MORPHOMETRIC VARIATION, MEASUREMENT ERROR, AND FLUCTUATING ASYMMETRY IN THE RED FIG-EATING BAT (*STENODERMA RUFUM*)

MICHAEL R. GANNON, MICHAEL R. WILLIG, AND J. KNOX JONES, JR.
Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409-3131

ABSTRACT.—Morphometric data were collected from 174 specimens of the red fig-eating bat (*Stenoderma rufum*) from the Tabonuco Rain Forest of Puerto Rico. Specimens were grouped by age and sex, and secondary sexual dimorphism was examined for 19 cranial and dental characters using univariate and multivariate techniques. Adult females were larger than adult males for 18 characters, whereas juvenile females were larger than juvenile males for 17 characters. For each specimen, measurement error was assessed using three non-consecutive measurements for each of the 19 characters. Results showed no detectable measurement effects. Additionally, eight paired measurements of the right and left sides were made for each specimen, and analyzed quantitatively for asymmetry. After correcting for directional asymmetry and antisymmetry, one character differed significantly in the amount of fluctuating asymmetry present between sexes. *Key words*: fluctuating asymmetry; morphometrics; *Stenoderma*; sexual dimorphism; Chiroptera.

Morphometric variation long has been used as an indicator of a diverse array of taxonomic and evolutionary phenomena including studies 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). Morphological variation is a reflection of the evolutionary factors that shape organismal phenotypes. Moreover, the manner in which individual variation is compartmentalized among groups can provide insight into the processes of speciation and the maintenance of phenotypic integrity (Simpson, 1944; Mayr, 1964).

Although morphometric studies have added important contributions to the study of mammalian systematics in the past, most have dealt with samples spanning relatively large geographic regions that contained a number of potentially different populations (see, for example, Husson, 1962; Handley, 1976; Koopman, 1978). Differences among populations, however, cannot be investigated based on such widely scattered collections. Sample sizes adequate to conduct intrademic analyses have been available to few investigators. Notable exceptions include works on *Liomys* (Genoways, 1973), *Cratogeomys* (Hollander, 1990), and a number of Brazilian bat species (Willig, 1983).

Secondary Sexual Variation

Variation between the sexes has interested biologists for many years (Darwin, 1859, 1871; Ralls, 1976; Myers, 1978; Swanepoel and Genoways, 1979; Williams and Findley, 1979). Sexes of a taxon often

differ morphologically to such an extent so as to appear as different species (for example, males are nearly twice the size of females in *Hypsignathus monstrosus*). However, the reasons for such differences (or lack thereof) are not always clear. Two major hypotheses have been presented to explain sexual variation in organisms. The first is that of sexual selection. Darwin (1859, 1871) suggested that natural selection can shape the anatomical or morphological traits that function in obtaining mates. Competition among individuals of one sex (usually males) for reproductive access to the other sex will act as a selection process on morphological 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 that is the object of competition. Large size frequently is advantageous in competitive encounters leading to access to females; larger males thus should be favored without similar size-related effects on females. A second hypothesis, suggested by Selander (1966, 1972), is the contention 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 constrains prey choice, then differences in prey-size selection between age or sex classes could lead to considerable dietary variation within a population of predators, a reduction in niche overlap among individuals, and an expanded resource base for the species. Numerous examples demonstrate that differences between sexes in body size are related to differential food consumption (Earhart and Johnson, 1970; Schoener, 1967, 1968; Selander; 1966), although such dietary correlates are 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. This is true particularly for those in which females are larger than males. Ralls (1976) suggested that the phenomenon of females being larger than males 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. Reasons for this involve the stringent demands of pregnancy and nursing, which may represent more powerful selection pressures than those produced by sexual selection differentially favoring large 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 measuring error has been ignored in many morphometric studies in the past (Pimentel, 1979; Reyment et al., 1984; Willig, 1983), 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 were 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).

Asymmetry

When examining morphological variation in a natural population, slight but measurable differences often can be detected between bilateral structures. These differences, resulting in asymmetry of otherwise bilaterally symmetrical organisms, have been of interest to evolutionary biologists for some time (Van Valen, 1962; Soulé, 1967; Jackson, 1973). More recently, renewed interest in this phenomenon has occurred because factors implicated in causing fluctuating asymmetry, such as systemic or environmental stress, inbreeding, contact in hybrid zones, 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 (Siegel and Doyle, 1975a, 1975b; Graham and Felley, 1985; Palmer and Stroebeck, 1986; Wayne et al., 1986; Willig and Owen, 1987a; Owen and McBee, 1990).

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 will have enhanced development (right side minus the left side for a particular character is not normally distributed). Each of these conditions is considered to have potential adaptive value (Soulé, 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 (Soulé, 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). Fluctuating asymmetry appears to have no obvious adaptive value and may represent the inability of developmental control systems to buffer against accidental variation during development (Van Valen, 1962; Soulé, 1967). Some individuals have a higher susceptibility to accidental variation, and as a result manifest a higher degree of asymmetry. Accidents that induce this condition may be intrinsic, extrinsic, or an interaction of the two. Nonetheless, such disruption, if manifested via homoeotic mutations, could play a critical role in the evolution of novel phenotypic body plans (Raff and Kaufmann, 1983).

Distribution

The red fig-eating bat, *Stenoderma rufum*, first was 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 first were captured in 1957 on St. John, Virgin Islands, confirming the contemporary existence of this bat. 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 (1960) 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 measurements, Hall and Tamsitt (1968) 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.*

S. rufum still is known only from the islands of Puerto Rico, St. John, and St. Thomas. As a result, it is a little-studied species and is relatively rare in scientific collections. 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). Thus, *S. rufum*, appears to be a good

candidate in which to examine all three aspects of morphometric variation. A geographically restricted population of this endemic insular species occurs in the Tabonuco Rain Forest of Puerto Rico. Indeed, almost all specimens we studied were obtained within a short distance (15 kilometers) of what is presently El Verde Field Station (18°19′ 18″ N, 65°49′ 12″ W). Moreover, analyses of home range and movement patterns reveal *S. rufum* to be extremely philopatric over long periods (Gannon, 1991). In addition, its habitat is affected by continual environmental disturbances of various scales ranging from tree falls, to landslides, to hurricanes. Recent data indicate that this Puerto Rican population of *S. rufum* may be extremely sensitive to large scale disturbances, which create severe reductions in population density and potential for genetic bottlenecks (Gannon and Willig, unpublished data). It is currently listed as a "sensitive" species by the U.S. Forest Service, but is presently under consideration for a change of status to either "threatened" or "endangered."

METHODS

Specimens of *S. rufum* collected in the Tabonuco Rain Forest of Puerto Rico were obtained from The Museum of Texas Tech University, The Royal Ontario Museum, and Carnegie Museum of Natural History (Appendix A). Individuals were sexed and aged as adult or juvenile (unossified epiphyses of the metacarpal-phalangeal joints—Anthony, 1988), as well as measured to the nearest 0.01 mm using Fowler digital calipers (Ultra-cal II, Fred V. Fowler Co., Inc., Newton, Massachusetts) for each of 19 morphometric characters (Appendix B). Of 174 specimens potentially used in univariate analysis, 125 were intact for all characters (adult males, N=45; adult females, N=58; juvenile males, N=17; juvenile females N=5) and were used in multivariate analyses. All measurements were made by the same individual. All statistical tests were performed via programs in SPSS-X (SPSS Inc., 1990).

Morphometric Variation

All bilateral measurements were taken from the right side of the skull or mandible. Systematic questions usually involve comparisons based upon a suite of characters; consequently, a multivariate approach is the preferred methodology (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. A multivariate test for homogeneity of variance (Box's M) was performed to evaluate the appropriateness of MANOVA, whereas univariate tests for homoscedasticity (Bartlett's Box Test) were performed on each character to determine the appropriateness of ANOVA.

Measurement Error

To evaluate the effects of variation due to measuring error, each character was measured three nonconsecutive times for all skulls. A two-way (age versus sex) nested (multiple measures per skull) ANOVA was preformed for each character separately (SPSS Inc., 1990) with the repeated measures factor reflecting the impact of measurement error. Because not all skulls were intact for all measurements, sample sizes varied with each analysis (see degrees of freedom in Table 3). In addition, significance of main treatment factors (age and sex) from these ANOVAs can identify important variables that contributed to significance in

TABLE 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: $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***.

Source	df	Pillias' trace	F
Age	19	0.41	3.79***
Sex	19	0.52	5.81***
Age by sex	19	0.28	2.13**
Error	103		

the MANOVA, with more powerful hierarchical *a priori* contrasts for each character used to compare 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. Eight bilaterally symmetrical cranial and dental characters (Appendix B) were measured on both right and left sides of each specimen. Of 174 specimens examined, 58 adult males and 78 adult females were intact for all eight characters and were analyzed for each of three different types of asymmetry following the analytical protocol described by Owen and McBee (1990). Each character first was made scale free by dividing its right minus left difference by the mean of its right and left measurement. This insured that asymmetry values were 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 using a *t*-test (Sokal and Rohlf, 1981). Corrections for directional asymmetry were achieved by substracting the mean asymmetry value of a character from the value of each individual 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, Box's M test was nonsignificant ($P > 0.05$), indicating homogeneity of variances in the treatment groups. MANOVA (Tables 1 and 2) detected significant age-specific and secondary sexual variation. The significant age-by-sex interaction indicated that the magnitude of difference between 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, an

TABLE 2. Mean (mm), followed by standard deviation in parentheses, of each mensural character used in morphometric analyses.

Character	Adult males N=45	Adult females N=58	Juvenile males N=17	Juvenile females N=5	Entire sample N=125
ZB	14.70(0.345)	15.20(0.281)	14.61(0.395)	14.86(0.514)	14.93(0.419)
GLS	22.19(0.413)	22.83(0.353)	21.94(0.676)	21.76(0.828)	22.44(0.589)
CBL	18.72(0.327)	19.46(0.310)	18.65(0.472)	19.04(0.371)	19.07(0.505)
POC	5.40(0.117)	5.62(0.123)	5.34(0.202)	5.57(0.106)	5.50(0.196)
MB	12.16(0.253)	12.54(0.289)	12.11(0.347)	12.34(0.346)	12.34(0.342)
BBC	10.72(0.234)	10.81(0.216)	10.57(0.210)	10.67(0.230)	10.74(0.235)
RB	9.33(0.241)	9.70(0.200)	9.34(0.267)	9.61(0.230)	9.51(0.286)
BUM	9.36(0.212)	9.68(0.173)	9.32(0.227)	9.54(0.131)	9.51(0.252)
BUC	5.70(0.143)	5.91(0.144)	5.69(0.319)	5.70(0.122)	5.79(0.204)
LTM	6.79(0.189)	7.03(0.190)	6.70(0.220)	7.07(0.199)	6.90(0.236)
LUM	5.69(0.160)	5.92(0.176)	5.73(0.157)	5.96(0.105)	5.81(0.200)
GLM	12.02(0.240)	12.61(0.207)	12.04(0.294)	12.48(0.219)	12.32(0.371)
LMD	6.89(0.159)	7.12(0.154)	6.90(0.176)	7.04(0.134)	7.00(0.193)
DS	11.89(0.260)	12.12(0.280)	11.72(0.178)	11.76(0.375)	11.97(0.302)
LB	2.61(0.164)	2.64(0.177)	2.57(0.137)	2.61(0.233)	2.62(0.169)
WB	3.32(0.233)	3.35(0.198)	3.29(0.252)	3.32(0.169)	3.33(0.216)
WM	3.67(0.129)	3.83(0.146)	3.76(0.168)	4.06(0.231)	3.77(0.173)
WZ	7.25(0.219)	7.47(0.204)	7.06(0.222)	7.25(0.314)	7.32(0.260)
W2M	2.17(0.154)	2.22(0.125)	2.19(0.093)	2.10(0.069)	2.19(0.133)

implication substantiated by examination of group means. In particular, dimorphism is exaggerated in adults compared to the situation in juveniles (Table 2).

Bartlett's test for univariate homogeneity of variance was nonsignificant for each character; thus ANOVAs were considered appropriate indications of the contribution of particular characters to significance in the MANOVA. Two-way ANOVAs (Table 3) with three randomly repeated measurements nested within each character corroborated MANOVA results and revealed 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 indicated that measurement error was not significant for any character and had no discernible effect on the results of this study. More powerful *a priori* hierarchical contrasts (Table 3) showed adult males differed from adult females in 18 characters, and juvenile males were smaller than juvenile females in 14 characters. Adults, regardless of sex, were significantly larger than juveniles in 12 characters. Sample means of all 19 characters were 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. We proceeded, therefore, with some confidence that measurements used in this study are unbiased estimates of actual parametric values. Second, secondary sexual dimorphism exists in *S. rufum*, and this dimorphism is consistently exhibited by all characters separately within each age group. 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, secondary 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 dimorphism in size in six of 18 vespertilionid 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, three with larger males and 13 with larger females. However, in all cases the existing dimorphism was slight, less than five percent (Fleming, 1988). In Brazil, 11 of 17 bat species were dimorphic for eight or more external and cranial characters (Willig,

TABLE 3. Results of two-way ANOVA (age versus sex) with three random measurements nested within each cell, along with *a priori* contrasts. Some degrees of freedom were constant for each test (error = 8, age = 1, sex = 1, age by sex = 1), but because sample size varied with each analysis, denominator degrees of freedom (df) are provided. Significance: $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***.

						A priori contrasts		
						Sexual dimorphism		
Character	Age	Sex	Age by sex	Measure within age by sex	df	Adults	Juveniles	Adults vs juveniles
ZB	3735.11***	18811.13***	677.90***	0.01	470	230.17***	24.48***	24.11***
GLS	830.95***	890.80***	136.56***	0.07	479	177.52***	6.97***	58.33***
CBL	2002.27***	26081.79***	621.34***	0.01	468	457.94***	50.46***	17.98***
POC	47.24***	2511.19***	23.14***	0.09	500	109.22***	0.11	0.08
MB	790.41***	4848.65***	131.91***	0.02	470	189.61***	20.31***	15.74***
BBC	392.31***	128.94***	0.98	0.13	491	17.85***	6.23*	51.37***
RB	15.92**	63.58***	14.97**	1.04	492	177.46***	5.52*	16.57***
BUM	224.18***	1061.80***	107.49***	0.11	500	250.08***	17.37***	25.10***
BUC	224.99***	1214.79***	110.01***	0.06	495	139.28***	10.57***	12.69***
LTM	10.99*	2608.20***	3.93	0.15	498	522.80***	116.77***	1.70
LUM	289.78***	90.42***	23.96***	0.18	485	50.94***	1.21	53.56***
GLM	15.97**	3717.88***	29.44***	0.04	483	192.06***	59.62***	0.71
LMD	5.19	1905.10***	52.63***	0.08	492	266.49***	33.97***	0.43
DS	10.23*	1874.34***	109.72***	0.07	499	235.20***	22.80***	0.68
LB	97.03***	243.04***	18.87**	0.02	471	11.71***	0.87	2.17
WB	204.96***	45.04***	23.88***	0.02	396	2.87	0.02	3.22
WM	2029.62***	3728.17***	0.10	0.03	492	128.01***	32.48***	56.75***
WZ	2504.96***	4626.26***	2.98	0.02	468	109.84***	24.41***	44.68***
W2M	73.89***	3.83	179.30***	0.05	495	15.51***	2.26	4.05*

1983). Six taxa contained larger males, and five taxa contained larger females. Similarly, Willig (1985) found slight sexual dimorphism in *Neoplatymops* (Molossidae) from the semiarid Caatinga of South America, with males larger than females, as is true in some other molossids. Previously, Jones et al. (1971) examined a small number of adults of both subspecies of *S. rufum* for 10 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 greater or lesser extent, that none of the three theories presented to explain sex-related differences in size is independent of the others. Selection pressures due to sexual selection, diet breadth, and "big mother" phenomena in concert most likely affect the magnitude and direction of dimorphism in most species of bats (Willig, 1983).

Although males and females exhibit similar diets (unpublished data) as well as foraging patterns and home ranges (Gannon, 1991), characterization of other basic behavioral attributes 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 we do not know whether males compete for females. Male *S. rufum* do not maintain harems, or defend roost sites or feeding areas. Therefore, little opportunity exists for agonistic interactions between males, and sexual selection is probably not a primary selection pressure. Their solitary habits and the fact that they do not defend roost sites suggest that males contribute nothing to the care of offspring. The role of raising young is undoubtedly fulfilled by females. This might lend support for Ralls' theory, but the size differences are small. Although sex differences in body size for *S. rufum* appear similar in magnitude to those for other tropical bats, such slight variation is difficult to explain. Willig (1985) was able to relate slight size differences in cranial characters between sexes of *Neoplatymops* to the structural constraint of environmental factors involving roost sites, but factors affecting *S. rufum* are not at all clear, and until more information on the basic ecology of this bat is available, the reasons for the occurrence of slight sexual dimorphism cannot 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 4).

The Shapiro-Wilk test on values corrected for directional asymmetry indicated antisymmetry was present in two characters for males and in

TABLE 4. Results of asymmetry tests for adult male ($N = 55$) and adult female ($N = 78$) *S. rufum* from the Tabonuco Rain Forest. Magnitude, direction and significance (t-test) for directional asymmetry (values expressed as means) are shown for males and females. Positive values represent larger right sides. Significant asymmetry as indicated by Shapiro-Wilk statistics for both males and females. Fluctuating asymmetry values for males and females are expressed as variances corrected for other types of asymmetry. The F statistic evaluates the equality of fluctuating asymmetry in males and females via Levene's test. Occasional missing values (for example, a broken zygomatic arch) were encountered; therefore, sample size reported represents the maximum possible in each case. Significance: $P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***.

	Directional asymmetry		Antisymmetry		Fluctuating asymmetry		
Character	Males	Females	Males	Females	Males	Females	F
LTM	−0.004	−0.000	0.959	0.484***	0.0037	0.0015	0.05
LUM	0.001	−0.000	0.946*	0.741**	0.0003	0.0013	1.06
LMD	−0.001	0.002	0.983	0.970	0.0002	0.0003	0.06
LB	−0.002	0.002	0.960	0.968	0.0016	0.0016	2.62
WB	0.006	0.004	0.984	0.972	0.0016	0.0011	0.00
WM	0.003	0.001	0.969	0.979	0.0025	0.0039	0.87
WZ	0.001	−0.001	0.963	0.980	0.0057	0.0025	4.79*
W2M	0.019**	0.013**	0.949*	0.953*	0.0018	0.0012	0.05

three characters for females. Normalizing these data can be a significant problem and has been discussed by several authors (Van Valen, 1962; Owen and McBee, 1990). As a result, each group was evaluated separately for skewness and kurtosis, different aspects of non-normality. Each character revealed high levels of skewness but not kurtosis; therefore, the Box-Cox procedure was chosen to transform the data to normality as suggested by Owen and McBee (1990). Because the null hypothesis for testing fluctuating asymmetry within males or within females is that the group variance equals zero, within-group tests cannot be performed because the test statistic is undefined (zero appears in the denominator of the test statistic). 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 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 (Modi et al., 1987; Willig and Owen, 1987a), results showed elevated levels of fluctuating asymmetry when compared to other felids, but no differences between sexes. Although results indicated 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 a noteworthy 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. A more definitive evaluation should include inter-site comparisons of the same species from distinct populations, or interspecific comparisons with other chiropterans from the same locality. However, few specimens (less than 10) of *S. rufum* have been collected from outside the Tabonuco Rain Forest, making such options untenable at present. The occurrence of high variance in these data, after adjustment for directional asymmetry and antisymmetry may reflect the genetic consequences of ecological and biogeographic isolation, which is further exacerbated by reduced population size after disturbance events such as hurricanes.

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Present address of Gannon: Department of Biology, The Pennsylvania State University, 3000 Ivyside Park, Altoona, Pennsylvania, 16601.

APPENDIX A
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 Luquillo Experimental 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 B
Cranial and Dental Characters

ZB, zygomatic breadth—greatest distance parallel to long axis of skull across zygomatic arches.

GLS, greatest length of skull—distance from most anterior part of rostrum (excluding teeth) to posterior point of skull.

CBL, condylobasal length—distance from anterior-most edge of premaxillae to posterior-most projection of occipital condyles.

POC, postorbital constriction—least distance across top of skull posterior to postorbital process.

MB, mastoid breadth—greatest width of skull including mastoid.

BBC, breadth of braincase—greatest width across braincase posterior to zygomatic arches.

RB, rostral breadth—greatest width across rostrum anterior to zygomatic arches.

BUM, breadth across upper molars—maximum width from outer alveolus of one molar to outer alveolus of the opposite molar.

BUC, breadth across upper canines—width from outer alveolus of one canine to outer alveolus of the other canine.

*LTM, length of maxillary toothrow—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—maximum length from the anterior edge of alveolus of first cheektooth to the posterior edge of the alveolus of last molar.

GLM, greatest length of mandible—length from anterior-most point on ramus (excluding teeth) to posterior-most point on coronoid process.

*LMD, length of mandibular toothrow—length of anterior edge of alveolus of canine to posterior edge of alveolus of last molar in mandible.

DS, depth of skull—shortest distance perpendicular to the long axis of skull from the ventral-most portion of the auditory bullae to the sagital crest.

*LB, length of bullae—greatest distance of auditory bullae along the long axis of skull.

*WB, width of bullae—greatest distance of auditory bullae along the short axis of skull.

*WM, width of maxilla—distance from the midline of the skull at the anterior-most point on the posterior edge of the palate to the outer alveolus of molar M2.

*WZ, width of zygomatic arch—distance from ventral midline of skull parallel to long axis of skull to the outer edge of the zygomatic arch.

*W2M, width of molar M2.

*indicates bilaterally symmetrical measurements taken for both the left and right side of each specimen.