 21:161-169.
- NICOLAS, V., AND M. COLYN. 2003. Seasonal variations in population and community structure of small rodents in a tropical forest of Gabon. *Canadian Journal of Zoology* 81:1034-1046.
- NICOLAS, V., P. BARRIÈRE, S. GUIMONDOU, AND M. COLYN. 2004. Variabilité structurale des peuplements forestiers de rongeurs (Muridae) et musaraignes (Soricidae) dans les Monts Doudou, Gabon. Pp. 107-127 in *Monts Doudou, Gabon: A floral and faunal inventory, with reference to elevational variation* (B. Fisher, ed.). *Memoirs of the California Academy of Sciences* No. 28, San Francisco
- NICOLAS, V., W. WENDELEN, E. VERHEYEN, and M. COLYN. 2003. Population structure and reproduction of *Heimyscus fumosus* (Brosset *et al.*, 1965) in southwestern Gabon. *Rev. Ecol. (Terre Vie)* 58(2):209-216.
- NOWAK, R.M. 1999. *Walker's mammals of the world*. Sixth edition, vol. 2. Johns Hopkins University Press, Baltimore.
- QUÉROUIL, S. 2001. Intérêts et Limites de l'approche Moléculaire pour Aborder la Biogéographie et la Spéciation: Quelques Exemples chez les Mammifères d'Afrique Tropicale. Ph.D. thesis, University of Rennes 1, Rennes, France.
- QUÉROUIL, S., R. HUTTERER, P. BARRIÈRE, M. COLYN, J.C. KERBIS PETERHANS, AND E. VERHEYEN. 2001. Phylogeny and evolution of African Shrews (Mammalia: Soricidae) inferred from 16s rRNA sequences. *Molecular Phylogenetics and Evolution* 20(2):185-195.
- QUÉROUIL, S., E. VERHEYEN, M. DILLEN, AND M. COLYN. 2003. Patterns of diversification in two African forest shrews: *Sylvisorex johnstoni* and *Sylvisorex ollula* (Soricidae, Insectivora) in relation to paleo-environmental changes. *Molecular Phylogenetics and Evolution* 28:24-37.
- QUÉROUIL, S., P. BARRIÈRE, M. COLYN, R. HUTTERER, A. DUDU, M. DILLEN, AND E. VERHEYEN. 2006. A molecular insight into the systematics of African *Crociodura* (Crociodurinae, Soricidae) using 16s rRNA sequences. Pp. 99-113 in *The Biology of the Soricidae II* (J.F. Merritt, S. Churchfield, R. Hutterer and B.I. Sheftel, eds.). *Carnegie Museum of Natural History Special Publication*, Pittsburgh.
- RAY, J.C. 1998. Temporal variation of predation on rodents and shrews by small African forest carnivores. *Journal of Zoology* 244:363-370.

- RAY, J.C. 2001. Carnivore biogeography and conservation in the African forest. Pp. 214-232 in African Rain Forest Ecology and Conservation: An Interdisciplinary Perspective (W. Weber, L.J.T. White, A. Vedder, and L. Naughton-Treves, eds.). Yale University Press, New Haven.
- RAY, J.C., AND R. HUTTERER. 1995. Structure of a shrew community in the Central African Republic based on the analysis of carnivore scats, with the description of a new *Sylvisorex* (Mammalia: Soricidae). *Ecotropica* 1:85-97.
- ROSEVEAR, D.R. 1969. The rodents of west Africa. Trustees of the British Museum (Natural History), London.
- SCHEMSKE, D.W., AND N. BROKAW. 1981. Treefall and the distribution of understory birds in a tropical forest. *Ecology* 62:938-945.
- STRUHSAKER, T.T. 1998. Ecology of an African rain forest. University Press of Florida, Gainesville.
- TUCKER, C.J., D.M. GRANT, AND J.D. DYKSTRA. 2004. NASA's global orthorectified Landsat data set. *Photogrammetric Engineering & Remote Sensing* 70:313-322.
- TURKALO, A.K., AND J.M. FAY. 2001. Forest elephant behavior and ecology. Pp. 207-213 in African Rain Forest Ecology and Conservation: An Interdisciplinary Perspective (W. Weber, L.J.T. White, A. Vedder, and L. Naughton-Treves, eds.). Yale University Press, New Haven.
- TUTIN, C.E.G., L.J.T. WHITE, AND A. MACKANGA – MISSANDZOU. 1997. The use by rain forest mammals of natural forest fragments in an equatorial African savanna. *Conservation Biology* 11(5):1190-1203.
- VAN DER STRAETEN, E., E. LECOMPTE, AND C. DENYS. 2003. *Praomys petteri*: une nouvelle espèce des Muridae africains (Mammalia, Rodentia). *Bonner Zoologische Beiträge* 50(4):329-345.
- VOLOBOUEV, V.T., V.M. ANISKIN, E. LECOMPTE, AND J.F. DUCROZ. 2002. Patterns of karyotype evolution in complexes of sibling species within three genera of African murid rodents inferred from the comparison of cytogenetic and molecular data. *Cytogenetic and Genome Research* 96:261-275.
- WHITE, L.J.T. 1994. Biomass of rain forest mammals in the Lope Reserve, Gabon. *Journal of Animal Ecology* 63:499-512.
- WHITE, L.J.T. 2001. The African rain forest: climate and vegetation. Pp. 3-29 in African Rain Forest Ecology and Conservation: An Interdisciplinary Perspective (W. Weber,

- L.J.T. White, A. Vedder, and L. Naughton-Treves, eds.). Yale University Press, New Haven.
- WHITESIDES, G. H., J.F. OATES, S.M. GREEN, AND R.P. KLUBERDANZ. 1988. Estimating primate densities from transects in a western African rain forest: A comparison of techniques. *Journal of Animal Ecology* 57:345-367.
- WILLIAMS, D.F., AND S.E. BRAUN. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. *Journal of Wildlife Management* 47:841-845.
- WILLIAMS, S.E., H. MARSH, AND J. WINTER. 2002. Spatial scale, species diversity, and habitat structure: Small mammals in Australian tropical rain forest. *Ecology* 83(5):1317-1329.
- WILSON, D.E. 1983. Checklist of mammals. Pp. 443-447 in *Costa Rican Natural History* (D.H. Janzen, ed.). University of Chicago Press, Chicago.
- YALDEN, D.W. 1988. Small mammals of the Bale mountains, Ethiopia. *African Journal of Ecology* 26:281-294.