Is there a field proxy for brain size in great-tailed grackles (*Quiscalus mexicanus*)?

Corina Logan, Christin Palmstrom

There is an increasing need to validate and collect data approximating brain size on individuals in the field to understand what evolutionary factors drive brain size variation within and across species. We investigated whether we could accurately estimate endocranial volume (a proxy for brain size) as measured by computerized tomography (CT) scans, using external skull measurements and/or by filling skulls with beads and pouring them out into a graduated cylinder for male and female great-tailed grackles. We found that while females had much stronger correlations than males, estimations of endocranial volume from external skull measurements or beads did not correlate with CT volumes at a standard that surpassed our strict criteria. We found no accuracy in the ability of external skull measures to predict CT volumes because prediction intervals from data points overlapped extensively. We conclude that we are unable to detect individual differences in endocranial volume using external skull measurements. These results emphasize the importance of validating and explicitly quantifying the predictive accuracy of brain size proxies for each species, and each sex, under consideration.

2   Is there a field proxy for brain size in great-tailed grackles (*Quiscalus mexicanus*)?

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12   **Abstract**

13   There is an increasing need to validate and collect data approximating brain size on individuals in the

14   field to understand what evolutionary factors drive brain size variation within and across species. We

15   investigated whether we could accurately estimate endocranial volume (a proxy for brain size) as

16   measured by computerized tomography (CT) scans, using external skull measurements and/or by

17   filling skulls with beads and pouring them out into a graduated cylinder for male and female great-

18   tailed grackles. We found that while females had much stronger correlations than males, estimations of

19   endocranial volume from external skull measurements or beads did not correlate with CT volumes at a

20   standard that surpassed our strict criteria. We found no accuracy in the ability of external skull

21   measures to predict CT volumes because prediction intervals from data points overlapped extensively.

22   We conclude that we are unable to detect individual differences in endocranial volume using external

23   skull measurements. These results emphasize the importance of validating and explicitly quantifying

24   the predictive accuracy of brain size proxies for each species, and each sex, under consideration.

Introduction

While comparing brain sizes across species has led to a greater understanding of the evolutionary factors correlated with brain size variation at a broad scale (e.g., Iwaniuk & Nelson 2003, Sakai et al. 2011, Sol et al. 2005), little is known about the within species causes and consequences of variation in brain sizes (see Gonda et al. 2013, Thornton & Lukas 2012). Additionally, the accuracy of brain size proxies, which are frequently used in such comparisons, are not often validated. Therefore, the accuracy of these measures and how they compare to measures in other species is questionable (Healy & Rowe 2007). Intraspecies brain size comparisons are rare perhaps due to the difficulty of obtaining data on a number of factors (e.g., biometric measurements, reproductive success, dominance rank, position in the social network, cognitive abilities, etc.) for the same individuals. Acquiring such data is key for understanding what contributes to the evolution of brain size among individuals, as well as across species (Gonda et al. 2013, Logan & Clutton-Brock 2013, Thornton & Lukas 2012).

We investigated whether endocranial volume, a proxy for brain size (Iwaniuk & Nelson 2002), can be approximated using measurements of the external skull in great-tailed grackles (*Quiscalus mexicanus*, JF Gmelin, 1788). Finding such a proxy would greatly ease the collection of data on brain sizes since head measurements can be taken on live birds, thus allowing for correlations with any number of other factors on which data are gathered on this species in the field and the lab. Great-tailed grackle body sizes are sexually dimorphic (Johnson et al. 2000), therefore we expect sex differences in brain sizes and we investigate proxies for each sex independently. We used endocranial volumes calculated from computerized tomography (CT) scans to represent actual endocranial volumes since this measure is the most precise. We compared CT volumes to skull length, width, and height measurements to determine whether the correlation between these two methods and the accuracy of external measures in predicting CT volumes warrants their use as a proxy for endocranial volume. We also evaluated the bead method of generating endocranial volume, where glass beads are poured into

50   the skull and then out into a graduated cylinder, to increase the value of our research by determining

51   whether this widely used method also accurately predicts actual endocranial volume as estimated by

52   CT scans in this species.

53

54   **Methods**

55   *Specimens*

56   We collected data from February through September 2014 on 40 great-tailed grackle skulls (Table S1),

57   20 female and 20 male (some analyses have 19 males because on one of their skulls the bill was broken

58   off, thus we could not acquire its skull length measurement), obtained from the Museum of

59   Southwestern Biology (n=24, Albuquerque, NM), the Ornithology Division of the University of

60   Kansas (KU) Biodiversity Institute (n=15, Lawrence, KS), and the Santa Barbara Museum of Natural

61   History (n=1, Santa Barbara, CA). Skulls of unknown age were aged by Andy Johnson if they were

62   from the Museum of Southwestern Biology or by us if they were from KU. Skulls were aged using the

63   percentage of ossification to classify each as adult (100% ossified unless it was collected in February-

64   May because this would mark the start of that individual's first breeding season after having hatched

65   June-August in the previous year) or immature (<100% ossified when collected September-December

66   indicating it had hatched that year; del Hoyo et al. 1992, Winker 2000, Pyle 1997).

67

68   *Collecting endocranial volume measurements*

69   Linear measurements: Linear measurements of skulls were collected using calipers as would be

70   measured on a live bird in the field. We recorded skull length from the base of the bill to the back of

71   the skull along the occipital crest (Figure 1), height from the posterior edge of the foramen magnum to

72   the top of the skull along the frontal region (Figure 2), and width at the widest part of the brain case

73   along the squamosal bones (Figures 3). All measurements were taken to the nearest 0.1mm. We

74   estimated endocranial volume using a number of volumetric shapes and data transformations to

75   determine which best correlated with actual endocranial volumes from CT scans. The volumetric

76   shapes included were: cube (Length x Width x Height), sphere ($\frac{4}{3}\pi r^3$, where r=$\frac{1}{2}$L or $\frac{1}{2}$W or $\frac{1}{2}$H),

77   ellipsoid ($\frac{4}{3}\pi abc$, where a=$\frac{1}{2}$L, b=$\frac{1}{2}$W, c=$\frac{1}{2}$H), and cone/pyramid ($\frac{1}{3}$bh, where b=W, h=H). We

78   included log, natural log, and exponential transformations of the data, and also allowed polynomial

79   terms.

80

81   CT scans: Skulls were CT scanned at the Pueblo Radiology Medical Group in Santa Barbara,

82   California using a Siemans 16-slice Somatom Sensation 16 (1mm slices, 100Kv, 150MAs, 380mm

83   FOV, soft tissue window, analyzed with bone algorithm on). Endocranial volume (cm^3) was calculated

84   using the DICOM viewer OsiriX v5.8.5 (32-bit, Pixmeo SARL, Switzerland; Figure 4) for 1x1mm

85   slices (regular) and for 1x1mm slices that were taken with the CT scanner bed moved 0.5mm forward

86   (offset), using the average endocranial volume ($\frac{regular + offset}{2}$) in analyses. The offset was

87   added to increase the precision of the endocranial volume measurements since grackle craniums are

88   small (approximately 20mm in length), resulting in about 20 slices per scan (one slice every 1mm).

89   The offset allowed us to measure more area (one slice every 0.5mm) by increasing the number of slices

90   to approximately 40 per skull.

91

92   Beads: Endocranial volume was measured by pouring 1mm diameter glass beads (BioSpec Products,

93   catalog number 11079110) into the cranium through the foramen magnum until full. The skull was

94   repeatedly shaken to settle the beads and then filled again until the beads reached the posterior foramen

95 magnum without falling out (Figure 5). The volume was calculated by pouring the beads out of the

96 skull and into a graduated cylinder (5ml in 0.1ml graduations, World Precision Instruments, Inc.,

97 catalog number CG-0160; note that 1ml=1cm^3). In cross-species comparisons, there is mixed evidence

98 about whether pouring the beads into a graduated cylinder introduces error when compared with

99 pouring the beads onto a scale and converting their mass into volume (4% difference: Miller 1997, 0%

100 difference: Isler et al. 2008). However, addressing this issue in an intraspecies study means ensuring

101 that the same amount of error, if any, is introduced for each skull, thus making sure that the relative

102 differences between skulls remains unaffected. This measurement error was controlled in our study

103 because we used the same methods on every skull.

104

105 *Statistical analyses*

106 The female and male data (analyzed separately) were normally distributed (Anderson Darling

107 normality test p>0.05).

108   We used generalized linear models (GLMs) to determine how well linear and bead

109 measurements correlated with volumes from CT scans, while examining whether the year the skull was

110 collected improved the model fit. GLMs were carried out in R v3.0.2 (R Core Team 2014) using the

111 MCMCglmm function (MCMCglmm package, Hadfield 2010), while applying the dredge function

112 (MuMIn package, Barton 2012) to select the top model using the Akaike weight (Akaike 1981).

113 Females and males were evaluated in separate models. Full models included endocranial volumes from

114 CT scans as the response variable with the following explanatory variables: volume of a cube or sphere

115 or ellipsoid or cone + age * year collected, or skull length + skull width + skull height + age * year

116 collected. GLMs were conducted on the top model for each sex to explore whether the adjusted

117 coefficient of determination (adjusted r^2) improved by transforming the explanatory variable

118 endocranial volume proxy in the following ways: squared, cubed, quadratic, exponential, square root,

119   log, log base 10, and a polynomial with a degree of two or three. Of these, the model with the highest

120   adjusted r^2 was chosen as the final top model for that sex and included in the results below.

121   Since we want to *predict* CT volumes from linear measures, we validated whether this was

122   possible by generating prediction intervals: the interval in which new observations would occur with

123   95% probability. We applied the predict function in the MCMCglmm package to the top model for

124   each sex and evaluated whether fitted values (predicted CT volumes) had credible intervals small

125   enough such that there was little to no overlap with other fitted values, thus allowing the discrimination

126   of individual differences.

127

128   *Data availability*

129   The data from skull measurements and intraobserver reliability, and the R code are available at the knb

130   repository (*will be posted soon*).

131

132   **Results**

133   *Intraobserver reliability*

134   CP had a very high degree of intraobserver reliability for volume measurements when data included

135   both sexes (Pearson's product moment correlation: linear method r^2=0.86, p=0.0003, n=9; bead method

136   r^2=0.90, p=0.0001, n=9; CT scans r^2=0.94, p=0.005, n=5) and a substantial amount of reliability for

137   individual linear measurements (skull height r^2=0.71, p=0.004, n=9; skull width r^2=0.69, p=0.003, n=9;

138   skull length r^2=0.83, p=0.001, n=9; Landis & Koch 1977). Intraobserver reliability was also very high

139   when evaluating males independently, though the sample size for the CT volumes was too small to be

140   significantly correlated (linear method r^2=0.84, p=0.02, n=7; bead method r^2=0.89, p=0.008, n=7; CT

141   scans r^2=0.96, p=0.12, n=3). Female data could not be analyzed separately due to the small sample size

142   (n=2 for CT scan volumes, n=1 for other measures). We can rule out that males and females were

143   measured with different levels of accuracy, which might have caused the poor correlations between

144   bead volumes/linear measures and CT volumes for males in the analyses below. Male skulls had

145   narrower length and width ranges for individual linear measurements than females, making accuracy

146   more difficult in males (see data at the knb repository). Therefore, it is likely that female intraobserver

147   reliability would be at least as high for female skulls as it was for male skulls.

148

149   *Correlations between methods*

150   Volumes from CT scans were poorly (for males) to moderately (for females) correlated with volumes

151   from linear measurements, with the sphere being the best fitting shape for both sexes according to the

152   Akaike weights (the radius was based on skull width for males and skull height for females). The top

153   female model showed a positive relationship between CT volumes and volumes from using the skull

154   height as the radius for a sphere, volumes were larger for immatures than for adults, and volumes

155   slightly   decreased   over   the   years   collected   (Akaike   weight=0.60,

156    $y = 0.00002 \times VolumeSphere + 1.10 \times Age - 0.007 \times Year + 1.44$, adjusted r^2=0.80, p<0.0001,

157   model 1; Figure 6a). The top male model showed a positive correlation between CT volumes and

158   volumes using a quadratic polynomial of the skull width as the radius for a sphere, volumes were

159   slightly larger for immatures than for adults, and volumes decreased slightly over the years collected

160   (Akaike   weight=0.26,

161    $y = 0.47 \times VolumeSphere + 0.19 \times VolumeSphere^2 + 0.12 \times Age - 0.003 \times Year + 5.25$,

162   adjusted r^2=0.39, p=0.02, model 2; Figure 6b). Transformations of the explanatory volume variables or

163   substituting volume for individual linear measurements (length, width, height, or some combination of

164   these) did not improve the adjusted r^2 for females.

165   Volumes from CT scans were only moderately positively correlated with volumes from the

166   bead method for both sexes: the top female model showed that endocranial volumes decreased slightly

167   over time (Akaike weight=0.74, adjusted r^2=0.77, p<0.0001,

168     $y = 0.37 \times VolumeBead - 0.0005 \times Year + 11.24$, model 3; Figure 7a), while the top male model

169   included age, with immatures having smaller volumes than adults (Akaike weight=0.45, adjusted

170   r^2=0.68, p<0.0001, $y = 0.66 \times VolumeBead - 0.09 \times Age + 0.66$, model 4; Figure 7b). None of the

171   models from the bead method or linear measurements had high enough Akaike weights to make strong

172   inferences about the data (Burnham & Anderson 2002).

173   None of the correlations between CT volumes and linear measures met our subjective minimum

174   criteria (r^2>0.88) for a strong enough relationship to predict endocranial volumes from linear

175   measurements of live birds in the field. Since we want to *predict* CT volumes from linear measures, we

176   determined whether this was possible by generating prediction intervals for the top female and male

177   models for the linear measurements (models 1 and 2) and bead method (models 3 and 4). We found

178   that the lower and upper limits of the 95% confidence intervals of the predicted values for both sexes

179   show extensive overlap such that individual differences would not be able to be resolved if a new,

180   unvalidated data point was obtained (Table 1).

181

182   *Comparing method means*

183   Endocranial volume means were significantly different from each other when comparing across

184   methods (mean±standard deviation: females: volumeCT 2.29cm^3±0.20, volumeSphere

185   32459.1mm^3±4344.7, volumeBead 2.60ml±0.28; males: volumeCT 2.54cm^3±0.15, volumeSphere

186   59292.1mm^3±2360.4, volumeBead 2.91ml±0.21; Welch two sample t-test: females: CT x Sphere t=31,

187   p<0.0001, df=19; Sphere x Bead t=-31, p<0.0001, df=19; Bead x CT t=4, p=0.0003, df=34; males: CT

188   x Sphere t=96, p<0.0001, df=19; Sphere x Bead t=-96, p<0.0001, df=19; Bead x CT t=6, p<0.0001,

189   df=35).

190

Discussion

192   While female great-tailed grackle endocranial volumes from linear measurements were moderately

193   correlated with volumes from CT scans, which we consider a more accurate proxy for brain size, the

194   correlation did not meet our criteria of having a coefficient of determination (r^2) greater than 0.88 – a

195   level of correlation that might allow the resolution of individual differences in endocranial volumes.

196   This correlation was weak in males, which is likely due to the sexual dimorphism in this species and

197   potentially influenced by traits that correlate with male reproductive success (tail length and

198   iridescence; Johnson et al. 2000). Perhaps additional biometric measurements would explain more of

199   the variation in their endocranial volumes from CT scans, however we only had access to skulls for

200   most of the specimens and therefore could not test this hypothesis.

201   We were more interested in whether a given value of x (some external skull measurement)

202   could accurately *predict* y (actual endocranial volume from CT scans), rather than setting a subjective

203   criterion about how high r^2 should be, especially given the extensive debate around the latter approach

204   (e.g., Legates & McCabe Jr. 1999, Müller & Büttner 1994). In particular, r^2 does not allow one to

205   investigate differences in the variance of individual data points because it "…describes the proportion

206   of the *total* variance in the observed data that can be explained by the model" (Legates & McCabe Jr.

207   1999, p. 233, *emphasis added*). Our predictive analyses showed that prediction intervals for new data

208   points overlapped to such a degree (within 95% credible intervals) that it was not possible to

209   distinguish among individuals, as we would need to when collecting linear measurements on new

210   individuals in the field. Therefore, we must conclude that there is not a field proxy accurate enough yet

211   to estimate endocranial volume, and thus brain size, in great-tailed grackles.

212   Predictive analyses are crucial for determining the accuracy of predicting individual data points

213   by a particular method and should be applied extensively in future research, rather than relying solely

214   on correlation coefficients (r) or coefficients of determination (r^2). The omission of such an analysis

215   leaves data uninterpretable for its purported use of discerning intraspecies differences in a

216   morphological feature. Additionally, we caution against using a proxy validated in one species as

217   evidence that the same proxy will apply to other species (e.g., great tits: Dreyer 2012). Until

218   intraspecies validations of brain size proxies using skull or head measurements have been validated

219   across species, we cannot assume that what works (or not) for one species will work (or not) for

220   another.

221   The bead method was only moderately correlated with CT volumes in both sexes and prediction

222   intervals also extensively overlapped for individual data points. Iwaniuk and Nelson (2002) validated

223   the strong relationship between the endocranial volumes from beads and actual brain masses in 81 bird

224   species (r^2=0.98, p<0.01). Great-tailed grackles appear to be an anomaly since this relationship does

225   not hold for them. However, great-tailed grackles and common grackles are among the species with the

226   largest ranges in endocranial volumes (as measured using the bead method) when compared with the

227   other species in Iwaniuk & Nelson's (2002) study (common grackles: mean $\pm$ SD=2.59ml $\pm$ 0.37;

228   Iwaniuk & Nelson 2002; great-tailed grackles: female 2.60ml $\pm$ 0.28, male 2.91ml $\pm$ 0.21; this study).

229   It appears that grackle skulls are more variable than skulls in other species and it is not clear how this

230   variation relates to brain size.

231   To infer differences in brain size among individuals of the same species, and of the same sex,

232   there must be a high degree of accuracy to have the ability to detect actual individual differences

233   (Legates & McCabe Jr. 1999, Logan & Clutton-Brock 2013). Our results highlight the need to validate

234   brain size proxies and their predictive power for each species under investigation, and for each sex if

235   they are sexually dimorphic. It is unfortunate that there is not an easier, more accurate way to

236 approximate brain size in the field where we have the potential to understand how evolutionary factors

237 drive brain size variation within species. However, this study accentuates the importance of knowing

238 how accurate brain size measures are when including such data in analyses.

239

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250

251 **References**

252 Akaike H. 1981. Likelihood of a model and information criteria. *Journal Econometrics* 16: 3-14.

253 Barton K. 2012. MuMIn: Multi-model inference. R package version 1.7.7. Available: http://CRAN.R-

254   project.org/package=MuMIn. Accessed 3 Jan 2015.

255 Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-

256   theoretic approach. New York: Springer.

257 del Hoyo J, Elliot A, Christie DA. 1992. Handbook of the Birds of the World. Barcelona: Lynx

258   Edicions.

259 Dreyer, S. 2012. Cranium size and fitness measures in a wild population of great tits (*Parus major*).

260   Masters thesis, University of Oslo.

261 Gonda A, Herczeg G, Merilä J. 2013. Evolutionary ecology of intraspecific brain size variation: a

262   review. *Ecology and Evolution* 3:2751-2764.

263 Hadfield JD. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The

264   MCMCglmm   R   Package.   *Journal*   *of*   *Statistical*   *Software*   33:1-22.

265   http://www.jstatsoft.org/v33/i02/. Accessed 3 Jan 2015.

266 Healy SD, Rowe C. 2007. A critique of comparative studies of brain size. *Proceedings of the Royal*

267   *Society B* 274:453-464.

268 Isler K, Christopher Kirk E, Miller J, Albrecht GA, Gelvin BR, Martin RD. 2008. Endocranial volumes

269   of primate species: scaling analyses using a comprehensive and reliable data set. *Journal of*

270   *Human Evolution* 55:967-978.

271 Iwaniuk AN, Nelson JE. 2002. Can endocranial volume be used as an estimate of brain size in birds?

272   *Canadian Journal of Zoology* 80:16-23.

273 Iwaniuk AN, Nelson JE. 2003. Developmental differences are correlated with relative brain size in

274   birds: a comparative analysis. *Canadian Journal of Zoology* 81:1913-1928.

275 Johnson K, DuVal E, Kielt M, Hughes C. 2000. Male mating strategies and the mating system of great-

276   tailed grackles. *Behavioral Ecology* 11:132-141.

277 Landis JR, Koch GG. 1977. The measurement of observer agreement for categorical data. *Biometrics*

278   33:159-174.

279 Legates DR, McCabe Jr. GJ. 1999. Evaluating the use of "goodness-of-fit" measures in hydrologic and

280   hydroclimatic model validation. *Water Resources Research* 35:233-241.

281 Logan CJ, Clutton-Brock TH. 2013. Validating methods for estimating endocranial volume in

282   individual red deer (*Cervus elaphus*). *Behavioral Processes* 92:143-146.

283   Miller JMA. 1997. A hierarchical analysis of primate brain size and body size: patterns of

284   morphometric variation. Ph.D. dissertation, University of Southern California, Los Angeles.

285   Müller R, Büttner P. 1994. A critical discussion of intraclass correlation coefficients. *Statistics in*

286   *Medicine* 13:2465-2476.

287   Pyle P, Howell SN, DeSante DF. 1997. *Identification guide to North American birds* (pp. 421-422).

288   Bolinas, CA: Slate Creek Press.

289   R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for

290   Statistical Computing, Vienna, Austria. http://www.R-project.org. Accessed 3 Jan 2015.

291   Sakai ST, Arsznov BM, Lundrigan B, Holekamp KE. 2011. Brain size and social complexity: a

292   computed tomography study in hyaenidae. *Brain, Behavior and Evolution* 77:91-104.

293   Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005. Big brains, enhanced cognition, and

294   response of birds to novel environments. *Proceedings of the National Academy of Sciences of the*

295   *United States of America* 102:5460-5465.

296   Thornton A, Lukas D. 2012. Individual variation in cognitive performance: developmental and

297   evolutionary perspectives. *Philosophical Transactions of the Royal Society B* 367:2773-2783.

298   Winker K. 2000. Obtaining, preserving, and preparing bird specimens. *Journal of Field Ornithology*

299   71:250-297.

1

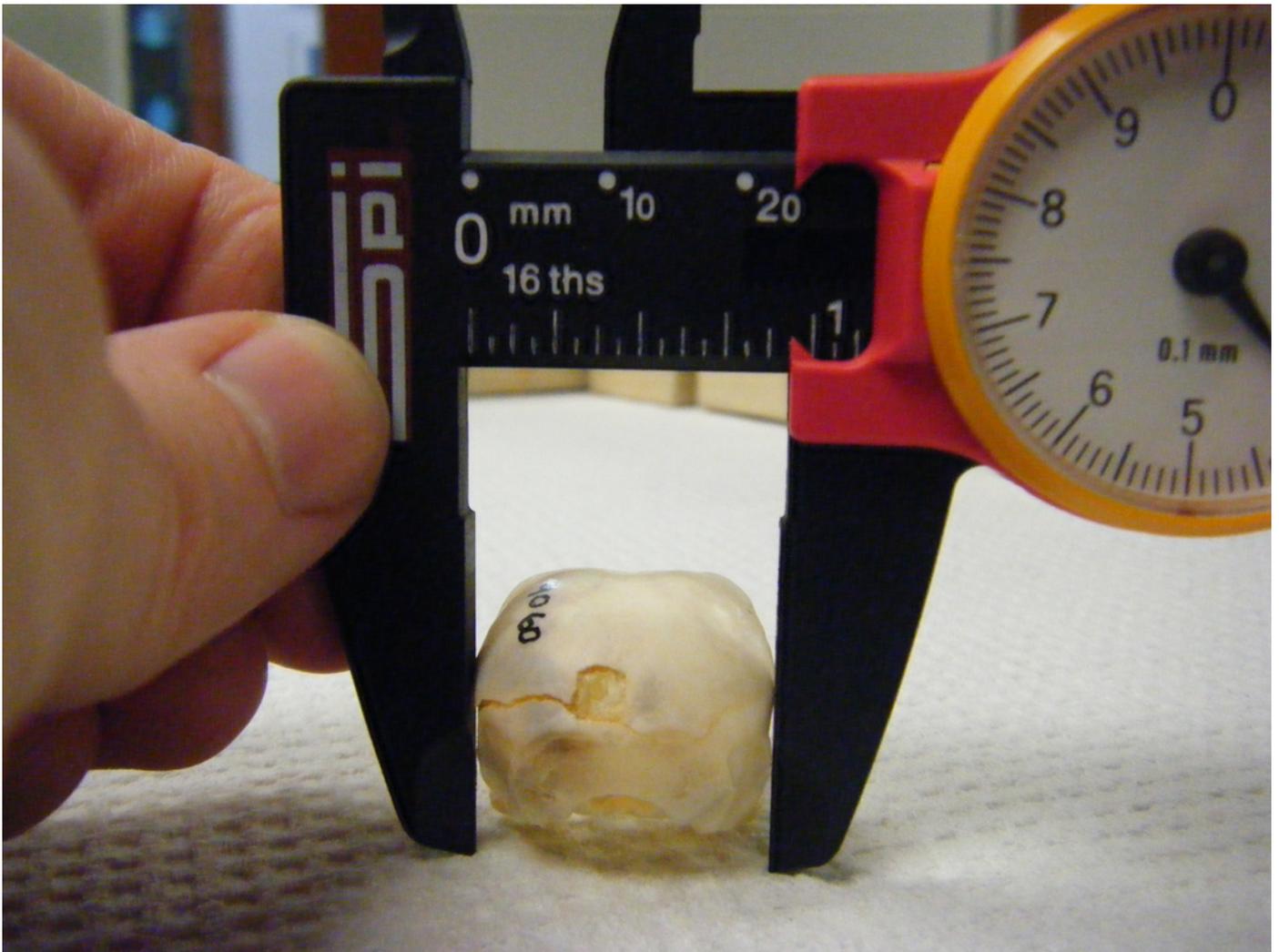
Skull length

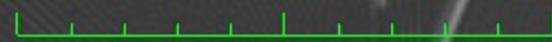
Measuring skull length as it is measured on live birds

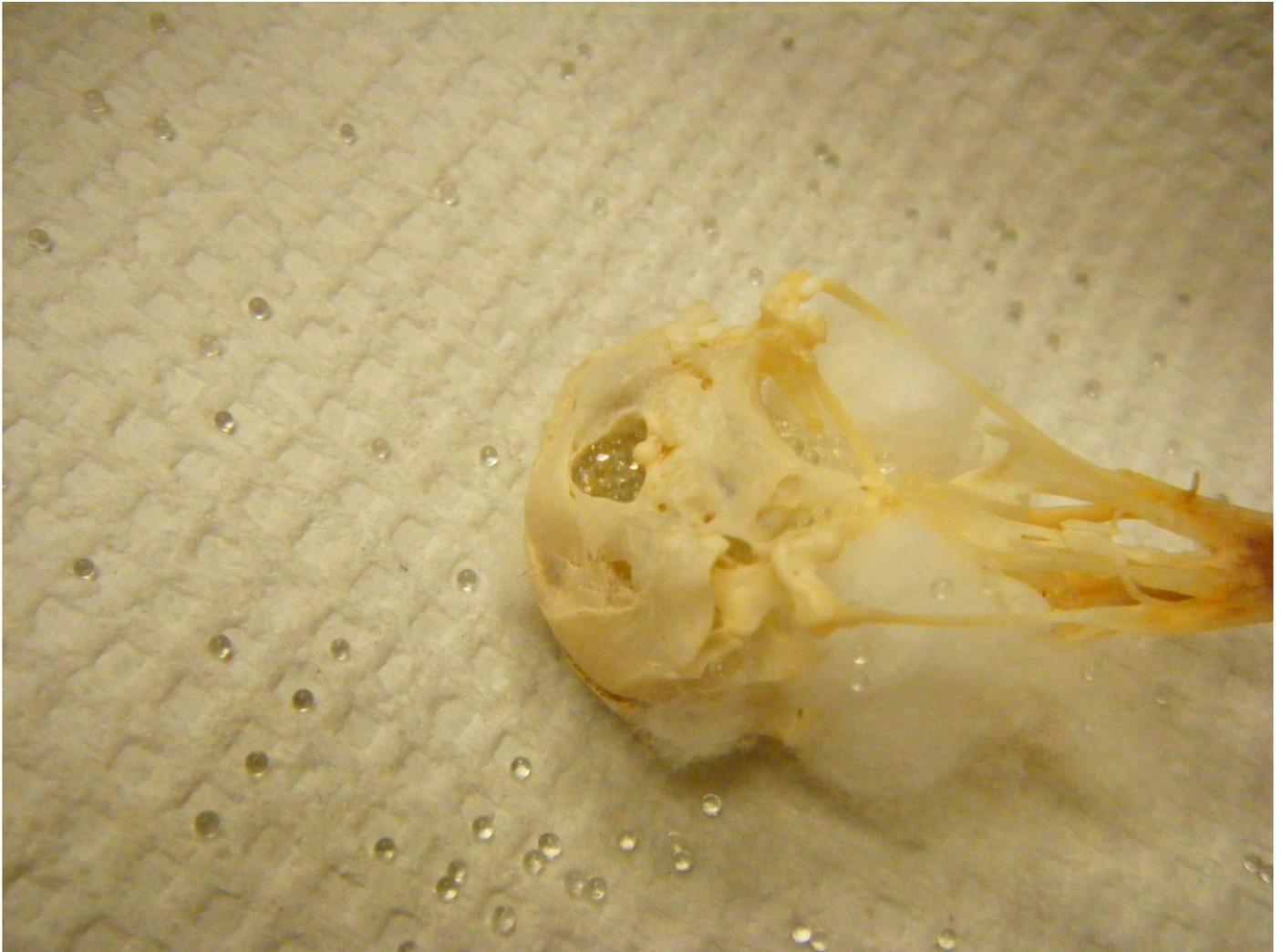
Skull height

Measuring skull height, replicating the height that can be measured on live birds

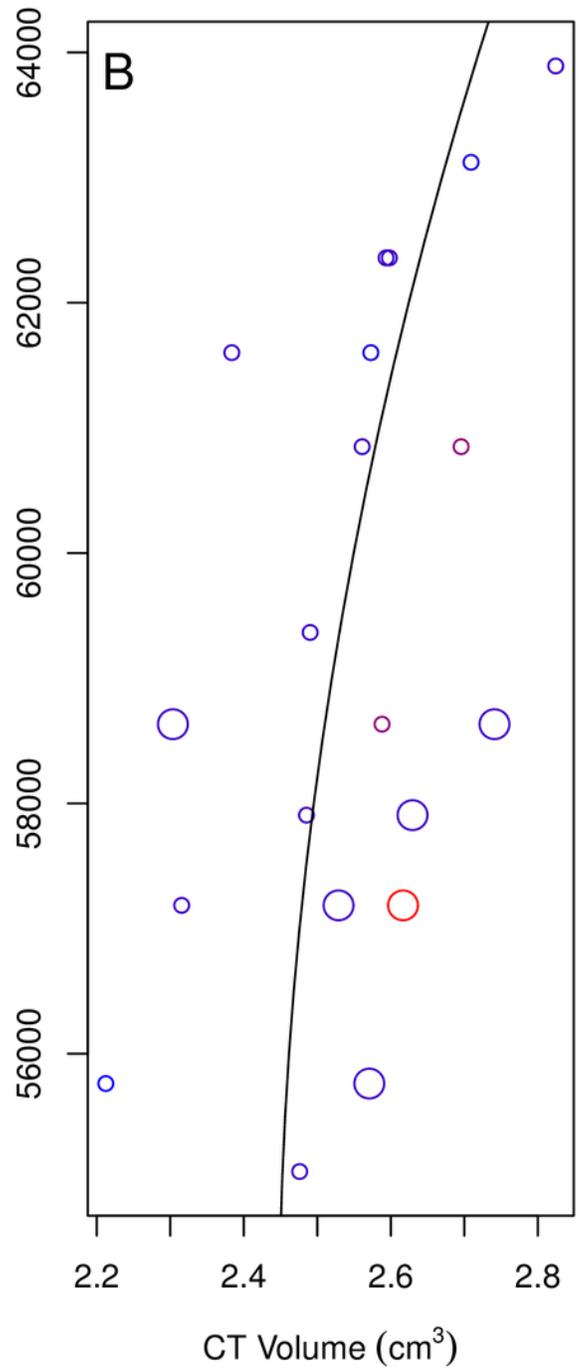
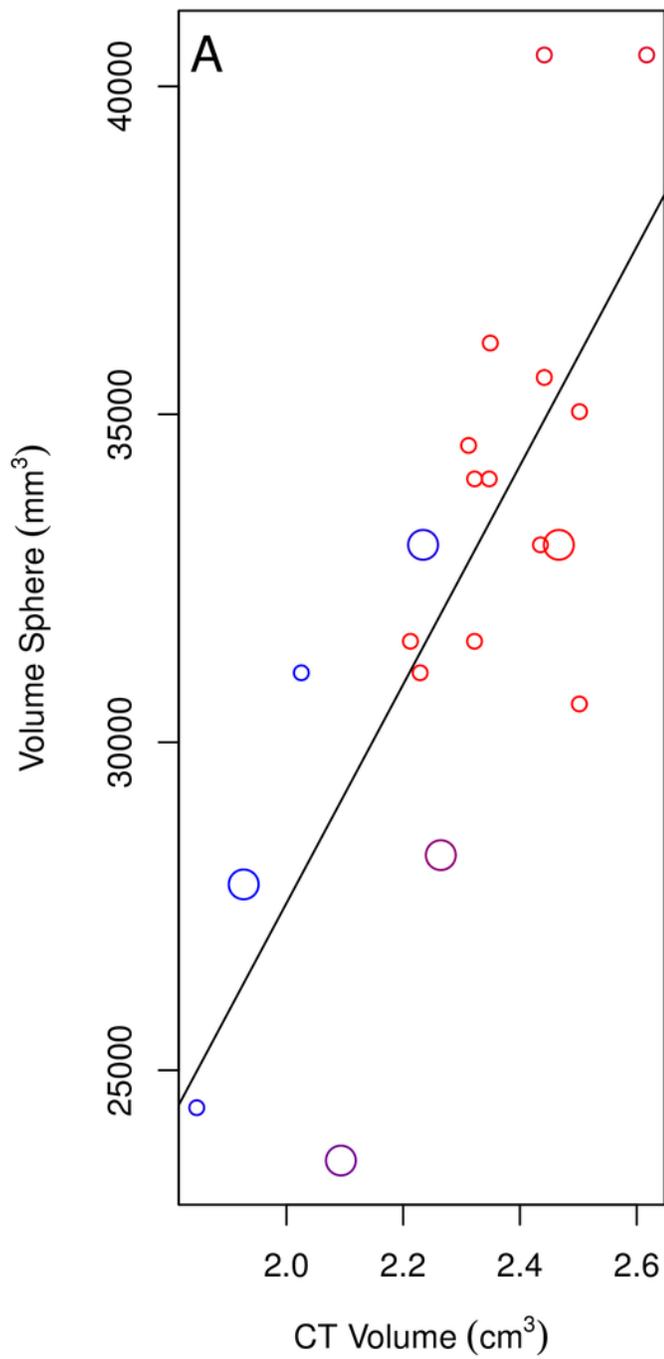
Skull width

Measuring skull width at the widest part of the braincase as it would be measured on live birds

CT scan of grackle skulls

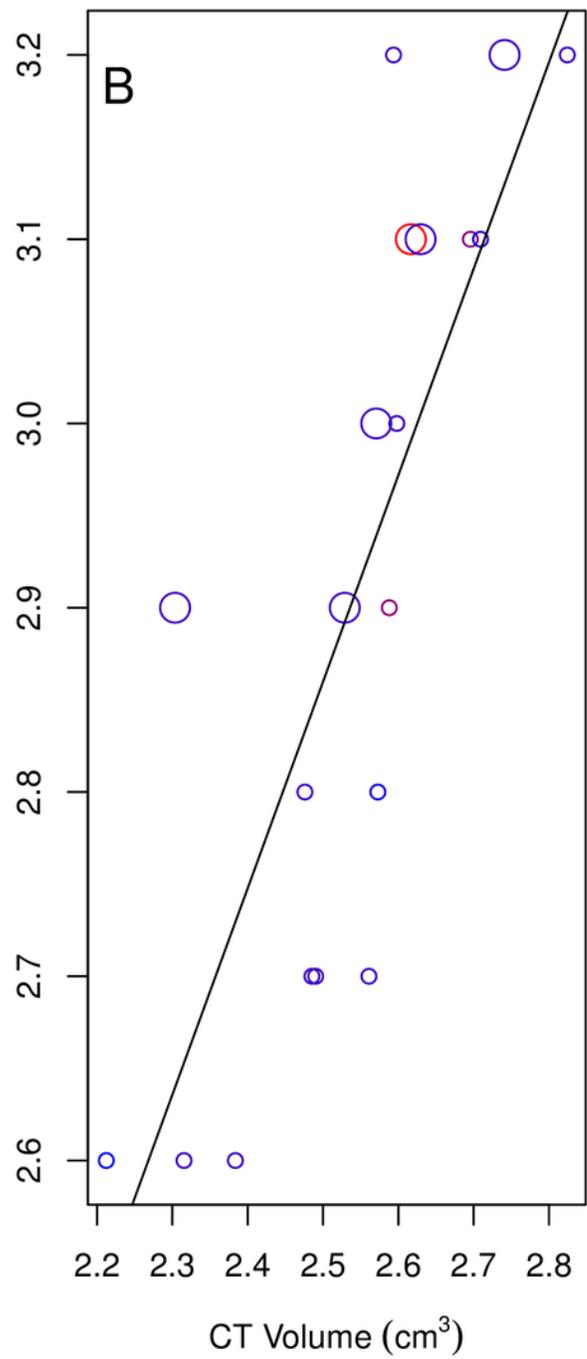
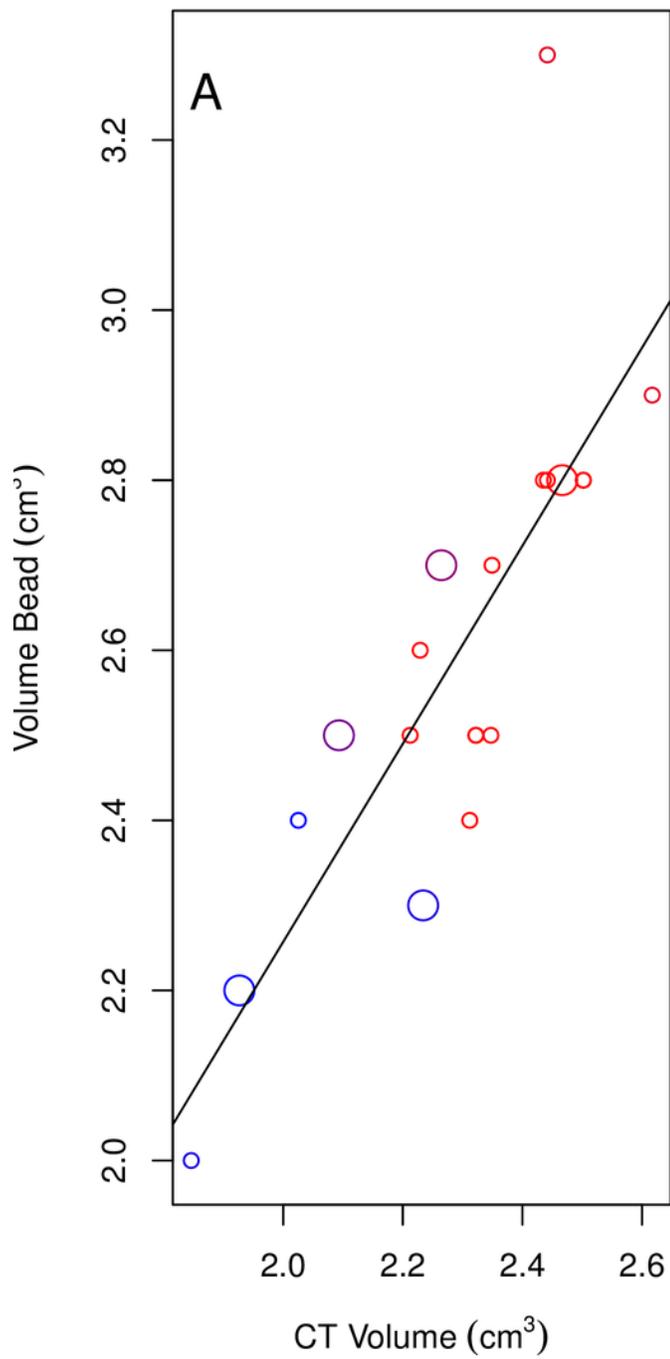
CT scan showing five grackle skulls using OsiriX

Bead method

Skull holes are plugged with cotton and then the cranium is filled with glass beads

6

Plots of the correlations between Volume Sphere and Volume CT for females and males

Correlations between CT volumes and the volume of a sphere as calculated from linear measurements for female (A) and male (B) adults (small circles) and immatures (large circles), with the year the skull was collected represented by a red-blue spectrum (earlier years are redder and recent years are bluer). Note that regression lines only reflect VolumeSphere~VolumeCT and do not correct for age or year (factors in the top model for both sexes) as in the GLMs.

7

Plots of the correlations between Volume Bead and Volume CT for females and males

Correlations between CT volumes and bead volumes for female (A) and male (B) adults (small circles) and immatures (large circles), with the year the skull was collected represented by a red-blue spectrum (earlier years are redder and recent years are bluer). Note that regression lines only reflect VolumeBead~VolumeCT and do not correct for age (in the top male model) or year (in the top female model) as in the GLMs.

Grackle skulls on the CT scanner

Predicted CT volumes and their prediction intervals

Predicted CT volume values (fitted value) and the predicted intervals in which these new data points would occur with 95% credible intervals based on inputs from linear measures or the bead method in the top female and male models for each method.

2   Table 1. Predicted CT volume values (fitted value) and the predicted intervals in which these new data

3   points would occur with 95% credible intervals based on inputs from linear measures or the bead

4   method in the top female and male models for each method.

Linear Measurements						Bead Method					
Males			Females			Males			Females		
Fitted value	Lower	Upper	Fitted value	Lower	Upper	Fitted value	Lower	Upper	Fitted value	Lower	Upper
2.72	2.37	3.07	2.23	2.03	2.42	2.61	2.42	2.80	2.30	2.07	2.48
2.41	2.17	2.73	2.08	1.86	2.29	2.43	2.23	2.61	2.21	1.99	2.42
2.40	2.12	2.69	1.87	1.61	2.07	2.37	2.18	2.55	1.90	1.63	2.11
2.60	2.33	2.92	1.99	1.78	2.22	2.70	2.52	2.90	2.02	1.78	2.26
2.42	2.10	2.70	2.20	2.02	2.39	2.50	2.34	2.68	2.05	1.81	2.30
2.52	2.22	2.83	2.30	2.10	2.51	2.55	2.35	2.75	2.42	2.22	2.62
2.77	2.45	3.07	2.43	2.23	2.60	2.76	2.54	2.94	2.39	2.16	2.59
2.67	2.41	2.94	2.39	2.20	2.58	2.70	2.50	2.89	2.28	2.07	2.52
2.35	2.06	2.64	2.32	2.14	2.53	2.37	2.17	2.56	2.31	2.11	2.54
2.55	2.30	2.84	2.51	2.30	2.71	2.50	2.31	2.67	2.57	2.31	2.81
2.46	2.21	2.72	2.51	2.30	2.71	2.43	2.25	2.63	2.43	2.20	2.64
2.64	2.40	2.92	2.39	2.19	2.59	2.63	2.45	2.82	2.32	2.10	2.53
2.53	2.24	2.77	2.48	2.27	2.70	2.44	2.26	2.63	2.46	2.20	2.70
2.58	2.31	2.85	2.40	2.21	2.60	2.37	2.18	2.57	2.32	2.11	2.52
2.55	2.31	2.85	2.32	2.13	2.52	2.47	2.28	2.67	2.31	2.11	2.56
2.64	2.39	2.94	2.41	2.23	2.60	2.76	2.57	2.97	2.43	2.20	2.64
2.54	2.29	2.82	2.36	2.16	2.55	2.61	2.40	2.80	2.43	2.22	2.66
2.55	2.24	2.80	2.42	2.21	2.60	2.67	2.49	2.87	2.43	2.20	2.65
2.52	2.26	2.80	2.32	2.13	2.52	2.48	2.27	2.68	2.36	2.15	2.57
2.51	2.24	2.80	2.02	1.82	2.13	2.57	2.38	2.74	1.98	1.74	2.18