

GEOMETRIC MORPHOMETRIC APPROACHES TO THE STUDY OF SEXUAL SIZE DIMORPHISM IN MAMMALS

CRAIG S. HOOD

*Department of Biological Sciences, Loyola University, New Orleans, LA, USA 70118,
and Tulane University Museum of Natural History, Belle Chasse, LA, USA 70037.
email: chood@loyno.edu*

ABSTRACT - Sexual size dimorphism (**SSD**) has been extensively documented in many organisms, from vascular plants to vertebrates, including mammals. Geometric morphometric methods offer new, powerful tools for the study of **SSD**. The investigation of shape variability has not been previously pursued in traditional SSD studies and is a unique contribution of geometric morphometrics to this field. The combining of Procrustes methods with multivariate statistical analyses supports all traditional SSD experimental designs and allows new studies of shape variability and its relationship with size and other variables. Intraspecific and interspecific examples comparing traditional and geometric morphometric approaches to the study of **SSD** within several mammalian taxa are presented.

Keywords - geometric morphometrics, sexual size dimorphism, allometry, Rensch's rule

INTRODUCTION

The study of sexual dimorphism has attracted the interests of biologists ever since Darwin (1859, 1874). Sexual size dimorphism (**SSD**), the differences in body size between sexes, is a common feature of many organisms, from vascular plants to invertebrates and vertebrates, including mammals (for reviews see, Clutton-Brock and Harvey, 1983; LaBarbara, 1989; Short and Balaban, 1994; Fairbairn, 1997). Within mammals, a large literature of descriptive studies of **SSD** exists and numerous papers continue to be published (e.g., Clutton-Brock et al., 1977; Ralls, 1977; Jungers, 1985; Weckerly, 1998).

Hypotheses explaining the origin and maintenance of **SSD** include a) sexual selection (especially in mate choice or mating system), b) selection on reproductive life history traits, and c) intersexual ecological divergence. The association of **SSD** with sexual selection has been a dominant theme among studies of mammals (Clutton-Brock

et al., 1977; Leutenegger, 1978; Jungers, 1985; Ford, 1994; Weckerly, 1998). Studies of reproductive life history traits, often including overall body size as a variable, evaluate how size constrains life history features (Leutenegger and Cheverud, 1985; Heske and Ostfeld, 1990; Soderquist, 1995). Intersexual ecological divergence hypotheses, whereby males and females diverge in size due to their different ecological roles, address how foraging, behavioral activity patterns, and inter and intraspecific competition varies between the sexes (Myers, 1978; Willig, 1983; Willig and Hollander, 1995; Sullivan and Best, 1997).

SSD has been traditionally described using body size measures, including body mass, single linear measures capturing total length, or the length of some specific body part. In many studies, one body size measure is used as a covariate for another. A commonly calculated index of **SSD**, $\log(\text{male size})/\log(\text{female size})$, is often generated to compare levels of dimorphism in various taxa (LaBar-

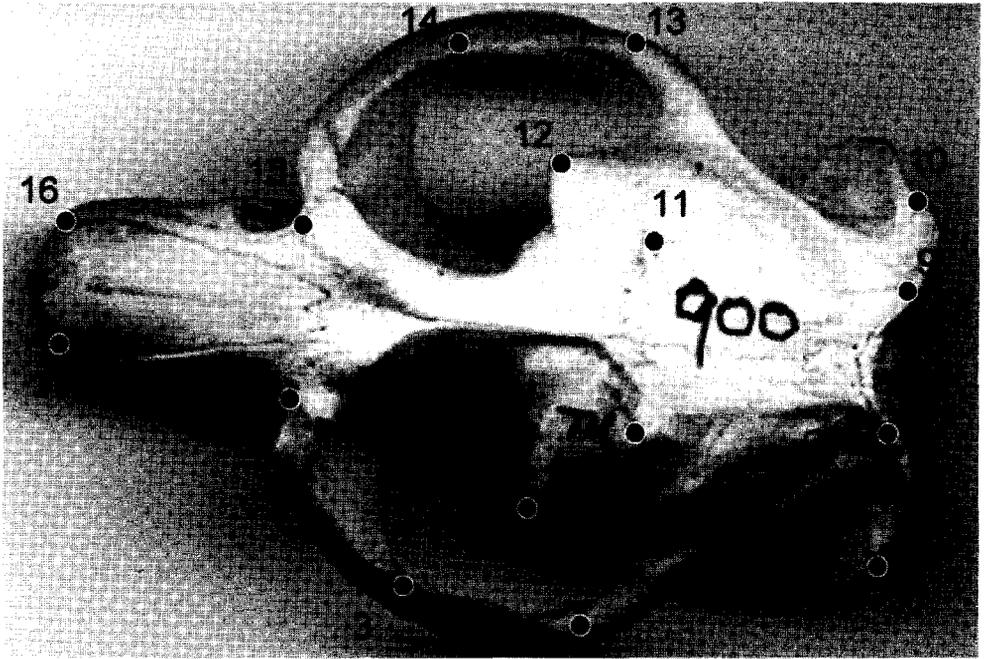


Fig. 1. Landmarks used to capture cranial size and shape in the muskrat, *Ondatra zibethicus*. Skulls were placed on a stage and aligned by their maxillary tooththrows to a stable plane.

bara, 1989; Gibbons and Lovich, 1990; Lovich and Gibbons, 1992). The validity of generating and using such ratios notwithstanding, comparative SSD studies have also regressed log-transformed size variables against one another to evaluate the allometric relationship of dimorphism in overall body size (see discussions by Abouheif and Fairbairn, 1997; Fairbairn, 1997).

A number of recent studies have assessed sexual dimorphism in both size and shape using traditional morphometric approaches (e.g., see Wiig, 1986; Lynch and Hayden, 1995; Lynch et al., 1996b). The application of one of several size correction methods (Burnaby, 1966; Rohlf and Bookstein, 1987; Bookstein, 1991) has allowed these studies to evaluate shape dimorphism.

Rensch's rule describes the general tendency observed in many comparative studies, that the magnitude of SSD increases with overall body size in taxa where males are the larger of the two sexes (Rensch, 1960; Fairbairn,

1997). Recently, Abouheif and Fairbairn (1997) have evaluated statistical tests of Rensch's Rule and of the allometric relationship in interspecific SSD studies. They identified important factors effecting these analyses including the inappropriate use of simple linear regression models for estimating allometric relationships and the lack of phylogenetic independence in comparing taxa within a larger phylogenetic context.

The goals of the present paper are to investigate the use of geometric morphometric methods in SSD studies, to identify the unique contributions these new tools bring to SSD, and to suggest approaches for future studies. Geometric morphometric methods provide powerful tools to describe and analyze biological form (Bookstein, 1991, 1996; Rohlf and Marcus, 1993; Marcus and Corti, 1996). In addition to capturing shape variability that can be analyzed by traditional multivariate statistical designs and visualized by the thin-plate spline interpolating func-

tion, these methods also yield a geometrical-based measure of size – centroid size.

Whereas most geometric morphometric studies addressing questions at the intraspecific level have evaluated sexual dimorphism as an initial experimental design step (e.g., Auffray et al., 1996; Corti et al., 1996; Astua de Moraes et al., 1999; Hingst-Zaher et al., 2000), only a few studies have focused on questions concerning sexual dimorphism with these methods (Ahlstrom, 1996; Lynch et al., 1996a; Wood and Lynch, 1996). The present paper presents two examples, one addressing SSD at the intraspecific and the other at an interspecific (comparative) level.

MATERIALS AND METHODS

Specimens. The specimens used in this study are housed in the Mammal Collections of the Tulane University Museum of Natural History. Crania and mandibles of the muskrat, *Ondatra zibethicus* (Rodentia: Muridae, Arivicolinae) collected from three major lo-

calities along the Louisiana coastal marshes in two trapping seasons during 1939-40, were used for the infraspecific study. Gould and Kreeger (1948) reported traditional morphometric results based on 358 specimens aged as adults by tooth wear criteria, noting significant geographic variation. In the present study, 148 of these specimens were examined with the following specific localities and sample sizes: Calcasieu and Sabine lake marshes, Cameron Parish, Louisiana?USA (46 males, 37 females), Delacroix island marshes, St. Bernard Parish, Louisiana, USA (24 males, 41 females).

Crania of representative pteropodid bat taxa used for the interspecific study, were as follows (n = 5 males and 5 females for each species): *Eidolon helvum*, Bata, Rio Muni, West Africa; *Epomops franqueti*, Bata and Evuenam, Rio Muni, West Africa; *Rousettus aegyptiacus*, Mt. Bong and Moka, Rio Muni, West Africa; *Myonycteris torquata* Bata, Rio Muni, West Africa; *Megaloglossus woermanni*, Evuenam, Rio Muni, West Africa; *Micropteropus pusillus*, Bata, Rio Muni, West

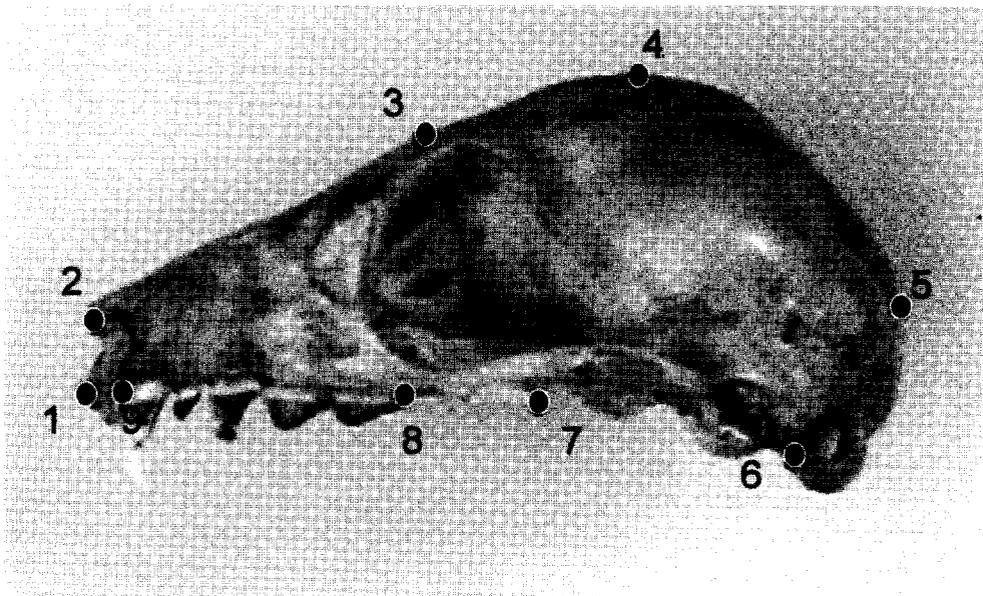


Fig. 2. Landmarks used to capture cranial size and shape in pteropodid bats: all landmarks were located on midline of the skull in each specimen.

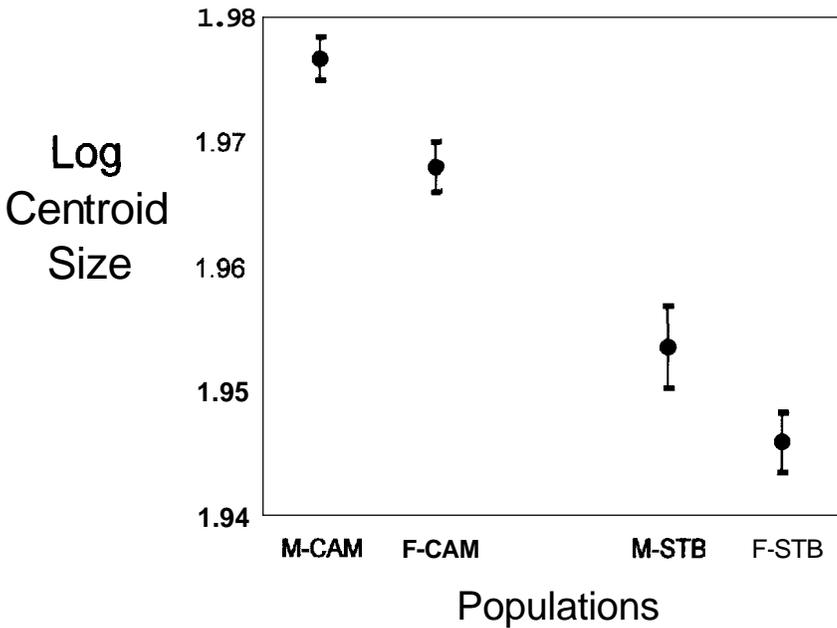


Fig. 3. Plot of log centroid size in *Ondatra zibethicus* from two localities, Cameron parish, and St. Bernard parish, Louisiana, USA, illustrating sexual size dimorphism Mean \pm 1 SE.

Africa; *Cynopterus sphinx*, Prachinburi, Thailand; *Macroglossus minimus*, Nakonsithamraj, Thailand. The natural history, ecology, and traditional morphometric measurements for the Rio Muni collections were reported by Jones (1971, 1972). All specimens included in the present study, had field-collected measurement data, including body weights.

Morphometric data collection and analysis.

Landmarks were collected on each individual (Figs. 1 and 2) using a two-dimensional video-based data capture system that included a BW CCD video camera, PCVISION+ framegrabber installed in a Windows 95-based pc. Landmarks were obtained using the digitizing software program MORPHOSYS (ver. 2.18), imported into a spreadsheet program (EXCEL) and analyzed by morphometric (tpsREGR ver. 1.18; tpsRELW ver. 1.14; MORPHEUS et al.)

and statistical programs (SAS ver. 6.12; BIOMSTAT ver. 3.2; NTSYS ver. 2.).

Measures of size analyzed in the intraspecific study were linear cranial measurements (in mm, originally taken by Gould and Kreeger, 1948) and centroid size (CS). Size variables used in the interspecific study were body mass (weight in gr., originally taken in field by Jones, 1971) and centroid size (CS). Body weight is a traditionally-used measure of size in many mammalian SSD studies. It's wide variability among individuals, especially during different seasons and reproductive conditions (e.g., winter/summer, pregnancy in female) has been noted as needing careful evaluation in the SSD literature. Centroid size is a geometrically-based measure of size that is the square root of the sum of the squared distances of the landmarks to their centroid (for discussion see Bookstein, 1989, 1991).

Both body mass and CS were log transformed for use in statistical analyses.

Shape changes were described using geometric morphometric methods (Bookstein, 1991, 1996; Rohlf and Marcus, 1993; Marcus et al., 1993, 1996). Shape variables were extracted from the landmark data using the procedures implemented in the software program tpsREGR. Briefly, landmark configurations for each specimen were aligned, translated, rotated, and scaled to a unit centroid size by the generalized least squares fit criterion (CLS) as described by Rohlf and Slice (1990) using the consensus configuration of all specimens as the starting form (i.e., tangent configuration of Rohlf et al., 1996). Partial warps representing the non-uniform shape variables, and uniform components estimated using Bookstein's (1996) formula were obtained using tpsREGR and used in subsequent analyses. The thin-plate spline interpolating function (TPS) was used to visualize overall, uniform, and non-uniform shape changes.

Because our focus concerns testing for sexual dimorphism, sexes were treated separately throughout the statistical analyses. Tests for sexual dimorphism in size and shape were conducted using ANOVA and MANOVA, respectively, following Adams and Funk (1997). A relative warps analysis (RWA) was conducted to explore shape variability within and among sexes (Bookstein, 1991; Rohlf, 1993). All deformation illustrations in this paper were generated using the program tpsREGR or tpsRELW.

In the interspecific study (comparing sexual dimorphism among pteropodid bat taxa), sexual dimorphism was assessed within each taxon and comparisons among taxa were made following traditional SSD designs. Traditional designs include plotting male versus female size variables and calculation of regressions to test Rensch's rule. As discussed by Abouheif and Fairbairn, (1997) and Fairbairn (1997), simple linear regression models used in many published SSD studies are not statistically robust, as

both size variables (males and females) are measured with error (see also Sokal and Rohlf, 1995). Thus, major axis rotation regressions were estimated for evaluation of Rensch's rule (Fairbairn, 1997).

RESULTS AND DISCUSSION

Assessing sexual dimorphism in intraspecific studies.

The muskrat data set used as an example of an intraspecific SSD study exhibits a strong pattern of sexual size dimorphism. Two-way ANOVAs and MANOVAs of nine linear cranial measurements (originally taken by Could and Kreeger, 1948) revealed highly significant sexual dimorphism and geographic variation (two-way MANOVA, sex, Wilks' lambda 0.533, $F = 12.87$, $P < 0.0001$; locality, Wilks' lambda 0.395, $F = 9.68$, $P < 0.0001$; interaction, Wilks' lambda 0.0464, $F = 0.87$, n.s.). Similarly, a two-way ANOVA of centroid size was highly significant for both sex and locality, demonstrating both sexual dimorphism and geographic variation (sex, $F = 3.964$, $P = 0.004$; locality, $F = 3.964$, $P = 0.004$; interaction, $F = 0.912$, n.s.; Fig. 3).

Sexual dimorphism in shape was highly significant by sex and locality (two-way MANOVA of non-uniform shape variables, sex, Wilks' lambda 0.571, $F = 3.43$, $P < 0.0001$; locality, Wilks' lambda 0.483, $F = 4.90$, $P < 0.0001$; interaction, Wilks' lambda 0.754, $F = 1.50$, n.s.). Relative warps analysis was conducted to explore shape variability within the data set. Plots of relative warps 1 and 2 and one set of visualizations of shapes within those warps provide insight into shape variability within the sample (Fig. 4). Along relative warp axis 1, positive deviations yield shorter rostra, narrower zygomatic processes, and longer braincases, whereas negative deviations include forms with longer rostra, broader zygomatic processes and shorter braincases.

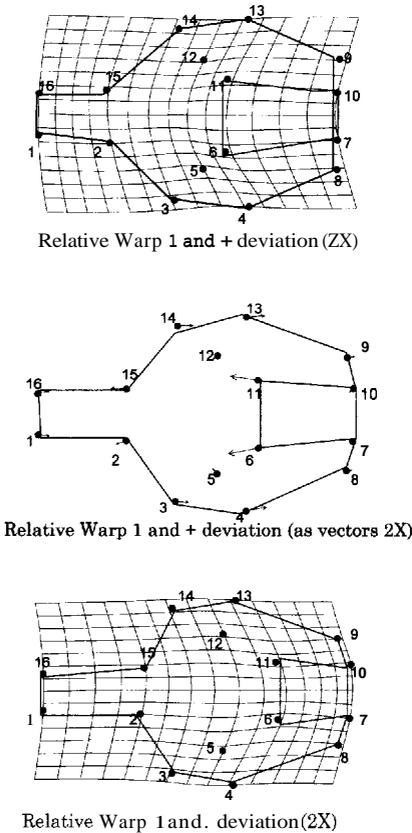


Fig. 4. Thin-plate-spline reconstructions of shape variability along relative warp 1 following a relative warps analysis. Positive deviation is in direction of male shape variability, negative is towards female shapes.

Along this relative warp, males from the sample are generally aligned with positive deviations and females with negative deviations. As discussed by Rohlf (1993) and Rohlf et al. (1996), relative warp plots such as these simply depict two axes of variation and should be interpreted with caution. However, if shape variability is aligned with some interpretable grouping factor (e.g., sex along RW1 in this example), its visualization can be a useful exploratory exercise. The localization of shape change in a portion of

the form (e.g., the rostrum, zygoma, and braincase in this example) might suggest specific hypotheses for further study.

Reduction of the dimensionality of the variability by conducting a canonical variates analysis (CVA) would be appropriate to explore shape variability within homogeneous samples (Rohlf et al., 1996; Adams and Funk, 1997). The CVA conducted for one locality, the Cameron Parish sample, produced good separation of the sexes (Fig. 5).

Additional variables, including body weight, other life history variables, behavioral or environmental data could be included in shape analyses using multivariate regression models (Rohlf et al., 1996; Rohlf, 1998; Zelditch et al. 1998; Monteiro, 1999). Multivariate regression of shape on body size variables allow for direct tests of major factors that explain the origin and maintenance of SSD. Multivariate regressions of shape on centroid size and total body length for the Cameron parish population were not significant. therefore shape change does not accompany increasing size at this locality. The significant geographic factor in the analyses of Cameron and St. Bernard parish

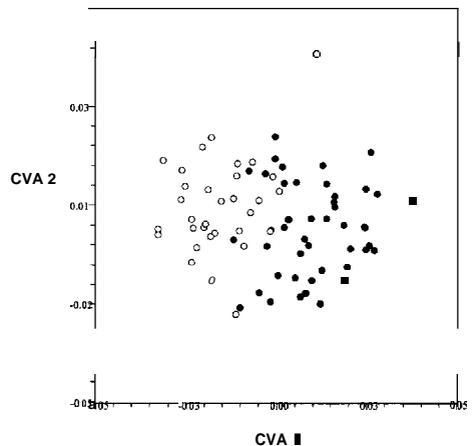


Fig. 5. Plot of canonical variate scores for landmarks of *Ondatra zibethicus* males (solid circles) and females (open circles) from Cameron Parish.

populations suggests that some variable(s) that differ in specimens from the two localities should be studied. The vegetation of the two localities was markedly different at the time of specimen collection (Lynch et al., 1947; O'Neil, 1949). Whereas plant species composition and primary productivity in Cameron parish reflect a healthy freshwater marsh, the St. Bernard locality was characterized as a brackish/intermediate marsh that is less favored by muskrats (Lay et al., 1942; Lynch et al., 1947; O'Neil, 1949; Lowery, 1974). Because ecological data collected with the specimens only included qualitative descriptions of vegetation patterns for 3 sub-groups of the Cameron parish population, inultivariate regression would not be an appropriate analysis for this data set. However, where such data are available, a multivariate regression would provide a test of factors impacting sexual dimorphism.

Assessing sexual dimorphism in interspecific studies.

The pteropodid bat data set used as an example of an interspecific SSD study shows that, some taxa possess significant sexual size dimorphism, while other taxa do not (Fig. 6). Body weight and centroid size exhibit nearly identical patterns of SSD. Significant SSD in body weight (with male bias – males being larger) exists in the three largest pteropodids, *Eidolon helvum*, *Rousettus aegyptiacus*, and *Epomops franqueti*, with other taxa being non-significant. Similar results apply for centroid size, although *Myonycteris torquata* (a medium-sized bat) is non-significant with female-biased dimorphism. The presence of male-biased SSD in these African pteropodid taxa is well known, having been found in previous morphometric and systematic studies (e.g., Jones, 1971; Bergmans, 1979, 1988, 1989, 1994). Furthermore, the epomorphine bats, including *Epomops*, *Epomophorus*, *Micropteropus*, and *Megaloglossus* examined in this study, are remarkable among

pteropodids in having several qualitative sexually dimorphic features associated with social organization and mate choice (Andersen, 1912; Kingdon, 1974; Zeller, 1984). Behavioral and ecological studies have shown these taxa to possess some of the most complex social structures and breeding systems among mammals (Wickler and Seibt, 1976; Bradbury, 1977a, 1977b; Marshall and MacWilliam, 1982). Thus, the pattern of SSD is consistent with patterns of mate choice, which have been proposed as a causal factor for sexual selection hypotheses of SSD.

Body weight and centroid size both exhibit Rensch's rule; the largest taxa have the greatest magnitudes of SSD and are male-

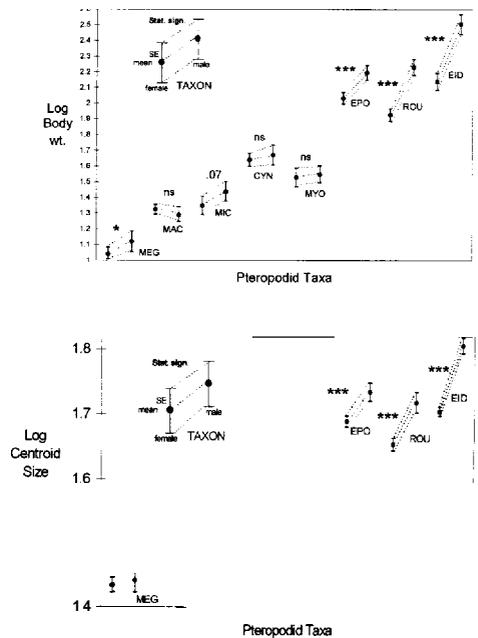


Fig. 6. Plots of centroid size illustrating sexual size dimorphism in pteropodid bats. For each species, the male data are on the right and female on the left. Asterisks indicate significant sexual dimorphism in that taxon by ANOVA at $P < 0.0001$.

biased (Fig. 7). The major axis regressions for both size variables are significant and account for large proportions of sample variability. In this example, the largest taxa (*Eidolon*, *Epomops*, *Rousettus*) include one (*Epomops*) that was mentioned above as having a breeding system consistent as a causal factor for SSD. *Eidolon helvum* and *Rousettus aegyptiacus* have generalized promiscuous breeding systems, not usually associated with sexual selection. Other epomorphine taxa that have qualitative sexual dimorphic features (e.g., *Micropteropus* and *Megaloglossus*) did not have detectable SSD. Thus, the interpretation of SSD patterns and their potential causal factors in the pteropodid taxa studied is not simple.

MANOVA tests of shape dimorphism were not possible due to small sample sizes. However, inspection of mean male and female forms visualized by the thin-plate spline interpolating function shows shape dimorphism in most of the taxa (Fig. 8). Substantial shape differences are evident among taxa, reflecting their distinct evolutionary histories. Comparison of male and female shapes within each taxon reveals that both uniform and non-uniform shape changes occur (both components are illustrated in Fig. 8). The magnitude of shape change does not appear to be substantially different in comparing the 3 largest taxa which had significant SSD (*Eidolon*, *Epomops*, and *Rousettus*) to the others.

CONCLUSIONS.

Geometric morphometric methods support the analysis of sexual size dimorphism that incorporate traditional SSD designs. In many traditional SSD studies, body size measurements (e.g., linear measurements capturing total body length, the lengths of body parts or regions, and body weight) are used both as variables to define SSD, as well as co-variables to evaluate factors explaining the origin and maintenance of SSD. The introduction of centroid size as a size variable makes an important new contribu-

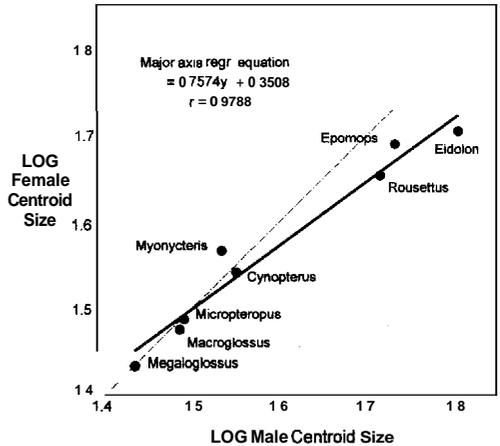
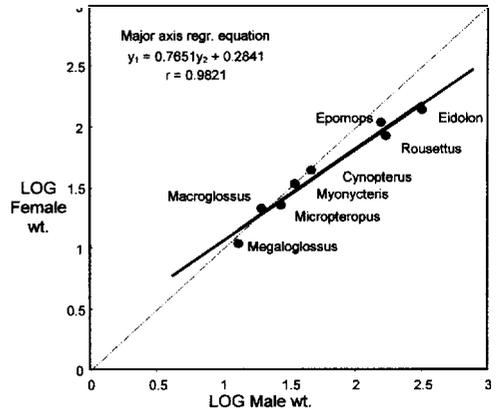


Fig. 7. Logarithmic plots of male and female size variables for 8 pteropodid taxa. Upper graph plots body weight as in a traditional SSD analysis; lower graph plots centroid size. Values represent mean male and female value for each taxon.

tion to SSD studies. Given that centroid size is a geometrically-based measure of size that is independent of landmark shape variability (in the absence of allometry), it can serve as a primary size variable to investigate SSD in a taxon. The use of other size variables as factors to explain the origin and maintenance of SSD, especially body weight, is therefore strengthened.

Female

Male

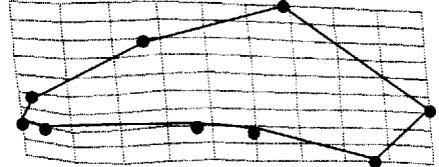
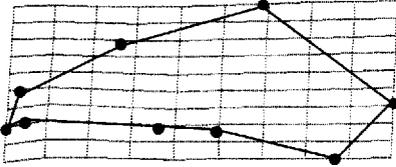
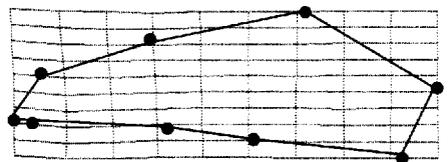
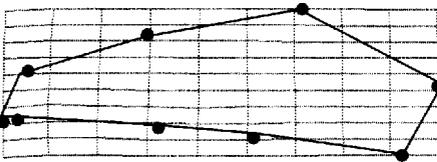
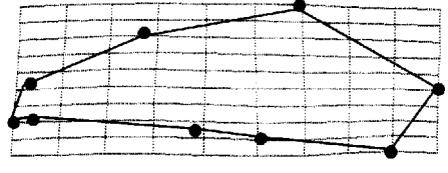
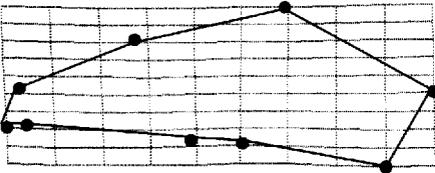
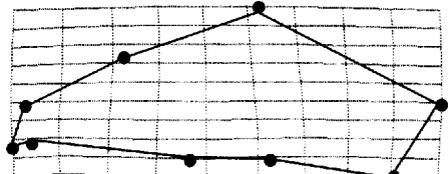
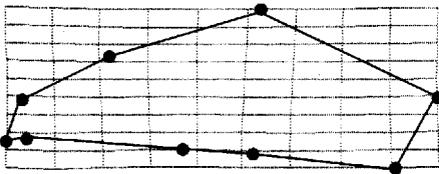
Eidolon helvum*Epomops franqueti**Rousettus egyptiacus**Myonycteris torquata*

Fig. 8. Reconstructions of mean male and female skulls for representative pteropodid taxa. As described in text, each pair of deformations is based on data for males and females in a given species, not the entire pteropodid data set.

Geometric morphometric methods provide tools to extend the study of sexual dimorphism to include shape. Shape variability can be integrated into SSD studies in several ways. Shape variables can be assessed for dimorphism, yielding a sexual shape dimorphism that can be the primary focus of the study. Body size variables, as well as behavioral, metabolic, or ecological variables can be tested as factors explaining shape dimorphism. If the focus of a study is indeed SSD, then shape variables can be evaluated as explanatory factors. Of course, the role that shape variables take in an experimental design depends on the biological questions being investigated. One of the most powerful components of geometric morphometric analysis is the visualization of shape variability through the thin-plate spline interpolating function. Relative warps analysis supports an exploration of shape variability within a data set and can provide visualization of shape change within a RW. For data sets that are appropriate for canonical variates analysis, shape variability among individuals or among defined groups can be visualized. In intraspecific studies, sexual dimorphism in size and shape can be described by standard descriptive statistics and evaluated by ANOVA and MANOVA designs. Depending on the nature of the biological problem being studied, appropriate choice of samples and experimental designs can lead to tests of the factors that might explain the origin and/or maintenance of sexual dimorphism. For example, whereas some populations in a study might be characterized (*a priori*) as having a breeding system that is predicted to accentuate sexual selection through mate choice, others do not. In the muskrat example, there was significant geographic variation in size and shape, although the magnitude of SSD was similar. Muskrats are not known to possess breeding systems that are likely to lead to sexual selection, and no evidence is available to suggest that these populations have been subjected to sexual selection (O'Neil, 1949; Errington,

1963). Thus, ecological or environmental factors are reasonable variables to investigate in subsequent studies.

Rensch's rule, the tendency for the magnitude of SSD to increase with increasing body size in male-biased taxa, is not usually evaluated for intraspecific problems. Rensch (1960) described this trend for comparative studies, but noted that this relationship might also hold within species. Fairbairn (1997) observed that Rensch's rule has not been well studied at the intraspecific level. In the muskrat data set, the magnitude of SSD was not different between populations, yet body size was highly significantly different (see Fig. 3). Thus, Rensch's rule did not hold true in this specific case.

In interspecific studies, sexual dimorphism in size and shape for each taxon can be described by standard descriptive statistics and evaluated by ANOVA and MANOVA designs. The comparison of the magnitude of sexual dimorphism across taxa, especially to evaluate Rensch's rule, has been approached by regressing a SSD index against an overall body size variable. Lack of phylogenetic independence among taxa in a data set poses a significant problem for this comparison. Care must be taken to separate historical effects from those that are the primary focus of the study. When phylogenetic distance data are available for all the taxa in a study, then techniques such as independent contrasts might be applied (see discussion by Abouheif and Fairbairn, 1997; Fairbairn, 1997). For the pteropodid bat data set, evolutionary relationships among some of the taxa seem well established (i.e., for several of the African forms), whereas the phylogenetic position of others is uncertain (Hood, 1989; Juste et al., 1997; Bergmans, 1997). The taxa with the greatest magnitudes of SSD (*Eidolon*, *Rousettus*, and *Epomops*) were the largest in overall body size. These taxa are not closely related to one another and those that are (*Myonycteris* to *Rousettus*; *Micropteropus* and *Megaloglossus* to *Epomops*) do not have detectable SSD.

ACKNOWLEDGMENTS

The specimens used in this study were collected, prepared, and deposited in the Tulane Museum of Natural History. Acknowledgement is due to Dr. Clyde Jones for making the original collections of African pteropodid bats and Dr. Harley Gould for assembling the collection of muskrats. I thank my undergraduate research students Nga Vu and Nicole Lorenz for assisting in data capture. Morphometrics software used in this paper is available from the SUNY Stony Brook morphometrics website located at <http://life.bio.sunysb.edu/morph>. Funding support was provided by a sabbatical leave and the J.H. Mullahy Fund, Loyola University. Imaging hardware was acquired with support from a National Science Foundation grant (BSR 8723 153) to the author.

REFERENCES

- Abouheif, E., and D.J. Fairbairn. 1997. A comparative analysis for sexual size dimorphism: assessing Rensch's rule. *Am. Nat.*, 149: 540-562.
- Adams, D.C., and D. J. Funk. 1997. Morphometric inferences on sibling species and sexual dimorphism in *Neochlamisus bebbianae* leaf beetles: multivariate applications of the thin-plate spline. *Syst. Biol.*, 46: 180-194.
- Ahlstrom, T. 1996. Sexual dimorphism in medieval human crania studied by three-dimensional thin-plate spline analysis. In: L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor, and D.E. Slice (eds.), *Advances in Morphometrics NATO ASI Series vol. 284*, Plenum Press, New York: 415-421.
- Andersen, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum. 2nd ed., vol. 1: Megachiroptera. *British Mus. (Nat. Hist.)*, London, 854 pp.
- Astua de Moraes, D., G. Marroig, E. Hingst-Zaher, and R. Cerqueira. 2000. Shape analyses in didelphid marsupial mandibles using traditional and 2D geometric morphometrics: different approaches for morpho-functional interpretations. *Hystrix, It. J. Mamm.* 115-130.
- Auffray, J.-C., P. Alibert, C. Latieule, and B. Dod. 1996. Relative warp analysis of skull shape across the hybrid zone of the house mouse (*Mus musculus*) in Denmark. *J. Zool. London*, 240: 441-455.
- Bergmans, W. 1979. Taxonomy and zoogeography of the fruit bats of the People's Republic of Congo, with notes on their reproductive biology. *Bijdragen tot de Dierkunde*, 48: 161-186.
- Bergmans, W. 1988. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 1. General introduction; materials and methods; results: the genus *Epomophorus* Bennett, 1836. *Beaufortia*, 38: 75-146.
- Bergmans, W. 1989. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 2. The genera *Micropteropus* Matschie, 1899, *Epomops* Gray, 1870, *Hypsignathus* H. Allen, 1861, *Nanonycteris* Matschie, 1899, and *Pterotes* Andersen, 1910. *Beaufortia*, 39: 89-153.
- Bergmans, W. 1994. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 4. The genus *Rousettus* Gray, 1821. *Beaufortia*, 44: 79-125.
- Bergmans, W. 1997. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 5. The genera *Lissonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899, and *Megaloglossus* Pagenstecher, 1885; general remarks and conclusions; annex: key to all species. *Beaufortia*, 47: 11-.
- Bookstein, F.L. 1989. "Size and shape": a comment on semantics. *Syst. Zool.* 38: 173-180.
- Bookstein, F.L. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge Univ. Press, New York, 435 pp.

- Bookstein, F.L. 1996. Combining the tools of geometric morphometrics. In: L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor, and D.E. Slice (eds.). *Advances in Morphometrics*. NATO ASI Series vol. 284, Plenum Press, New York: 131-152.
- Bradbury, J.W. 1977a. Lek mating behavior in the hammer-headed bat. *Zeit. Saugtierk.*, 45: 225-255.
- Bradbury, J.W. 1977b. Social organization and communication. In: W.A. Wimsatt (ed.), *Biology of bats*. Vol. 3, 1-72. Academic Press, New York.
- Burnaby, T.P. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics*, 22: 96-110.
- Clutton-Brock, T.H., and P.H. Harvey, 1983. The functional significance of variation in body size among mammals. In: Eisenberg, J.F., and D.G. Kleiman (eds.). *Advances in the Study of Behavior*, Special Publication number 7, American Soc. Mammalogists, Lawrence, KS., 632-663.
- Clutton-Brock, T.H., P.H. Harvey, and B. Rudder. 1977. Sexual dimorphism, socioeconomic sex ratio and body weight in primates. *Nature*, 269: 797-800.
- Corti, M., C. Fadda, S. Simson, and E. Nevo. 1996. Size and shape variation in the mandible of the fossorial rodent *Spalax ehrenbergi*. A Procrustes analysis in three dimensions. In: L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor, and D.E. Slice (eds.), *Advances in Morphometrics*. NATO ASI Series vol. 284, Plenum Press, New York: 303-320.
- Darwin, C.R. 1859. *On the Origin of Species*. Murray, London. 597 pp.
- Darwin, C.R. 1874. *The Descent of Man and Selection in Relation to Sex*. 2nd ed., Amer. Publ. Corp., New York, 705 pp.
- Errington, P.L. *Muskrat Populations. Population Dynamics on an Important Species*. Iowa State Univ. Press. Ames, 665 pp.
- Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annu. Rev. Ecol. Syst.*, 28: 659-687.
- Ford, S.M. 1994. Evolution of sexual dimorphism in body weight in Platyrrhines. *Am. J. Primatol.*, 34: 221-244.
- Gibbons, J.W. and J. E. Lovich. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trichemys scripta*). *Herpetol. Monogr.* 4: 1-29.
- Gould, H. N., and F. B. Kreeger. 1948. The skull of the Louisiana muskrat (*Ondatra zibethica rivalicia*): I. The skull in advanced age. *J. Mammal.*, 29: 138-149.
- Heske, E.J. and R.S. Ostfeld. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. *J. Mammal.*, 71: 510-519.
- Hingst-Zaher, E., L.F. Marcus, and R. Cerqueira. 2000. Morphological integration during ontogeny in *Calomys tener* (Sigmodontinae, Rodentia). *Hystrix*, It. J. Mamm: 99-113.
- Hood, C.S. 1989. Comparative morphology and evolution of the female reproductive tract in macroglossine bats (Mammalia, Chiroptera). *J. Morphol.* 1989: 207-221.
- Jones, C. 1971. The bats of Rio Muni, West Africa. *J. Mammal.*, 52: 121-140.
- Jones, C. 1972. Comparative ecology of three pteropid bats in Rio Muni, West Africa. *J. Zool., London*, 167: 353-370.
- Jungers, W.L. (ed). 1985. *Size and Scaling in Primate Biology*. Plenum Press, New York, 491 pp.
- Juste, J.B., C. Ibanez, and A. Machordom. 1997. Evolutionary relationships among the african fruit bats: *Rousettus egyptiacus*, *R. angolensis*, and *Myonycteris*. *J. Mammal.*, 78: 766-774.
- Kingdon, J. 1974. *East African mammals: an atlas of evolution in Africa*. IIA: insectivores and bats. Academic Press. London, 446 pp.
- LaBarbara, M. 1989. Analyzing body size as a factor in ecology and evolution. *Annu. Rev. Ecol. Syst.*, 20: 97-117.

- Lay, D.W., and T. O'Neil. 1942. Muskrats on the Texas coast. *J. Wild. Manage.* 6: 301-312.
- Leutenegger, W. 1978. Scaling of sexual dimorphism in body size and breeding system in primates. *Nature*, 272: 610-611.
- Leutenegger, W., and J. Cheverud. 1985. Sexual dimorphism in primates. The effects of size. In, Jungers, W.J. (ed.) *Size and Scaling in Primate Biology*. Plenum Press, New York: 33-60.
- Lowich, J.E., and J.W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. *Growth, Devel. Aging*, 56: 269-281.
- Lowery, G.H.. Jr. 1974. *The mammals of Louisiana and adjacent waters*. Louisiana State University Press. Baton Rouge, 565 pp.
- Lynch, J.J., T. O'Neil, and D.W. Lay. 1947. Management significance of damage by geese and muskrats to Gulf Coast marshes. *J. Wild. Manage.*, 11: SO-76.
- Lynch, J.M. and T.J. Hayden. 1995. Genetic influences on cranial form: variation among ranch and feral American mink *Mustela vison* (Mammalia: Mustelidae). *Biol. J. Linnean Soc.*, 55: 293-307.
- Lynch, J.M., C.G. Wood. and S.A. Luboga. 1996a. Geometric morphometrics in primatology: craniofacial variation in *Homo sapiens* and *Pan troglodytes*. *Folia Primatol.*, 67: 15-39.
- Lynch, J.M., J.W.H. Conroy, A.C. Kitchenner, D.J. Jefferies, and T.J. Hayden. 1996b. Variation in cranial form and sexual dimorphism among five European populations of the otter *Lutra lutra* (L.). *J. Zool.*, London, 238: 81-96.
- Marcus, L.F., and M. Corti. 1996. Overview of the new, or geometric morphometrics. In: L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor, and D.E. Slice (eds.). *Advances in Morphometrics NATO ASI Series vol. 284*, Plenum Press, New York: 1-13.
- Marcus, L.F., E. Bello and A. Garcia-Valdecasas. 1993. Contributions to Morphometrics. *Monografias del Museo Nacional de Ciencias Naturales*. 8, Madrid, 264 pp.
- Marcus, L.F., M. Corti, A. Loy, G.J.P. Naylor, and D.E. Slice (eds.). 1996. *Advances in Morphometrics NATO ASI Series vol. 284*, Plenum Press, New York, 587 pp.
- Marshall, A.G., and A.N. McWilliam. 1982. Ecological observations on epoinophorine fruit-bats (Megachiroptera) in West African savanna woodland. *J. Zool.*, London. 198: 53-67.
- Monteiro. L.R., 1999. Multivariate regression models and geometric morphometrics: the search for casual factors in the analysis of shape. *Syst. Biol.* 48: 192-199.
- Myers, P. 1978. Sexual dimorphism in size of vespertilionid bats. *Am. Nat.* 112: 701-711.
- O'Neil, T. 1949. *The muskrat in Louisiana coastal marshes*. Louisiana Dept. Wildlife Fisheries, New Orleans. 152 pp.
- Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.*, 111: 917-938.
- Rensch, B. 1960. *Evolution above the Species Level*. Columbia Univ. Press. New York, 419 pp.
- Rohlf, F.J. 1993. Relative warp analysis and an example of its application to mosquito wings. In: Marcus, L.F., E. Bello, and A. Garcia-Valdecasas (eds.), *Contributions to Morphometrics. Monografias del Museo Nacional de Ciencias Naturales*. 8. Madrid: 131-159.
- Rohlf, F.J. 1998. On applications of geometric morphometrics to studies of ontogeny and phylogeny. *Syst. Biol.* 47: 147-158.
- Rohlf, F.J., and F.L. Bookstein. 1987. A comment on shearing as a method of "size correction". *Syst. Zool.* 36: 356-367.
- Rohlf, F.J., and L.F. Marcus. 1993. A revolution in morphometrics. *Trends Ecol. Evol.*, 8: 129-132.

- Rohlf, F.J., and D.E. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst. Zool.* 39: 40-59.
- Rohlf, F.J., A. Loy, and M. Corti. 1996. Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) using partial-warp scores. *Syst. Biol.* 45: 344-362.
- Shine, R. 1994. Sexual size dimorphism in snakes revisited. *Copeia*, 1994: 326-346.
- Short, R.V., and E. Balaban. 1994. *The Differences Between the Sexes*. Cambridge Univ. Press, Cambridge, 479 pp.
- Soderquist, T.R. 1995. Ontogeny of sexual dimorphism in size among polytocous mammals: tests of two carnivorous marsupials. *J. Mammal.*, 76: 376-390.
- Sokal, R.R., and F.J. Rohlf. 1995. *Biometry*. 3rd edition, W.H. Freeman and Company, New York, 887 pp.
- Sullivan, R.M. and T.L. Best. 1997. Effects of environmental on phenotypic variation and sexual dimorphism in *Dipodomys simulans* (Rodentia: Heteromyidae). *J. Mammal.*, 78: 798-810.
- Weckerly, F.W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.*, 79: 33-52.
- Wickler, W., and U. Seibt. 1976. Field studies on the African fruit bat *Epomophorus wahlbergi* (Sundevall), with special reference to male calling. *Zeit. Saugtierk.*, 40: 345-376.
- Wiig, Q. 1986. Sexual dimorphism in the skull of minks *Mustela vison*, badgers *Meles meles* and otters *Lutra lutra*. *Zool. J. Linn. Soc.*, 87: 163-179.
- Willig, M.R. 1983. Composition, microgeographic variation, and sexual dimorphism in Caatingas and Cerrado bat communities from northeastern Brazil. *Bull. Carnegie Mus. Nat. Hist.*, 23:1-131.
- Willig, M.R., and R.R. Hollander. 1995. Secondary sexual dimorphism and phylogenetic constraints in bats: a multivariate approach. *J. Mammal.*, 76: 981-992.
- Wood, C.G., and J.M. Lynch. 1996. Sexual dimorphism in the craniofacial skeleton of modern humans. In: L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor, and D.E. Slice (eds.), *Advances in Morphometrics NATO ASI Series vol. 284*, Plenum Press, New York: 407-414.
- Zelditch, M.L., W.L. Fink, D.L. Swiderski, and B.L. Lundrigan. 1998. On applications of geometric morphometrics to studies of ontogeny and phylogeny: a reply to Rohlf. *Syst. Biol.*, 47: 159-167.
- Zeller, V.U. 1984. Zur Kenntnis des Stimmapparates der epauletten flughunde (Epomophorini, Pteropodidae, Megachiroptera). *Zeit. Saugtierk.*, 49 :205-225.