

**Wither the subspecies?: an ecological perspective on taxonomic, environmental
and sexual determinants of phenotypic variation in Big-eared woolly bats,
*Chrotopterus auritus***

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Running Header: Wither the subspecies?

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13 Continuous phenotypic variation reflecting geographic clines can be difficult to
14 distinguish from subspecific discontinuities when specimens are few and
15 heterogeneously distributed. Nonetheless, increases in the holdings of museum
16 collections over the last decades contribute to our ability to resolve more fine-scaled
17 phenotypic gradients for many species. Although the Big-eared woolly bat is not
18 commonly encountered and thus poorly represented in museum collections, sufficient
19 numbers have accumulated to allow an assessment of sub-specific, sexual, spatial and
20 environmental components of phenotypic variation. I examined 123 specimens from
21 across the distribution of *Chrotopterus auritus* and characterized phenotype based on
22 external, cranial and mandibular characteristics and decomposed variation into
23 components based on univariate and multivariate statistical analyses. All components
24 accounted for significant phenotypic variation. Nonetheless, when examined together
25 and after accounting for correlated variation among components, only sexual, spatial
26 and environmental components accounted for significant unique variation. This,
27 combined with the observation that all qualitative characteristics used to define
28 subspecies of *C. auritus* can be observed throughout its geographic range, suggest that
29 phenotypic variation is clinal and not characterized by discontinuities reflective of
30 subspecies. Clinal variation was most related to temperature and its seasonality
31 highlighting the important role that these climatic characteristics play in many aspects of
32 the biology of Phyllostomidae.

A ubiquitous characteristic of life is phenotypic variability that manifests as numerous qualitatively different forms related to ontogeny, sex, geography or species-specific affinity to name only a few. Phylogenetic conservatism predisposes similarity of sister taxa (Wiens et al. 2010) and this combined with geographic variation within these same taxa (Endler 1977) challenges taxonomy and resultant understanding of phylogenetic relationships. Indeed, the phenotype is highly responsive to environmental gradients that underlie patterns of geographic variation (Endler 1977). For example, biogeographic “rules” of phenotypic variation, in particular Allen’s Rule (Allen 1877), Bergmann’s Rule (Bergmann 1847) and Gloger’s Rule (Gloger 1833), define general phenotypic patterns related to temperature and humidity. Even at smaller scales, gradients in phenotypic variation are fairly ubiquitous. For many mammals, microgeographic phenotypic variation can be detected even below the level of subspecies (Willig 1983, Nevo 2001) that often corresponds to environmental gradients related to climate (Stevens et al. 2016).

One major taxonomic/systematic limitation is that it is often difficult to distinguish phenotypic clines resulting from environmental gradients from discontinuities reflective of infraspecific groupings such as subspecies (Huxley 1938) without large numbers of specimens spanning much to the entire geographic distributions of species. One shortfall of modern biology that is true to this day, I coin the Merriamian shortfall, that is simply lack of museum specimens that prevents fully resolved description of variation of characteristics measured across the geographic distribution of a species. The Merriamian shortfall joins a number of other shortfalls (e.g., Darwinian, Eltonian, Hutchinsonian, Grinnellian, Linnean, Prestonian and Wallacean, Rosado et al. 2015)

that identify and point to where the scientific community needs to focus in terms of efforts to collect basic data describing the biota. Growth and maintenance of scientific museum collections is just one of those areas (Malaney and Cook 2018, Cook and Light 2019, Colella et al. 2020).

Because of the Merriamian shortfall, geographic gradients and taxonomic status of many relatively rare taxa are unresolved or tenuous. Another implication of the Merriamian shortfall is that only the most common species are associated with robust data and substantive additional effort is needed to accumulate a sufficient number of specimens across a sufficient number of sites in order to characterize phenotypic variability across the entire distribution of many species. Nonetheless, scientific collecting has been robust over the last 200 years (Malaney and Cook 2018) and now the opportunity exists to revisit a number of relatively rare taxa, especially when specimens are amassed across institutions.

A perfect example involves the Big-eared woolly bat, *Chrotopterus auritus*. This species is widely distributed from Mexico to Argentina (Medellin 1989). Nonetheless, because of the very nature of its large size and carnivorous trophic status, *C. auritus* is fairly uncommonly encountered. Subspecies were defined long ago (Thomas 1905), but have been disputed for many years (Handley 1966, Koopman 1994, Simmons and Voss 1998). We now finally have enough museum specimens to rigorously evaluate phenotypic variation in this species across much of its geographic distribution.

Thomas (1905) defined subspecies of *C. auritus* during an era of proliferation of species and subspecies discovery (Natural History's great age of discovery [Goetzmann 1986, Patten 2010]). Often and because of the Merriamian shortfall that was much

more of a limitation during this era, subspecies often were described based on small or geographically isolated samples from different places on geographic clines (James 2010). Subspecies are typically defined as interbreeding populations with a distinct allopatric or parapatric distributions, but perhaps more importantly that are phenotypically distinct from other populations of the species (Mayr 1969, Avise 2004, James 2010, Remsen 2010). Phenotypic discontinuities and not clinal variation warrant subspecific status (James 2010). To this end subspecific designations should account for significant variation among individuals over and beyond that due to clinal variation, a scenario that reflects the distinct nature of phenotypic variation reflected in subspecies. Because of the limited geographic scope of specimens used to describe subspecies of *C. auritus* in the past, I predict that once a geographically expansive sample of numerous specimens is examined, the inconsistent differences among subspecies defined by Thomas (1905) will be better characterized as spatial/climatic clines and not discrete subspecies.

Other forms of phenotypic variability also warrant examination. Many species of bats exhibit secondary sexual dimorphism (Ralls 1976), phyllostomids in particular (Swanepoel and Genoways 1979). Much evidence suggests that larger mothers have greater reproductive success and this drives larger size in female bats (Ralls 1976, Stevens et al. 2013). I predict significant secondary sexual dimorphism in *C. auritus* whereby females are larger than males. In addition, a number of bat species (Fukui et al. 2005, Aeshita et al. 2006, Wu et al. 2016), in particular phyllostomids (Willig 1983, Marchan-Rivadeneira et al. 2012, Ramirez-Mejia 2021), exhibit strong spatial gradients in phenotypic variation, with some directly related to climate (Jiang et al. 2010, Stevens

et al. 2016, Mutumi 2017). Because *C. auritus* possesses such a large geographic range spanning from Mexico to Argentina, I predict significant spatial gradients in morphometric variation. Moreover, because the main spatial gradient across its distribution is latitudinal, I predict that those environmental characteristics most associated with that spatial gradient, namely environmental seasonality, will be most related to spatial variation in morphometric characteristics. Related to these gradients in phenotypic variation I predict that once climatic clines are accounted for, there will be no significant variation accounted for by subspecies designations, supporting the doubts of validity of subspecies of *C. auritus* by others (Handley 1966, Koopman 1994, Simmons and Voss 1998).

MATERIALS AND METHODS

Systematics of *Chrotopterus auritus*.-- Controversy involving the status of subspecies of *C. auritus* is primarily due to the inconsistency of differences, even within local populations, used in their definition (Simmons and Voss 1998). Thomas (1905) described three subspecies of *C. auritus* (*C. a. auritus*, *C. a. australis* and *C. a. guianae*) from three individuals from Mexico, Paraguay and Venezuelan Guiana, respectively. Comparisons by Thomas (1905) of the Mexican form with the two others were made using the description of *C. auritus* by Peters (1856). *Chrotopterus a. guianae* was distinguished by broadly white wing tips with both the terminal phalanges of the third digit and the membrane white, the edge of the dactylopatagium white between digits four and five, a slight trace of white on the edge of the membrane leading to the foot and the base of the first digit almost without hairs and fur of body and forearm not extending onto the membranes. *Chrotopterus a. australis* was

distinguished by much reduced white on wing tips with only the third terminal phalanx whitened, membrane lighter but not white, the edge of the dactylopatagium not white between digits four and five, fur patch at the base of digit-1 conspicuous, body hair extending onto the wing membrane below and onto the interfemoral membrane dorsally. Thomas (1905) didn't actually examine the specimen from Mexico but relied on the description of Peters (1856) stating "but in his most careful and detailed description he mentions no white at all on the tips of the wings, nor is any shown in the plate, and I therefore conclude that the Mexican *Chrotopterus* is again different from either of the two races now described". Questions as to the status of subspecies of *C. auritus* have been longstanding (Handley 1966, Koopman 1994, Simmons and Voss 1998) and are primarily due to the inconsistency of differences described by Thomas (1905), even within local populations, used in their definition (Simmons and Voss 1998).

I examined 123 *C. auritus* distributed across Mexico, Belize, Guatemala, El Salvador, Honduras, Costa Rica, Panama, Venezuela, Guyana, Suriname, Ecuador, Peru, Brazil, Bolivia, Paraguay, and Argentina (Figure 1). Initially, this investigation aimed only to address environmental and spatial gradients in morphometric variation in *C. auritus* across its geographic range. Perhaps half-way through the measuring process it became apparent that examination of subspecific status would be necessary because while most authorities consider this species to be monotypic, others had considered three subspecies. I used Medellín (1989) to define the geographic distribution of each of the 3 subspecies defined by Thomas (1905). From 63 of the 123 specimens I examined qualitative characteristics described by Thomas (1905) to define subspecies: degree to which wing tips were white (one-Dark, two-small white tip, three-

broad white tip), number of digit 3 phalanges that were white (one-0, two-1, three-2), shading of the edge of dactylopatigium between digit-4 and digit-5 (dark-1, trace of white-2), presence of a conspicuous metacarpal patch on the thumb (absence/presence), ventral fur that extended onto the wing (absence/presence) and dorsal fur that extended onto the uropatagium between the legs (absence/presence). I used a canonical correspondence analysis (ter Braak and Verdonschot 1995) to examine the degree to which subspecies defined geographically (Medellin 1989) corresponded to the qualitative phenotypic definitions of subspecies suggested by Thomas (1905).

I also measured with digital calipers to the nearest 0.01 mm, eleven cranial and five mandibular measurements plus forearm length to estimate quantitative phenotypic variation among individuals. Greatest length of skull (GLS) was measured from the most anterior point on the rostrum (excluding incisors) to the most posterior point of the occipital bone. Condylbasal length (CBL) was from the most posterior point on the occipital condyles to the anterior most point on the premaxillae. Mastoid breadth (MAB) was the greatest distance between the two mastoid bones. Zygomatic breadth (ZYGO) was the greatest distance across the zygomatic arches. Breadth of the upper canines (BUC) was the greatest distance between the canines at the edge of the alveolus on the cranium. Breadth across the upper molars (BUM) was the greatest distance between the outer sides of the molar tooth rows measured at the edge of the alveolus on the cranium. Maxillary toothrow length (MAX) was the distance between the most anterior point of the canine at the alveolus to the most posterior point of the last molar at the alveolus. Length of the toothrow (LTR) was the distance from the anteriormost point on

the first incisor to the posterior most point on the last molar at the alveolus on the cranium. Height of the cranium (HOC) was the greatest distance between the sagittal crest and the basioccipital. Breadth of the braincase (BBC) was the greatest width across the braincase, posterior to the zygomatic arches. Breadth across the post-orbital constriction (POC) was the smallest breadth across the frontals posterior to the postorbital processes. Length of the mandibular toothrow (LMTD) was the distance from the anteriormost point on the first incisor to the posterior most point on the last molar at the alveolus on the mandible. Length of the dentary (LDEN) was the most posterior point on the condyloid process to the most anterior point of the mandible. Width of the dentary (WDEN) was the greatest distance between the outsides of the angular process. Width of the lower canines (WLC) was the greatest distance between the canines at the edge of the alveolus on the mandible. Width of the lower molars (WLM) was the greatest distance between the outer sides of the molar tooth rows measured at the edge of the alveolus on the mandible. Forearm length (FA) was the distance from the elbow to the wrist. All measurements were log-transformed prior to analyses. Although these linear measurements likely underlie a strong size element, size often varies geographically and is often an important characteristics used in systematic revision of taxa (Marcus 1990).

The combination of 17 morphometric characteristics measured across the 123 specimens generated 2091 measurements of which 24 were missing. I used a maximum likelihood approach (Little and Rubin 1987) to estimate these missing values. To examine significance of differences between sexes, among subspecies and their interaction (defined by Thomas [1905] and spatially delimited by Medellín) I used a two-

way multivariate analysis of variance (MANOVA). If this MANOVA was significant, I conducted two-way univariate analyses of variance (ANOVA) to determine which morphometric characteristics were likely contributing to the significant difference among multivariate centroids. MANOVA's and ANOVA's were conducted using the "car" package in R (Fox and Weisberg 2019).

To construct simple and complex spatial gradients from which to examine clines in morphometric variation I created Moran's eigenvector maps, in particular principal coordinates of neighbor matrices (PCNM's) using the dbmem function in the "adespatial" package of R (Dray et al. 2016). PCNM's are orthogonal spatial descriptors that capture variation that ranges from broad to fine spatial structures (Borcard et al. 2018). PCNM's were based on a Euclidean distance matrix calculated from geographic coordinates where *C. auritus* were collected. From these same coordinates I also characterized environmental characteristics of each site by capturing the 19 bioclimatic variables from WorldClim with a 30 second spatial resolution (Hijmans et al. 2005).

To estimate amount of variation in morphometric characteristics accounted for by subspecies, spatial gradients and environmental gradients I conducted three separate redundancy analyses (Legendre and Legendre 2012). Correlations of the original variables (loadings) were used to interpret the identity of axes accounting for maximal variation in morphometric characteristics. I also conducted variation partitioning analyses to partition variation into components unique to subspecies, sex, spatial and environmental gradients plus two-way, three-way and four-way correlated variation. Such an analysis identified the relative contribution of the different sets of characteristics to morphometric variability in general but also directly addressed the

status of previously defined subspecies of *C. auritus*. If subspecies were valid, they should account for significant variation over and beyond sexual differences and spatial and environmental clines. In other words, if subspecies are valid they should still account for significant phenotypic variation after accounting for continuous environmental and spatial variation. Redundancy and variation partitioning analyses were conducted using the “vegan” package in R (Oksanen et al. 2017).

Results

Subspecies defined geographically according to Medellín (1989) were not discrete from perspectives of qualitative external characteristics. Indeed, characteristics thought to be definitive of certain subspecies can be commonly found across all three (Table 1). Correspondence analysis indicated that subspecific distinctions were weakly ($R^2_{\text{adj}} = 0.11$) but significantly ($P < 0.001$) discernable based on external characteristics. Despite weak structure, dark wing tips and phalanges were found more often but not always in *C. a. auritus*. This was the only characteristic used to distinguish subspecies (Thomas 1905) that exhibited any consistent differences, though weak (Figure 2).

Individuals of *C. auritus* were variable in terms of cranial, mandibular and wing morphology (Table 1). Multivariate analysis of variance indicated no significant two-way subspecies by sex interaction in group centroids ($F_{34,204} = 1.44$, $P = 0.067$), meaning that significance of these two main effects were independent and could be interpreted simply. Multivariate analysis of variance indicated a highly significant difference among subspecies centroids ($F_{34,204} = 6.34$, $P < 0.001$) and a moderately significant difference between female and male centroids ($F_{17,101} = 1.75$, $P = 0.046$). Significant univariate

differences among subspecies existed for 11 of 17 characters. Significant differences among females and males existed for 12 characters and in all cases involved females being larger than males.

Variation partitioning indicated that 37% of cranial and mandibular morphometric variation of *C. auritus* could be accounted for by unique and correlated components of subspecies, sex, spatial proximity and climate (Figure 3) and this was highly significant ($P < 0.001$). Once correlated variation was accounted for, all components but subspecies accounted for significant unique variation in phenotypic characteristics. Eight of the nine percent of phenotypic variation expressed as differences among subspecies could be accounted for by variation shared with spatial and climatic gradients. In fact, only 1 percent of cranial and mandibular variation could be accounted for uniquely by subspecies.

When examined by themselves, sexual, climatic and spatial variables were all significantly related to cranial and mandibular phenotypic variability in *C. auritus* (Table 3). Differences in size between females and males, with females being larger for most characteristics determined the sexual difference. The canonical axis separating sexes accounted for 3.1 percent of the variation among individuals and was significant ($P = 0.008$).

Morphometric characteristics of *C. auritus* exhibited strong ($R^2_{\text{adj}} = 0.198$) and significant (Variation Partition B, Table 3; $p < 0.001$) spatial gradients in the New World (Table 3). Length and breadths of most cranial and mandibular characteristics were strongly related to spatial gradients measured by PCNM's (Figure 4 a and b). The

strongest spatial gradients involved the second and third PCNM's that reflect more broadscale spatial variation.

Climatic gradients accounted for approximately 19.5 percent of the variation in morphometric characteristics (Figure 4 c and d) and this was highly significant (Table 3; $P < 0.001$). Forearm length, height of the cranium, mastoid breadth, length of the cranial toothrow, width across the post-orbital constriction, breadth of the braincase, width of the lower canines and width of the dentary were all strongly related to climatic gradients, in particular those involving temperature seasonality, mean temperature in the coldest quarter, minimum temperature in the coldest month, isothermality and mean temperature in the driest quarter. Size and breadths of the cranium were larger in seasonal environments that were colder and relatively more variable on a daily basis (Fig 4).

All three components of sex, climate and spatial differences also accounted for significant unique variation in morphometric characteristics (Table 3). Spatial and climatic gradients exhibited the most redundancy that reflected the spatial nature of climatic gradients. Separate partial redundancy analyses indicated that climate gradients accounted for slightly more variation than did spatial gradients in morphometric characteristics, and both were highly significant. The unique climatic component accounted for by this partial redundancy analysis expressed climatic variation that was unrelated to spatial gradients, or the non-spatial climatic variation. Bioclim characteristics related to temperature, especially involving magnitude in summer or the wet season were the most important climatic characteristics uniquely related to morphometric variation. Morphometric characteristics related to cranial size

and dentary width were positively related to higher temperatures suggesting that once the spatial component of climatic variation is accounted for, crania become longer and mandibles become wider in areas of higher temperature (Figure 4E and F). Uniquely spatial gradients remained after accounting for spatial variation related to climate. Uniquely spatial gradients involved the 3rd, 6th, and 15th PCNM indicating that this spatial variation involved broad, intermediate and small-scale patterns, respectively (Figure 4G and H).

Discussion

Chrotopterus auritus is phenotypically variable across its geographic distribution from perspectives of qualitative external and quantitative morphometric characteristics involving wing size, the cranium and mandible. While subspecies did exhibit tendencies for particular external characteristics, those originally reported as distinct (Thomas 1905) could be found in all three subspecies and were not reliable population-level indicators. Morphometric variation exhibited distinct sexual, spatial and climatic components. Moreover, subspecies designations accounted for little unique variation when sexual, spatial and climatic gradients were considered in the same analysis suggesting that the existing morphometric variation is better described by clines than by subspecific designations.

Wither subspecies of C. auritus? —Even when examined by themselves and not considering correlations with sex, space and climate, subspecies designations, while

significant, only accounted for approximately 11 percent of the variation among individuals in qualitative external characteristics. Moreover, characteristics suggested as indicative of the different subspecies by Thomas (1905) could be found in all subspecies, yet in different proportions (Table 2). This is consistent with the observations of Simmons and Voss (1998) who found a similar pattern at the local site of Paracou, French Guiana, namely that all distinctions made by Thomas (1905) for the three different subspecies could be found among individuals within this single local population. As with external characteristics, cranial and mandibular morphometric variation exhibited significant differences among subspecies when considered alone but did not contribute significantly when considered in the same analysis with sexual, spatial and climatic gradients. Morphological differences described by Thomas (1905) likely seemed distinctive because they were taken from three widely separated marginal localities (Mexico, Venezuelan Guiana and Paraguay). It is likely that clinal variation will not be appreciated from examination of specimens from widely separated marginal localities without examination of intervening material. I agree with Simmons and Voss (1998) as well as Handley (1966) and Koopman (1994) that it is likely more productive to consider *C. auritus* as monotypic.

Environmental gradients.—As indicated by the correspondence of vectors of morphometric characteristics and climatic variables illustrated in Figure 4, *Chrotopterus auritus* exhibited strong and significant clines in morphometric variation related to a number of climatic gradients. Larger forearms, cranial heights, toothrow lengths and widths of the dentary, canines, braincase and the mastoid were related to areas of

colder and more seasonal temperatures. Cold seasonal environments are likely important limiting factors in the distribution of many phyllostomid bat species. Tropical mammals, in particular bats, have poorer insulation than temperate species as reflected in lower conductance (McNab 1969). Moreover, larger phyllostomids, in particular *C. auritus*, maintain relatively constant body temperatures by increasing their metabolic rate at lower ambient temperatures (McNab 1969). Larger body size may be a means to mitigate effects of more variable temperatures in colder seasonal environments (i.e. Bergmanns Rule [Bergmann 1847]) and might explain the positive relationship between size and seasonality and the negative relationship between size and cold temperatures in *C. auritus*.

Morphometric variation in *C. auritus* also exhibited significant spatial gradients and much related to spatial PCNM's remained after accounting for climate (i.e., spatially structured climatic gradients). The set of PCNM's that most contributed to the significant non-climatic spatial structure ranged from those that spanned broad (MEM3) to intermediate (MEM6) to very local (MEM15) spatial gradients. The environmental identity of these spatial gradients remains unclear. Indeed, they are not related to temperature and precipitation gradients, at least those captured by the very indices I measured. A likely possibility is that this form of spatial structure in morphometric characteristics of *C. auritus* is related to environmental gradients not captured by the climatic variables I used (Diniz-Filho et al. 2003).

Wither the subspecies concept? —Recently there has been increased interest in more explicitly defining and rigorously applying the subspecies concept to infraspecific

353 taxonomy (Patton and Conroe 2017, Richardson 2018, Schiaffini 2020, Burbrink et al.
354 2022). Important characteristics of subspecies are that they are definable geographic
355 variants that represent phenotypic discontinuities (Mayr 1942). In particular, if
356 phenotypic differences simply represent clinal variation, as demonstrated here for *C.*
357 *auritus*, then subspecies should not be defined (Patten 2010). In fact, competing a
358 hypothesis of categorical variation with one of continuous spatial variation is a more
359 rigorous test than simply demonstrating significant phenotypic differences among
360 distant populations. Likely most subspecies-rich taxa span large
361 geographic/environmental gradients (Koopman 1994). Such taxa may warrant
362 reexamination of subspecific status. Fortunately, scientific collections may be finally
363 mature enough such that we can more rigorously and statistically address morphometric
364 variation in even some of the most uncommon or rare taxa, *C. auritus* being a fine
365 example. Indeed, we should not beat up older studies, such as that of Oldfield Thomas
366 (1905) that were relatively specimen poor and could not benefit from the many more
367 museum specimens available today. Moreover, as the 117 years of growth of museum
368 specimens since Thomas (1905) exemplifies, efforts to build museum collections are
369 exceedingly valuable to understanding distribution and abundance, systematics and all
370 of the many other forms of variation (Malaney and Cook 2018) that can be
371 characterized from this important form of scientific infrastructure. Indeed, while the
372 subspecies concept does not wither in light of the analyses performed here, perhaps its
373 application will to some degree. This is because upon further examination of a greater
374 number of specimens, especially those that intervene geographically disparate sites
375 used as the basis for diagnosable differences in the past, a number of subspecific

designations may be demonstrated to merely represent different ends of phenotypic
clines. In such cases we should refrain from using the subspecies concept.

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Data Availability Statement

Data underlying this work are available from the author upon reasonable request.

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Figure Legends

Figure 1. Distribution of sites used to characterize subspecific, sexual, spatial and climatic determinants of morphometric variation in *C. auritus*. Red shading indicates geographic distribution of *C. auritus* according to Rojas et al. (2018).

Figure 2. Biplot illustrating relationships of subspecies of *C. auritus* (arrows) with qualitative external characteristics (triangles) used to define them by Thomas (2005). Position of arrows and triangles relative to the end of each axis defines the importance of subspecies and characteristics to the kind of variation represented by that axis.

Figure 3. Venn diagram describing partitions of variation in morphometric variability of *C. auritus* related to subspecies, sex, climate and spatial characteristics. Numbers inside partitions correspond to R^2_{adj} . Only $R^2_{adj} > 0.00$ shown.

Figure 4. Star diagrams describing loadings of morphometric, climatic and spatial variables onto axes generated from redundancy (A, B, C, D) and variation partitioning (E, F, G, H) analyses. Figures A-D demonstrate relationships among variables without accounting or correlations with the other two effects (spatial VS climate) whereas Figures E-H correspond to variation partitions characterizing the unique effects of spatial versus climatic variables after accounting for variation correlated with the other. Length and direction of vectors indicate the degree to which they are correlated with each RDA axis. For rows of plots, correspondence of lengths and directions of morphometric and climatic/spatial variables indicate the degree to which pairs are correlated with each other.

556 Table 1.—Distribution of qualitative phenotypic characteristics across
 557 three subspecies of *C. auritus*.

Subspecies	<i>C. a. auritus</i>	<i>C. a. australis</i>	<i>C. a. guianae</i>
Number examined	27	28	8
Wingtip Dark	3	1	0
Small white tip	13	23	4
Broad white tip	11	4	4
Dark III phalanges	1	0	0
Most distal III white	7	16	2
Two distal III white	19	12	6
Dactylopatagium edge white	10	5	8
Metacarpal patch on thumb	27	27	5
Ventral body fur extension	18	28	7
Dorsal body fur extension	12	25	2

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Table 2.—Results from MANOVA and ANOVA examining significance of differences between subspecies (SSP), sex and their interaction. SSP-F and SSP-P correspond to the F-statistic and associated p-value for each subspecies contrast. Sex-F and Sex-P correspond to the F-statistic and associated p-value for each sex contrast. SXS-F and SXS-P correspond to the F-statistic and associated p-value for the subspecies by sex interaction.

Characteristic	SSP-F	SSP-P	Sex-F	Sex-P	SXS-F	SXS-P
Multivariate Difference	6.34	<0.001	1.75	0.046	1.44	0.067
Greatest Length of Skull	2.54	0.083	1.79	0.184	1.35	0.263
Condylbasal Length	9.97	<0.001	7.28	0.008	3.32	0.040
Mastoid Breadth	9.84	<0.001	7.66	0.007	1.07	0.347
Zygomatic Arch Breadth	8.43	<0.001	10.14	0.002	1.04	0.356
Breadth of Upper Canines	0.35	0.706	12.33	<0.001	0.11	0.898
Breadth of Upper Molars	2.72	0.070	5.48	0.021	2.71	0.071
Maxillary Toothrow Length	1.78	0.173	1.99	0.161	0.08	0.922
Length of Toothrow	11.59	<0.001	8.29	0.005	0.54	0.582
Height of Cranium	31.94	<0.001	4.41	0.038	0.85	0.430
Breadth of Braincase	17.37	<0.001	3.87	0.052	0.11	0.899
Width of Post-Orbital Constriction	7.42	<0.001	7.67	0.007	0.03	0.975
Length of Mandibular Toothrow	5.65	0.005	4.78	0.031	0.26	0.773
Length of the Dentary	4.10	0.019	4.93	0.028	0.70	0.500

Width of the Dentary	0.26	0.774	4.12	0.045	0.12	0.892
Width of the Lower Canines	0.21	0.810	3.08	0.082	1.06	0.349
Width of Lower Molars	5.05	0.008	11.20	<0.001	1.56	0.215
<u>Forearm Length</u>	<u>20.52</u>	<u><0.001</u>	<u>3.75</u>	<u>0.055</u>	<u>4.44</u>	<u>0.014</u>

Table 3.—Results redundancy analyses and variation partitions decomposing morphometric variation in *C. auritus* into unique and additive partitions of variation of sexual, spatial and climatic to decompose spatial variation into climatic and nonclimatic components. Total R^2_{adj} and Total P-value correspond to results from redundancy analysis examining a particular effect without accounting or correlations with the other two effects whereas Unique R^2_{adj} and Unique P-Value correspond to variation partitions characterizing the unique effects of a particular effect after accounting for variation correlated with the other two effects.

Statistic	Sex	Space	Climate
Total R^2_{adj}	0.031	0.198	0.195
Total P-value	0.008	<0.001	<0.001
Unique R^2_{adj}	0.047	0.103	0.125
Unique P-Value	<0.001	<0.001	<0.001

