ALLEN'S RULE IN BEARS: AN INTER- AND INTRASPECIES ANALYSIS IN THE URSINAE SUBFAMILY

Daniel Babnigg

I. INTRODUCTION

Allen's rule states that groups of closely allied endothermic species with large geographical ranges show a decreasing relative extremity size with increasing latitude (Allen 1877). This trend is traditionally explained by selection and plasticity to optimize for thermoregulation in an environment (Alho et al 2011). While ecogeographical rules like Allen's rule are sometimes contested and unsupported, they can still provide potential context on how climate can induce morphological constraints on an organism (Nudds and Oswald 2007).

There are no detailed studies on Allen's rule in bears, *Ursidae*, which is a family of species that have a widespread geographic range and therefore thrive in a variety of climates and temperatures. The species in the *Ursinae* subfamily of *Ursidae* includes polar bears (*Ursus maritimus*), brown bears (*Ursus arctos*), American black bears (*Ursus americanus*), Asian black bears (*Ursus thibetanus*), sun bears (*Ursus malayanus*), and sloth bears (*Ursus ursinus*). The *Ursus* genus comprises of polar bears, brown bears, and both species of black bears. **Figure 1** shows the geographic distributions of these species; broadly, the *Ursinae* subfamily spans a large latitude and temperature range, and all species in the *Ursus* genus individually also span large latitudes (Kumar et al. 2017). Bears have already been studied in context to Bergmann's rule, an ecogeographical rule that suggests that animals show larger sizes in colder regions; however, for the widespread brown bears species, size is dependent on proximity to prey, and independent of latitude (Bergmann 1847; Meiri et al. 2007).

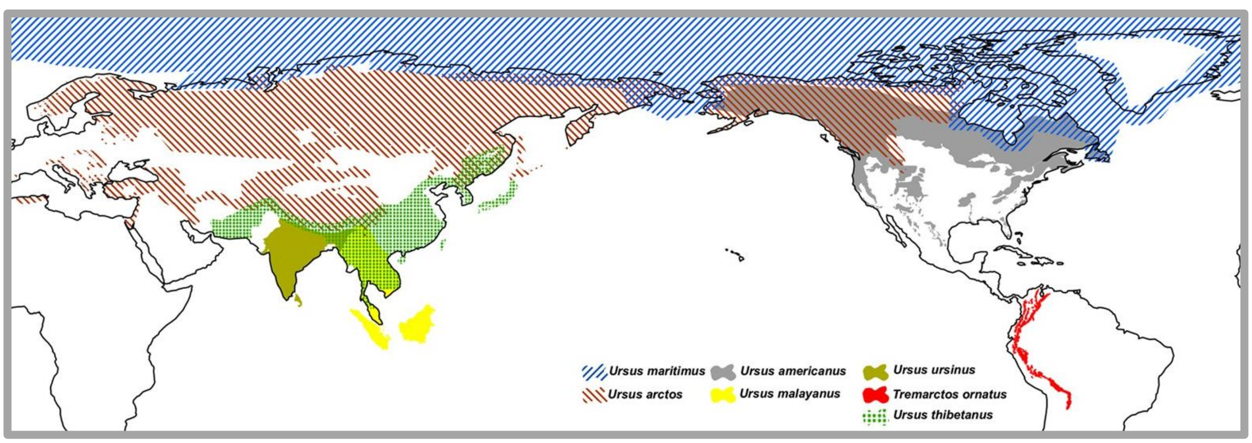

Figure 1: geographic distributions of bear species (Kumar et al. 2017)

This context provides motivation to study Allen's rule in bears, as species of *Ursinae* have large geographic ranges and Bergmann's rule does not consider proportions of extremities like Allen's rule. While Allen's rule can be studied in a single species, larger groups can be considered; for example, studying genera of species, like rabbits or hares, or even families of species, like toucans or penguins, can be well-motivated due to general morphological similarities. Additionally, several ratios and proportions can be used in context to Allen's rule, like tail to head length, or beak to head length (Stevenson 1986; Symonds and Tattersall 2010). With this context, I chose to study the ear to head area ratios of the *Ursinae* subfamily of bears, also separately analyzing the *Ursus* genus and a few species individually. The ear to head ratio is related to Allen's rule because ears are an extremity on bears, and a higher relative surface area of an ear allows for a higher degree of heat transfer; larger ears can dissipate heat faster, which is best for species living in warmer climates (Nudds and Oswald 2007). Correlations and patterns both inter- and intraspecies will be considered, in a dataset of *Ursinae* observations that includes the species of bear, the ear to head area ratios, and the mean annual temperature of a given observation. Statistic based conclusions will be made on bears in context to Allen's rule, and therefore on bears' plasticity and natural selection depending on their climate.

II. METHODS

Before performing analysis, sufficient data must be gathered: ear to head ratio, mean annual temperature, and bear species for each observation. iNaturalist was a good place to collect observations of bears, where citizen scientists can share images of wild organisms, with a crowdsourced species identification system for easy data collection (iNaturalist). To collect images of the *Ursinae* species, I simply searched up the name and filtered results such that they were verifiable, research grade, and wild observations; since results often included bear tracks or feces rather than actual bears, sorting by most liked observations helped bring quality captures of a given species to the first few pages. Only observations that had face-on bears and distinguished ear and head shapes were considered. The map feature on iNaturalist was simultaneously used, to ensure a collection with variation in latitude, and therefore diverse mean annual temperatures.

Figure 2: two example bear observations with marked ear and head areas

Once observations were collected – including the observation images, the bear species, along with the location in latitude and longitude – a macro in ImageJ was used to measure the areas of heads and ears using ellipses consistently and conveniently for each observation. Figure 2 displays a couple bear observation examples, an Asian black bear and a polar bear, with overlaid ellipses representing head and ear areas. Due to bears' morphology, even clear and face-on pictures can present difficulties in distinguishing head and ear areas; to mitigate potential error, the head area was defined as a roughly circular area where the ears met the body while not including the snout or protruding fur on a bear's face, and the ear area was defined as an ellipse that followed the outer edge of the ear again without protruding fur. The Asian black bear in Figure 2 is a demonstration of ignoring protruding fur when looking at area; the red circle indicating area for the head doesn't expand as horizontally as the face appears to be, as area outside of the circle on the face is mostly protruding fur. The ImageJ macro presented a table with ear and head area measurements after ellipses were placed, and these values were copied into a Microsoft Excel spreadsheet with other relevant information for each observation. The actual ear to head area ratio was then directly calculated using Excel.

A single source for mean annual temperature was used: CHELSA bioclimatic variables, which includes yearly and monthly means in temperature and other variables from 1981 to 2010 with a horizontal resolution of 30 arcseconds (Karger et al. 2017). Mean annual temperature data was downloaded as a GeoTIFF file, which is a georeferenced image with metadata that allows for a map projection to be spatially encoded with mean annual temperatures. This file could be loaded into QGIS (an open-source geographic information system) as raster data, along with the bear observations spreadsheet as a csv which include observations' latitudes and longitudes from iNaturalist (QGIS.org). Using QGIS, the raster layer was sampled with the given locations in the bear dataset, which returned a new column with imputed mean annual temperatures. The CHELSA raster data layer along with the bear species csv layer in QGIS is shown in figure 3.

Figure 3: CHELSA raster data and bear data layers in QGIS

A total of 155 observations were recorded using observations from iNaturalist, with calculated ear to head area ratios with the ImageJ macro in Excel and with the mean annual temperature for the location of each observation. A total of around 40 observations were recorded each for American black bears, brown bears, and polar bears; around 20 observations were recorded for sloth bears; and 7 observations were recorded each for sun bears and Asian black bears. Figure 3 additionally displays the geographic distributions of the collected data, with the goal of having latitude and therefore temperature data being varied as much as possible for a given species.

Allen's rule suggests an ear to head ratio dependance on mean annual temperature, so a regression analysis was used to test for indication of the rule. Python code along with various libraries were used to load data, implement visualizations, and compute variables from a regression analysis (Harris et al. 2020; Hunter 2007; McKinney et al. 2010; van Rossum 1995; Virtanen et al. 2020). This analysis used a linear least-squares regression to calculate a Pearson correlation coefficient R, with the square of R being the coefficient of determination. A p-value was also calculated, with a null hypothesis that the regression slope is 0, using the Wald test and two-sided t-distribution of the test statistic (Wald 1943). The results were cross-checked with data analysis in Excel to ensure consistency across regression analyses.

III. RESULTS

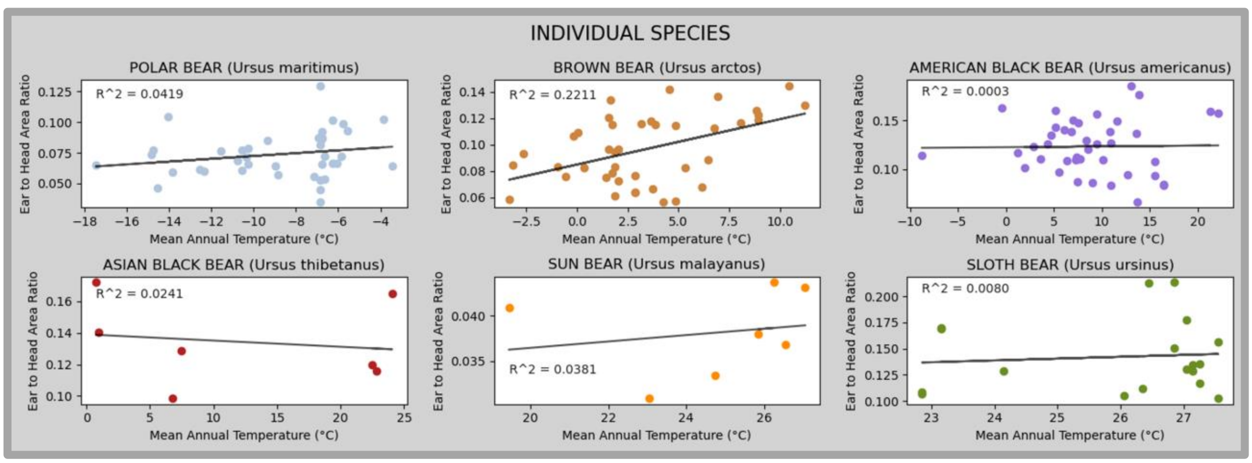

Figure 4: Regression analyses on each species of *Ursinae*

Figure 4 shows the data points for each species individually – the observation's mean annual temperature and ear to head area ratio – and overplots a linear least-squares regression line, along with the coefficient of determination, R^2. The Pearson correlation coefficient, R, for the brown bear species was 0.47, with a p-value of 1.92E-3; this suggests a weak positive correlation between the variables. For other species, the absolute value of the correlation coefficient was under 0.25, and the corresponding p-value was above 0.05; this suggests no correlation.

Figure 5 shows all data points, color coded by species, on the same two-dimensional space and axes as the plots in **figure 4**. It overplots a linear least-square regression line, the coefficient of determination, R^2, and the best-fit line equations for both the *Ursinae* subfamily and the *Ursus* genus. The *Ursinae* subfamily regression analysis has a correlation coefficient of 0.427, with a corresponding p-value of 3.01E-8; this suggests a weak to moderate positive correlation. The *Ursus* genus regression analysis has a correlation coefficient of 0.597, with a corresponding p-value of 6.45E-14; this suggests a moderate positive correlation. Note also that the slope is higher for *Ursus*. Residuals, the predicted area ratio given mean annual temperature subtracted from the actual area ratio of an observation, are plotted in **figure 6** for both the *Ursinae* subfamily and the *Ursus* genus from the regression lines. The *Ursus* regression residuals are more consistent, as the best-fit line was not skewed by the high-leverage sun bear datapoints.

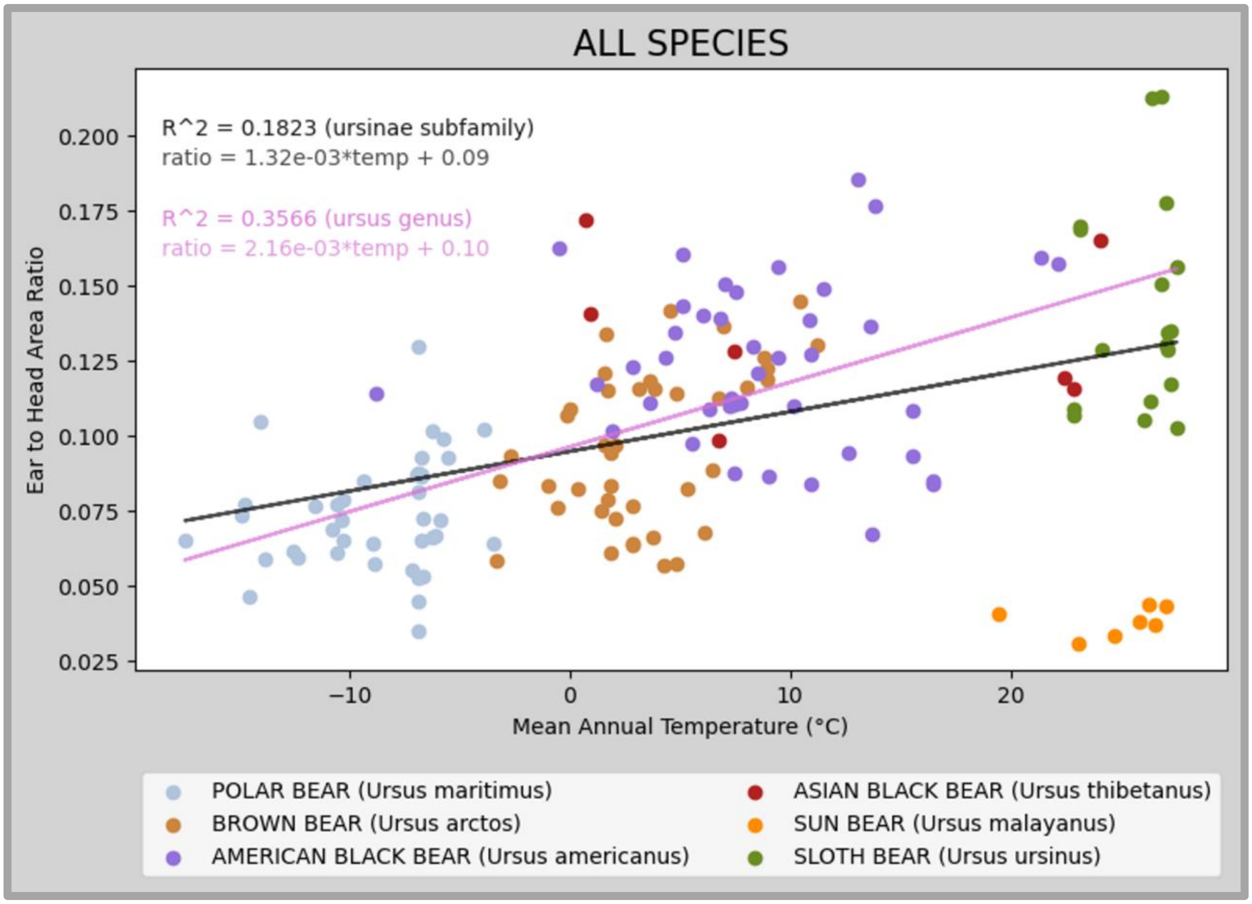

Figure 5: *Ursinae* and *Ursus* datapoints along with regression analyses

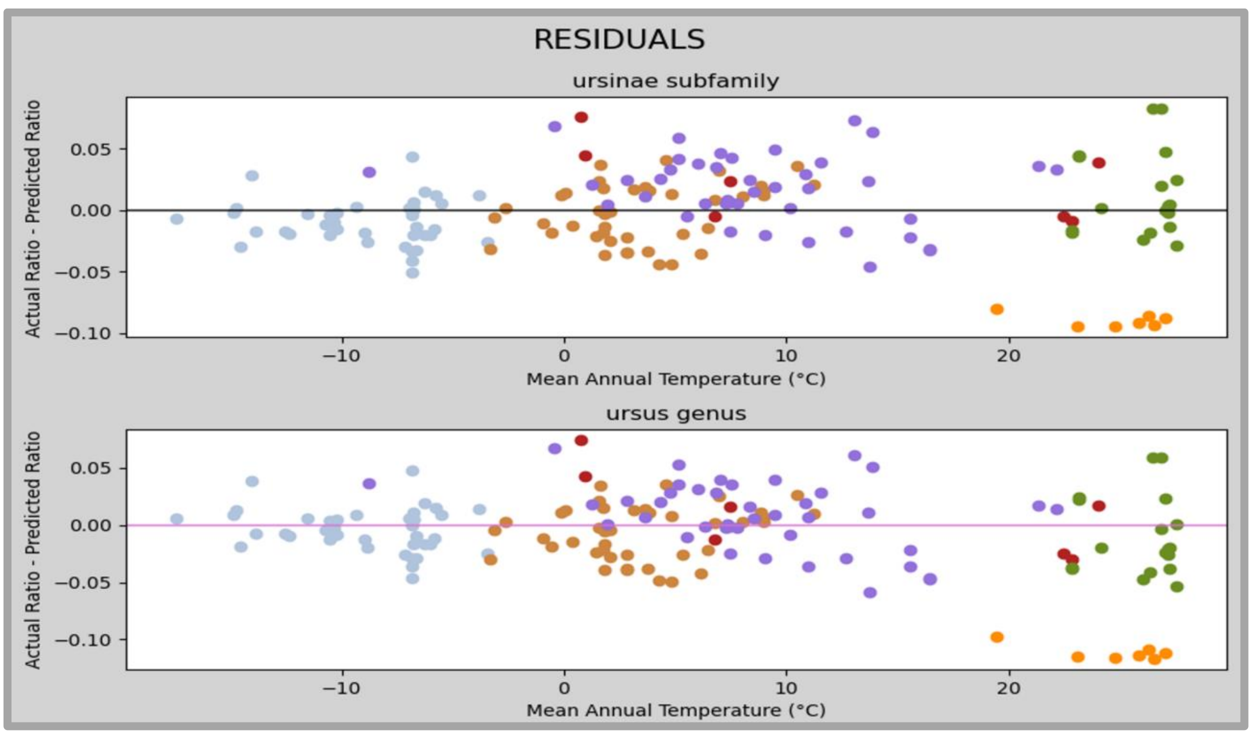

Figure 6: Residuals from the two regression analyses from figure 5

IV. DISCUSSION

According to the results, there is weak to moderate positive correlation between mean annual temperature and ear to head ratios for the brown bear species, the *Ursus* genus, and the *Ursinae* subfamily. These results suggest that Allen's rule holds for these three groupings of bears, with p-values significantly under 5% and weak to moderate positive correlation coefficients. The positive correlations imply that for increasing temperature, the ear to head ratio of a bear increases; this is consistent with Allen's rule. While regression analyses were done for each Asian black bears, sun bears, and sloth bears, the regression results cannot be as conclusive when compared to species with both high amount of datapoints and temperature variation like polar bears, brown bears, and American black bears. Low amount of data was due to lack of quality observations on iNaturalist for especially sun bears and Asian black bears, and low temperature variation for the sun bear and sloth bear was due to relatively small geographic ranges. However, these species' datapoints can still hold value and give additional context in the larger groupings of *Ursus* and *Ursinae*, where Allen's rule does indeed hold for both the genus and the subfamily. This can even be seen visually in **figure 5**; the species' datapoints, excluding sun bears, qualitatively seem to move up in ear to head ratio as mean annual temperature increases – and the statistics back this claim up.

There are many potential sources of error for this dataset. Consistency in measuring the ear to head ratios correctly was likely a significant source of error; this is partly due to bears' morphology, where it is often difficult to distinguish head and ears for even the highest quality images with extraneous fur on ears and faces along with inconveniently large bodies behind a face-on head. As described in the methods section, steps were taken to ensure consistency; even if the ratios themselves were always under or over-predicting, a regression can still be concluded with a systematic inaccuracy in ratios. Smaller sources of error on ratio measurement include sexual dimorphism and age; in a paper describing sexual dimorphism in polar bears, there were significant differences in body mass, body length, head length, and head width when using a sample of captured and measured bears (Derocher et al. 2005). This systematic error also shows variation over different species, age, and occasionally latitude, which complicates things further (Cameron et al. 2020). Observation mean annual temperature may have also induced some errors, as it comes from a dataset that uses interpolation and sampling to model empirical data; however, these errors likely did not have an impact on the correlation due to higher systemic errors in ratio measurement. In general, using a large set of datapoints helped mitigate the errors, and allow for more well-motivated conclusions on the regression analysis findings.

A clear outlier in **figure 5** is the sun bear, where the observations had characteristically low ear to head area ratios for the temperature range they were observed in when compared to the other species in the *Ursinae* subfamily. This extremity creates reason to explore an important distinction – that ear to head area ratio is not the only indicator of Allen's rule, and that Allen's rule is not the only way to relate morphological aspects with heat dissipation. Sun bears can still dissipate heat favorably in their geographic range, despite their ears being relatively small – sun bears do not have underfur like other bears and are the smallest bear species (Huber and van Manen 2019). Smaller volumes have more relative surface area to radiate off heat, and a lack of underfur also allows for easier heat dissipation – both optimal for the warm climate where sun bears live. This is to say that it is not surprising that correlations were not found in some instances in this study, and that outliers can be expected as ear to head ratios and Allen's rule are only a small part of the context on how climate constrains morphology on bears.

If the scope of this project were expanded, this study could include collecting more data, by taking images of the selected species of bears from other resources rather than just iNaturalist. More data can help better prove or disprove Allen's rule in each subgroup of bears, with a higher statistical confidence. Additionally, other indicators of Allen's rule – for example, body length compared to leg length – could be included to induce a better understanding of whether Allen's rule generally is seen for bears in other ways. Although beyond the scope of a project using just images, correction for errors could also lead to an improved comprehension. However, the correlation results within the collected dataset are statistically real and suggests that Allen's rule is seen for brown bears, the *Ursus* genus, and the *Ursinae* subgroup. This study adds to the literature about plasticity, natural selection, and morphological constraints all induced by the various climates in which the subfamily *Ursinae* of bears live within.

Project GitHub: https://github.com/babnigg/UCHI_PROJECTS/tree/main/BIOS_10140

WORKS CITED

Alho JS, Herczeg G, Laugen AT, RäSänen K, Laurila A, Merilä J. 2011. Allen's rule revisited: quantitative genetics of extremity length in the common frog along a latitudinal gradient. Journal of Evolutionary Biology. 24(1): 59–70.

Allen, JA. 1877. The Influence of Physical Conditions in the Genesis of Species. Radical Review. 1: 108-140.

Bergmann C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien. 3(1): 595–708.

Cameron MD, Hilderbrand GV, Joly K, Schmidt JH, Gustine DD, Mangipane LS, Mangipane B, Sorum MS. 2020. Body size plasticity in North American black and brown bears. Ecosphere. 11(8): Article e03235.

Derocher AE, Andersen M, Wiig Ø. 2005. Sexual Dimorphism of Polar Bears. Journal of Mammalogy. 86(5): 895–901.

Harris CR, Millman KJ, van der Walt SJ, Gommers R, Virtanen P, Cournapeau D, et al. 2020. Array programming with NumPy. Nature. 585: 357-62.

Huber Đ, van Manen FT. 2019. Bear Morphology. Encyclopedia of Animal Cognition and Behavior.

Hunter JD. 2007. Matplotlib: A 2D Graphics Environment. Computing in Science & Engineering. 9(3): 90-95.

iNaturalist. Available from https://www.inaturalist.org. Accessed 2024.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder P, Kessler M. 2017. Climatologies at high resolution for the Earth land surface areas. Scientific Data. 4: 170122.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder P, Kessler M. Data from: Climatologies at high resolution for the earth's land surface areas. Dryad Digital Repository.

Kumar V, Lammers F, Bidon T, Pfenninger M, Kolter L, Nilsson MA, Janke A. 2017. The evolutionary history of bears is characterized by gene flow across species. Scientific Reports. 7: Article 46487.

McKinney W et al. 2010. Data structures for statistical computing in python. In Proceedings of the 9th Python in Science Conference 445: 51–56.

Meiri S, Yom-Tov Y, Geffen E. 2007. What determines conformity to Bergmann's rule?. Global Ecology and Biogeography. 16: 788-794.

Nudds RL, Oswald SA. 2007. An Interspecific Test of Allen's Rule: Evolutionary Implications for Endothermic Species. Evolution. 61(12): 2839–2848.

QGIS.org. 2024. QGIS Geographic Information System. QGIS Association.

Stevenson RD. 1986. Allen's Rule in North American Rabbits (Sylvilagus) and Hares (Lepus) Is an Exception, Not a Rule. Journal of Mammalogy. 67(2): 312–316.

Symonds MR, Tattersall GJ. 2010. Geographical variation in bill size across bird species provides evidence for Allen's rule. Am Nat. 176(2):188-97.

Virtanen P, Gommers R, Oliphant TE, Haberland M, Reddy T, Cournapeau D, Burovski E, Peterson P, Weckesser W, Bright J, van der Walt SJ, Brett M, Wilson J, Millman KJ, Mayorov N, Nelson ARJ, Jones E, Kern R, Larson E, Carey CJ, Polat İ, Feng Y, Moore EW, VanderPlas J, Laxalde D, Perktold J, Cimrman R, Henriksen I, Quintero EA, Harris CR, Archibald AM, Ribeiro AH, Pedregosa F, van Mulbregt P, and SciPy 1.0 Contributors. 2020. SciPy 1.0: Fundamental Algorithms for Scientific Computing in Python. Nature Methods. 17(3): 261-272.

van Rossum G. 1995. Python tutorial, Technical Report CS-R9526. Centrum voor Wiskunde en Informatica (CWI).

Wald A. 1943. Tests of Statistical Hypotheses Concerning Several Parameters When the Number of Observations is Large. Transactions of the American Mathematical Society. 54: 426-482.