Osteological Variation within the Baldwin County, Georgia, Population of Didelphis virginiana

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Osteological Variation within the Baldwin County, Georgia, Population of *Didelphis virginiana*

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Abstract - We analyzed intraspecific and sexually dimorphic osteological variation within the Baldwin County, GA, population of *Didelphis virginiana* (Virginia opossum). Where possible, 20 measurements (11 cranial/mandibular and 9 postcranial) were obtained from each of 59 road-killed adult opossums (47 males, 12 females). Although range overlaps exist between the sexes for all measurements, males are significantly larger ($P \leq 0.05$) for the following characteristics: greatest length of skull, condylobasal length, basal length, postpalatal length, nasal length, bicanine width, zygomatic breadth, length of mandible, scapula length, humerus length, radius length, femur length, and fibula length. Males exhibit significantly less ($P \leq 0.05$) variation in mandibular tooth row length and significantly greater ($P \leq 0.05$) variation in scapula length and fibula length. Intraspecific variation ranges from 14–54% for cranial/mandibular and 29–73% for postcranial measurements. Sexual dimorphism is most pronounced in cranial/mandibular dimensions. Comparisons with multi-state samples indicate that the continent-wide population of the Virginia opossum is very similar in terms of osteological dimension. The combination of low variation index and nonsignificant difference between the sexes in mandibular tooth row length suggests that this measure may be useful for distinguishing fossil opossum species.

Introduction

Although there have been several studies on *Didelphis virginiana* Kerr 1792 (Virginia opossum) collected throughout Middle and North America (e.g., Allen 1901, Coues 1872, Elftman 1929, Gardner 1973, Jenkins 1971, Jenkins and Weis 1979, Lowrance 1949, Petrides 1949, Tague 2003, White 1989), little is written about the variability of skeletal characteristics within a localized population. Allen (1901) analyzed skeletal and external characteristics of approximately 350 pelts and 100 opossum skulls (*D. virginiana* included in sample) collected from across the United States and Middle America. Lowrance (1949, 1957) assessed developmental characteristics, maturation rate, and correlation of linear postcranial dimensions to skull weight and length using 150 specimens collected from eastern Kansas. Petrides (1949) outlined a method for age determination using 49 carcasses collected from a 10-county area in Ohio. Gardner (1973) studied the systematics of the Virginia opossum and *D. marsupialis* Linnaeus (southern opossum) using 2800+ specimens

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from Middle and North America. Most recently, Tague (2003), using 95 specimens collected from a 12-state geographic area within the United States (e.g., Florida, Texas, Illinois, Pennsylvania), addressed intraspecific pelvic variability.

The analysis of osteological variation in the Virginia opossum is complicated by delayed epiphyseal fusion and closure of cranial sutures. Allen (1901) observed that the degree of sagittal and occipital crest development was age-related and concluded that variation between specimens from different localities was likely due to age rather than discernable geographic differences. Washburn (1946) determined that epiphyseal fusion was anatomically regionally sequential, progressing from the girdle to the elbow, feet, wrist, hip, ankle, and then knee. Lowrance (1949) documented the same pattern in a different sample and concluded that the determination of skeletal maturity must be based on tooth eruption. Petrides (1949) also found that sagittal crest development and epiphyseal closure were not as useful in age determination when compared to the sequence of molar eruption. Gardner (1973) reanalyzed Allen's sample along with an additional 2700+ specimens and concurred that cranial development occurred throughout life and skull dimensions are linked to the nutritional richness of the local environment. He also noted that skulls exhibit high individual variation correlated with age and sex, and tooth wear in adults may be related to abrasiveness of diet rather than age. More recently, Tague (2003) pointed out that delayed epiphyseal fusion and differential growth rates for males and females could greatly influence measurements of sexual dimorphism.

Sexual dimorphism and intraspecific variation in a species can provide valuable information in both a paleontological and ecological context (Clutton-Brock et al. 1977, Ralls 1977, Weckerly 1998, Willig and Hollander 1995). Quantification of variation within a modern mammalian population provides a baseline for the analysis of extinct species. Also, osteological sexual dimorphism within an extant population may have multiple implications concerning the social and ecological habits of the species. A general conclusion for the presence of sexual dimorphism is that differences in size could indicate an intense level of mating competition; larger males being dominant to smaller and thus gaining mating privileges. In the Virginia opossum, males are aggressive to one another, and violent interactions may end in death of the weaker (Gardner 1982, McManus 1974). Alternately, a difference in size of certain skeletal characteristics between males and females could reflect different ecological habits for the two sexes or, as indicated for this species, differential growth rates following sexual maturity (Gardner 1973, 1982).

The Virginia opossum provides an excellent subject for scientific research, mainly due to large population numbers and ease of collection. It is a relatively ubiquitous species found in large population numbers within the

eastern and extreme western portions of the United States. Current classification includes four subspecies: *D. v. virginiana* Kerr, *D. v. pigra* Bangs, *D. v. californica* Bennett, and *D. v. yucatanensis* Allen (Gardner and Sunquist 2003). Little has been written concerning the specific skeletal characteristics of the Georgia population of the Virginia opossum (Golley 1962). In the previously mentioned morphological studies, only 8 of approximately 1350 US specimens were collected in Georgia (Allen 1901, Gardner 1973, Lowrance 1949, Tague 2003). The present study explored the intraspecific and intersexual variation within a localized population of the Virginia opossum from the Georgia Piedmont. Variation within the localized sample was compared to published samples that included specimens from much larger geographical areas.

Materials and Methods

The 59 specimens (47 males, 12 females) of the Virginia opossum analyzed in this study were collected as road-kill within Baldwin County, central Georgia Piedmont, in the winter months (January–March) of 2002 and 2004. The specimens were tagged, sexed, weighed, and skeletonized using dermestid beetles. Baldwin County lies on the border of the range of two subspecies, *D. v. virginiana* and *D. v. pigra* (Golley 1962). Based on characteristics given by Gardner (1973), the specimens analyzed in this study belong to *D. v. pigra*. However, Tague (2003) found no statistical differences in osteological characteristics between the two subspecies, so the issue of some specimens being *D. v. virginiana* rather than *D. v. pigra* should have no bearing on this analysis.

Due to the way in which these animals died, each specimen contained numerous broken bones. When possible, 11 cranial/mandibular and 9 postcranial measurements were obtained from each skeleton. The extent of skeletal damage in conjunction with the initial unbalanced sample created large disparities between the numbers of males and females for some measurements. The cranial/mandibular measurements (from Martin et al. 2001) include greatest length of skull (GLS), condylobasal length (CL), basal length (BL), postpalatal length (PL), nasal length (NL), bicanine width (BW), zygomatic breadth (ZB), postorbital constriction (PC), maxillary tooth row length (P2–M4: MxTR), length of mandible (LM), and mandibular tooth row length (p2–m4: MnTR). The postcranial measurements (greatest length unless otherwise noted) include scapula length (SL), humerus length (HL, head to intercondylar sulcus), radius length (RL), ulna length (UL), epipubis length (EL), pelvis length (LP), femur length (FL, trochanteric sulcus to intercondylar sulcus), tibia length (TL), and fibula length (FiL). Chicago Brand digital calipers accurate to 0.01 millimeters were used to take measurements. All skeletons are housed in the Georgia College and State University Recent Mammal Collection (GCM).

Each specimen was placed in an approximate age group based upon stage of tooth eruption and was considered an adult at 10–11 months (Gardner 1973, Tague 2003). The assigned groups were derived from molar eruption as described by Petrides (1949). All of the analyzed specimens exhibited degrees of tooth eruption consistent with those of mature individuals of age classes 5 and 6 of Gardner (1973). For each measurement within both sexes, the mean, range, standard deviation, and coefficient of variation were calculated. An intraspecific variation index (VI = largest individual measurement ÷ smallest individual measurement) was determined for each character. Variation between the sexes was computed using the dimorphism ratio (DR = male mean value ÷ female mean value). The significance of the difference between each osteological character's mean male and female value was determined using the Student's t-test and considered significant at the $P \leq 0.05$ level. Levene's test was used to analyze the significance ($P \leq 0.05$) of the relative variation between sexes (Van Valen 2005) for each osteological character (MnTR,

Table 1. Summary of cranial osteological measurements (mm) and statistics for *Didelphis virginiana* (Virginia opossum) from Baldwin County, GA. GLS = greatest length of skull, CL = condylobasal length, BL = basal length, PL = postpalatal length, NL = nasal length, BW = bicanine width, ZB = zygomatic breadth, PC = postorbital constriction, MxTR = maxillary tooth row length, LM = length of mandible, MnTR = mandibular tooth row length, SD = standard deviation, CV = coefficient of variation, VI = largest individual measurement ÷ smallest individual measurement, and DR = male mean value ÷ female mean value. *P*-value pertains to Student's t-test for comparison of means.

Character	Sex	Mean	Range	N	SD	CV	VI	DR	P
GLS	M	126.99	101.11–139.17	16	11.42	8.99	1.38	1.17	<0.001
	F	109.00	104.07–112.65	5	3.58	3.28			
CL	M	121.98	100.52–132.84	15	9.98	8.18	1.32	1.14	<0.001
	F	106.94	100.57–111.73	5	4.25	3.97			
BL	M	117.94	95.58–132.15	15	10.61	9.00	1.39	1.15	<0.001
	F	102.21	95.29–106.49	5	4.35	4.26			
PL	M	47.02	37.25–52.02	15	4.96	10.55	1.48	1.20	<0.001
	F	39.26	35.06–41.24	5	2.50	6.37			
NL	M	58.11	47.87–64.50	23	4.57	7.86	1.35	1.11	<0.001
	F	52.58	51.13–54.49	6	1.56	2.97			
BW	M	10.95	8.80–13.52	23	1.02	9.32	1.54	1.09	0.01
	F	10.07	9.71–10.57	4	0.39	3.87			
ZB	M	68.45	57.45–74.81	14	5.05	7.38	1.42	1.19	0.003
	F	57.34	52.69–61.99	4	3.88	6.77			
PC	M	11.82	11.23–12.84	20	0.43	3.64	1.16	0.99	0.826
	F	11.89	11.06–12.75	5	0.65	5.47			
MxTR	M	34.22	28.53–36.98	20	2.00	5.84	1.30	1.02	0.347
	F	33.42	32.71–36.22	6	1.66	4.97			
LM	M	100.30	84.24–111.34	28	7.67	7.65	1.34	1.15	<0.001
	F	87.16	82.91–91.39	6	3.99	4.58			
MnTR	M	37.21	34.53–39.35	41	1.06	2.85	1.14	1.01	0.479
	F	36.84	35.44–39.19	10	1.47	3.99			

SL, HL, RL, UL, FL, TL, and FiL) with at least 8 measurements for both sexes (Schultz 1985).

Results

Summaries of the cranial/mandibular and postcranial measurements and statistical values are presented in Tables 1 and 2. Although the ranges overlap for all the cranial measurements, males average larger in all characters except PC. GLS, CL, BL, PL, NL, BW, ZB, and LM are significantly larger in males. The average male cranial coefficient of variation (CV) (7.38) exceeds the average female value (4.59). Males exhibit greater CVs for GLS, CL, BL, PL, NL, BW, ZB, MxTR, and LM. Females show greater variability in PC and MnTR, of which the MnTR relative variation is significantly greater. Intraspecific variation (VI) ranges from 1.14 (MnTR) to 1.54 (BW). The range of sexual dimorphism (DR) varies from 0.99 (PC) to 1.20 (PL).

Overlapping ranges also exist for all postcranial measurements. All mean male values are larger than mean female values. The SL, HL, RL, LP, FL, TL, and FiL measurements are significantly larger in males. The average male postcranial CV (8.22) exceeds the female's (7.31). Males exhibit greater relative variation in SL, HL, LP, FL, TL, and FiL, with SL and FiL variability being significantly greater. Females exhibit larger CVs for RL, UL, and EL. Intraspecific variation (VI) ranges from 1.29 (LP) to

Table 2. Summary of postcranial osteological measurements (mm) and statistics for *Didelphis virginiana* (Virginia opossum) from Baldwin County, Georgia. SL = scapula length; HL = humerus length; RL = radius length; UL = ulna length; EL = epipubis length; LP = pelvis length; FL = femur length; TL = tibia length; FiL = fibula length. See Table 1 for additional abbreviations.

Character	Sex	Mean	Range	N	SD	CV	VI	DR	P
SL	M	67.73	55.43–79.08	32	6.52	9.63	1.43	1.13	<0.001
	F	59.98	55.79–62.32	9	3.04	5.06			
HL	M	70.50	59.05–79.59	43	5.36	7.60	1.36	1.09	<0.001
	F	64.69	58.50–71.37	11	3.34	5.16			
RL	M	87.22	69.06–98.11	41	6.44	7.38	1.45	1.10	0.008
	F	79.12	67.76–88.71	8	6.32	7.99			
UL	M	71.25	56.75–80.56	40	5.16	7.24	1.42	1.04	0.271
	F	68.67	59.08–73.73	10	6.61	9.63			
EL	M	40.22	31.45–49.30	19	4.78	11.88	1.73	1.03	0.614
	F	38.86	28.57–46.06	7	6.21	15.98			
LP	M	87.73	76.49–98.72	23	5.60	6.38	1.29	1.06	0.031
	F	83.14	78.62–87.73	6	3.61	4.34			
FL	M	82.64	67.95–98.71	43	6.81	8.24	1.45	1.07	0.007
	F	77.31	70.26–84.24	10	4.47	5.78			
TL	M	88.58	71.93–101.75	41	6.6	7.45	1.43	1.06	0.018
	F	83.48	71.15–89.54	11	5.57	6.67			
FiL	M	84.94	72.50–98.39	40	6.97	8.21	1.36	1.06	0.007
	F	79.91	74.95–86.64	10	4.15	5.19			

1.73 (EL). The range of sexual dimorphism (DR) varies from 1.03 (EL) to 1.13 (SL).

Discussion

Although variability of the Virginia opossum skeleton has been documented in previous analyses (Coues 1872, Gardner 1973, Lowrance 1949, Tague 2003), these studies have included specimens from large geographic regions. In comparison to the regional, multi-state sample of Tague (2003), the Baldwin County sample exhibits nearly identical male and female mean values for GLS, ZB, and LM. For males, CVs are higher than those of Tague (2003) for GLS and LM. For females, CVs are lower for GLS, ZB, and LM. When compared to the Middle American sample of Gardner (1973), male and female GLS, CL, ZB, PC, and LM values average larger in the Baldwin County sample, perhaps reflecting the differences between the subspecies *D. v. pigra* and *D. v. californica*. For males, CVs are higher than those of Gardner (1973) for GLS and LM. For females, CVs are lower for GLS and LM. The VI for GLS, CL, ZB, PC, and LM in the Baldwin County sample averages 15.5% (13–19%) less than that for comparably aged specimens within Gardner's (1973) Middle American sample. Maximum and minimum values are not provided in Tague's (2003) analysis, so VI values could not be compared.

Coues (1872) noted the sexually dimorphic nature of the upper canines in the Virginia opossum. Allen (1901) also noted the differences in canines and described the female skull as generally narrower and more slender. Gardner (1982) quantified the canine sexual dimorphism and proposed a method of sexing skulls using canine dimensions and molar eruption and wear. The present study illuminates additional dimorphic cranial measurements. The Baldwin County sample displays a range of sexual dimorphism (DR) from 1.09 to 1.20 for the cranial characters found to be significantly different between the sexes. The DR values for GLS, CL, ZB, and LM average 4.3% greater in comparison to the Middle American sample presented by Gardner (1973). Also, DR values for GLS and LM are 3.5% and 3.6% greater, respectively, in comparison to the eastern US sample of Tague (2003). However, DR values for ZB are identical between the Baldwin County sample and Tague's (2003) regional sample.

In comparison to the multi-state sample of Tague (2003), the Baldwin County sample exhibits humeral and femoral mean values that are 5.1% and 4.7% smaller for males and 5.0% and 5.4% smaller for females. For males, CVs are higher than those of Tague (2003) for HL and FL. For females, CVs are lower for HL and FL. Comparable measurements are not available for the Middle American sample of Gardner (1973). Postcranial sexual dimorphism is not as well documented as that for cranial characteristics. Lowrance (1957) noted sexual dimorphism in epipubis length in

the Kansas sample. Also, Tague (2003) found that males were significantly larger for 14 of 16 pelvic measurements. The DR values for HL and FL are virtually identical for the Baldwin County sample and Tague's (2003) regional sample.

In the Baldwin County sample, MnTR exhibits the smallest VI values. MnTR also has a DR of 1.01. The relative constancy of MnTR is interesting given the dimorphism noted in the other cranial measurements. The relative lack of inter- and intra-sexual variation is likely correlated to the similar feeding habits of the sexes (Gardner 1982) and the fact that the mandibular tooth row is fully developed at sexual maturity and does not lengthen as the animal continues to mature physically. The low VI and DR for the MnTR suggest that it may be the most useful skeletal character for distinguishing fossil opossum species.

The sexually dimorphic measurements obtained in this study suggest that the Baldwin County sample contains males with larger cranial (GLS, CL, BL, PL, NL, and LM) and shoulder (SL and HL) dimensions. The larger head and shoulders in males could indicate a functional adaptation correlated to male-male competition for mating privileges (Allen 1901, Gardner 1982, McManus 1974). As mentioned previously, parts of the Virginia opossum skeleton have been shown to increase in size throughout life (Gardner 1973, Lowrance 1949, Tague 2003). The rate of development appears to slow significantly at sexual maturity, with the females exhibiting a lower rate of growth compared to males (Gardner 1973). Developmental heterochrony would explain the observed sexual dimorphism; however, the inability to age specimens beyond sexual maturity complicates the analysis.

The present study appears to show that more males than females (47 males: 12 females) are being killed on Baldwin County roads during the winter months, suggesting that males are more active and wider ranging than females during this time of year. Allen et al. (1985) found that on the Georgia Piedmont, male Virginia opossums are significantly wider ranging than females. Gardner (1982) and Ryser (1995) noted that males are more active during the winter resulting in greater highway mortality. Ryser (1995) found that in Florida, female home-range size was approximately half that of males, and males tend to travel farther than females as a result of natal dispersal, mate searching, and the need for increased food acquisition related to larger body mass. The peak of the breeding season for Virginia opossums in Georgia is early February (Golley 1962). It is likely that the males in Baldwin County were actively seeking mating opportunities during the winter months of 2002 and 2004, increasing the probability of death on roadways.

Within the Baldwin County population of the Virginia opossum, males are generally larger and exhibit greater CVs than females (however, only 2 of 8 measurements are considered statistically significant using

Levene's test). For the characteristics analyzed, this sample averages slightly larger than the Middle American sample yet shows 15% less osteological variability (VI), supporting the hypothesis that variation would be greater in a geographically expansive sample of mixed populations when compared to a local sample. Alternately, Gardner's (1973) Middle American sample (77 males, 91 females) is larger than the Baldwin County sample and the observed differences in osteological variability may be a function of sample size rather than geographic area. Also, due to the presence of different subspecies, the possibility arises that differences noted here are due to previously unreported subspecific differences. The Baldwin County sample is identical for cranial and, on average, 5.0% smaller for humeral and femoral measurements in comparison to a regional US sample. However, the comparatively higher male CVs and lower female CVs indicate the need for further exploration. The Baldwin County sample averages 2.4% greater for cranial DR and is nearly identical for postcranial DR in comparison to the regional sample. The differences between these two samples may reflect the tendency to collect and prepare large specimens for museum collections (source of specimens for regional sample), potentially muting the recognition of sexual dimorphism that may exist within the species. Alternately, the under-representation of females in the Baldwin County sample may have significantly influenced the DR values for this sample. Recognizing these differences, this study suggests that the continent-wide population of the Virginia opossum is quite similar in osteological dimension.

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