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Texas Tech University
Doctoral Dissertation
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Doctoral Dissertation
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# TABLE OF CONTENTS

ACKNOWLEDGMENTS

ABSTRACT

LIST OF TABLES

LIST OF FIGURES

CHAPTER

I. INTRODUCTION

II. SITE FIDELITY, HOME RANGE, AND FORAGING PATTERNS

III. MORPHOMETRICS

iv
ABSTRACT

Tropical forests account for much of the world’s forested areas, yet many of these regions are increasingly subjected to disturbance and deforestation as a result of both natural and anthropogenic agents. In many tropical systems, bats are dominant nocturnal organisms and keystone species because they make a critical contribution to forest succession as both seed dispersers and pollinators. As such, knowledge of their autecology contributes to an understanding of the integration of structure and function in food webs and the manner in which biotic elements may hasten the process of recovery from disturbance at a variety of scales.

*Stenoderma rufum* is a dominant frugivorous bat of the Luquillo Experimental Forest of Puerto Rico. Various aspects of the autecology of this species were investigated and include: foraging patterns and home range, intrademic morphometric variation and fluctuating asymmetry, reproductive biology, and ectoparasitic associations.

Home range and a variety of foraging parameters were examined over a 2-year period via radio telemetry. Day and night “capture” points were used to determine foraging behavior, home range, and roosting behavior. Results indicate that the Red Fig-eating Bat is extremely philopatric and forages within a relatively small area that includes its day roost.

Nineteen cranial and mandibular characters were examined for morphometric variation between age and sex groups using a variety of parametric techniques. Eight bilaterally symmetrical characters were tested
for differences in fluctuating asymmetry between males and females. *S. rufum* exhibits significant morphometric variation between age and sex groups, with females larger than males. One morphometric character was found to exhibit different fluctuating asymmetrically values between males and females.

Seasonal differences in reproductive activity exist for males, but not for females, which are asynchronously polyestrous. These results are compared to two other bat species from the Tabonuco Rain Forest, *Artibeus jamaicensis* and *Monophyllus redmani*.

Patterns of ectoparasite association of bats from the Tabonuco Rain Forest were examined with respect to the effects of age and sex of host, as well as season. Infestation levels vary due to host age but not sex, with juveniles more heavily infested than adults. Significantly different parasite assemblages on adult males, adult females, and juvenile on *Artibeus jamaicensis*; moreover, *S. rufum*, *A. jamaicensis*, and *Monophyllus redmani* each have a statistically distinctive ectoparasite assemblage.
LIST OF TABLES

1.1--Bat fauna of Puerto Rico............................................................... 12

2.1--Home range characteristics of radio tracked S. rufum from the Tabonuco Rain Forest............................................................. 50

2.2--Mean (m²), followed by standard deviation in parentheses, for each type of home range calculated for S. rufum........................................ 53

2.3--Effects of age and sex on MCP home range of S. rufum based upon pure model I two-way analysis of variance............................... 54

2.4--Effects of age and sex on MCP foraging range of S. rufum based upon pure model I two-way analysis of variance............................... 54

2.5--Effects of age and sex on MAP (0.95) home range of S. rufum based upon pure model I two-way analysis of variance............................... 55

2.6--Effects of age and sex on MAP (0.95) foraging range of S. rufum based upon pure model I two-way analysis of variance............................... 55

2.7--Effects of age and sex on MAP (0.50) home range of S. rufum based upon pure model I two-way analysis of variance............................... 56

2.8--Effects of age and sex on MAP (0.50) foraging range of S. rufum based upon pure model I two-way analysis of variance............................... 56

2.9--Movement parameters (means in meters, followed by standard error in parentheses of S. rufum during dark and light phases of the moon.................................................................................. 57

2.10--Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on mean total distance traveled during foraging by S. rufum based upon a pure model I two-way analysis of variance.................................................. 58
2.11--Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on maximum distance traveled during foraging by *S. rufum* based upon a pure model I two-way analysis of variance ................................................................. 58

2.12--Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on minimum distance traveled during foraging by *S. rufum* based upon a pure model I two-way analysis of variance ................................................................. 59

2.13--Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on mean distance per move traveled during foraging by *S. rufum* based upon a pure model I two-way analysis of variance ................................................................. 59

2.14--Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on number of moves per hour during foraging by *S. rufum* based upon a pure model I two-way analysis of variance ................................................................. 60

2.15--Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on time spent in night roost during foraging by *S. rufum* based upon a pure model I two-way analysis of variance ................................................................. 60

3.1--Two-way MANOVA results for *S. rufum* using 19 morphometric characters as dependent variables ......................... 95

3.2--Mean (mm) followed by standard deviation in parentheses of each mensural character used in morphometric analyses .... 96

3.3--Results of two-way ANOVA (age versus sex) with three random measurements nested within each cell, along with a priori contrasts ................................................................. 99
3.4--Results of asymmetry tests for adult male (N = 55) and adult female (N = 78) S. rufum from the Tabonuco Rain Forest. 102

4.1--Reproductive characteristics of bats in the Tabonuco Rain Forest during dry and rainy seasons. 119

5.1--Host-parasite associations and their abundance for bats from the Tabonuco Rain Forest. 141

5.2--Ectoparasites from S. rufum captured in the Tabonuco Rain Forest of Puerto Rico. 145

5.3--Significance levels from a series of two-way ANOVAs evaluating the effects of host age-sex (adult males, adult females, and juveniles) and season of collection (rainy and dry) in incidence levels of each of four categories of P. iheringi on S. rufum. 147

5.4--Ectoparasites from A. jamaicensis from the Tabonuco Rain Forest of Puerto Rico. 148

5.5--Significance levels from a series of two-way ANOVAs evaluating the effects of host age-sex (adult males, adult females, and juveniles) and season of collection (rainy and dry) in incidence levels of each of five different ectoparasites that occur on A. jamaicensis. 151

5.6--Ectoparasites from M. redmani from the Tabonuco Rain Forest of Puerto Rico. 152

5.7--Significance levels from a series of two-way ANOVAs evaluating the effects of host age-sex (adult males, adult females, and juveniles) and season of collection (rainy and dry) in incidence levels of each of four different ectoparasites that occur on M. redmani. 155

5.8--Significance levels from a series of two-way ANOVAs evaluating if levels of infestation among the three host taxa A. jamaicensis, S. rufum, and M. redmani or differ between seasons (rainy and dry). 156
LIST OF FIGURES

1.1--The island of Puerto Rico showing the location of the Luquillo Experimental Forest (LEF)........................................ 14

1.2--A three-dimensional image of the Luquillo Experimental Forest looking toward the southeast........................................ 16

2.1--Diagramatic representation the location and extent of trails in the Tabonuco Rain Forest........................................ 61

2.2--Frequency distribution of MCP home range sizes for individual 974, generated by computer simulation (n=200) using the mean and variance of movement segment lengths for that individual........................................ 63

2.3--Cumulative home range estimates over time for all male and female S. rufum (age categories combined).................. 65

2.4--Bar diagram of MCP home range and foraging range of S. rufum in the Tabonuco Rain Forest........................................ 67

2.5--Bar diagram of MAP home range and foraging range of S. rufum in the Tabonuco Rain Forest........................................ 69

2.6--Schematic representation of the size and shape of the minimum convex polygon (MCP) home range for 12 S. rufum in the Tabonuco Rain Forest........................................ 71

2.7--Detailed movement records every 5 minutes (over an 8 hour period) for an adult male S. rufum. ........................................ 73

3.1--Dorsal, ventral, and lateral views of cranium, as well as lateral and occlusal views of the lower jaw of an adult female S. rufum from the Tabonuco Rain Forest (modified from Genoways and Baker, 1972)......................................... 104
4.1--Frequency of adult male and female S.rufum in the rainy and dry season that were reproductively active (males: testes descended; females: pregnant or lactating)................................. 120

4.2--Distribution of embryo sizes in museum specimens of S. rufum for rainy and dry seasons................................................................. 122
CHAPTER I
INTRODUCTION

Tropical forests account for much of the world's forested areas, yet many of these regions are increasingly subjected to disturbance and deforestation as a result of anthropogenic activities. The characteristic structure and function of any ecosystem may be viewed as a dynamic condition affected by disturbance and recovery (Pickett and White, 1985). The impact of a disturbance is predicated upon its severity, spatial extent, duration, and frequency of occurrence, whereas the recovery of the system is mediated by a variety of biotic elements whose importance during secondary succession varies depending upon forest-type and disturbance regime. Natural treefalls, landslides, and hurricanes, as well as selective and clear cutting are the major forms of disturbance in humid tropical systems. Few studies of tropical systems have focused on the role of consumers during secondary succession (see Pickett and White, 1985). Nonetheless, vertebrates are ascribed an important role in the colonization of disturbed habitats by pioneer species (Fleming, 1988; Wiens, 1985). Many authors (e.g., Charles-Dominique, 1986; de Foresta et al., 1984) indicate that bats make a critical contribution to tropical forest succession by widely dispersing the seeds of early successional plants. The seeds of small, fleshy-fruit plants dominate tropical soil seed banks and are the source of colonists in recently disturbed areas (de Foresta et al., 1984; Swaine and Hall, 1983; Uhl et al., 1981). Such bat-dispersed plants, with large and pervasive seed banks, are capable of responding rapidly to a
variety of patch-generating phenomena. Bats have also been implicated to have an important role in flower pollination in a number of tropical systems (Gould, 1978; Howell, 1974; Ng, 1978; Sazima and Sazima, 1978; Stuart and Marshall, 1976). As such, bats are critical keystone species; knowledge of their autecology contributes to a general understanding of the integration of structure and function in tropical food webs and of the manner in which biotic elements hasten the process of recovery (secondary succession) from disturbance at a variety of scales.

This dissertation is a compilation of four manuscripts examining various aspects of the autecology of *Stenoderma rufum darioi*, a common frugivorous bat inhabiting the Tabonuco Rain Forest of Puerto Rico. The first manuscript investigates several aspects of social spacing, including site fidelity, home range, and foraging parameters. The second paper deals with intrademic morphometric variation among age-sex groups. The third examines reproductive biology and considers various factors which may regulate it. The last manuscript defines the composition of the ectoparasitic fauna of *S. rufum* and compares it to the ectoparasitic fauna of other species of bats in the Tabonuco Rain Forest.

**Study Site**

Puerto Rico stands as an island fulcrum between the Greater and Lesser Antilles, and contains floral and faunal elements of both regions. The tropical forests of Puerto Rico have been a focus for forestry and ecological research throughout this century (Brown et al., 1983; Mosquera
and Feheley, 1984). The Caribbean National Forest (18° 10' N, 65° 30' W), also known as the Luquillo Experimental Forest (LEF), contains the only tropical rain forest protected by the U.S. National Forest System. It comprises about 28,000 acres and constitutes the largest single area of natural, intensively managed forest on the island. It has been designated an experimental forest and a biosphere reserve in the UNESCO Man and Biosphere Program.

The LEF is located in the northeast corner of the island within the Luquillo Mountains (Fig. 1.1), about 20 miles southeast of San Juan. A detailed description of the area is available in Brown et al. (1983). This area encompasses El Verde Field Station, which is occupied under a use agreement with the U. S. Forest Service, and is currently administered by the Center for Energy and Environment Research (CEER) and the University of Puerto Rico. The history of ecosystem research at this site began in 1963 with the Rain Forest Project under the direction of Howard Odum. Unlike many other tropical sites, a wealth of background information is available and includes 80 years of climatic observation, 30 years of data on forest growth and composition, complete inventories of vegetation, soil and geologic maps, and a good understanding of plant and animal taxonomy. The Luquillo Experimental Forest (LEF) has been the subject of intensive ecological study for the last 20 years. Increasing elevation in the Luquillo Mountains is accompanied by changes in climate, soil, and vegetation structure and composition. As a result, four distinct vegetation types occur within its bounds (Ewel and Whitmore, 1973):
Tabonuco Rain Forest, Palo Colorado Forest, Elfin Woodland, and Palm Forest.

The Tabonuco Forest is located on lower mountain slopes below 650 meters (Fig. 1.2). It occupies the greatest land area within the forest and has been the area subject to the most intensive ecological studies. Rainfall is substantial and varies between 2,000 and 4,000 mm annually. Average monthly temperature ranges from 21° to 25° C.

The Tabonuco Rain Forest consists of tall, straight trees that reach about 30 m in height and have huge crowns that merge into a thick closed canopy. Most trees are devoid of branches on their lower half, creating an open mid-section in the forest. Over 150 species of trees are present in the rainforest. The more common ones are Dacryodes excelsa (Tabonuco), Cecropia schreberiana (= C. peltata, Trumpet Tree), Didymopanax morototoni (Matchwood), Ochroma lagopus (Balsa), and Prestoea montana (Sierra Palm). Although P. montana and C. schreberiana are the both more abundant in the area than D. excelsa, Tabonuco is present in the greatest numbers within the largest tree size class (40+ cm dbh), hence the name of the life zone. A variety of ferns, epiphytes, and fruit-bearing plants occur throughout the understory. For a more detailed description, see Wadsworth (1951) and Smith (1970).

Bat Fauna

Although the Tabonuco Rain Forest has been extensively studied, relatively little is known about the ecology and behavior of resident
mammals. The present composition of the mammalian community appears to be a product of biogeographic, abiotic, and human-mediated events (Willig and Gannon, 1991). Most previous work on Puerto Rican mammals has been limited to taxonomic description, specimen collection, and anecdotal observation (Anthony, 1918, 1925; Tamsitt and Valdivieso, 1970). Bats compose the major portion of the Puerto Rican mammal fauna in terms of species richness and density (Willig and Bauman, 1984; Willig and Gannon, 1991). Moreover, the 14 extant bat species (Table 1.1) are the only indigenous Puerto Rican mammals. All other mammal species were introduced in recent times. Four bat species (Artibeus jamaicensis, Stenoderma rufum, Brachyphylla cavernarum, and Erophylla sezekorni) are frugivores. Bat populations in the Tabonuco Rain Forest maintain a much lower density than might be expected of island species, which frequently experience competitive release causing elevated densities when compared to taxa on the mainland (MacArthur and Wilson, 1967). In contrast, other vertebrate taxa in the forest, such as Eleuthrodactylus (frogs) and Anolis (lizards) clearly do maintain high densities. Bat-netting success in the Tabonuco Rain Forest is considerably less (5-20%) than that of other tropical and subtropical mainland sites (Willig and Gannon, 1991).

Stenoderma rufum, the Red Fig-eating Bat, was first reported by Geoffroy St.-Hilaire (1818) as "le Sténoderme roux" based upon examination of a single specimen, believed to have come from Egypt. This designation appears to have been the basis for the name Demarest (1820) used in his original description of stenoderma rufa (the generic name was
not capitalized in the original description). At that time, the type locality was listed as "unknown" because of its doubtful origin, complicated by the observation that the one known specimen more closely resembled New World bats than those known from Egypt or the Old World. The distribution and status of this taxon remained an enigma for almost 100 years until Anthony (1918, 1925) discovered Sub-Recent fossil material in caves on Puerto Rico. Until relatively recent times, it was known only from such fossil records, and was thought to be extinct. Three live specimens were first captured in 1957 on St. John, Virgin Islands confirming the contemporary existence of this species. Since then, live individuals have been obtained from two localities on Puerto Rico, and from the islands of St. John and St. Thomas, Virgin Islands. Hall and Bee (1968) considered the St. John specimens to be indistinguishable from the holotype, and by inference established St. John as the type locality. Based on differences in cranial and external morphological measurements, they classified specimens from Puerto Rico as a new subspecies, S. r. darioi. Using similar morphometric characteristics, Choate and Birney (1968) characterized fossil remains from Puerto Rico as a separate subspecies, S. r. anthonyi.

*Stenoderma rufum* is still known only from the islands of Puerto Rico, St. John, and St. Thomas. As a result, it is a little studied species and its presence in scientific collections is rare. Of the two extant subspecies, only *S. r. darioi* from Puerto Rico has been collected in any appreciable numbers. Presently two populations are known from the island, and only
that in the Luquillo Mountains has been sampled and studied
morphometrically to any extent (Jones et al., 1971). *S. rufum* comprises
at least 25% of the bats in the Tabonuco Rain Forest (Willig and Bauman,
1984) and almost all data currently available on this species are derived
from work done on this population. Nonetheless, little is known
concerning the autecology of *S. rufum*. Few accounts of any aspect of its
feeding behavior have been published (Genoways and Baker, 1972; Scogin,
1982; Willig and Bauman, 1984; Willig and Gannon, 1991) and these are
neither detailed, nor inclusive of an entire year. Although its common
name implies a diet of figs, no published data support this. Stomach content
analyses (Willig and Gannon, 1991) indicate a diet mainly of *C.
schreberiana, Manilkara bidentata, and Prestoea montana* fruit. Similarly,
reproductive data are neither extensive nor well documented. Willig and
Bauman (1984), as well as Genoways and Baker (1972), suggested that *S.
rufum* exhibits polyestry in the Tabonuco Rain Forest, but reproductive
patterns of the population remain undefined.


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<th>Taxon</th>
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<th>LEF</th>
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CHAPTER II
SITE FIDELITY, HOME RANGE, AND FORAGING PATTERNS

Introduction

Foraging is an essential activity of consumers and often occupies a large portion of their daily time budget. As a result, movement patterns associated with foraging may, to a large extent, determine various aspects of social spacing. The fundamental behavior that optimal foraging theories predict is that, as a result of natural selection, animals tend to adhere to a strategy of obtaining food that maximizes the difference between benefits and costs (Stephens and Krebs, 1986). A variety of potential strategies for gathering food occur; the primary objective of foraging ecology is to determine which strategies exist in nature and to identify environmental factors which affect or constrain a particular consumer's feeding behavior. Foraging movements are ecologically important for several reasons. First, they represent responses to conflicting ecological or evolutionary pressures. Second, the movements of consumers can affect the distribution and genetic structure of plant populations through seed and pollen dispersal (Heithaus, 1982; Heithaus and Fleming, 1978). Third, ecosystem integration and response to perturbation may be mediated by keystone flower pollinators and seed disseminators.

Four general foraging "decisions" must be made by all consumers (Pyke et al., 1977; Stephens and Krebs, 1986); these involve the choice of
habitats or patches in which to forage, the choice of foods to consume, the
decision of when to leave a patch, and the selection of search strategies. A
variety of prey characteristics affect these decisions and include prey size,
prey density, costs associated with locating and processing prey, and the
risk of predation while foraging.

Small volant endotherms such as bats are ideal organisms for
investigation of foraging because they appear to be energy limited (Howell
and Hartl, 1980). Nonetheless, until recently, most of the data concerning
foraging behavior of frugivorous bats had been anecdotal because volant
nocturnal organisms are difficult to observe under even the best of
circumstances. Conclusions were usually based on either few visual
observations or mark-recapture studies. Chemiluminescent tags (Buchler,
1976) permit tracking the movement of individuals over short distances
(200-300 m) for short periods of time (up to four hours); however, once
an individual is out of sight, it is virtually impossible to locate again. The
advent of sophisticated, light-weight, radio-telemetry equipment has
renewed interest in bat foraging ecology and social spacing (Brigham,
1983; Barclay, 1985; Fenton, 1983; Fenton et al., 1985; Fleming, 1988;
Jacobsen et al., 1986; Morrison, 1978a, 1978b, 1980; Vehrencamp et al.,
1977), and it has become the method of choice for studying activity and
movement patterns of bats (Wilkinson and Bradbury, 1988), because it has
made such research practical and affordable. Telemetry affords several
benefits over other methods. These include (1) the location and
monitoring of individuals over large distances for long periods of time;
(2) simultaneous detection of several “tagged” individuals based upon
unique transmission frequencies; (3) facilitation of direct visual observation, during both day and night; and (4) discrimination among activities (e.g., flying and resting) based upon changes in signal pulse.

Home Range

Numerous definitions have been applied toward the term home range. One popular definition considers it as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943). Radio tracking data can be used to estimate home range. This approach is superior to mark-recapture methods because it enables the position of animals to be specified independently of behavior and movements (Wilkinson and Bradbury, 1988). In order to quantify home range, a more precise operational definition is necessary. The simplest way to estimate home range size is the convex polygon method which draws the smallest possible convex polygon through the outermost capture points (Odum and Kuenzler, 1955). Although this method is sensitive to sample size and may over- or underestimate home range (Jennrich and Turner, 1969; Kenwood, 1987; Schoener, 1981), it does facilitate comparisons with other studies (Fleming and Heithaus, 1986). Nonetheless, the current methods of choice involve probabilistic models and nonparametric techniques (Fourier Transformation, Anderson, 1982; Minimum Area Versus Probability Method, Ford and Krumme, 1979; Bivariate Normal Method, Jennrich and Turner, 1969) because they weight estimates of home range size by frequency of use. A comparison of the accuracy of these methods via Monte Carlo simulation studies suggests
that the Fourier Transformation Method is the most reliable (Anderson, 1982) and not sensitive to small sample size (Wilkinson and Bradbury, 1988). Nonetheless, a potential problem exists in using short interval observations in this manner because they may produce a high inter-sample dependency which can result in biased estimations (Dunn and Gibson, 1977). However, serial correlation is not as serious a problem in home range estimation for bats as it is for terrestrial mammals. Bats have a greater potential for swift movements and change position rapidly. As a result, little serial correlation should exist between samples separated by two to three hours.

Probabilistic models represent space use as a bivariate probability distribution in which the z-axis is the probability of encountering an animal at a particular point in space. The nonparametric method uses an animal's actual pattern of movement rather than an assumed movement distribution (as in parametric methods) to generate spatial utilization distributions (UDs). Estimates of home range size are easily calculated as an area defined by a probability level (e.g., 0.50, 0.95, and 1.00) which specifies the proportion of time that an organism was observed inside that area. These estimates are referred to as "minimum area versus probability" home ranges [MAP (0.50), MAP (0.95), and MAP (1.00) corresponding to each of the previously defined probability levels, respectively].

The number of captures required to accurately assess home range depends on the pattern of spatial variation exhibited by the animal over time (Wilkinson and Bradbury, 1988). Both Mares et al. (1980) for
Eastern chipmunks (*Tamias*), and Munger (1984) for horned lizards (*Phrynosoma*), demonstrated that the number of captures could considerably alter the home range estimates. At low capture numbers, the addition of another capture substantially increased home range size. As more capture points were added, the amount of change in home range size approached zero. Wilkinson and Bradbury (1988) have demonstrated that for at least *Desmodus rotundus*, the size of telemetrically obtained home ranges asymptotically stabilize after two to five nights of radio tracking.

**Foraging Behavior**

Foraging behavior, as revealed by radio-tracked bats, previously has been examined in a handful of taxa (Brigham, 1983; Fleming et al., 1977; Leonard and Fenton, 1983; McCracken and Bradbury, 1981; Thomas and Fenton, 1978; Williams and Williams, 1970). Only a few are New World frugivores.

Energy expended in commuting from day roosts to night feeding areas constitutes a critical part of the daily energy budget of a frugivorous bat. Morrison (1978b) noted that commuting distances of *Artibeus jamaicensis* vary greatly between habitats, and appear to be related to the density and distribution of trees that bear ripe fruit. In addition, bats must allocate time to search for new sources of food as they deplete currently utilized areas. Although this may be accomplished while commuting, individuals have been observed to make long extended scouting flights to find new feeding areas (Fleming, 1982). Frugivorous bats are pure searchers (Schoener, 1969), in that they need not pursue or subdue food
once it is located. This reduces both the magnitude of food handling costs and the variation of costs for different types of food. Depending on spatial distribution of food, some bats may commute directly to a feeding area before beginning to search for food (Fleming and Heithaus, 1981). This is a "separate" strategy and is usually noted in bats with restricted diets or when food occurs in isolated patches. Other species commute and search simultaneously. This "mixed" strategy occurs in species with broad diets or when feeding areas are evenly distributed. Three species of frugivorous bats in Panama, *A. jamaicensis* (Morrison, 1978a; 1978b), *A. literatus*, and *Vampyrodes caraccioli* (Morrison, 1980), exhibited foraging strategies similar to each other. Although roost sites were changed daily, individuals had a generalized fidelity to a small number of roost sites. No evidence for adjustment of day roost site location to minimize commuting distance to sources of ripe fruit was obtained for these three species or for *Epomophorus wahlbergi*, an Old World frugivore (Fenton et al., 1985). This suggests that predation risk, in addition to the energetic costs associated with foraging, may influence the selection of day roost sites in these habitats.

Foraging locations and behavior can also be influenced by social structure (Fleming, 1982). Morrison (1979) has documented that male bats which maintain harems (5-25 females) commuted significantly shorter distances than did females. Males may exclude females from areas closer to the roost or they themselves may be forced to forage close to the communal roost in order to prevent competing males from establishing dominance at the roost site.
Some small mammals are capable of detecting varying light conditions and alter their behavior in response to it (Clarke, 1983; Kaufman, 1974; Kotler, 1984). *A. jamaicensis* (Morrison, 1975, 1978c) and *D. rotundus* (Wilkinson, 1985) significantly reduce activity during periods of high lunar illumination. This behavior, termed "lunar phobia," suggests that flying in moonlight may significantly increase the risk of predation by visually oriented hunters. Predation pressure is the most probable cause of this behavior because neither resource abundance and distribution nor social activity in bats is correlated with lunar illumination. At these times, *A. jamaicensis* and *D. rotundus* restrict foraging activity and retreat to roosts during the brightest part of the night. *C. perspicillata* (Fleming, 1988; Fleming and Heithaus, 1981; Heithaus and Fleming, 1978; Stashko, 1982) also was found to be lunar phobic, but only in the dry season when loss of leaves on roost trees would expose them to predators.

**Hypotheses**

This paper elucidates the factors which influence social spacing of *S. rufum* in the Tabonuco Rain Forest. In general, the data gathered for this study facilitate comparison of home range, and foraging and roosting behavior between the sexes, as well as between age groups.

When examining the manner in which an animal uses space, one must first consider if the concept of home range is an ecologically meaningful construct within the context of the biology of the focal species. All home range estimation techniques can be applied to a set of capture points regardless of the site fidelity of the species. However, the home range of a
randomly wandering animal should differ strikingly from that of one which exhibits fidelity to an area. This study establishes whether S. rufum maintains a non-random home range or a home range which is merely the enclosed area of a randomly moving individual. Secondly, one must evaluate the number of samples required to accurately estimate home range. Estimates of home range in many mammals usually plateau after between 20 to 40 samples have been taken; not enough information exists to determine whether this can be extended to bats (Wilkinson and Bradbury, 1988). In order to evaluate this methodological concern, cumulative home range calculations are examined over time.

Do male and female S. rufum differ in home range size? Differences between sexes in patterns of space use are known to exist for a variety of mammalian species including bats. Males and females of A. jamaicensis (Morrison, 1975) and C. perspicillata (Fleming, 1988) differ in patterns of space use. One evolutionary explanation frequently invoked for such differences is related to reproductive strategies. Gaulin and Fitzgerald (1986) suggest that larger male home ranges should be favored by species with promiscuous or polygynous mating systems. However, A. jamaicensis has a social system characterized by harem polygeny, in which males defend harem roost sites and range significantly shorter distances from these sites than do females (Morrison, 1975). This study examines parameters of space use related to sex and whether these parameters result in differences in home range size between males and females.

Do adult and juvenile S. rufum differ in home range size? Differences between age groups in patterns of space use are also known to
exist. Young individuals may tend to stay close to day roosts. Older juveniles without much foraging experience or knowledge of food resources might exhibit expanded ranges. This paper evaluates whether age differences affect home range estimates of S. rufum, and if so, in what manner.

Unlike most mainland settings, the Tabonuco Rain Forest harbors few chiropteran predators. Marsupials are absent; snake species richness and density is low (the Puerto Rican Boa, the only potential bat predator in the forest, is an endangered species because of its rarity); large bat-eating owls are not present (Willig and Gannon, 1991). In the absence of significant predation, I evaluated if reduced foraging activity characterizes S. rufum during periods of high lunar illumination.

Methods

Bats were captured via mist nets at sites established within the Tabonuco Rain Forest. Sites were chosen based on previous netting success. Approximately 15 nets were set along the unimproved road entrance to El Verde Field Station, and 10 additional nets were placed nearby in natural forest openings. Age, sex, weight, and reproductive condition were determined for each captured specimen. Selected S. rufum were fitted with radio transmitters (Holohil Systems, Ltd., Ontario, Canada, model BD-2) by attachment to the dorsal pelage using "Skin Bond" surgical glue (Pfizer Hospital Products Group, Inc., Largo, Florida, U.S.A.), as described by Fenton and Thomas (1981). These transmitters each weighed 1.2 grams, approximately 5% of body weight
for all but the smallest (19 g) "tagged" individuals. Transmitters were well under the maximum weight recommended to minimize flight and behavioral disturbance (Fenton and Thomas, 1981; Fleming and Heithaus, 1981; Heithaus and Fleming, 1978; Wilkinson and Bradbury, 1988). In March of 1989, I also began to mark bats via attachment of small neck chains, each carrying a uniquely numbered aluminum band (Gey Band and Tag Co., Norristown, Pennsylvania, U.S.A). After release, bats were tracked by two observers using hand held telemetry receivers and antennas (Wildlife Materials, Inc., Carbondale, Illinois, U.S.A., model TRX-1000X).

Error Assessment

Errors from telemetry signals used to locate the position of a radio tagged animal can result in several ways. The first is an inherent error due to the directionality and precision of receiving equipment (Kenwood, 1987; Wilkinson and Bradbury, 1988). Sampling error of this type usually has no systematic deviation from true bearings, and thus no bias. If the exact location of individuals is important to the study, then assessing the magnitude of equipment precision is critical. The second source of error is a function of the study area and its topographical features. Signals from transmitters may be deflected or hidden by obstructions such as hills, trees, or buildings. Errors arising from this type of error may give rise to grossly inaccurate locational information.

In order to assess the accuracy of this telemetry system in the Tabonuco Rain Forest, several exercises were performed prior to the
collection of data used in this study. The first was conducted by two observers simultaneously recorded the location of a third person who moved through the study area with a transmitter. For each of a set of previously designated triangulation points, possible sources of error due to reflection were noted. While tracking bats, if either reflection or obstruction of the transmitter signal was suspected, a third and periodically a fourth bearing were recorded in order to confirm location. On some occasions it was not possible to acquire additional bearings prior to animal movement. These bearings were discarded from analyses.

A second exercise to further test system accuracy was performed utilizing one of the 25 meter canopy towers present in the forest. As an observer with a radio receiver moved away from the base of the tower in increments of 25 meter distances (25 m to 250 m), bearings were taken on transmitters placed at six different heights on the tower (0 m, 5 m, 10 m, 15 m, 18 m, 22 m). Each test was repeated three times in different directions from the tower. I then compared these bearings to actual compass bearings to assess accuracy at different distances and for different transmitter heights.

Telemetry

Location of individual bats was determined by triangulation of signals simultaneously obtained by two field receivers. Each bat was located once during the day, and as many times as possible each night. With constant tracking over a six hour period, I usually was able to telemetrically "capture" each bat between one and three times per night.
Tracking continued as long as transmitters continued to function. Although Fleming and Heithaus (1986) reported that bats usually carry transmitters for an average of 10 to 12 days before they are scratched from the pelage, my experience indicates a minimum mean attachment time of 25 days (range, 13-38; n=26). Field triangulation was facilitated by superimposing a cartesian coordinate system over the study area with 0 degrees at magnetic north. Logistics were simplified because of the series of well maintained trails throughout the forest (Figure 2.1). Two-way radios allowed field observers to make simultaneous measurements which could be verified immediately while in the field.

Site Fidelity

Most definitions of home range consider it to be an area of restricted use by an animal. "Restricted" implies that daily activities are constrained to occur within a subset of the space within which they could occur based upon the locomotor capabilities of the species. Nonetheless, most studies of home range fail to distinguish between an area traversed by an animal because of microgeographic associations and area produced as an artifact of random wanderings. As the mechanisms that generate each of these two types of home range are different, so the ranges they generate should be distinguishable. For each individual bat, the Minimum Convex Polygon (MCP) home range was calculated, as well as a set of vectors which connected successive capture points. Using the mean length and variance of these vector movement segments, program HomeRange (Huber and Willig, unpublished.) created a new set of vectors with order and direction
of each successive capture point randomly assigned. This generated a new set of random coordinates for which a new MCP home range could be calculated. The simulation was performed 200 times for each bat. These 200 simulated MCPs form a distribution under the null hypothesis (random movement) to which the observed MCP could be compared. If site tenacity occurs, and bats actually remain within a limited region, then the observed home range should be statistically distinguishable from randomly generated home ranges with the same segment length mean and variance. In particular, actual MCP home ranges should be smaller than those obtained by random movement. Similar protocols have been used by Case and Sidell (1983) to evaluate size assortment in neotropical avian fauna, by Willig and Moulton (1989) to examine processes structuring neotropical bat communities, and by Munger (1984) to evaluate lizard movement patterns.

Home Range

To estimate the number of nights of radio telemetry data needed to accurately evaluate home range size, cumulative mean MAP estimates for adult males, adult females, and juveniles were plotted for data obtained during the first field season. Data were plotted separately for MAP (0.50) and MAP (0.95) values.

Home range estimates for S. rufum were calculated in different ways. As first approximations, the MCP was plotted using program HomeRange (Huber and Willig, unpublished.) for home range and foraging range. Foraging range can be distinguished from home range by excluding the
location of day roosts from the estimation of range size. I also calculated both MAP (0.95) and MAP (0.50) home range using another option in program HomeRange (Huber and Willig, unpublished.) which is a modification of program MacAnders (Anderson, 1982; Wilkinson and Bradbury, 1988). These MAP values of the home range utilization distribution were chosen because they are the suggested analytical standards (Anderson, 1982; Wilkinson and Bradbury, 1988). MAP (0.95) is used because it is appropriate to the standard definition of home range suggested by Burt (1943). However, when using large MAP estimates, occasional outlier points may lead to large errors when evaluating home range (Anderson, 1982). Because smaller percent MAPs are less sensitive to outlier generated error, I also have conducted analyses using MAP (0.50) home range estimates. MAP (0.50) values are as useful as MAP (0.95) values for comparison purposes, but have the advantage of representing smaller core areas which reduce the effects of occasional outlier points on the resulting estimate.

Estimating a utilization distribution is no different from estimating a probability density function. The resulting three dimensional plots are, in effect, a series of histograms throughout the plane where an animal may be found (i.e., real space). The height of the histogram, or z-axis, is the probability of locating that individual at each point at any given time. Higher peaks indicate higher probability. These figures can therefore be used to qualitatively evaluate the pattern of space use for each bat.

The effects of age (adult versus juvenile) and sex (male versus female) on home range was evaluated via two-way analysis of variance
(ANOVA) and orthogonal a priori tests (Sokal and Rohlf, 1981). Separate analyses were conducted on home range based upon MCP and MAP estimates.

Foraging Behavior

In addition to continuing data collection to estimate home range for S. rufum in 1989, I began collecting data on location and movement of focal individuals during an entire night. Each bat was continuously tracked over one or two periods, which spanned most of the night (2000 hrs - 0400 hrs). Bat location and activity were recorded every 5 minutes to generate a log of nightly activity patterns. I determined the number, size, and location of each individual's feeding area (defined as any area away from the day roost in which a bat remains for 30 minutes or more); the rate of movement between feeding areas; night-to-night fidelity to feeding areas; total commuting distance flown each night from the day roost to feeding areas; the location of, fidelity to, and number of nocturnal feeding roosts employed within a feeding area; and the location of, fidelity to, and number of diurnal roost sites. For each individual, a log of nightly activity was constructed and observations on distance traveled per hour, maximum distance traveled per move, minimum distance traveled per move, mean distance traveled per move, number of moves per hour, and percent of time spent in night roosts (versus foraging) were recorded. These data also were examined for association with phases of lunar illumination. Eight individuals were observed as described above during periods of new moon, when lunar illumination was absent (dark phase). The remaining
eight were tracked during periods of full moon, when lunar illumination was at its peak light phase). Two-way ANOVA was used to ascertain the effect of lunar phase and age-sex group on each movement parameter. All juveniles, regardless of sex, were combined together in order to meet sample size criteria for these tests.

Results and Discussion

Telemetry Accuracy

Errors due to distance of telemetry signals above the ground and distance from the receiver were examined in the Tabonuco Rain Forest. Error decreased as a function of the height of the transmitter. At ground level, the amount of error ranged from 0 to 30 degrees, depending on the topography. At the height of 5 meters, error ranged from 0 to 20 degrees, and from 0 to 8 degrees at 10 meters. The canopy heights of 15, 18, and 22 meters were of particular interest, as these were heights where bats would tend to be found while roosting and foraging. Here, the error ranged from 0 to 2 degrees in all tests up to 200 meters from the tower, except in one, where it reached 3 degrees. Between 200 and 250 meters, error ranged from 0 to 3 degrees, with only one test achieving an error of 4 degrees. Although signal strength decreased as linear distance from the transmitter increased, this factor did not have a substantial affect on accuracy. Instead, height in the canopy and topography of the area seemed to have a combined effect on the accuracy of received signals. At heights over 15 meters, the error rates were reduced substantially. With a maximum error of 4
degrees at distances of 250 m or less, the bearings used to pinpoint the location of bats should be, at most, no greater than 10 m from its true location. These errors simply become "noise" which do not bias the result, but may reduce the chance of obtaining statistically significant differences (Kenwood, 1987).

One other potential source for error may result when a tagged animal cannot be located. For these animals, the home range estimate could be severely biased (underestimated) because the individual may be well outside the range in which it thus far has been recorded or may be involved in some unusual activity. This sort of problem tends to bias against recording large ranges (Kenwood, 1987). In actuality, this was rarely the case with bats in the Tabonuco Rain Forest. Most bats that were "captured" repeatedly and could be located at all times. However, on certain occasions some individuals could not be found. Search of the study area on foot and from canopy towers, where tests showed signals could be received from 2 to 4 kilometers, failed to locate these bats. Subsequent to each departure from the study area, bats were later located within known feeding areas. At times a bat suddenly "disappeared" and radio contact was lost for 20 to 60 minutes. Such individuals always "reappeared" within known feeding areas where they continued to forage for the remainder of the night. Two possible explanations apply to these occurrences. First, these bats may have stopped at a night roost or area which sufficiently obstructed or reduced the strength of the radio signal to prevent reception. The times during which these bats were "missing" are well within the normal length of time S. rufum is known to remain inactive in night roosts. A second
possibility is that these bats were flying long search flights outside the previously recorded home range (greater than 4 km away), possibly to gather information on other feeding areas. Both *A. jamaicensis* (Morrison, 1975) and *C. perspicillata* (Fleming, 1988) demonstrate this behavior while assessing new food sources. However, in the case of *S. rufum*, it does not appear likely that all of these individuals left the area to forage at a second feeding site. The commuting time to and from another area almost 4 km away, as well as the time spent foraging and feeding in that area, would well exceed the period in which most were out of radio contact. Also, fruit availability in the Tabonuco Rain Forest is only slightly seasonal and large amounts strike the forest floor unconsumed (Devoe, 1990). This indicates an excess of fruit is available to frugivores year round. There would appear to be little need to spend large amounts of time and energy searching for new food sources. Although *S. rufum* may make occasional short sorties outside of its normal home range, longer search flights appear to be rare, and not characteristic of most individuals.

**Home Range**

MCP home ranges for each individual were first compared to computer generated simulations. If bats move randomly, then observed home ranges would be expected to fall outside the lower 5% tail of the randomly generated home ranges. This was not the case for any individual in this study. All home ranges were much smaller than would be expected by chance if movements were random (Table 2.1; Figure 2.2). For most individuals, 100% of the randomly generated home ranges were larger
than the actual home range. Clearly, *S. rufum* is not nomadic; individuals remain within a well-defined area for long periods of time. My netting observations support this. Several banded bats have been captured in the same locality and in the same nets months after initial capture.

When cumulative mean MAP estimates were plotted over time (Figure 2.3), it became evident that mean MAP (0.95) values did not stabilize over the three to four week period for which they were measured. Even after 20 days, the addition of capture points noticeably increased home range size. MAP (0.50) values, which represent a more stable core area and are less sensitive to occasional outlier points, stabilized between 5 and 10 nights of radio tracking. Based on this, only individuals which were captured on 10 or more nights of tracking were included in home range analyses.

Forty-one *S. rufum* were tagged with radio transmitters during 1988 and 1989 to estimate home range size. Of these, 26 (8 adult male, 10 adult female, 6 juvenile male, 2 juvenile female) were captured via telemetry sufficiently often to estimate spatial parameters. All individuals were reproductively inactive when they were tagged (females were neither pregnant or lactating; testes were not descended in males). Reproductively inactive individuals were selected for two reasons. First, this minimized confounding effects such as increased energy demands for pregnant or lactating females which might manifest itself in longer foraging bouts or larger home ranges. Second, *S. rufum* is a "sensitive" species according to U. S. Forest Service criteria. As I wished to prevent negative effects with reproductive success of pregnant females, I avoided tagging them with
transmitters. Adding the weight of a transmitter, even as small as 1.2g, to an individual already burdened with carrying a developing fetus, could have detrimental effects on reproduction.

Results of MCP analyses for home range and foraging range were identical (Table 2.3 and 2.4). Regardless of sex, both home range and foraging range were significantly larger for juveniles than for adults (home range a priori test $F_{(1,22)}=9.27, 0.05>p>0.01$, foraging range a priori test $F_{(1,22)}=9.02, 0.05>p>0.01$; Figure 2.4).

Although the actual size of areas estimated by MAP (0.50) and MAP (0.95) methodologies differ, the statistical conclusions concerning the effects of age and sex on these spacial parameters are the same. No significant differences in mean home range size were related to age or sex (Tables 2.5 and 2.7). Similarly, the results of analyses of foraging range based upon the two MAP methods are identical: the foraging range of juveniles was significantly larger that that of adults (MAP (0.50) a priori test, $F_{(1,22)}=8.72, 0.05>p>0.01$, MAP (0.95) a priori test, $F_{(1,22)}=9.72, 0.05>p>0.01$; Figure 2.5), and this difference was consistent in both sexes (Tables 2.5 and 2.7). All age and sex categories maintain indistinguishable home range sizes, but juveniles forage over a broader range within those areas than do adults. This pattern of space use is consistent with the idea that S. rufum do not form harem associations and that juveniles forage more widely because of inexperience or behavioral interactions with conspecifics.

Because MAP estimations determine an area which encompasses either 95% or 50% of the capture points, it is possible for foraging range
to be larger than home range, as in the case for juveniles (Table 2.2). This can happen if day roosts occur in one or a few clusters, night roosts are widely dispersed, or by some combination of the two. Dense clusters of day roosts can result in 95% or 50% of capture points being concentrated in a small area, thus yielding a small MAP estimate. When day roosts are eliminated from analyses, and foraging areas, constructed only from the more widely dispersed night roosts, a larger area is needed to encompass both 95% and 50% of the captures. Smaller MAP estimates should be more sensitive to this effect, particularly if clusters of day roost are centrally located within the home range.

I examined space utilization of each bat qualitatively based upon three dimensional plots of the utilization distribution (Appendix A). These figures generally appear similar in shape (high towards the center which decreases towards the edges) and thus indicate similar patterns of space use for all individuals. Home range comprises an area with high utilization towards the center, with occasional minor peaks on otherwise decreasing use of peripheral space. The emerging view of total home range of an individual is one in which space use is heterogeneous, with areas of intense use (peaks) and infrequent use (valleys) giving rise to a varied topography.

This study indicates that sex related differences in home range size based upon MCP or MAP methods do not occur in S. rufum. The social system of this species, as inferred from by telemetry, indicates that males and females occupy solitary roosts, with no indication of polygeny or harem formation. Moreover, considerable spacial overlap in home range characterizes all individuals regardless of sex (Figure 2.6). However, the
inability to detect differences in overlap or size may be influenced, at least in part, by the fact that only individuals which were reproductively inactive at the time of initial capture were tagged with radio transmitters. Any change in home range or foraging patterns which would result as a consequence of the onset of reproductive activity would remain undetected by these analyses.

Age differences in home range size were demonstrated only when based upon MCP; with juveniles ranging significantly farther than adults. Bat movement patterns have been reported to be age dependent. Young bats may travel with their mother, as occurs in *Desmodus rotundus* (Wilkinson, 1985) and *Eptesicus fuscus* (Brigham and Brigham, 1989), or they may remain close to day roosts, as occurs in *Myotis lucifugus* (Anthony and Kunz, 1977). Because it was not possible for *S. rufum* smaller than 19 grams to carry transmitters, data on very young bats are not available. Older juveniles that were tagged, not only demonstrated larger home ranges than adults, but also evidenced considerable range overlap with other adults and juveniles. These results are consistent with several behavioral hypotheses. Juveniles may at times be excluded from feeding in areas with trees having high fruit set. However, because of the high amount of spatial overlap and long term site tenacity exhibited by all individuals, it would probably be difficult and costly to attempt to defend such a food source against other bats for any length of time, especially in light of relatively high year round abundance of fruit in the Tabonuco Rain Forest (Devoe, 1990). Young bats may be flying greater distances because of inexperience or unfamiliarity with the feeding area. As experience is
gained over time, they likely increase efficiency and reduce flight time and range as they forage. This is a plausible explanation because capture records indicate that at least some bats remain faithful to the same feeding area for an extended period of at least several months or years.

Foraging Behavior

Of 41 S. rufum tagged with radio transmitters, 16 were chosen for detailed monitoring of nightly movements and foraging behavior. Actual tracking time averaged 6.05 hours per individual (range 2.33 to 8.00 hrs.). All tracked bats exhibited fidelity to only one feeding area, which persisted over a period of at least several weeks. Day roosts often were located within or on the periphery of the feeding area, thus commuting time to feeding area was negligible. Bats changed day roosts almost daily and seldom utilized the same site more than once or twice. Each evening, bats departed from their day roost between 1830 and 1930 hrs. Individuals left their night roosts an average of 3.79 times each hour and characteristically made several passes among fruiting trees. They usually remained in flight for ten or more minutes (occasionally up to 40 minutes) when selecting fruit; however, the majority of their time (approximately 73 %) was spent in night roosts, ostensibly consuming and digesting food. Night roosts were changed frequently, with a mean distance of about 59 meters separating consecutive sites. Typically two or three "major" roosts were visited repeatedly throughout the night (Figure 2.6a), in contrast to many "minor" roosts which were occupied only once or twice. These data, when superimposed on long term home range suggest that night roosts are
scattered throughout the home range and that occasional long distance sorties outside the previously observed home range occur (Figure 2.6b). The entire area utilized on any particular night usually encompasses 75% or less of the total home range, but occasional forays outside the home range suggest that S. rufum utilizes a strategy sensitive to detecting emerging food sources in the nearby surrounding habitat.

Night activity and movement parameters for S. rufum are shown in Table 2.9. For all parameters measured (Tables 2.10 to 2.15), no significant differences were found due to either treatments or their interaction. This indicates that nightly foraging activity of S. rufum does not vary due to sex, age, or lunar illumination. Lunar phobia and other predation avoidance behaviors can incur high costs to foraging by increasing energy or time needed to obtain resources. In the absence of predators, one might expect the absence of lunar phobia as well as the absence of other predation avoidance behaviors. As S. rufum is endemic to an area where nocturnal predation pressure is low, predation would appear to have little impact on the evolution of its foraging behavior.

Forest Gap Use

Disturbance and gap formation are major forces in the regeneration of rain forests (Pickett and White, 1985). Differential gap use in tropical forests has been inferred (Crome and Richards, 1988). The degree to which seed dispersers differentially utilize disturbed areas within a forest is of interest because of the implications in forest recovery. Some bats have been known to follow gaps in the forest canopy (Charles-Dominique, 1966)
and this appears to be true in the Tabonuco Rain Forest as well. Large open areas such as roads, powerline cuts, clearcuts, streams, and fence lines are areas of preferred utilization by bats (Devoe, 1990). Telemetry data for *S. rufum* support this. Home range and foraging data were almost always centered around one or more of the large aforementioned canopy gaps present in the study area. Bats frequently moved through these areas while foraging, and night roosts were often located near gap edges. Further evaluation of bat-disturbance by comparison of bat home ranges and the location of various gaps in the forest was to be a major focus of this study. However, prior to the detailed mapping of gaps, Hurricane Hugo struck the Tabonuco Rain Forest and drastically altered forest structure by damaging or destroying many of the trees and defoliating virtually all hardwoods.

**Summary**

*Stenoderma rufum* is the first species of bat with a demonstrated site fidelity and a quantified home range. The foraging behavior of this species is influenced by a variety of factors. Because *S. rufum* is solitary, is foliage roosting, lives in a habitat that has a year round food surplus, lacks any significant predators, and has few other vertebrate competitors, little of its foraging and roosting behavior appears to be greatly limited by energetic constraints. Day roosts are located in feeding areas where individuals remain for extended periods of time. Commuting time is practically eliminated and search time is effectively absent. Total distance flown by *S. rufum* in a night is much less than for other tropical bat species for which foraging data are available, such as *A. jamaicensis* or *C. perspicillata*, and
foraging behavior is not influenced by variation of lunar illumination. Selection of both day and night roost sites appears to be opportunistic, as these sites are seldom, if ever, revisited.

Sex had little effect on home range; however age did, with juveniles frequently flying farther than did adults. Differences due to age are likely related to juvenile inexperience or unfamiliarity with the habitat. No differences due to sex were detected during nightly foraging behavior.

Predation pressure and food availability seem to be foremost considerations in shaping foraging and roosting behavior in other neotropical bats. Both *A. jamaicensis* (Morrison, 1975; 1978a; 1978b; 1978c) and *C. perspicillata* (Fleming, 1986; 1988; Stashko, 1982) modify their behavior in response to those factors. Because *S. rufum* on Puerto Rico does not appear limited by either predation or fruit availability, the foraging and roosting behaviors it exhibits are greatly different from the aforementioned species.
Literature Cited


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<td>25,444</td>
<td>173,975</td>
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</tr>
<tr>
<td>179</td>
<td>J</td>
<td>M</td>
<td>27</td>
<td>18,502</td>
<td>104,225</td>
<td>0.00</td>
</tr>
<tr>
<td>218</td>
<td>A</td>
<td>F</td>
<td>47</td>
<td>28,687</td>
<td>187,825</td>
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<tr>
<td>238</td>
<td>A</td>
<td>M</td>
<td>14</td>
<td>26,287</td>
<td>68,650</td>
<td>0.03</td>
</tr>
<tr>
<td>239</td>
<td>J</td>
<td>M</td>
<td>29</td>
<td>26,432</td>
<td>140,750</td>
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</tr>
</tbody>
</table>
### Table 2.1 continued

<table>
<thead>
<tr>
<th>Specimen number</th>
<th>Age</th>
<th>Sex</th>
<th>Number of relocations</th>
<th>MCP (m²)</th>
<th>Mean area from randomizations (m²)</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>255</td>
<td>A</td>
<td>M</td>
<td>23</td>
<td>16,507</td>
<td>78,175</td>
<td>0.00</td>
</tr>
<tr>
<td>259</td>
<td>A</td>
<td>M</td>
<td>28</td>
<td>17,505</td>
<td>81,100</td>
<td>0.00</td>
</tr>
<tr>
<td>279</td>
<td>A</td>
<td>F</td>
<td>56</td>
<td>22,062</td>
<td>205,175</td>
<td>0.00</td>
</tr>
<tr>
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<td>A</td>
<td>F</td>
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<td>19,240</td>
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<tr>
<td>579</td>
<td>A</td>
<td>M</td>
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<td>80,850</td>
<td>0.05</td>
</tr>
<tr>
<td>635</td>
<td>A</td>
<td>F</td>
<td>27</td>
<td>14,677</td>
<td>69,600</td>
<td>0.00</td>
</tr>
<tr>
<td>846</td>
<td>J</td>
<td>F</td>
<td>21</td>
<td>40,365</td>
<td>164,125</td>
<td>0.00</td>
</tr>
<tr>
<td>897</td>
<td>J</td>
<td>M</td>
<td>29</td>
<td>36,307</td>
<td>345,425</td>
<td>0.00</td>
</tr>
<tr>
<td>907</td>
<td>J</td>
<td>M</td>
<td>15</td>
<td>29,465</td>
<td>96,700</td>
<td>0.01</td>
</tr>
<tr>
<td>936</td>
<td>A</td>
<td>F</td>
<td>17</td>
<td>23,402</td>
<td>186,000</td>
<td>0.00</td>
</tr>
<tr>
<td>967</td>
<td>A</td>
<td>F</td>
<td>23</td>
<td>20,115</td>
<td>97,975</td>
<td>0.00</td>
</tr>
<tr>
<td>974</td>
<td>J</td>
<td>F</td>
<td>25</td>
<td>20,582</td>
<td>133,125</td>
<td>0.00</td>
</tr>
<tr>
<td>996</td>
<td>A</td>
<td>F</td>
<td>19</td>
<td>22,577</td>
<td>156,650</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Table 2.2--Mean (m$^2$), followed by standard deviation in parentheses, for each type of home range calculated for *S. rufum*. MCP = Minimum Convex Polygon, MAP (0.50) = 50% Minimum Area Probability, MAP (0.95) = 95% Minimum Area Probability; home range is based upon both day roost and night roost captures, whereas foraging range is defined by night roost captures only.

<table>
<thead>
<tr>
<th>Group</th>
<th>N</th>
<th>MCP home range</th>
<th>MCP foraging range</th>
<th>MAP (0.50) home range</th>
<th>MAP (0.50) foraging range</th>
<th>MAP (0.95) home range</th>
<th>MAP (0.95) foraging range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>18</td>
<td>20,967 (1365)</td>
<td>11,623 (1353)</td>
<td>6,671 (948)</td>
<td>5,208 (716)</td>
<td>20,670 (2397)</td>
<td>15,309 (1847)</td>
</tr>
<tr>
<td>Adult males</td>
<td>8</td>
<td>20,018 (2116)</td>
<td>10,830 (2390)</td>
<td>8,120 (1945)</td>
<td>6,271 (1486)</td>
<td>24,244 (4533)</td>
<td>17,601 (3856)</td>
</tr>
<tr>
<td>Adult females</td>
<td>10</td>
<td>21,727 (1844)</td>
<td>12,257 (1604)</td>
<td>5,513 (607)</td>
<td>4,357 (436)</td>
<td>17,812 (2169)</td>
<td>13,476 (1227)</td>
</tr>
<tr>
<td>Juveniles</td>
<td>8</td>
<td>31,064 (3740)</td>
<td>19,615 (2476)</td>
<td>7,086 (1194)</td>
<td>10,259 (2476)</td>
<td>23,636 (3442)</td>
<td>27,727 (5917)</td>
</tr>
<tr>
<td>Total</td>
<td>26</td>
<td>24,074 (1717)</td>
<td>14,082 (1454)</td>
<td>6,799 (740)</td>
<td>6,762 (993)</td>
<td>21,583 (1949)</td>
<td>19,130 (2436)</td>
</tr>
</tbody>
</table>
Table 2.3.--Effects of age and sex on MCP home range of *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares x 10^{-5}</th>
<th>Mean squares x 10^{-5}</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td>44,815.2</td>
<td>44,815.2</td>
<td>7.36</td>
<td>0.01</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>9.5</td>
<td>9.5</td>
<td>0.02</td>
<td>0.90</td>
</tr>
<tr>
<td>Age X Sex</td>
<td>1</td>
<td>69.9</td>
<td>69.9</td>
<td>0.12</td>
<td>0.74</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td>13,400.0</td>
<td>609.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.4.--Effects of age and sex on MCP foraging range of *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares x 10^{-5}</th>
<th>Mean squares x 10^{-5}</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td>4,638.4</td>
<td>4,638.4</td>
<td>11.23</td>
<td>0.03</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>1,080.3</td>
<td>1,080.3</td>
<td>2.62</td>
<td>0.12</td>
</tr>
<tr>
<td>Age X Sex</td>
<td>1</td>
<td>543.4</td>
<td>543.4</td>
<td>1.32</td>
<td>0.26</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td>9,066.3</td>
<td>412.1</td>
<td></td>
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</tr>
</tbody>
</table>
Table 2.5.--Effects of age and sex on MAP (0.95) home range of *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares x 10^-5</th>
<th>Mean squares x 10^-5</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td>727.4</td>
<td>727.4</td>
<td>0.73</td>
<td>0.40</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>6.4</td>
<td>6.4</td>
<td>0.01</td>
<td>0.94</td>
</tr>
<tr>
<td>Age X Sex</td>
<td>1</td>
<td>1,643.0</td>
<td>1,643.0</td>
<td>1.65</td>
<td>0.21</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td>21,900.0</td>
<td>995.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.6.--Effects of age and sex on MAP (0.95) foraging range of *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares x 10^-5</th>
<th>Mean squares x 10^-5</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td>8,319.0</td>
<td>8,319.0</td>
<td>6.35</td>
<td>0.02</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>28.4</td>
<td>28.4</td>
<td>0.02</td>
<td>0.88</td>
</tr>
<tr>
<td>Age X Sex</td>
<td>1</td>
<td>1,086.4</td>
<td>1,086.4</td>
<td>0.08</td>
<td>0.37</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td>28,800.0</td>
<td>1,309.1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.7.--Effects of age and sex on MAP (0.50) home range of *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares x 10^{-5}</th>
<th>Mean squares x 10^{-5}</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td>18.0</td>
<td>18.0</td>
<td>0.12</td>
<td>0.73</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>14.8</td>
<td>14.8</td>
<td>0.10</td>
<td>0.75</td>
</tr>
<tr>
<td>Age X Sex</td>
<td>1</td>
<td>185.2</td>
<td>185.2</td>
<td>1.27</td>
<td>0.27</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td>3,218.2</td>
<td>146.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.8.--Effects of age and sex on MAP (0.50) foraging range of *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares x 10^{-5}</th>
<th>Mean squares x 10^{-5}</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td>1,361.7</td>
<td>1,361.7</td>
<td>6.29</td>
<td>0.02</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>1.3</td>
<td>1.3</td>
<td>0.01</td>
<td>0.94</td>
</tr>
<tr>
<td>Age X Sex</td>
<td>1</td>
<td>195.2</td>
<td>195.2</td>
<td>0.90</td>
<td>0.35</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td>4,765.7</td>
<td>216.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.9.--Movement parameters (means in meters, followed by standard error in parentheses) of *S. rufum* during dark and light phases of the moon. Light phase = full moon, dark phase = new moon, total = combination of light and dark phase.

<table>
<thead>
<tr>
<th>Group</th>
<th>N</th>
<th>Tot. Dist/HR</th>
<th>Max. Dist.</th>
<th>Min. Dist.</th>
<th>Mean Dist./Move</th>
<th>Moves/HR</th>
<th>% Time/Roost</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light Phase</td>
<td>8</td>
<td>232.5 (41.6)</td>
<td>146.5 (13.9)</td>
<td>19.3 (8.6)</td>
<td>63.9 (9.0)</td>
<td>3.6 (0.3)</td>
<td>72.0 (8.0)</td>
</tr>
<tr>
<td>Dark Phase</td>
<td>8</td>
<td>223.2 (30.2)</td>
<td>152.0 (17.3)</td>
<td>15.2 (1.4)</td>
<td>54.5 (6.0)</td>
<td>4.0 (0.3)</td>
<td>74.2 (4.2)</td>
</tr>
<tr>
<td>Total</td>
<td>16</td>
<td>227.8 (24.9)</td>
<td>149.2 (10.7)</td>
<td>21.3 (3.5)</td>
<td>59.2 (5.3)</td>
<td>3.8 (0.2)</td>
<td>73.1 (4.4)</td>
</tr>
</tbody>
</table>
Table 2.10.--Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on mean total distance traveled during foraging by *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moon (A)</td>
<td>1</td>
<td>40.4</td>
<td>40.4</td>
<td>0.00</td>
<td>0.95</td>
</tr>
<tr>
<td>Age-Sex (B)</td>
<td>2</td>
<td>6,152.2</td>
<td>3,077.1</td>
<td>0.34</td>
<td>0.72</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>2,948.0</td>
<td>1,474.0</td>
<td>0.16</td>
<td>0.85</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>9,016.9</td>
<td>9,016.9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.11.--Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on maximum distance traveled during foraging by *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moon (A)</td>
<td>1</td>
<td>239.7</td>
<td>239.7</td>
<td>0.10</td>
<td>0.76</td>
</tr>
<tr>
<td>Age-Sex (B)</td>
<td>2</td>
<td>642.3</td>
<td>321.1</td>
<td>0.13</td>
<td>0.88</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>1,952.3</td>
<td>976.2</td>
<td>0.40</td>
<td>0.69</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>24,999.4</td>
<td>2,499.9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.12.—Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on minimum distance traveled during foraging by S. rufum based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moon (A)</td>
<td>1</td>
<td>1,022.8</td>
<td>1,022.8</td>
<td>2.50</td>
<td>0.15</td>
</tr>
<tr>
<td>Age-Sex (B)</td>
<td>2</td>
<td>144.9</td>
<td>72.5</td>
<td>0.18</td>
<td>0.84</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>41.7</td>
<td>20.8</td>
<td>0.05</td>
<td>0.95</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>4,089.4</td>
<td>408.9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.13.—Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on mean distance per move traveled during foraging by S. rufum based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moon (A)</td>
<td>1</td>
<td>319.2</td>
<td>319.2</td>
<td>0.55</td>
<td>0.48</td>
</tr>
<tr>
<td>Age-Sex (B)</td>
<td>2</td>
<td>595.4</td>
<td>297.7</td>
<td>0.51</td>
<td>0.62</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>26.3</td>
<td>13.1</td>
<td>0.02</td>
<td>0.98</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>5,855.9</td>
<td>585.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.14.—Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on number of moves per hour during foraging by *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moon (A)</td>
<td>1</td>
<td>0.58</td>
<td>0.58</td>
<td>0.55</td>
<td>0.48</td>
</tr>
<tr>
<td>Age-Sex (B)</td>
<td>2</td>
<td>0.21</td>
<td>0.10</td>
<td>0.10</td>
<td>0.90</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>0.35</td>
<td>0.18</td>
<td>0.17</td>
<td>0.84</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>10.14</td>
<td>1.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.15.—Effects of age-sex group (adult males, adult females, or juveniles) and moon phase on time spent in night roost during foraging by *S. rufum* based upon a pure model I two-way analysis of variance.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moon (A)</td>
<td>1</td>
<td>722.5</td>
<td>722.5</td>
<td>0.06</td>
<td>0.81</td>
</tr>
<tr>
<td>Age-Sex (B)</td>
<td>2</td>
<td>737.5</td>
<td>368.8</td>
<td>0.03</td>
<td>0.97</td>
</tr>
<tr>
<td>A x B</td>
<td>2</td>
<td>23,856.3</td>
<td>11,928.1</td>
<td>1.01</td>
<td>0.40</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>118,450.0</td>
<td>11,845.0</td>
<td></td>
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CHAPTER III
MORPHOMETRICS

Introduction

Morphometric variation has long been used as an indicator of a diverse array of taxonomic and evolutionary phenomena dealing with ecology, population biology, geographic variation, and sexual dimorphism (Bookstein, 1982; Findley and Wilson, 1982; Reyment et al., 1984; Willig, 1986; Willig and Moulton, 1989). It is of interest in its own right, as a reflection of the evolutionary factors which shape organismal phenotypes. Moreover, the manner in which individual variation is compartmentalized among groups can give insight into the processes of speciation and the maintenance of phenotypic integrity (Simpson, 1944; Mayr, 1964).

Although morphological studies have added important contributions to the study of mammals, in the past, most have dealt with samples spanning large geographic regions containing a number of potentially different populations (e.g., Husson, 1962; Handley, 1976; Koopman, 1978). Differences among populations cannot be investigated based on such wide scale collection. Few studies have had adequate sample sizes to conduct intrademic analyses. Notable exceptions include works on Liomys (Genoways, 1973), Cratogeomys (Hollander, 1990), and a number of Brazilian bat species (Willig, 1983).
Secondary Sexual Variation

In particular, secondary sexual variation has interested biologists for many years (Darwin, 1859, 1871; Myers, 1978; Ralls, 1976; Swanepoel and Genoways, 1979; Williams and Findley, 1979). Often the sexes of a taxon differ morphologically to such an extent so as to appear a different species (e.g., males are nearly twice the size of females in *Hypsognathus monstrosus*). However, the consequences of such differences (or lack thereof) are not always clear. Two major hypotheses have been presented to explain sexual variation in organisms. The first, that of sexual selection (Darwin 1859, 1871), suggested that natural selection can shape, among other things, the anatomical or morphological mechanisms that function in obtaining mates. Competition among individuals of one sex (usually males) for reproductive access to the other sex (usually females) will act as a selection process on phenotypic and behavioral traits. Trivers (1972) further refined this idea to include parental investment, indicating that the sex with the greater investment in the offspring (usually females in mammals) will be the one which is the object of competition. Because large size is usually advantageous in competitive encounters which provide access to females, larger males should be favored without similar size related effects on females. A second hypothesis, suggested by Selander (1966, 1972), imparts that size differences between sexes may reduce intraspecific competition for resources. This is also true for differences in size related to age. If predator size, due to differences associated with age or sex, constrains prey choice, then differences in prey-size selection between age or sex classes could lead to considerable dietary variation within a
population, a reduction in niche overlap among individuals, and an expanded resource base for the species. Numerous examples demonstrate that body size differences between sexes are related to differential food consumption (Earhart and Johnson, 1970; Schoener, 1967; 1968; Selander; 1966), although this is not always clear (Gannon et al., 1990).

These theories are neither mutually exclusive, nor sufficient, individually or collectively, to account for all cases of sexual variation, particularly those in which females are larger than males. Ralls (1976) suggested that this phenomenon of larger females does not appear to be commonly associated with type of mating system, degree of parental investment, aggressiveness and dominance of females, or other factors commonly associated with sexual selection. She presented the "Big Mother Hypothesis" which posits that big mothers are better or more fit mothers for a number of reasons. These involve the stringent demands of pregnancy and nursing, which may represent more powerful selection pressures than those produced by sexual selection differentially acting on males.

Measurement Error

A certain amount of error is associated with making any kind of measurement. Because morphometric analyses are concerned with detecting differences among and within groups, the consequences of measuring error, the variability of repeated measurements of a particular character from the same individual relative to its variability among individuals in a particular group (Bailey and Byrnes, 1990), can be
substantial. Although many morphometric studies have ignored measuring error in the past (Pimentel, 1979; Reyment et al., 1984), various methods have been suggested to deal with this problem. Each method has limitations. For example, Dillon (1984) chose to measure morphological variables that differ significantly among known groups, but his method is inadequate because measurements are not repeated on any given individual. Zink (1983) utilized a method in which he repeated measurements of each character for a group of individuals and compared the means of the two sets of measurements. Similarly, Lee (1982) and Pankakoski et al. (1987) measured a set of individuals many times. If variation does occur among individuals, a reasonably large sample is needed to evaluate measuring error (Bailey and Byrnes, 1990). Since sample sizes were small or statistical comparisons invalid in previous analyses, they were inadequate or inaccurate assessments of within-individual variation and its consequences to higher level questions of group difference.

Asymmetry

When examining morphological variation in a natural population, slight but measurable differences can often be detected between bilateral structures. These differences, resulting in asymmetry (the difference between the right side and left side of a character) of otherwise bilaterally symmetrical organisms, have been of interest to evolutionary biologists for some time (Jackson, 1973, Soulé, 1967; Van Valen, 1962). More recently, a renewed interest in this phenomenon has occurred because factors implicated to cause fluctuating asymmetry, such as environmental stress,
inbreeding, or genetic bottlenecks, have important biological consequences of their own. These agents ostensibly disrupt genomic organization or coordination. Thus fluctuating asymmetry may reflect past or current disruption of coadapted gene complexes (Graham and Felley, 1985; Owen and McBee, 1990; Palmer and Stroebeck, 1986; Wayne et al., 1986; Willig and Owen, 1987a).

It is important to distinguish among three different types of asymmetry, any of which can occur together for any one character. Directional asymmetry occurs when normal development is greater on one side of a plane than on the other. For a particular mensural character (as in the mammalian heart), this occurs when the population mean of the right side minus the left side is not statistically equal to zero. In contrast, antisymmetry is a condition where asymmetry exists, but it is variable as to which side of the plane on which it occurs will have greater development (i.e., right side minus the left side for a particular character is not normally distributed). An example of this phenomenon is right- and left-handedness in humans. Both these conditions are considered to have some adaptive value (Soule, 1967). Fluctuating asymmetry is the remaining variation, which is expressed within a population after the signed differences between paired structures are normally distributed with a mean of zero (Soule, 1967). Generally, an examination of fluctuating asymmetry evaluates the variance of this normal (or normalized) distribution with respect to that of another reference population (Owen and McBee, 1990). This phenomenon appears to have no obvious adaptive value and may result from the inability of an organism to develop in precisely predetermined paths, which in turn
Fluctuating asymmetry may represent the inability of developmental control systems to buffer against accidental variation during development (Soule, 1967; Van Valen, 1962). Some individuals have a higher susceptibility to accidental variation and as a result will manifest a higher degree of asymmetry. Accidents which induce this condition may be intrinsic, extrinsic, or an interaction of the two. Fluctuating asymmetry has been postulated to occur under a variety of conditions including inbreeding, hybrid zones, and systemic or environmental stress which may result in the critical disruption of the genome (Owen and McBee, 1990; Palmer and Stroebeck, 1986). Such disruption, if manifested via homoeotic mutations, could play a critical role in the evolution of novel phenotypic body plans (Raff and Kaufmann, 1983).

The effects resulting from environmental stress have been of particular interest. Whereas some researchers have found positive associations between environmental stress and increased levels of fluctuating asymmetry (Palmer and Stroebeck, 1986; Siegel and Doyle, 1975a), others have found results to be inconclusive (Owen and McBee, 1990; Siegel and Doyle, 1975b).

*Stenoderma rufum* appears to be a good candidate in which to examine fluctuating asymmetry. An endemic island species with a geographically restricted population, this species has only rarely been captured outside the Tabonuco Rain Forest. Moreover, home range and movement pattern analyses reveal it to be extremely philopatric to one site over long periods of time (see Chapter III). In addition, its habitat is
affected by constant environmental disturbances of various scales ranging from tree falls, to landslides, to hurricanes. Recent data indicate that this population of S. rufum may be extremely sensitive to large scale disturbances creating severe reductions in population density with the potential for genetic bottlenecks (Gannon and Willig, unpublished).

Hereafter, I investigate morphometric variation within a single population of S. rufum. Measuring error, secondary sexual variation, and asymmetry were evaluated using multivariate and univariate statistical techniques.

Methods
Specimens of S. rufum collected in the Tabonuco Rain Forest were obtained from The Museum of Texas Tech University, The Royal Ontario Museum, and Carnegie Museum of Natural History. A complete list of specimens appears in Appendix A. Cranial and mandibular measurements were made to the nearest 0.01 mm (Figure 3.1, Appendix B) using Fowler digital calipers (Ultra-cal II, Fred V. Fowler Co., Inc., Newton, Massachusetts). All measurements were made by the author.

Morphometric variation
Skulls of S. rufum were classified by age (adult or juvenile) and sex (male or female), and measured for each of 19 morphometric characters (Appendix B). All bilateral measurements were taken from the right side of the skull or mandible. Because systematic questions involve comparison of a suite of characters, a multivariate approach is preferred (Willig et al.,
1986; Willig and Owen, 1987b). Two-way multivariate analysis of variance (MANOVA) was used to ascertain the existence of significant variation due to age or sex. Univariate two-way (age versus sex) analyses of variance (ANOVA) were performed on each character to identify important variables that contribute to significance in the MANOVA. A multivariate test for homogeneity of variance (BoxM) was performed to evaluate the appropriateness of MANOVA, whereas univariate tests for homogeneity of variance (Bartlett’s Box) were performed on each character to determine the appropriateness of ANOVA. All statistical tests were performed via programs in SPSS (SPSS Inc., 1990)

Measurement error

To evaluate the effects of variation due to measuring error, each of the 19 characters (Appendix B) was measured three non-consecutive times for all skulls. A two-way (age versus sex) nested (multiple measures per skull) ANOVA, was performed for each character separately (SPSS Inc., 1990). In addition, more powerful hierarchical a priori contrasts were made for each character comparing adult males to adult females, juvenile males to juvenile females, and adults to juveniles regardless of sex.

Asymmetry

Asymmetry tests were performed only on adult males and females in order to eliminate variation due to age, which is difficult to evaluate or control. Eight bilaterally symmetrical cranial and dental characters (Appendix B) were measured on both right and left sides of each specimen.
Data were analyzed for each of three different types of asymmetry following the analytical protocol described by Owen and McBee (1990). Each character was first made scale free by dividing its right minus left difference by the mean of its right and left measurement. This insures that asymmetry values are comparable among characters. Scale independence was evaluated using product moment correlations (Zar, 1981) between each individual’s asymmetry value and the right minus left mean for that individual.

Directional asymmetry was assessed for males and females separately, by comparing the sample mean of each character to zero via a t-test (Sokal and Rohlf, 1981). Corrections for directional asymmetry were achieved by subtracting a character’s mean asymmetry value from each individual’s value for that character. Skewness and kurtosis reflect antisymmetry and were tested on corrected values (adjusted for directional asymmetry) with the Shapiro-Wilk statistic (Zar, 1981) for males and females separately. Prior to testing for fluctuating asymmetry, significant antisymmetries (non-normal distributions) were corrected using Box-Cox transformations (Sokal and Rohlf, 1981) to produce normality. Differences in fluctuating asymmetry between males and females were evaluated using Levene’s test (Schultz, 1985). Because this test is particularly robust with respect to undetected non-normal tendencies, normalization was not an overwhelming concern.
Results and Discussion

Morphometric variation

For multivariate analyses, BoxM test was non-significant (p>0.05), indicating homogeneity of variances in the treatment groups. MANOVA (Table 3.1, Table 3.2) detected significant age specific and secondary sexual variation for S. rufum. The significant age by sex interaction indicates that the magnitude of difference between the sexes depends upon age (age and sex do not interact independently). Significance of each of the main effects implies that the interaction is one of magnitude rather than direction. Similarly, a comparison of means for each character separately indicates exaggerated dimorphism in adults compared to the situation in juveniles (Table 3.2).

Bartlett’s test for univariate homogeneity of variance was non-significant for each character, thus ANOVAs may be considered appropriate indications of the contribution of characters to significance in the MANOVA. Two-way ANOVAs (Table 3.3) with three random measurements nested within each character corroborate MANOVA results and reveal highly significant interactions for all but four characters (width of maxilla, width of zygomatic arch, breadth of braincase, and length of maxillary toothrow). Moreover, they indicate that measurement error is not significant for any character. Therefore, measurement error, has no discernible effect on the results of this study. More powerful a priori hierarchical contrasts (Table 3.3) showed adult males different from adult females for 18 characters, and juvenile males different from juvenile
females for 14 characters. Adults, regardless of sex, were significantly larger than juveniles for 12 characters. Sample means of all 19 characters are larger for adult females than for adult males and for 17 of 19 characters, juvenile females are larger than juvenile males.

These analyses clearly indicate two main conclusions. First, measurement error is negligible for cranial and mandibular characters. One can therefore proceed with some confidence that measurements used in this study are unbiased estimates of actual parametric values. Second, secondary-sexual dimorphism exists in *S. rufum* for almost all characteristics examined, with females of both age groups (adult and juvenile) larger than males. Nonetheless, the magnitude of dimorphism, estimated by mean ratios of adult males to adult females (range 1.00 to 1.04) and juvenile males to juvenile females (range 1.00 to 1.06) is small.

Within the Chiroptera, sexual dimorphism is primarily limited to size, although other characteristics, such as dimorphic glands, are not uncommon in the Emballonuridae and Molossidae (Bradbury, 1977). In many species of bats, females tend to be larger than males. This is particularly marked in the vespertilionids and emballonurids. Myers (1978) examined 28 taxa of vespertilionids, and only found sexual dimorphism in which females were larger than males. Williams and Findley (1979) found sexual size dimorphism in 6 of 18 taxa, with females larger than males; one taxon was dimorphic with males larger than females. Swanepoel and Genoways (1979) summarized morphometric data on phyllostomid bats. Of 25 species for which data were available, 16 were dimorphic, 3 with larger males and 13 with larger females. However, in all
cases the existing dimorphism was slight, less than 5% (Fleming, 1988). In Brazil, 11 of 17 phyllostomids examined were found to be dimorphic in eight or more of the external and cranial characters (Willig, 1983). Six taxa contained larger males, and five taxa contained larger females. Similarly, Willig (1985) found slight sexual dimorphism to exist in Neoplatymops (Molossidae) from South America, with males larger than females. Previous work with S. rufum (Jones et al., 1971) examined a small number of adults for ten cranial and external characters using only a univariate approach. Their results indicated the presence of secondary sexual dimorphism for all characters, with females larger than males. Most authors agree, to a greater or lesser extent, that none of the three theories presented to explain sex-related differences in size is independent of the other. Selection pressures due to sexual selection, diet breadth, and “Big Mother” phenomena in concert affect the magnitude and direction of dimorphism in most Chiroptera (Willig, 1983).

Although males and females exhibit similar diets (Willig, unpublished) as well as foraging patterns and home ranges (see Chapter II), characterization of basic behavior of S. rufum is lacking. Available evidence indicates that size differences do not appear strongly related to feeding strategies. Currently, no details concerning mating behavior exist, and nothing suggests that males do or do not compete for females. Male S. rufum do not maintain harems, or defend roost sites or feeding areas. They probably have little contact with other individuals except when seeking mates. As such, little opportunity exists for agonistic interactions between males, and sexual selection is probably not a dominant selection pressure.
Moreover, because of their solitary nature and failure to defend roost sites, males presumably contribute little effort to the care of their offspring. The role of raising young is undoubtedly fulfilled by females. This might lend support for Ralls' theory, if not for the fact that size differences are so small. Although sex differences in body size for S. rufum appear similar in magnitude to those for other tropical bats, reasons for such slight variation are difficult to explain. For example, Willig (1985) was able to relate slight size differences in cranial characters between sexes of Neoplatymops to the constraint of environmental factors involving available roost sites. Factors affecting S. rufum are not as clear, and until more information on its basic ecology is available, the reasons for the occurrence of slight sexual dimorphism can not be elucidated with confidence.

Asymmetry

All asymmetry values were found to be scale free, indicating that they are comparable among characters. Even though only one character showed significant results for directional asymmetry, character means of the right side were dominant for both males and females, with five of eight characters skewed in this direction for each sex (Table 3.4). However, lack of significance for all but one character indicates a weak right-sided prevalence, which could be expected to occur due to chance alone.

The Shapiro-Wilk test on values corrected for directional asymmetry indicated antisymmetry was present in two characters for males and females, as well as one additional character for females alone. Further analysis for fluctuating asymmetry requires that these samples be normally
distributed. Normalizing these data can be a significant problem and has been discussed by several authors (Owen and McBee, 1990, Van Valen, 1962). Each group was evaluated individually for skewness and kurtosis. All five revealed high levels of skewness; therefore the Box-Cox procedure was chosen to correct the data, as suggested by Owen and McBee (1990). Because the null hypothesis for testing fluctuating asymmetry within males or females alone is that the group variance equals zero, within group tests cannot be performed. Nonetheless, differences in fluctuating asymmetry between sexes for each character were evaluated using Levene’s test and showed one character, width of zygomatic arch, to differ significantly between males and females (Table 3.4).

The cheetah is one of few rare and isolated animals that has been examined for morphometric variation, genic diversity, and fluctuating asymmetry (Wayne et al., 1986). Although certain methodological considerations of this work have been questioned (Willig and Owen, 1987; and Modi et al., 1987), results showed elevated levels of fluctuating asymmetry when compared to other felids, but no differences between sexes. Although results indicate the presence of fluctuating asymmetry in cheetahs, it appears to be identical in direction and magnitude for males and females. In the present study, one character differed significantly in the amount of fluctuating asymmetry present between sexes of S. rufum, also a rare and isolated animal. This is an encouraging result because the fluctuating asymmetry present in each sex for all characters is large, especially when compared to values reported for Sigmodon and Peromyscus (Owen and McBee, 1990), some of which were exposed to
clastogens on toxic waste sites. The occurrence of high variance in these data, after adjustment for directional asymmetry and antisymmetry, suggests that fluctuating asymmetry in this bat population may reflect the genetic consequences of biogeographic isolation and ecologically reduced population size after disturbance events. A more definitive evaluation should include inter-site comparisons of the same species from distinct populations, or interspecific comparisons with other chiroptera from the same locality. However, few specimens (less than ten) of S. rufum have ever been collected from outside the Tabonuco Rain Forest, making such options untenable at present.
Literature Cited


Table 3.1.--Two-way MANOVA results for *S. rufum* using 19 morphometric characters as dependent variables. Pillias', Hotellings', and Wilks' criteria yielded identical F-values and significance, only Pillias' Trace is reported here. Significance: $p \leq 0.05^*$, $p \leq 0.01^{**}$, $p \leq 0.001^{***}$.

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<tr>
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<td>Adult Females N=58</td>
<td>Juvenile Males N=17</td>
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Table 3.2 continued.

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<td>Sexual dimorphism</td>
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CHAPTER IV
REPRODUCTION

Introduction


Four basic reproductive patterns are known for neotropical bat populations: seasonal monestry, seasonal polyestry, seasonal bimodal polyestry, and aseasonal polyestry (Fleming et al., 1972; Willig, 1985a; Wilson, 1973). These general patterns appear to be geographically widespread, particularly among the phyllostomids (Wilson, 1979), and are likely regulated by abiotic variables (Racey, 1982; Wilson, 1979). Timing of birth in several tropical bats is known to vary with environmental factors including ambient temperature, photoperiod, and rainfall (Racey, 1982). In particular, rainfall appears to be the most important climatic factor affecting bat reproductive cycles in the tropics because it directly affects the availability of food via the phenology of both fruit bearing plants and insects. Nonetheless, a diversity of patterns persist throughout the tropics. For example, in a number of seasonally breeding Old World bats, births occur just before the appearance of peaks in rainfall (Mutere, 1967, 1970, 1973). Phyllostomid bats in Costa Rica are cyclic and avoid
reproduction during the dry season (Mares and Wilson, 1971). In many
eotropical species which annually produce two young, the births coincide
with maximum food levels at the end of the dry season and the middle of the
rainy season (Fleming et al., 1972). Moreover, species in Panama, whose
food sources remain abundant over most of the year and are not limited by
rainfall produce two litters annually (Bonaccorso, 1979). In contrast, in
Colombia, where its food supply is abundant all year long, Artibeus
literatus breeds throughout the year (Tamsitt and Valdivieso, 1963, 1964).
In semiarid Northeast Brazil, several phyllostomid frugivores (Carollia
perspicillata, Vampyrops lineatus, A. jamaicensis, and A. literatus) exhibit
bimodal polyestry, with parturition and lactation concentrated during the
rainy season, whereas the phyllostomid nectarivore, Glosophaga soricina,
exploits pollen and nectar, as well as fruit, and thereby exhibits bimodal
polyestry with a birth peak in both rainy and dry seasons (Willig, 1985a,
1985c).

The reproductive biology of Puerto Rican bats is poorly documented
(Willig and Gannon, 1991). Because of its limited range and rarity in
scientific collections, little information has been published concerning
reproduction in S. rufum. Most previous reports (Genoways and Baker,
1972; Jones et al., 1971; Tamsitt, 1970; Tamsitt and Valdivieso, 1971;
Willig and Bauman, 1984) have been anecdotal and included observations
on few individuals. Based on such information, Wilson (1979) suggested
that S. rufum may be polyestrus, but noted that data are lacking to be
confident of that conclusion.
The reproductive biology of *Artibeus jamaicensis* is much better known throughout its range in Central and South America. Reproductive patterns vary greatly among localities (Wilson, 1979). Few observations have been documented from Puerto Rico. Herein, I describe reproduction of *S. r. darioi*, *A. jamaicensis*, and *Monophyllus redmani*, three of the most common bats from the Tabonuco Rain Forest of Puerto Rico, including sex ratios for males and females of each species in both the rainy and dry season.

**Methods**

**Field Studies**

Bats were netted in the Tabonuco Rain Forest during 1988 and 1989. Each bat was identified to species, sexed, and weighed. Males were considered reproductively active if testes were descended (TD), or inactive if testes were not descended (TND). Females were classified as pregnant (determined by abdominal palpation), lactating, pregnant and lactating, or inactive. All individuals were released after capture.

**Museum Studies**

Specimens of *S. rufum* collected in the Tabonuco Rain Forest were obtained from The Museum of Texas Tech University, The Royal Ontario Museum, and Carnegie Museum of Natural History (Appendix B) and evaluated for reproductive condition. When available, reproductive information for individuals preserved as dried skins was obtained from
specimen tags and field notes. The majority of examined museum specimens was preserved in fluid. These were dissected and reproductive condition evaluated directly by necropsy. Both museum and field specimens were classified as to the season (rainy or dry) in which they were captured. In addition, the embryos of all pregnant females preserved as fluid specimens were measured to estimate their developmental stage.

For both S. rufum and A. jamaicensis, G-tests (Sokal and Rohlf, 1981) were used to compare reproductive activity in wet and dry seasons for males and females separately. Year to year variation in reproductive activity was compared in the same manner. Binomial tests (Sokal and Rohlf, 1981) were used to determine whether observed sex ratios differed significantly from a ratio of 1:1.

Results and Discussion

Fifty-five adult S. rufum, 54 adult A. jamaicensis, and 19 adult M. redmani were captured in the Tabonuco Rain Forest during 1988 and 1989. Ninety-eight adult S. rufum were obtained from museums.

Reproductive Patterns

Although field (Figure 4.1A) and museum (Figure 4.1B) data for S. rufum suggest some differences in the seasonality of male reproductive activity, no appreciable differences exist for females. When data are combined from both sources and analyzed statistically, no significant differences were detected in female reproductive activity between rainy
(67.5% of 77 adult females pregnant or lactating) and dry (80.0% of 25 adult females pregnant or lactating) seasons (G-Test of independence: G=0.58, df=1, 0.50>p>0.01). Moreover, the same wide range of embryo sizes characterized both seasons (Figure 4.2). Such a broad overlap in the frequency size distributions of embryos throughout the year indicates an extended period during which fertilization occurs (Mares and Wilson, 1971). The presence of simultaneously pregnant and lactating females suggests that S. rufum is polyestrous, but the polyestry is asynchronous in that reproductive activity occurs throughout the year. Such asynchronous polyestry is characteristic of species whose food does not vary greatly in abundance on a seasonal basis (Wilson, 1979). Observations in the Tabonuco Rain Forest suggest that fruit availability at this location is only slightly seasonal and the major disseminator of most animal dispersed fruits are bats (Devoe, 1990). Still, the intensity of arboreal frugivory is low, consistent with the observations that a large portion of the fruit crop strikes the ground without being consumed (Devoe, 1990). This indicates that excess fruit exists in ample supply year round. For S. rufum, imposition of modalities in reproductive behavior may not be advantageous from an energetic perspective at this locality.

The results for A. jamaicensis (Table 4.1), when compared with data from Willig and Bauman (1984), demonstrate that the proportion of reproductively active females of this species during the rainy season is statistically variable (G-Test of Independence: G = 6.16, df = 2, 0.025 > P > 0.01) from year to year. Of 45 adult females, 68.8% were pregnant or
lactating in 1982 (Willig and Bauman, 1984), whereas 36.6% (N = 30 adult females) were reproductively active in field samples from 1988 and 1989. In part, this difference may be a methodological one. The latter samples were based solely on field palpation of live females, which may underestimate true reproductive activity, whereas the 1982 data were based on necropsy. Few data exist for *A. jamaicensis* during the dry season in Puerto Rico. Two of 6 adult females were reproductively active during 1988 and 1989. These data do not suggest differences beyond the variation characteristic within a season.

**Parturition**

Two instances of parturition for *S. rufum* have been recorded (Genoways and Baker, 1972; Tamsitt and Valdivieso, 1966). Both occurred by head presentation; the body of young were well-furred at birth. Tamsitt and Valdivieso (1966) provided measurements of one newborn individual (weight, 7g; length of head and body, 45 mm). On 17 July 1989, I observed one individual abort a fetus. A pregnant female (33.5g) was netted at 0330 hrs. Upon capture a small volume of fluid and blood discharged from the vagina. The individual was returned to the laboratory, placed in a holding cage, and observed periodically over the next 20 hours. By 1200 hours, vaginal blood and fluid were no longer visible, but by 1830 hrs., fluid discharge was noted again. Although parturition was not observed in entirety, the fetus was delivered by head presentation and persisted over a 15 minute period from 1930 to 1945 hrs.
The fetus was stillborn and remained hanging head down from the female, with the umbilical chord attached. During the next four hours, the female continued to be motionless, but alert. At no time did she attempt to lick, move, or dislodge the fetus. The blood and fetal membranes continued to dry during this period. At 2330 hrs. the fetus was removed from the female and examined. A male, it appeared almost fully developed, but lacked substantial quantities of hair. It weighed 3.5 g, with a crown-rump length of 37 mm, considerably smaller measurements than for surviving newborns. The adult female weighed 22.5 g after parturition. She appeared normal in general good health, appearance, and activity until her release two hours later.

**Sex Ratio**

Sex ratios of Puerto Rican bats from the Tabonuco Rain Forest have not been reported previously. Male to female sex ratios were calculated for museum and field samples (Table 4.1) for three species of bats. In general, although females appear more abundant in both seasons for two species, results did not statistically differ from an equal sex ratio in most cases. Only museum data for *S. rufum* from the rainy season revealed a sex ratio highly skewed toward females (Binomial Test, P < 0.001). Field data for *M. redmani* in the rainy season (Binomial Test, P < 0.004) was also demonstrative of unequal sex ratios in that no females were captured in that season.
Sex ratios of neotropical bats appear to depend on locality, season, and age. For example, the sex ratio for *A. jamaicensis* in Costa Rica (Mares and Wilson, 1971) is female biased. Willig (1983) also reported sex ratios of fifteen bats from northeastern Brazil. Of 11 phyllostomids, six were female biased, including *A. jamaicensis*, and five had equal sex ratios. Four other non-phyllostomids had equal ratios. Silva Taboada (1979) found 1:1 ratios in adult *A. jamaicensis* on Cuba, as well as in four other phyllostomids and ten species of non-phyllostomids from the same location. Similar ratios were obtained for *A. jamaicensis* in Panama (Morrison, 1975). In Costa Rica, *Carollia perspicillata* exhibits a male biased secondary sex ratio (birth), but in adults it was virtually 1:1 (Fleming, 1988).

Female biased sex ratios may be a result of differential mortality rates between the sexes and between age groups, as appears to be the situation for *C. perspicillata*. However, behavior patterns may have influence also. McNab (1963), Smith (1968), and Thomas (1972) suggest that the presence of greater number of females in a population sample may be a result of increased energy requirements of pregnant and lactating females. This would manifest itself in longer foraging bouts, larger home ranges, or both, and thus increase the likelihood of capture. It has been demonstrated for *S. rufum*, that males and females in Puerto Rico exhibit similar home range sizes and foraging behavior (see Chapter II), however, these results were obtained from reproductively inactive individuals.
Sex ratio theory (Fisher, 1930) indicates that if offspring are equal in 
cost, parents will invest an equal amount of resources in both males and 
females. Secondary ratios (those after birth) should be biased toward the 
sex that is “less costly” to produce. Details of investment or cost associated 
with offspring at birth or weaning for *S. nufum* are unavailable, but there is 
evidence that juvenile males are smaller, on average, than juvenile females 
(see Chapter III). However, according to Fisher (1930) this should yield 
male biased sex ratios. Results involving the museum specimens should be 
interpreted with caution. These data were obtained by numerous different 
collectors over a period of 20 years. Although it would appear that 
information thus gathered would be a good indication of trends over a long 
period of time, alternatively it might exhibit a bias by collectors who 
selectively kept or released individuals of one sex or another. Field data 
represent a complete sample of all bats captured and likely is a better 
representation of actual sex ratios in this population. Results indicating 
equal sex ratios for both species of frugivores consider only tertiary (adult) 
ratios. Birth and mortality rates may vary at either conception or birth. 
Basic information on survivorship, both pre- and post-weaning, as well as 
many other areas of life history of *S. nufum*, is needed to draw further 
conclusions on both reproduction and sex ratios, and the factors that 
influence them.
Literature Cited


Table 4.1.--Reproductive characteristics of bats in the Tabonuco Rain Forest during dry and rainy seasons. Total numbers are reported, followed by number breeding. Museum data is based upon specimens collected over a 20 year period. An asterisk (*) indicates a sex ratio that statistically differs from 1:1.

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CHAPTER V
ECTOPARASITES

Introduction

Ectoparasites are organisms that live and feed on external surfaces at the expense of their host. Relatively little is understood concerning host characteristics that affect ectoparasite population densities or the variation in composition of species assemblages on individual bats. Although ectoparasites provide no benefit, under normal conditions they do not cause host mortality. Whereas most ectoparasites have piercing or sucking mouthparts and feed on blood or other body fluids, deleterious effects on their hosts have been limited by evolution, and seem to cause little permanent harm or physical damage (Whitaker, 1988). Nonetheless, ectoparasites may cause host injury through irritation, skin damage, or loss of blood. They also have been implicated in the spread of infections (Constantine, 1988) and may have significant effects on the host’s daily energy expenditure (Burnett and August, 1981). It is unclear for bats, as it is unclear for most mammals, whether parasites have an appreciable effect on population level processes (Anderson, 1982; Holmes, 1983; May, 1983).

Many bat ectoparasites are highly host specific because of the ecologically and geographically isolated nature of their hosts. All species show some degree of host limitation (Marshall, 1982). Some groups appear more host specific than others. Thus, the potential exists to use host-parasite relationships as taxonomic characters in the same way that morphological characteristics are used in systematics (Whitaker, 1988).
However, the capacity for successful invasion of new hosts may present major limitations on such utility.

Bat ectoparasites usually spend their entire life either on the body of the host, where they continually feed, or remain in the host’s roost, where they feed during periods of host inactivity (Marshall, 1981). Continuous feeders remaining with the host usually exhibit a small and flattened form and are capable of movement over the surface of the host; however, most show a distinct preference for particular locations on the body. This may reduce the possibility of being removed or dislodged. Host grooming is the major source of mortality for most species of bat ectoparasites (Marshall, 1982).

Over 687 species of arthropods parasitize bats (Marshall, 1982). Phyllostomids harbor a large assemblage of ectoparasites, comprising over 250 species (Webb and Loomis, 1977). Details concerning the interspecific relationships between bats and their ectoparasites are sketchy at best, as few species have been studied from an ecological perspective. It is clear that individual bats may be associated with complex communities of ectoparasites, which comprise seven or more species. Nonetheless, two to three species are most common. In general, the number per host appears correlated with relative size of the parasite, with highest infestations recorded for the smallest species (Marshall, 1982). The diversity of ectoparasites associated with an individual is related to many factors, including host distribution, behavior, size, and roost type; these factors may affect differences not only between species, but also between age or sex
groups within a species. For example, if roosting behavior either facilitates or precludes ectoparasite dispersal, then colonial roosters would tend to have a more even or random ectoparasite distribution, whereas solitary roosters would exhibit clustered distributions. Competition among ectoparasites may influence their diversity (Wenzel and Tipton, 1966). Nevertheless, even if interspecific competition among ectoparasites affects population density per host individual, it remains unclear whether it is sufficient to manifest a community-wide response (Moulton and Pimm, 1986; Willig and Moulton, 1989).

Knowledge of bat-ectoparasite associations in Puerto Rican bats are based upon serendipitous collections from one or a few host specimens, fewer than ten individuals for most bat species. Published data do not address the ecology of these arthropods or interactions with their hosts. In addition to providing an updated list of ectoparasites for bats from the Tabonuco Rain Forest of Puerto Rico, I examined population and community characteristics of the ectoparasite fauna, such as density, infestation levels, and species composition. More specifically, I addressed questions on the effects of host age and sex, as well as seasonal variation, on the distribution of ectoparasites. Differences among age-sex groups within a host species, as well as differences among host taxa constitute habitat variation for ectoparasites. The effects of both of these sources of variation on ectoparasite community structure are evaluated for the three common bat hosts in the Tabonuco Rain Forest.
Methods

Bats were collected during the dry (March) and rainy (June - August) seasons of 1988 and 1989. Specimens were captured in mist nets at various localities in the Tabonuco Rain Forest near El Verde Field Station. Upon capture, each bat was held in a separate cloth bag until it could be inspected for ectoparasites. All examinations were performed on live specimens within 20 minutes of capture. Wing and tail membranes, pelage, ears, and face were thoroughly examined for the presence of arthropods. All ectoparasites were removed and placed in vials containing 70% ethyl alcohol, using a separate vial for each bat. Species, age, and sex were recorded for the host prior to its release. The number of individuals of each category [adult male, adult female and immature (nymphs and larvae)] of each ectoparasite species was recorded for each bat host. If an adequate host sample size was obtained, several host-ectoparasite parameters were estimated. These include: incidence (the percentage of bats infested), prevalence (mean ectoparasites per bat), and density (mean ectoparasites per infested bat) which are useful for examining host parasite relationships, but not for assessing community attributes (Whitaker, 1988). When sample size was sufficient, analysis of variance (ANOVA) was used to evaluate whether differences in infestation occurred due to host age-sex (adult males, adult females, juveniles) or due to differences in season (rainy or dry) of capture (Sokal and Rohlf, 1981). Age-sex was used as a single factor because sample sizes of juvenile males and females for all hosts were
small. More powerful a priori tests were performed to compare adult males to adult females, and adults regardless of sex to juveniles.

Interspecific and seasonal comparisons of ectoparasitic infestation were performed for *P. iheringi*, *Trichobius* sp. and all ectoparasite taxa via separate pure model I two-way ANOVAs. Similarly, Tukey's a posteriori multiple comparison for unequal sample size (Zar, 1981) was used to evaluate pairwise differences between host species for all three ectoparasite categories. Season and the season by species interaction in the more powerful ANOVAs were nonsignificant, hence seasons were combined in these a posteriori comparisons of bat species.

For host specific distributional comparisons, the observed density function of parasites (regardless of species) was compared to a random density function (generated by the Poisson Distribution) via a goodness of fit test (Sokal and Rohlf, 1981). Significant hyperdispersion of parasites on a host is indicated by a CD>1, whereas hypodispersion is suggested when CD<1.

Comparisons of community composition were achieved via G-tests (Sokal and Rohlf, 1981) in two different circumstances. In the first, the effect of host age-sex on ectoparasite community development was determined for *A. jamaicensis*. In the second, comparison of ectoparasite community composition focused on potential interspecific differences among the common bats (*A. jamaicensis*, *S. rufum*, and *M. redmani*). In both circumstances, a sum of squares simultaneous test procedure was
performed as an a posteriori test to evaluate factors affecting significance in the G-test (Pimentel and Smith, 1986).

**Results and Discussion**

Eight species of ectoparasite were collected from five species of bats in the Tabonuco Rain Forest (Table 5.1). Only one ectoparasite (Periglischrus iheringi) was found to occur on all eight hosts. Most ectoparasites occurred on two or more bat species except for Megistopoda aranea, Nycterophilia sp., and Ornithodoros sp. were species-specific. The presence of Aspidoptera sp., Trichobius sp. and Spelaeorhynchus sp. on A. jamaicensis represents three new host records for Puerto Rican bats.

**Stenoderma rufum**

Although various authors (Tamsitt and Fox, 1970a, 1970b, Tamsitt and Valdivieso, 1970) have reported a number of ectoparasites of the Red Fig-eating Bat from the Tabonuco Rain Forest, only one species, P. iheringi, a spincturid mite, was obtained from tail and wing membranes of the host during this study (Table 5.2). Thirty-three of 95 captured individuals harbored this ectoparasite. Variation in level of infestation of P. iheringi is related to the age-sex of the host (Table 5.3). Juvenile bats harbored a significantly higher number of wing mites than did adult males or females (a priori test, F_{1,89} = 5.664, 0.025>p>0.01). This is largely due to the significantly greater number of male P. iheringi mites present on juvenile bats (a priori test, F_{1,89} = 5.342, 0.025>p>0.01). No differences in infestation of P. iheringi females or immatures were detected on any of the
bat age-sex groups. Finally, no differences in infestation level due to season existed for any of the ectoparasite groups. Moreover, the lack of significant interactions between main treatment effects indicates that the effect of age-sex is independent of season.

**Artibeus jamaicensis**

Eighty-two of 94 bats harbored ectoparasites comprising five different species (Table 5.4): *P. iheringi*, *Megistopoda aranea*, *Aspidoptera* sp., and *Trichobius* sp. (streblid batflies); and *Spelaeorhynchus* sp. (mite). Differences in the level of infestation of *P. iheringi* occur (Table 5.5) based upon age-sex of the host. Juvenile bats harbored a significantly higher number of adult male ectoparasites than did adult bats, regardless of sex (A priori test, $F_{1,88} = 39.98$, $p<0.001$). A similar overall trend was evident when all age groups of *P. iheringi* (adult males, adult females, and immatures) were combined (A priori test, $F_{1,88} = 41.63$, $p<0.001$). No difference in incidence could be attributed to seasonal variation for any *P. iheringi* group examined, and all interactions were non-significant, indicating that the effects of age-sex are independent of season. No significant differences (Table 5.5) in infestation of any of the other ectoparasite groups (*M. aranea*, *Aspidoptera* sp., *Trichobius* sp. and *Spelaeorhynchus* sp.) were detected due to host age-sex, season, or their interaction. Overall infestation of ectoparasites regardless of species varied significantly due to age-sex of host, but not season, with juvenile bats
consistently harboring more parasites than did adults (a priori test, $F_{1,88} = 22.57$, $p<0.001$).

**Monophyllus redmani**

Twelve of 21 adult *M. redmani* were infested with ectoparasites comprising four species, *P. iheringi*, *Nycterophilus* sp., *Trichobius* sp., and *Spelaeorrhynchus* sp. (Table 5.6). *M. redmani* harbored few individuals of *P. iheringi*. The dominant ectoparasite on this nectarivorous species was *Trichobius* sp., which infested 42.9% of the examined individuals (mean number per bat, 0.76) and was found on no other bat host. As in the case of *A. jamaicensis*, only females of *Spelaeorrhynchus* sp. were collected from *M. redmani*. Because of the small sample size, juvenile bats ($N=2$) and rainy season females ($N=0$) were eliminated from further analyses. Thus, host categories were restricted to three adult groups (rainy season males, dry season males, dry season females) Regardless of ectoparasite category (Table 5.7), no differences in infestation rate occurred among any adult host group.

**Erophylla sezekorni**

Six specimens of this bat were captured, four of which were infested with two types of ectoparasites. Individual bats harbored from one to 23 *P. iheringi* (mean number per bat, 10.25), all of which were female. Three bats were infested with a tick, *Ornithodoros* sp. One host was heavily parasitized with 41 ticks, most occurring on the dorsal pelage. The other
two individuals harbored two and three ticks, respectively. Because of the low host sample size, statistical comparisons were not attempted for any of these ectoparasites on E. sezekorni.

**Eptesicus fuscus**

All three specimens of this bat were infested at moderate levels by P. iheringi (mean number per bat, 7.0). Again, statistical comparisons were not attempted because of the low host sample size.

**Overview**

Some ectoparasites showed specificity for particular host taxa. Streblids (Aspidoptera sp. and M. aranea) occurred only on A. jamaicensis, whereas Trichobius sp. occurred on both A. jamaicensis and M. redmani. Streblids are obligate bat parasites whose distributions are, at least partially, due to ecological factors which are associated with colonial cave dwelling species; few have been found on bats restricted to forest habitats (Webb and Loomis, 1977). Streblids may be absent from S. rufum is consistent with the idea that it is a foliage roosting species. Nycterophila sp., also a streblid batfly, was found only on M. redmani, and only during the rainy season. The scarcity of Spelaeorhynchus sp. was not unusual. It is a rare species, the males of which are presently unknown (Webb and Loomis, 1977). Females have highly specialized features which appear to make adaptation to new hosts difficult (Webb and Loomis, 1977), thus accounting for its low numbers and limited host range on Puerto Rico. The
absence of male *Spelaeorhynchus* suggests that either males are free living, or that this species is parthenogenetic.

Infestation levels of some ectoparasites vary with the age of their frugivorous hosts, with juvenile bats supporting higher densities than adults. Although no ectoparasite numbers were affected by seasonal variation, numbers of *P. iheringi* varied with host age. Moreover, this occurred in both *A. jamaicensis* and *S. rufum*. It is possible, though unlikely, that juvenile bats represent a superior habitat which can support elevated ectoparasite population levels. However, if no major difference in host quality associated with age is assumed, two points of speculation remain. Either juvenile bats are more likely to acquire ectoparasites, or adults are more adept at displacing them. Age specific host behaviors are known to occur which might contribute to the differences in levels of ectoparasite infestation. Age groups, at least for *S. rufum*, have been demonstrated to differ in home range size and foraging patterns (Chapter II). By traveling longer distances and occupying a larger home range than adults, they may increase the likelihood of encountering additional ectoparasites. If so, other species of ectoparasites should increase as well, but this is not the case for *S. rufum*, or either of the other two species, *A. jamaicensis* and *M. redmani*. A more reasonable explanation is that adults are more adept at grooming and dislodging mites than are juveniles. *P. iheringi* is wingless and slow moving; it prefers exposed wing and tail membrane and may therefore, have a higher probability of being dislodged while a host is grooming than would other ectoparasites, such as batflies.
Clearly, these are speculations, the exact nature of host-parasite associations is difficult to elucidate, particularly in the absence of detailed knowledge of the biology and behavior of either host or parasite.

Within the Tabonuco Rain Forest, *P. iheringi* was the most widespread bat ectoparasite occurring on all species of phyllostomids. Although its incidence on most host species was low, *P. iheringi* was the dominant ectoparasite on *A. jamaicensis* (occurring on 69.1% of these hosts, mean density per bat, 4.96) and *S. rufum* (occurring on 34.7% of these hosts with a mean density per bat of 1.48 per individual). Although little is known of its ecology, its widespread distribution and numbers indicate a relatively well developed means of dispersal.

Ectoparasite spatial distributions are affected by differences among age-sex groups and are related to behavioral attributes of each species. *A. jamaicensis* ($X^2 = 6.48, df = 4, P>0.05$) and *M. redmani* ($X^2 = 1.15, df = 1, P>0.05$) exhibited a random spatial distribution of ectoparasites; whereas, *S. rufum* ($X^2 = 6.84, df = 1, P<0.01$) had a nonrandom ectoparasite distribution in which individuals were hyperdispersed. *A. jamaicensis*, and *S. rufum*, although both dominant frugivores in the Tabonuco Rain Forest, exhibit different diet preferences, foraging patterns, and roosting patterns (Chapter II). These behavioral characteristics may either facilitate the spread of ectoparasites from host to host, as in the case of colonial roosters such as *A. jamaicensis* and *M. redmani* (note, however, that data for roosting habits in the Tabonuco Rain Forest are unavailable), or serve as a barrier to ectoparasite transmission, as in the case of solitary roosters such
as S. rufum. Others have demonstrated that bats occupying long established roosts are known to exhibit higher species richness and larger numbers of ectoparasites (Wenzel et al., 1966). The apparent lack of fidelity to roosting sites by S. rufum (Chapter II) may preclude infestation by ectoparasites that spend part of their life cycle off the host in the roost area, such as Argasids (e.g., Ornithodoros sp.), or Streblids, which although widespread among phyllostomids, are not known to parasitize forest species.

Seasonal and Interspecific Comparisons

Only two species of ectoparasites (P. iheringi and Trichobius sp.) occurred on all three common bat species, thus interspecific comparisons of host infestation are restricted to these taxa and all ectoparasites. Seasonal and interspecific host comparison of infestation by P. iheringi, Trichobius sp., and all ectoparasites yielded the same results in all three cases based upon ANOVA. Consistent host-specific differences in ectoparasite infestation exist regardless of season (Table 5.8). Nonetheless, a posteriori contrasts revealed differences in the response of the ectoparasite categories to host species. For Trichobius sp., infestation levels were the same on S. rufum and A. jamaicensis (q(2,206) = 2.56, p>0.05), but levels on each of these bat species were less than on M. redmani (S. rufum: q(2,206) = 7.91, p<0.001; A. jamaicensis: q(2,206) = 9.70, p>0.001) In contrast, results of a posteriori comparisons of host infestation by P. iheringi and all ectoparasites were the same: S. rufum and M. redmani harbored
indistinguishable levels of infestation \((P. \text{ iheringi}}: q_{(2,206)} = 1.68, p>0.05;\) for all ectoparasites: \(q_{(2,206)} = 0.12, p>0.05\) and each of them differed from \(A. \text{ jamaicensis}\) in the level of infestation as well \((S. \text{ rufum}}: q_{(2,206)} = 5.76 p<0.01; M. \text{ redmani}}: q_{(2,206)} = 9.74, p>0.001).\)

Incidence and prevalence can provide an estimate of levels of parasitism for the entire host population. These numbers can be directly compared among species, and are thus appropriate for interspecific contrasts (Whitaker, 1988). Of the three species of bats for which an adequate sample size exists, \(A. \text{ jamaicensis}\) had the highest overall incidence (87.2%) and a much higher overall mean ectoparasitic load (6.32 ectoparasites per bat). \(M. \text{ redmani}\) was second with an incidence of 56.5% and a mean of 1.61 ectoparasites per individual, followed by \(S. \text{ rufum}\) of which 34.7% was infested with a mean of 1.48 ectoparasites per bat.

**Community Comparisons**

The proportional representation of ectoparasite species (species abundance distributions) can be used as measures of community composition (Pielou, 1974). Samples were sufficiently large to evaluate if ectoparasite community differences are evidenced by the age-sex categories of \(A. \text{ jamaicensis}\) based upon this measure. Differences among the three age-sex groups (adult males, adult females, and juveniles) were significant (G-test, \(G=16.64, df=8, P<0.03\)). Less powerful a posteriori comparisons failed to detect a significant difference between any two age-sex groups; however, the difference between adult females and juveniles approached
significance (G-test, G=15.42, df=8, P<0.052) and most likely contributed to the intergroup variation. Moreover, differential incidence of Trichobius sp. among these groups (G-test, G=17.30, df=8, P<0.05) was a significant contribution to the community-wide effect.

Summary

Few studies of bat ectoparasites have examined any aspect of their population dynamics. The results of this work indicate that bat-ectoparasite relationships on Puerto Rico are complex and vary at intraspecific, interspecific, and community levels. Still, many questions remain unanswered. For example, it is not clear why ectoparasite levels on most hosts remain low. Obviously, host behavior has a substantial effect on ectoparasites, and it is not possible to completely understand the complexity of ectoparasite ecology without detailed information on the roosting ecology and behavior of hosts. At this time little is known about specific behavioral aspects of of most bats on Puerto Rico, making further speculation difficult.
Literature Cited


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<th>Family</th>
<th>Abundance</th>
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<td>C</td>
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<td></td>
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<td>Labidocarpidae</td>
<td>--</td>
</tr>
<tr>
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<td>Labidocarpidae</td>
<td>R</td>
</tr>
<tr>
<td></td>
<td>Periglischrus iheringi 1,2,3,5,7*</td>
<td>Spinturnicidae</td>
<td>A</td>
</tr>
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<td></td>
<td>Periglischrus vargas 1,2*</td>
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<td>Aspidoptera sp. 7*</td>
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1 = Webb and Loomis, 1977
2 = Tamsitt and Valdivieso, 1970
3 = Tamsitt and Fox, 1970a
4 = Tamsitt and Fox, 1970b
5 = Rudnick, 1960
6 = Fain et al., 1967
7 = Gannon, 1991 (this volume)

* = known from the Tabonuco Rain Forest

A = abundant
C = common
R = rare
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<td>Radfordiella oudemansi 1,3</td>
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<td>--</td>
</tr>
<tr>
<td></td>
<td>Trichobius truncatus 1,3</td>
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<td>--</td>
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<td>Eptesicus fuscus</td>
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<tr>
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A = abundant  
C = common  
R = rare
Table 5.1 continued

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* = known from the Tabonuco Rain Forest
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C = common
R = rare
Table 5.2.--Ectoparasites from specimens of *S. rufum* captured in the Tabonuco Rain Forest of Puerto Rico. Host sample size = 95 (21 adult males, 35 adult females, 39 juveniles). Ectoparasites were classified into three groups: F = adult females, M = adult males, I = immatures (larvae and nymphs), T = total ectoparasites, and SD = standard deviation.

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<tr>
<td></td>
<td>F</td>
<td>M</td>
<td>I</td>
<td>T</td>
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<tr>
<td>Number Infested</td>
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<td>18</td>
<td>33</td>
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<tr>
<td>Adult males</td>
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<td>7</td>
<td>6</td>
<td>11</td>
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<tr>
<td>Adult females</td>
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<td>Juveniles</td>
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<td>11</td>
<td>17</td>
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<tr>
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<td>66</td>
<td>32</td>
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<td>9</td>
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<td>Juveniles</td>
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<tr>
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<td>26.3</td>
<td>18.9</td>
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<td>11.4</td>
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<td>4</td>
<td>15</td>
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Table 5.3.--Significance levels from a series of two-way ANOVAs evaluating the effects of host age-sex (adult males, adult females, and juveniles) and season of collection (rainy and dry) on incidence levels of each of four categories of *P. iheringi* [adult females (F), adult males (M), immatures (I) and totals (T) regardless of age or sex] that occur on *S. rufum*. An asterisk (*) indicates significance at $P = 0.05$.

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<thead>
<tr>
<th>Host Characteristics</th>
<th>df</th>
<th>F</th>
<th>M</th>
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<th>T</th>
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<tr>
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<td>0.34</td>
<td>0.29</td>
<td>0.35</td>
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<tr>
<td>Age/Sex (A)</td>
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<td>0.12</td>
<td>0.04*</td>
<td>0.07</td>
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<tr>
<td>S x A</td>
<td>2</td>
<td>0.37</td>
<td>0.44</td>
<td>0.44</td>
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Table 5.4.--Ectoparasites of *A. jamaicensis* from the Tabonuco Rain Forest of Puerto Rico. Host sample size = 94 (30 adult males, 36 adult females, 29 juveniles). Ectoparasites were classified into three groups: F = adult females, M = adult males, I = immatures (larvae and nymphs), T = total ectoparasites, and SD = standard deviation.

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<th>Trichobius sp.</th>
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<th>Total</th>
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</thead>
<tbody>
<tr>
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<td>F  M  T</td>
<td>F  M  T</td>
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<td>7  3  10</td>
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<td>3  1  4</td>
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<td>5  1  6</td>
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<th>Aspidoptera sp.</th>
<th>Trichobius sp.</th>
<th>Spelaerhynchus sp.</th>
<th>Total</th>
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<tbody>
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<td>F  M  T</td>
<td>F  M  T</td>
<td>T</td>
<td>T</td>
</tr>
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<td>25</td>
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<td>1 1 1</td>
<td>3</td>
<td>23</td>
</tr>
<tr>
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<td>4 1 4</td>
<td>1 2 3</td>
<td>1 0 1</td>
<td>3</td>
<td>22</td>
</tr>
<tr>
<td>Juveniles</td>
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<td>3 3 6</td>
<td>1 2 3</td>
<td>2 1 3</td>
<td>7</td>
<td>25</td>
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<tr>
<td>% Hosts Infested</td>
<td>50.0 50.0 54.2 69.1</td>
<td>23.4 19.1 35.1</td>
<td>14.9 13.8 21.3</td>
<td>10.6 2.1 11.7</td>
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<td>8.3 0 8.3</td>
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<td>28.6 28.6 42.9</td>
<td>14.3 21.4 25.0</td>
<td>14.3 3.6 14.3</td>
<td>7.1</td>
<td>96.4</td>
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Table 5.4 continued

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<th>Aspidoptera sp.</th>
<th>Trichobius sp.</th>
<th>Spelaerhynchus sp.</th>
<th>Total</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>F</td>
<td>M</td>
<td>I</td>
<td>T</td>
<td>F</td>
<td>M</td>
</tr>
<tr>
<td>Mean Parasites/Host</td>
<td>2.26</td>
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<td>1.40</td>
<td>4.96</td>
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<td>0.25</td>
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<tr>
<td>SD</td>
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<td>1.99</td>
<td>1.79</td>
<td>6.10</td>
<td>0.69</td>
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<tr>
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<td>0.93</td>
<td>1.75</td>
<td>4.97</td>
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<td>2.75</td>
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<td>0.19</td>
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<td>1.55</td>
<td>4.31</td>
<td>0.74</td>
<td>0.40</td>
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<td>2.59</td>
<td>7.17</td>
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<td>1.28</td>
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<tr>
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<td>2.13</td>
<td>1.69</td>
<td>6.16</td>
<td>0.84</td>
<td>0.58</td>
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<td>Adult males</td>
<td>3.57</td>
<td>1.50</td>
<td>2.54</td>
<td>5.61</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>SD</td>
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<td>0.91</td>
<td>1.85</td>
<td>5.37</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
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<td>2.31</td>
<td>2.12</td>
<td>4.71</td>
<td>1.43</td>
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<td>1.65</td>
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<td>10.23</td>
<td>1.50</td>
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<td>2.63</td>
<td>1.58</td>
<td>6.55</td>
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150
Table 5.5.--Significance levels from a series of two-way ANOVAs evaluating the effects of host age-sex (adult males, adult females, and juveniles) and season of collection (rainy and dry) on incidence levels of five different ectoparasites that occur on *A. jamaicensis*. When possible, incidence of each ectoparasite was analyzed separately for adult females (F), adult males (M), immatures (I), and totals (T) regardless of age or sex. An asterisk (*) indicates significance at $P = 0.05$.

<table>
<thead>
<tr>
<th>df</th>
<th>Periglischrus iheringi</th>
<th>Megistopoda aranea</th>
<th>Aspidoptera sp.</th>
<th>Trichobius sp.</th>
<th>Spelaeorhynchus sp.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>M</td>
<td>I</td>
<td>T</td>
<td>F</td>
<td>M</td>
</tr>
<tr>
<td>Season (S)</td>
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<td>0.32</td>
<td>0.71</td>
<td>0.96</td>
<td>0.33</td>
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<tr>
<td>Age-Sex (A)</td>
<td>2</td>
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<td>&lt;0.001*</td>
<td>0.03*</td>
<td>&lt;0.001*</td>
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<td>S x A</td>
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<td>0.72</td>
<td>0.92</td>
<td>0.86</td>
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Table 5.6.--Ectoparasites of *M. redmani* from the Tabonuco Rain Forest of Puerto Rico. R = rainy season, D = dry season. Host sample size = 21 (11 adult males-R, 4 adult females-D, 6 adult males-D). Ectoparasites were classified into three groups: F = adult females, M = adult males, I = immatures (larvae and nymphs), T = total ectoparasites, and SD = standard deviation.

<table>
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<tr>
<th>Host Characteristics</th>
<th><em>Periglischrus iheringi</em></th>
<th><em>Nycterophila</em> sp.</th>
<th><em>Trichobius</em> sp.</th>
<th><em>Spelaeorhynchus</em> sp.</th>
<th>Total</th>
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<tr>
<td></td>
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<td>F  M  T</td>
<td>F  M  T</td>
<td></td>
<td>T</td>
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<tr>
<td>Number Infested</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>1</td>
<td>1  1  2  3</td>
<td>1  2  3</td>
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<tr>
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<td>0  0  1  1</td>
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<td>0  1  1</td>
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<tr>
<td>Adult males-D</td>
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<td>0  0  0</td>
<td>2  3  4</td>
<td>1</td>
<td>4</td>
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<td>1  2  3</td>
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<td>17</td>
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<td>0</td>
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</tr>
<tr>
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<th>Spelaerhynchus sp.</th>
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<td>E  M  T</td>
<td>E  M  T</td>
<td>T</td>
<td>T</td>
</tr>
<tr>
<td>% Hosts Infested</td>
<td>4.7 4.7 9.5 14.3</td>
<td>4.7 9.5 14.3</td>
<td>28.6 28.6 42.9</td>
<td>14.3</td>
<td>57.1</td>
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<td>18.2 18.2 36.4</td>
<td>18.2</td>
<td>54.5</td>
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<td>0 0 0</td>
<td>0 25.0 25.0</td>
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<tr>
<td>Adult males-D</td>
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<td>0 0 0</td>
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<td>66.7</td>
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<td>4</td>
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<td>1 1 1</td>
<td>3 1 4</td>
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<td>4</td>
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<td>Adult females-D</td>
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<td>0 0 0</td>
<td>0 2 2</td>
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<td>2</td>
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<td>4</td>
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<td>Trichobius sp.</td>
<td>Spelaeorhynchus sp.</td>
<td>Total</td>
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<td>----------------</td>
<td>---------------------</td>
<td>-------</td>
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<tr>
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<td>F M T</td>
<td>F M T</td>
<td>T</td>
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<td></td>
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<td>0.09 0.18 0.27</td>
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<td>0 0</td>
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<td>1.00</td>
<td>1.17</td>
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<td>0.98</td>
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<td>0 0 0</td>
<td>0 0 0</td>
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<td>0.71</td>
</tr>
<tr>
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<td>0 0 0</td>
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<td>2.25</td>
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<tr>
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<td>0 0 0</td>
<td>0.71 1.00 0</td>
<td>0</td>
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</table>
Table 5.7.--Significance levels from a series of one-way ANOVAs evaluating the effects of host age-sex (adult males, adult females, and juveniles) on infestation levels of four different ectoparasites that occur on *M. redmani*. When possible, incidence by each ectoparasite was analyzed separately for adult females (F), adult males (M), immatures (I), and totals (T) regardless of age or sex. An asterisk (*) indicates significance.

<table>
<thead>
<tr>
<th></th>
<th>Periglischrus iheringi</th>
<th>Nycterophilia sp.</th>
<th>Trichobius sp.</th>
<th>Spelaeorhynchus sp.</th>
<th>Total T</th>
</tr>
</thead>
<tbody>
<tr>
<td>df</td>
<td>F</td>
<td>M</td>
<td>I</td>
<td>T</td>
<td>F</td>
</tr>
<tr>
<td>Between</td>
<td>2</td>
<td>0.66</td>
<td>0.66</td>
<td>0.30</td>
<td>0.97</td>
</tr>
</tbody>
</table>
Table 5.8.—Significance levels from a series of two-way ANOVAs evaluating if levels of infestation by particular ectoparasites differ among the three host taxa (A. jamaicensis, S. rufum, and M. redmani) or differ between seasons (rainy and dry season). An asterisk (*) indicates significance at $P = 0.05$.

<table>
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<tr>
<th>Parasite</th>
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<th>Periglischnus iheringi</th>
<th>Trichobius sp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species (Sp)</td>
<td>2</td>
<td>&lt;0.001*</td>
<td>&lt;0.001*</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>Season (S)</td>
<td>1</td>
<td>0.60</td>
<td>0.97</td>
<td>0.78</td>
</tr>
<tr>
<td>Sp x S</td>
<td>2</td>
<td>0.99</td>
<td>0.86</td>
<td>0.80</td>
</tr>
</tbody>
</table>
APPENDIX B
SPECIMENS EXAMINED
All *Stenoderma rufum* specimens listed below were taken from the following locality: **PUERTO RICO: El Verde Field Station (Center for Energy and Environment Research (University of Puerto Rico and The U. S. Department of Energy))** near Route 186 in the Caribbean National Forest (Luquillo Mountains), **Municipality of Rio Grande [18° 19' 18" N, 65° 49' 12" W].**

The Museum of Texas Tech University
8855, 8857-8880, 8882-8884, 9830, 22351-22375, 22377-22393, 43465-43495, 43497, 43498, 43500-43503, 43505-43507, 43538-43548, 45304, 46372-46378, 47888, 52899, 52900, 56141, 56142.

Carnegie Museum of Natural History
89965-90000.

The Royal Ontario Museum
40608, 43191, 43193, 45454.
APPENDIX C
MORPHOMETRIC CHARACTERS
CRANIAL AND DENTAL CHARACTERS

* indicates bilaterally symmetrical measurements taken for both the left (L) and right (R) side of each specimen. Letters in parentheses correspond with distances indicated in figure 3.1.

ZB - Zygomatic breadth (C-C) - greatest distance parallel to long axis of skull across zygomatic arches.

GLS - Greatest length of skull (M-Q) - distance from most anterior part of rostrum (excluding teeth) to posterior point of skull.

CBL - Condylobasal length (N-Q) - distance from anteriormost edge of premaxillae to posteriormost projection of occipital condyles.

POC - Postorbital constriction (E-E) - least distance across top of skull posterior to postorbital process.

MB - Mastoid breadth (A-A) - greatest width of skull including mastoid.

BBC - Breadth of braincase (B-B) - greatest width across braincase posterior to zygomatic arches.

RB - Rostral breadth (D-D) - greatest width across rostrum anterior to zygomatic arches.

BUM - Breadth across upper molars (G-G) - maximum width from outer alveolus of one molar to outer alveolus of the opposite molar.

BUC - Breadth across upper canines (H-H) - width from outer alveolus of one canine to outer alveolus of the other canine.
*LTM - Length of maxillary toothrow (F-K) - length of anterior edge of alveolus of first tooth present in maxillae to posterior edge of alveolus of last molar.

*LUM - Length of upper molariform toothrow (V-F) - maximum length from the anterior edge of alveolus of first cheek tooth to the posterior edge of the alveolus of last molar.

GLM - Greatest length of mandible (R-S) - length from anteriormost point on ramus (excluding teeth) to posteriormost point on coronoid process.

*LMD - Length of mandibular toothrow (T-U) - length of anterior edge of alveolus of canine to posterior edge of alveolus of last molar in mandible.

DS - Depth of skull (O-P) - shortest distance perpendicular to the long distance of skull from the ventralmost portion of the auditory bullae to the sagital crest.

*LB - Length of bullae (not illustrated) - greatest distance of auditory bullae along the long distance of skull.

*WB - Width of bullae (not illustrated) - greatest distance of auditory bullae along the short distance of skull.

*WM - Width of Maxilla (J-G) - distance from the midline of the skull at the anteriormost point on the the posterior edge of the palate to the outer alveolus of molar M2.

*WZ - Width of zygomatic arch (L-C) - distance from midline of skull parallel to long axis of skull to the outer edge of the zygomatic arch.