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Morphological comparison of two populations of Peromyscus maniculatus gambelii from the timberline of Mt. Shasta, California

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MORPHOLOGICAL COMPARISON OF TWO POPULATIONS OF *PEROMYSCUS MANICULATUS* GAMBELII FROM THE TIMBERLINE OF MT. SHASTA, CALIFORNIA

A THESIS

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INTRODUCTION

Ernst Mayr (1963:235) defines a subspecies as follows:

> A Subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the same species.

Inger (1961) discusses the problem geographically localized subdivision of the range brings to the concept. He gives examples where two named subspecies have broadly overlapping ranges, but upon examination turn out to be sympatric species. Some authors have named individual variates (Mayr, 1969); others have applied the term subspecies to sibling species or local populations.

Wilson and Brown (1953) elaborate on three areas of controversy that reduce the effectiveness of the subspecies concept: (1) discordant variation, (2) polytopic subspecies and (3) the arbitrary limits of the definition.

Discordant variation is a condition where character "A" may vary from north to south while character "B" varies east to west. Thus, at any one point in the range there may be great geographical variation, yet no coincidence in the regions of change of the various characters.

The term polytopic subspecies describes a condition where pheotypically similar population reoccur in geographically separate areas. Mayr, Linsley and Lusinger (1953) would describe polytopic subspecies as a single subspecies, while Inger (1961) sees their geographical isolation as indicative of more than one subspecies.

The last comment of Wilson and Brown (1953) was about the arbitrary limits of the subspecies definition. This leaves the researcher with no real boundary at the ends of the subspecific category. Any arbitrary amount of variation established cannot take into account samples with vague, untrustworthy characters falling above fixed limits while samples with often striking differences may fall below these limits.

Although the case built by Wilson and Brown (1953) does bring out the problems with the subspecies concept, few researchers (Blair, 1961) would agree with their final conclusion that it should be eliminated. Orr (1971) states that although the subspecies category is subjective, it does serve to express a concept.

The deer mouse *Peromyscus maniculatis* is a prime example of a mammal exhibiting a high degree of subspeciation. The pattern of variation in this species is known more completely than that of any other wild mammal (Fox, 1948). The large number of subspecies, as well as the abundance of animals in many situations, diversity of habitats and ease with which forms can be maintained and used in the laboratory makes this species of special value for study (Dice, 1968).

Pelage color and body dimensions are among characters used to distinguish subspecies (Dice, 1941). For example, *P.m. rubidus* is a very dark form found along the California and Oregon coast, while a lighter subspecies, *P.m. sonoriensis*, is found in the dry regions east of the Cascades and Sierras (Dice, 1941). In between, both geographically and colorwise, is a third subspecies, *P.m. gambelii* (Dice, 1941). Dice examined such body dimensions as tail length, total body length, hind foot length, length of the mandible, condylo-premaxillary skull length and other skull measurements. The only consistant difference he found between P.m. rubidus and its neighbors in body dimensions was in tail length. He also found that P.m. gambelii might be slightly smaller than P.m. sonoriensis, but his work did not show it conclusively as the original subspecies describer, Osgood (1909), claimed.

Dice (1941) found large, significant amounts of variation within individual subspecies of P. maniculatus. Therefore, within the range of a subspecies, there could be large amounts of variability. Yet the subspecies seem to be distinguishable from one to the next. Sumner (1932) found that mice from Calistoga, California within the range of P.m. gambelii more closely resembled P.m. gambelii from La Jolla, California, 500 miles to the south, than they did mice from Duncan Mills, California in the range of P.m. rubidus, only 27 miles to the west. This is more striking because there is no geographic barrier intervening between Calistoga and Duncan Mills. Dice (1940a) states that different genes can cause the same character. The fact that the mice from La Jolla and the mice from Calistoga have the same pelage color could be caused by the action of different genes in each population.

Another problem with the subspecies concept is whether major chromosomal races should be considered as separate subspecies even if there is a high degree phenotypic similarity among the races. It appears that this is not being done, but researchers do use the term chromosomal race, referring to organisms with similar karyotypes. Using techniques described by Nadler (1964) chromosomes can be examined to determine the similarity of karyotypes between populations. Bowers, et al. (1972)

examines the evolutionary relationships among different species of Peromyscus using karyotypes. He concludes that this type of research will enhance understanding of systematics of the species and will be another tool the researcher can use to determine to which subspecies a particular population belongs.

Doutt (1961) raises further questions about subspecies: (1) How much variation is to be expected as regards sex, age and locality? (2) What does this variation mean taxonomically? (3) What is the significance of rapid changes in populations?

Dice (1938), in a discussion of the above points, considers two populations to differ in a measurement if the means, plus or minus one standard error, do not overlap. He mentions no exact quantitative method of determining how many differing measurements it takes for two populations of Peromyscus to be distinct from one another. Fox (1948) in a similar study uses the same methods to distinguish one population from another. In the past 20-30 years methods of statistically determining significant differences among populations have become more sophisticated. Genoways and Jones (1971), for example, using multivariate analysis, are able to provide a more quantitative assessment of the similarity and dissimilarity of several populations.

Doutt's (1961) third point is that if a population can undergo change in a matter of years or decades, are we dealing with a new subspecies every time statistically significant changes are found? He discusses a study (Ford, 1945, in Doutt, 1961) in which a butterfly subspecies changed quite significantly in a matter of 5 to 10 years. Johnson and Sealander (1964) found morphological variation in distinct geographical populations of house sparrows but felt it did not warrant new subspecific designations because of the short period of time involved.

Doutt (1961) discusses a study of *Microtus* he has been trying to complete in which a comparison is to be made of two collections in the same locality separated by 25 to 50 years. This temporal problem in subspecific systematics is relatively unexplored within mammals; however, see Christianson (1967). Doutt (1961) states that he hopes other researchers will explore the time it takes various species to recognizably change. He concludes his discussion of this issue by suggesting that populations differing only in time and being significantly different not be named different subspecies, but simply that one should indicate that the populations vary over short periods of time.

From the above discussion it can be seen that there are many factors the taxonomist must consider when deciding if he has found a new subspecies. Morphology, ecology, location, karyotype, as well as time of collection are all important. Because some researchers weigh the above factors differently, the final judgement of subspecies is always subjective. In the following pages I have explained the factors I feel are important in the subspeciation of *Peromyscus maniculatus*.

The purpose of this study is to compare two populations of *Peromyscus maniculatus gambelii* from the same location, separated by about 80 years in an attempt to determine the degree of dissimilarity between them.

MATERIALS AND METHODS

Materials

A total of 204 specimens of *Peromyscus maniculatus gambelii* were examined in the course of this study. Of these, 84 were collected between 1892 and 1897 by R.T. Fisher, W.K. Fisher, W.H. Osgood and V. Bailey, all working for the U.S. Department of Agriculture. These 84 are presently housed in the United States National Museum in Washington D.C. Most of these specimens are represented by a skull and a study skin. The remaining 120 specimens were collected between 1972 and 1974 by Dr. Lee Christianson of the University of the Pacific and the author and are in the mammal collection at the University of the Pacific in Stockton, California. The specimens collected in the 1890's will be termed "old" population and the recent specimens will be called "new" for the remainder of this discussion.

Description of the Study Area

"Old" and "new" specimens were collected at the timberline of Mt. Shasta, California, on the south side. The habitat was primarily lodgepole pine. Mt. Shasta is of volcanic origin, and the rock in the study area was pumice and grey in color. The collection areas were in the open rocky locations at an elevation of about 7550 feet. To the best of my knowledge, there has been little environmental change in the collection area in the past 80 years.

Age Determination

The specimens were divided into six age groups based on visible wear to the upper molars according to a method of Christianson (1967) as follows:

Group 1: Third molar erupted, but not at height of first and second molar.

Group 2: Third molar at height of other two, but no visible wear.

Group 3: Slight wear apparent on third molar.

Group 4: Wear apparent on all molars.

Group 5: Extreme wear on all molars, cups partially worn off.

Group 6: All molars extremely worn, all cups completely worn off.

As far as I am aware, there has been no work done correlating exact chronological age with the above type of skeletal measurements on small mammals found in the wild.

Measurements

Standard external measurements were taken on the specimens collected before skin preparation; however, since they were taken by different individuals, they were not used in the analysis. There is no method of checking consistancy from one collector to the next with skins that are 80 years old.

Nineteen cranial measurements (adapted from Cockrum, 1962) were made on each specimen. All were made with the same dial micrometer to the nearest 0.01 millimeter. A dissecting microscope was used as an aid for the proper positioning of the micrometer calipers. If a specimen was so damaged as to make a particular measurement inaccurate or impossible, that measurement was omitted. The following is a list of the measurements used in this study and their abbreviations:

Condyle-premaxillary length (Condpr)--The distance from the posterior margin of an occipital condyle to the anterior part of the premaxilla on the same side.

Basilar length (Basil)--The distance down the midline of the skull of a line connecting the posterior edge of the alveoli of the upper incisors to the anterior edge of the foramen magnum.

Length of the maxillary tooth row (Maxtoo)--Distance from the anterior alveolus of the anterior molars to the posterior alveolus of the posterior molars.

Length of the maxillary diastema (Diast)--Greatest distance from the posterior bases of the upper incisors to the anterior edge of the first upper molar on the same side.

Palatilar length (Palat)--The distance from the posterior most extension of the palatine bone, along a midventral line, to the posterior bases of the upper incisors.

Postpalatal length (Pstpal)--The distance, in a midventral line from the anterior margin of the foramen magnum to the posteriormost extension of the palatine bone.

Greatest breadth across the upper molars (Brmol)--The greatest distance from the buccal side of the upper left molars to the buccal side of the upper right molars.

Mastoid breadth (Mastd)--The greatest width of the skull across the mastoid processes.

Length of the palatal bridge (Palbr)--The length of a line connecting the posterior margins of the anterior palatine foramina to the posterior extension of the palatine bones as measured along the midline of the skull.

Nasal length (Nasln)--Greatest anterior-posterior length of the nasal bones.

Frontal length (Front)--Greatest anterior-posterior length of the frontal suture.

Nasal width (Naswd)--Greatest distance across the nasal bones as measured perpendicular to the midline of the skull.

Zygomatic breadth (Zygomb)--Greatest distance between the outside margins of the two zygomatic arches perpendicular to the midside margins of the two zygomatic arches perpendicular to the midline of the skull.

Least interorbital constriction (Intero)--The least distance across the skull on the dorsal surface between the orbits.

Cranial breadth (Cranbr)--Greatest distance across the braincase immediately posterior to the zygomatic arches and perpendicular to the midline of the skull.

Condylo-aveolar length of mandible (Camand)--The greatest distance from the posterior margin of the alveolus of the lower incisor to the posteriormost extension of the mandibular condyle on the same side.

Mandibular tooth row (Mandth)--The greatest distance from the anterior margin of the first molar to the posterior margin of the third lower molar on the same side as measured from the alveolus.

Mandibular diastema (Manddi)--The greatest distance from the posterior margin of the alveolus of the lower incisor to the anterior margin of the first lower molar on the same side.

Methods of Analysis

Age and sex variation were examined using pairwise t-tests on each measurement. Of the 19 skull measurements made, five showed significant variation with age and four were missing on a large number of individuals (see Table 1). These nine measurements were omitted when a multivariate analysis was done. Skulls with any missing data in the remaining 10 measurements were excluded. This left 33 skulls in the "old" population and 47 in the "new" population. Then 33 were selected at random from the "new" population, thus equalizing both samples. A Principle Component Analysis was done on convariance matrices generated from those 10 variables. To increase the sample size to 48, three additional measurements were dropped, leaving a total of seven and the Principle Component Analysis was repeated. There were 33 skulls with complete data in 10 characters and 48 skulls with complete data in seven characters. See Table 2 for the lists of the two groups.

Computations were performed on the Burroughs B6700 computer at the University of the Pacific Computer Center in Stockton, California. Correlation matrices generated by SPSS (1975) Factor were manually converted into covariance matrices and a Principle Component Analysis was carried out using Numerals Numerical Analysis Program Library, subroutine Eigenvectors. All pairwise comparisons were made with Student t-tests using SPSS (1975) Breakdown. A significance level of 0.05 is to be assumed unless otherwise stated.

TABLE 1

A Comparison of Two Populations of *P. maniculatus* Showing Age Variation Between Christianson (1967) And This Study

Measurement	Significant in Christianson (1967)	Significant in This Study
Mastoid Breadth	X	
Nasal Length	X	
Nasal Width	X	
Condylo-Promaxillary Length	X	
Basilar Length	X	
Maxillary Diastema	X	
Mandibular Diastema	X	
Palatilar Length	X	X
Postpalatal Length	X	X
Molar Breadth, Uppers	X	X
Zygomatic Breadth	X	X
Condyl-Aveolar Length, Mandible	X	X

Table 2: Results of the Principle Component Analysis of *Peromyscus maniculatus gambelii* from Mt. Shasta, California

	From 10 by 10 Matrix									
Eigenvalue % of Variation	53%	22%	19%	2%	1%	1%	0%	0%	0%	1%
Eigenvalue	470.44	196.51	173.03	18.50	11.73	9.31	2.43	1.18	3.78	2.43
Measurements:										
Condpr	1.00	-.30	.09	-.03	.02	-.09	.04	.01	-.03	-.03
Basil	.22	1.00	-.82	-.18	.02	-.03	.04	-.01	-.03	.01
Maxtoo	.02	.05	-.01	.25	.10	.04	.33	-.06	1.00	-.51
Masdt	.05	.13	.00	.94	-.87	-.24	-.36	-.16	.08	.40
Pariet	.00	.11	.01	1.00	1.00	-.32	-.05	.04	-.08	-.09
Naswd	.03	.04	.00	.16	-.08	.15	-.03	1.00	.14	.23
Cranbr	.09	.83	1.00	-.15	.02	.03	-.03	-.01	-.01	-.02
Intero	-.02	.04	.04	.46	-.36	.07	1.00	.04	-.47	1.00
Manddi	.04	-.01	.02	.03	.35	.34	.30	-.22	.30	-.28
Diast	.09	.05	-.05	.46	.05	1.00	-.31	.10	-.14	-.28

	From 7 by 7 Matrix						
Eigenvalue % of Variation	65%	18%	8%	2%	1%	5%	1%
Eigenvalue	130.67	36.81	15.71	4.30	2.55	9.39	3.03
Measurements:							
Maxtoo	1.00	.00	.00	.00	.00	.00	.00
Masdt	.00	.06	-.22	.85	-.42	1.00	-.18
Pariet	.00	.19	.08	1.00	1.00	-.35	-.02
Cranbr	.00	1.00	-.50	-.25	-.05	-.08	-.03
Intero	.00	.15	.23	-.17	.33	.55	1.00
Manddi	.00	-.05	-.21	.64	-.83	-.67	.57
Diast	.00	.45	1.00	.15	-.46	-.06	-.17

RESULTS AND DISCUSSION

Age Variation

The few specimens available in age groups 1, 2 and 6 made it necessary from the onset to exclude these age groups from further analysis.

All 19 cranial measurements in the "old" population showed no age variation in groups 3, 4 and 5. Christianson (1967), while finding groups 5 and 6 to be statistically indistinct, found significant differences between groups 3, 4 and 5.

Christianson (1967) found little or no variation in seven of his measurements (see Table 1). Dice (1940b) and Christianson (1967) found that mice got progressively larger in age groups 3, 4 and 5. Fox (1948), studying samples of _P. maniculatus_ along the Columbia River, found no age variation in specimens showing at least slight wear on the last molar. This would correspond to age groups 3, 4, 5 and 6 in my study.

On the basis of my data it was decided to lump age groups 3, 4 and 5 in the "old" population into one group for the Principle Component Analysis.

Since 14 of the 19 cranial measurements in the "new" population showed no significant age variation, groups 3, 4 and 5 were also lumped together and treated as one group for further analysis. Christianson (1967), however, found significant age variation in 12 of his 19 measurements. Five of the measurements showed significant age variation in both studies (see Table 1, Figure 1). None of these five measurements were used in the Principle Component Analysis.

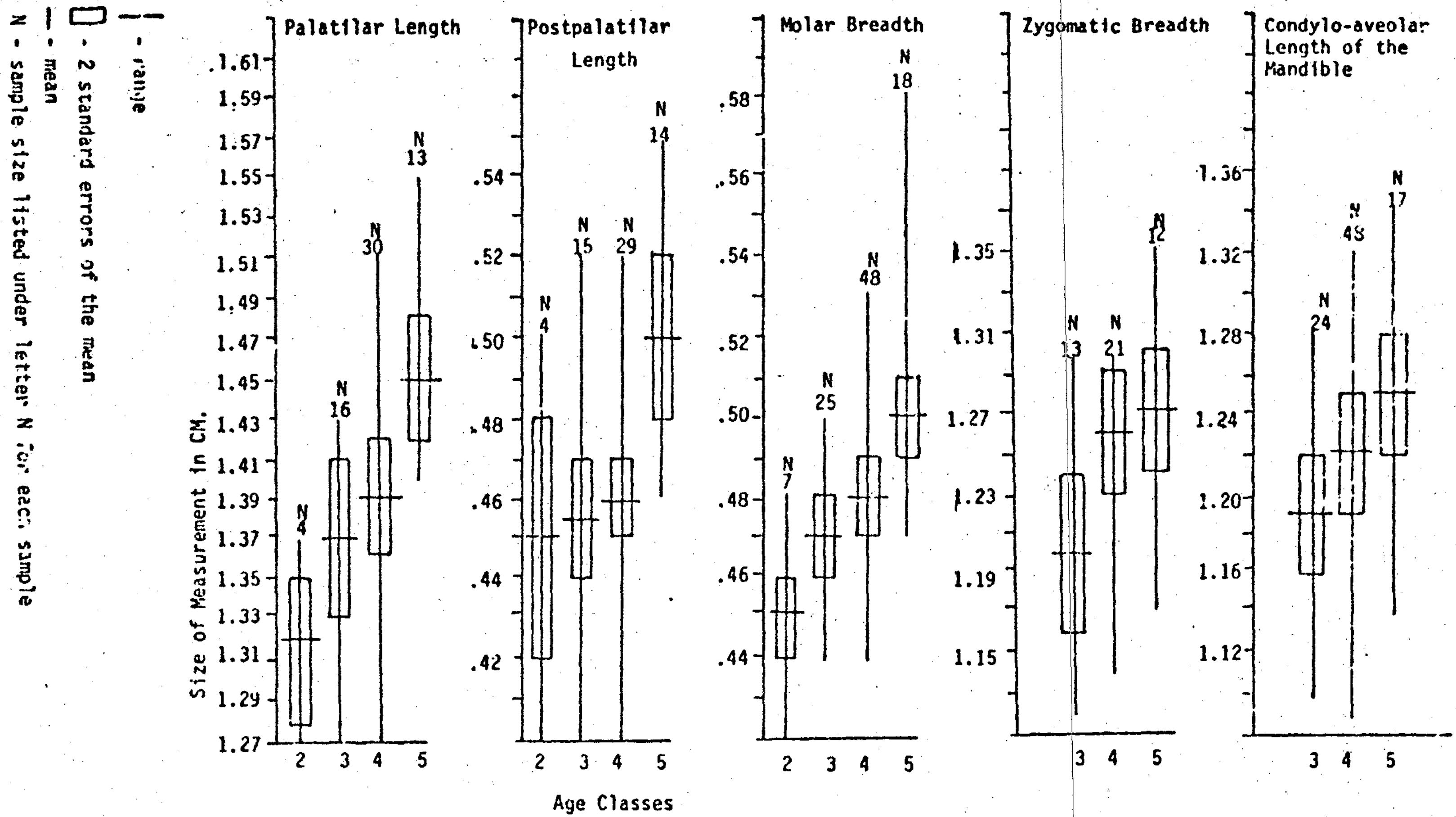


Figure 1: Age variation in P. *maniculatus gambelii* from the timberline of Mt. Shasta collected between 1972 and 1974.

Sexual Variation

Fox (1948) studied sexual dimorphism in several subspecies of Peromyscus maniculatus (P.m. oreas, P.m. austerus, P.m. rubidus, P.m. gambelii, and P.m. artemisiae) along the lower Columbia River and found a few locations where the female body length was larger than the male by about 4 times the standard error of the mean. In spite of these cases, it was not enough for him to conclude that the males and females needed to be studied separately. Dice (1932) found that in P.m. bairdii the males tend to have slightly larger foot length, weight, length of tail and bullar width than the female. He concluded that the differences were too slight to be significant. Christianson (1967) found a general tendancy for the females to be somewhat larger than the males in age group 4 of the population P.m. rufinus analyzed in Arizona. I found four measurements that showed some sexual variation but no strong patterns or trends. However, the degree of sexual dimorphism appears greater in the two measurements displaying variation in the"old" population than in the two from the "new" (see Figure 2). From the above I have concluded that the females and males need not be studied separately.

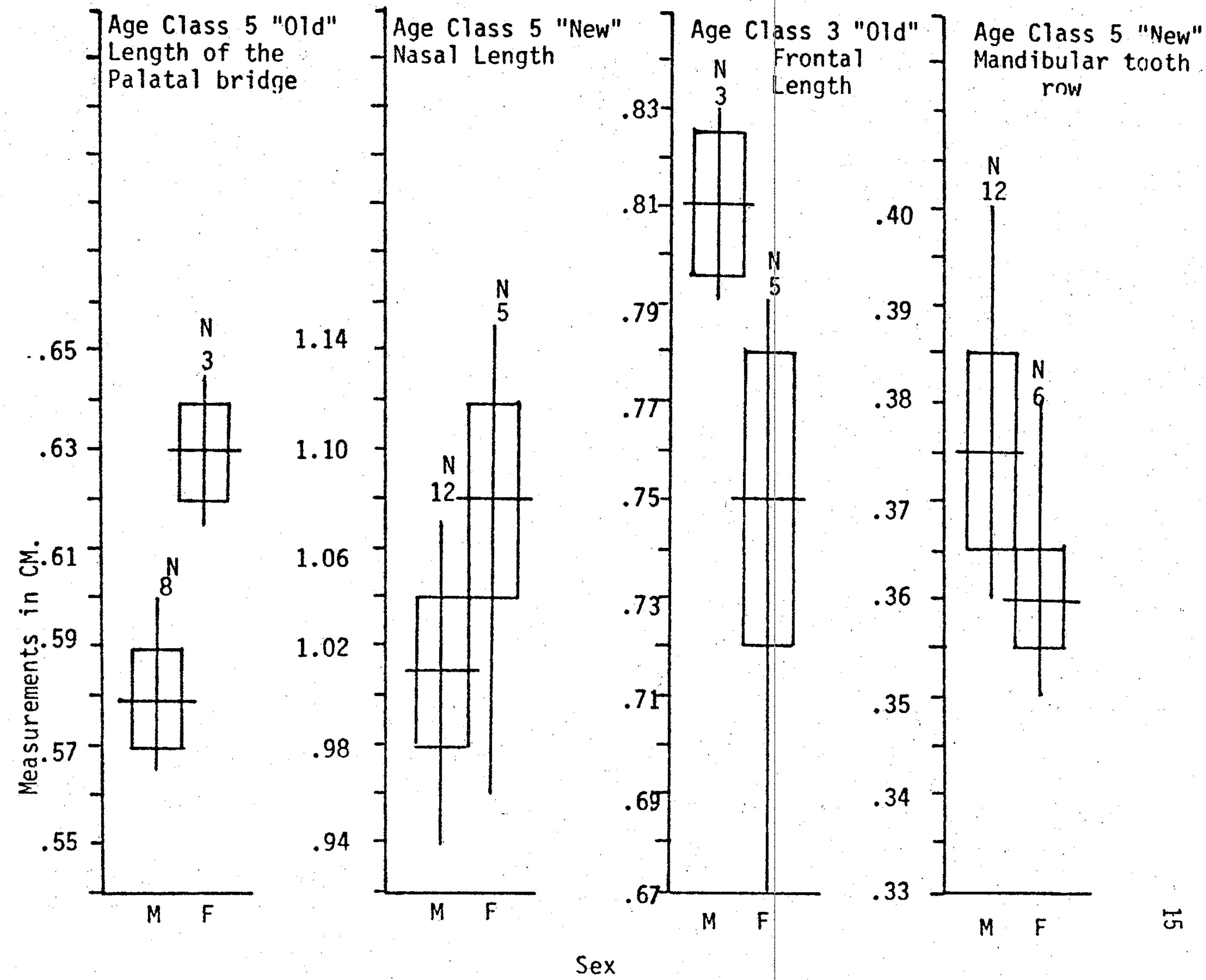


Figure 2: Sexual dimorphism in *P. maniculatus gambelii* from the timberline of Mt. Shasta, California collected between 1891 and 1897 ("Old") and between 1972 and 1974 ("New").

remainder of symbols see figure 1

F- female

M - male

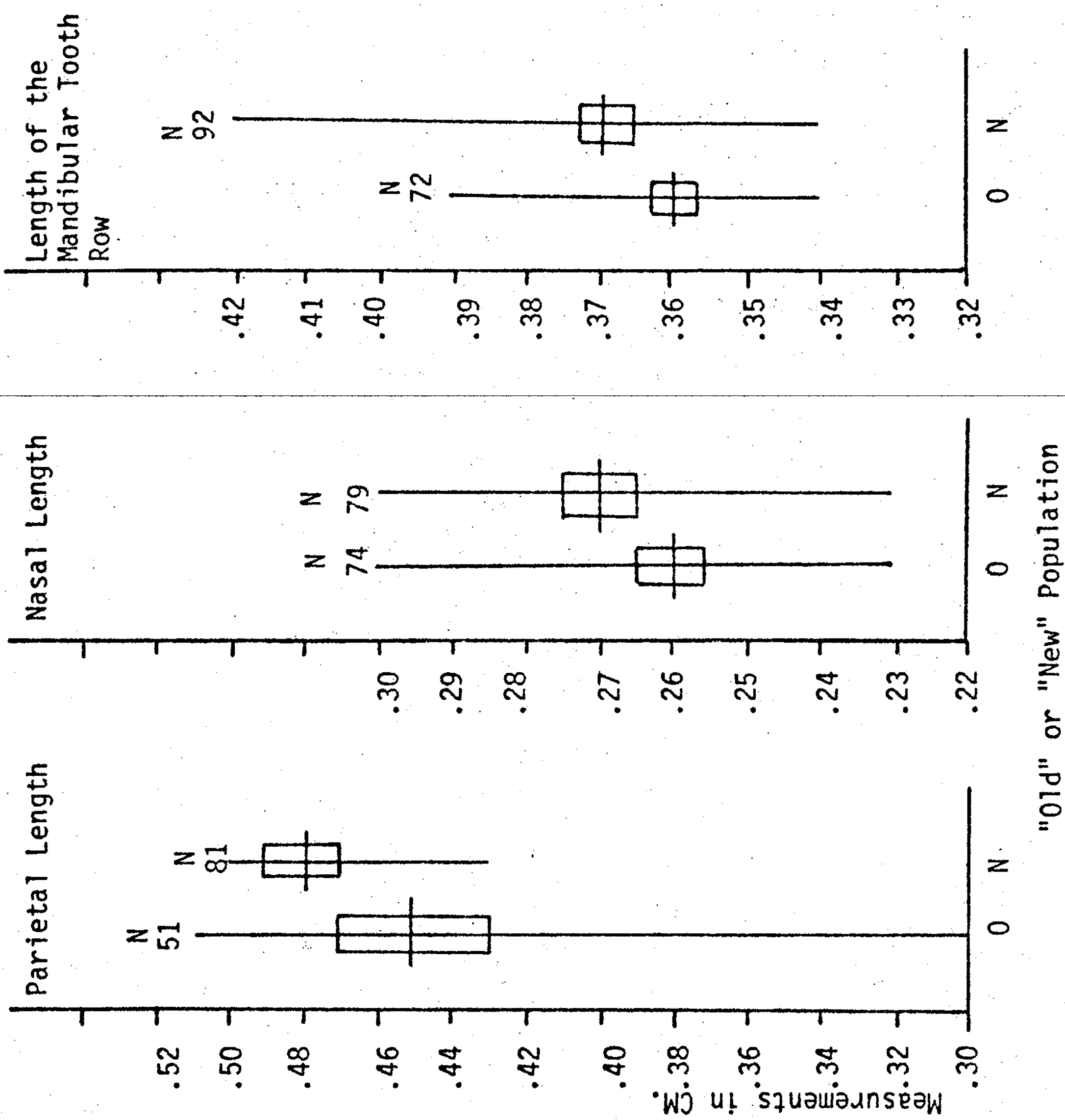
Difference Between "Old" and "New" Populations

Figure 3 illustrates the three measurements that showed significant variation between the "old" and the "new" populations using the Students t-test. These three measurements are parietal suture, nasal width and width of the mandibular tooth row.

Dice (1940c), while studying sychronic allopatric populations, examined the left mandible, condylo-premaxillary length, condylo-zygoma, bullar width of *P.m. bairdii* and *P.m. osgoodi* and found consistantly significant difference in skeletal measurements between the two synchronic populations. He did find large amounts of local variation within the subspecies. Dice (1941) collected data on five subspecies of *P. maniculatus* on the West Coast. Using the same skull measurement as above, there was no consistantly significant variation between them. In certain geographic locations *P.m. rubidus* has a greater bullar width than *P.m. gambelii*, but this is not true throughout the entire range. Also, condylo-zygoma and condylo-premaxilla length have a tendency to be larger in *P.m. rubidus*, but not significantly. Fox (1948) found that the mandibular diastema for *P.m. gambelii* is significantly smaller than that of its neighbors. Osgood (1909) says that one subspecies is different from another by merely having a slightly longer tail and slight cranial differences.

My results are consistant with the amount of skeletal variation found by other researchers. I did find slight cranial differences with three measurements showing significant variation (Figure 3).

The results of the Principle Component Analysis are summarized in Table 2 and Figure 3. Table 2 lists measurements, eigenvalues and their corresponding eigenvectors. Principle components were computed from the covariance matrix between the 10 measurements. The first three



0 - "Old" population

N - "New" population

remainder of symbols, see figure 1

Figure 3: Difference between two populations of P. m. gambelii from the timberline at Mt. Shasta, California collected 80 years apart.

principle components contained 94% of the variation and are thus the ones used in the analysis. The first principle component expressed 53% of the variation with condylo-premaxillary length and basilar length representing the highest reading. These two measurements describe skull length. The second principle component had 22% of the variability and revealed high positive values for mastoid breadth, parietal length, least interorbital constriction and mandibular diastema. These measurements define the shape of the skull. The third principle component shows a contrast between cranial breadth and nasal width.

In the 7 measurement matrix, 83% of the variation was displayed in the first two principle components. The first component had 65% of the variation with the maxillary tooth row being the only factor with high value. The second principle component had 18% of the variation, and, as in the 10 member matrix, parietal length and maxillary diastema length displayed large positive values.

The overall pattern displayed by the information points at the importance of length. It must be pointed out that the 7 member matrix showing only "0.00's" and "1.00" suggests that there might be some unknown problems associated with this particular covariance matrix.

The overall differences I observed appear to be no greater than those commonly found within any one subspecies (Sumner, 1932). Therefore, considering the results of the Principle Component Analysis along with the pairwise t-tests, the "old" and the "new" populations are too similar to consider designation as separate subspecies.

DISCUSSION AND CONCLUSION

There are several important questions still in need of consideration. The first is, "Why have I decided that the two populations are the same subspecies?"

Earlier researchers (Dice, 1941, Sumner, 1932), while examining the differences between two subspecies, often found only one or two characters that significantly varied between the populations. Those populations, however, usually differed in pelage color, thus making them more easily distinguishable from one another. Further, they were from different localities with different environments and were therefore better suited to Mayr's (1963) definition of subspecies. Later researchers (Genoways and Jones, 1971) used mathematical systems placing all the studied characters into a single Principle Component Analysis. Since (1) my Principle Component Analysis indicated no distinctness between the populations with respect to cranial measurement, (2) the pelage color was not usable and (3) only three individual characters showed variation, I have concluded that the populations do not differ enough in morphology to be considered as separate subspecies.

The second question is, "What amount of variation would I consider necessary to find separate subspecies?" A number of points are important to this issue. As indicated above and in the introduction, a complex of variables is used to separate two subspecies. However, the final conclusion rests with the subjective views of the party making the decision. It is a decision based on morphology, location, karyotype, type of collection and the environment where collected. This leads me to the conclusion that any decision based only on a pairwise testing of individual characters would be invalid.

The last question is, "Is it possible that the two populations should be considered as one subspecies even if they had been found to be statistically distinct?" As discussed above, morphological variation cannot be the only criteria for the subspecies. My study differs from that of Dice (1941) and Fox (1948) because they were studying populations in different environments, while I could find little evidence that the environment of Mt. Shasta had changed in the past 80 years. I could find no record of logging, volcanic action or other factors which would alter the environment and therefore influence natural selection. It appears that the major reason behind any large scale change must be random genetic drift. If the environment is the same, I am resistant to the idea of two separate subspecies.

To view the subspecies in this broad ecological framework does not over burden the literature with new forms every time a researcher finds significant morphological changes. In my opinion, to view the subspecies as an ecologic unit, taking into consideration the many factors the researcher must weigh in his determination, keeps the concept useful and viable.

SUMMARY

Nineteen cranial measurements were examined in two samples of *Peromyscus maniculatus gambelii* from the timberline at Mt. Shasta, California. One sample ("old") was a collection made between 1892 and 1897, and the other ("new") was taken between 1972 and 1975.

Age groups were assigned by observing tooth wear. There was little significant variation between the age groups. Significant sexual dimorphism was found in only a few cases.

A Principle Component Analysis revealed no significant differences between the two populations. Parietal length, nasal length and length of the mandibular tooth row differed significantly between "new" and "old" samples.

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Appendix A: Comparison of measurements for two populaions of _Peromyscus maniculatus gambelii_ collected between 1892-1897 ("Old") and 1972-1974 ("Old") at timberline of Mt. Shasta, California.

	AGE: 3				AGE: 4				AGE: 5			
	"OLD"		"NEW"		"OLD"		"NEW"		"OLD"		"NEW"	
	M	F	M	F	M	F	M	F	M	F	M	F
	Condylo-premaxillary length											
N	1	3	7	14	16	16	15	27	5	2	11	3
X̄	24.32	23.48	22.79	22.76	22.86	23.51	23.29	22.13	23.84	24.45	24.11	24.18
Min	-----	22.73	22.32	20.15	21.89	22.17	21.43	21.01	23.34	24.23	22.62	22.97
Max	-----	24.19	24.32	25.02	25.20	24.40	24.46	25.07	24.42	24.67	25.24	25.43
2s	-----	1.04	.86	.71	1.59	.34	.54	.13	.48	.62	.53	1.74
	Basilar Length											
N	3	5	8	16	19	16	14.	24	5	3	11	5
X̄	18.63	18.56	16.75	18.44	18.65	18.86	18.33	18.44	18.97	18.68	18.48	19.52
Min	17.35	18.19	17.13	16.35	17.58	17.87	14.67	17.13	18.07	18.59	18.28	18.55
Max	19.29	19.21	18.78	19.29	19.99	19.49	19.82	20.35	19.56	18.73	20.05	20.69
2s	1.56	.60	.25	.52	.34	.29	.72	.43	.60	.78	1.75	.82
	Length of the Maxillary Tooth Row											
N	3	7	9	16	29	22	18	31	10	3	12	6
X̄	3.46	3.52	3.64	3.57	3.57	3.53	3.55	3.54	3.49	3.50	3.54	3.46
Min	3.41	3.42	3.46	3.34	3.37	3.32	3.51	3.23	3.27	3.47	3.24	3.24
Max	3.52	3.77	3.80	3.76	4.57	3.91	3.82	3.90	3.68	3.55	3.79	3.74
2s	.08	.10	.26	.07	.10	.06	.08	.05	.09	.03	.08	.15
	Length of the Maxillary Diastema											
N	3	8	9	16	28	21	17	30	10	3	12	5
X̄	6.45	6.20	6.25	6.39	6.40	6.54	6.45	6.36	6.74	6.88	6.81	6.78
Min	5.68	5.24	5.92	5.52	5.93	6.07	5.86	5.49	6.43	6.37	6.05	6.58
Max	6.98	6.57	6.61	6.92	7.04	7.07	7.12	7.04	7.00	6.86	7.26	7.23
2s	.96	.32	.16	.22	.12	.13	.19	.15	.12	.38	.19	.26
	Palatilar Length											
N	3	5	5	11	21	19	9	21	6	3	9	4
X̄	14.08	13.94	13.48	13.79	13.93	14.27	13.95	13.82	14.25	14.80	14.57	14.47
Min	13.00	13.22	13.00	12.76	12.83	13.09	12.92	12.73	13.72	14.52	14.05	13.73
Max	14.68	14.54	14.19	14.67	15.24	15.82	14.68	15.12	14.70	14.95	15.17	15.48
2s	1.34	.48	.48	.39	.25	.26	.45	.34	.37	.34	.28	.84
	Postpalatal Length											
N	3	4	4	11	17	17	9	20	4	3	9	5
X̄	4.64	4.51	4.51	4.54	4.56	4.67	4.67	4.55	4.81	4.75	4.91	4.95
Min	4.29	4.02	4.02	3.53	4.22	4.22	4.19	4.00	4.56	4.49	4.57	4.62
Max	.56	4.84	4.71	5.02	5.06	5.16	5.17	5.12	5.06	5.01	5.33	5.48
2s		.22	.38	.28	1.01	.14	.19	.14	.30	.37	.19	.35
	Greatest Breadth Across the Upper Molars											
N	3.	8	9	16	28	20	17	31	10	3	12	6
X̄	4.73	4.74	4.71	4.70	4.80	4.87	4.77	4.80	4.92	4.89	4.98	5.04
Min	4.68	4.42	4.40	4.42	4.58	4.51	4.46	4.43	4.68	4.73	4.83	4.72
Max	4.82	5.04	4.96	4.59	5.16	5.82	5.31	5.26	5.12	5.02	5.22	5.80
2s	.12	.16	.13	.09	.05	.13	.12	.07	.12	.21	.07	.35

Mastoid Breadth												
N	3	5	8	15	22	20	16	31	8	3	12	6
$\bar{X}$	9.81	9.87	9.82	10.00	9.83	9.99	10.09	10.05	10.06	9.97	10.12	10.09
Min	9.40	9.18	9.16	9.41	9.12	9.39	9.69	9.16	9.39	9.63	9.72	9.42
Max	10.32	10.75	10.42	10.46	10.42	11.07	10.52	11.94	10.32	10.20	10.87	10.59
2s	.66	.58	.30	.14	.14	.18	.16	.19	.22	.42	.18	.37
Length of the Palatal Bridge												
N	3	5	5	7	20	19	8	21	6	3	8	3
$\bar{X}$	5.79	5.64	7.28	5.63	5.72	5.82	7.05	5.73	5.82	6.27	5.87	5.72
Min	5.72	5.28	5.43	5.27	5.22	5.32	5.28	5.32	5.73	6.18	5.26	5.18
Max	5.88	6.02	5.81	5.69	6.58	6.18	7.29	6.37	6.02	6.36	6.29	6.15
2s	.16	.28	3.91	.19	.13	.09	2.68	.15	.13	.13	.25	.69
Nasal Length												
N	1	8	8	14	28	21	14	28	9	3	12	5
$\bar{X}$	8.71	9.70	9.56	9.64	9.90	10.03	10.57	9.80	10.15	10.13	10.09	10.77
Min	-----	8.11	9.00	8.40	8.78	9.24	8.75	8.42	9.69	9.38	9.38	9.57
Max	-----	10.62	10.66	11.19	10.86	10.88	10.86	10.87	10.83	10.65	10.71	11.43
2s	-----	.60	.41	.41	.22	.22	1.43	.25	.30	.95	.28	.71
Frontal Length												
N	3	6	9	16	23	20	17	30	8	3	12	6
$\bar{X}$	8.06	7.48	7.76	7.63	7.79	7.76	7.71	7.75	8.18	7.95	8.02	8.03
Min	7.90	6.74	7.22	7.17	7.16	7.22	6.56	6.96	7.12	7.67	7.17	6.80
Max	8.28	7.94	8.94	8.28	8.75	8.42	8.62	8.90	8.63	8.19	9.48	8.79
2s	.28	.36	.38	.19	.20	.23	.24	.19	.38	.51	.38	.66
Parietal Suture Length												
N	3	5	9	16	20	20	17	31	8	3	12	6
$\bar{X}$	4.90	4.88	4.73	4.88	4.51	4.42	4.64	4.57	4.50	4.45	5.26	4.84
Min	4.39	4.53	4.49	4.29	3.82	3.00	4.27	3.24	3.87	4.22	4.47	4.42
Max	5.49	5.24	5.08	5.33	5.12	5.07	5.37	5.17	4.97	4.65	5.54	5.38
2s	.78	.30	.25	.17	.17	.23	.16	.16	.27	.31	.74	.29
Nasal Width												
N	3	8	8	13	29	22	14	27	9	3	12	5
$\bar{X}$	2.44	2.54	2.59	2.63	2.60	2.59	2.72	2.64	2.61	2.70	2.71	2.76
Min	2.41	2.33	2.32	2.38	2.27	2.34	2.41	2.42	2.42	2.58	2.56	2.52
Max	2.48	2.70	2.79	2.80	3.01	2.85	2.99	3.08	2.96	2.89	2.98	2.93
2s	.06	.10	.13	.08	.07	.07	.09	.07	.13	.24	.08	.17
Zygomatic Breadth												
N	2	-----	2	11	7	12	9	12	-----	-----	9	3
$\bar{X}$	11.90	-----	11.73	12.10	12.54	12.57	12.33	12.31	-----	-----	12.63	13.03
Min	11.72	-----	11.24	11.19	12.16	11.73	11.42	11.04	-----	-----	11.72	12.89
Max	12.80	-----	12.22	12.95	12.90	13.52	12.83	13.81	-----	-----	13.22	13.48
2s	.50	-----	1.38	.34	.23	.28	.42	.45	-----	-----	.36	.57
Cranial Breadth												
N	3	5	7	16	19	19	16	30	7	3	12	6
$\bar{X}$	11.27	11.45	13.23	11.29	11.37	11.29	11.39	11.35	11.43	11.58	11.55	11.49
Min	10.89	11.17	10.71	9.99	10.45	10.49	11.00	9.48	10.91	11.37	11.02	11.19
Max	11.59	12.08	11.50	11.85	12.24	11.78	11.93	11.94	11.72	11.82	12.42	11.92
2s	.50	.19	3.22	.23	.17	.17	.15	.17	.23	.33	.21	.24

	Least Interorbital Constriction											
N	3	6	8	16	28	19	17	30	10	3	12	6
$\bar{X}$	3.99	3.91	4.10	3.99	3.97	3.99	4.04	4.04	4.03	3.98	4.10	3.98
Min	3.86	3.63	3.78	3.82	3.71	3.72	3.67	3.65	3.79	3.85	3.72	3.70
Max	4.19	4.28	4.52	4.27	4.22	4.29	4.28	4.45	4.22	4.18	4.45	4.22
2s	.25	.24	.20	.07	.07	.08	.11	.10	.12	.25	.12	.22
	Condylo-aveolar Length of the Mandible											
N	3	8	9	15	29	20	18	30	10	3	11	6
$\bar{X}$	11.96	11.93	11.89	11.85	12.11	12.30	12.26	12.09	12.38	12.64	12.44	12.60
Min	11.05	10.56	11.02	10.78	11.49	11.75	11.09	11.07	12.87	12.50	11.55	12.04
Max	12.37	12.52	12.48	12.76	12.78	13.22	13.19	13.06	13.43	12.80	12.64	13.42
2s	1.12	.46	.33	.39	.02	.17	.28	.22	.28	.21	.28	.45
	Mandibular Tooth Row											
N	3	7	9	16	29	22	18	31	8	3	12	6
$\bar{X}$	3.58	3.57	3.72	3.69	3.63	3.63	3.67	3.64	3.65	3.67	3.75	3.58
Min	3.52	3.42	3.52	3.51	3.51	3.37	3.41	3.38	3.49	3.62	3.58	3.50
Max	3.63	3.75	3.88	3.90	3.79	3.92	4.16	3.92	3.78	3.71	3.95	3.82
2s	.09	.12	.88	..06	.03	.06	.08	.05	.09	.07	.08	.13
	Mandibular Diastema											
N	3	8	9	16	29	21	17	31	10	3	12	6
$\bar{X}$	3.12	3.15	3.48	3.13	3.01	3.09	3.06	3.13	3.18	3.00	3.15	3.23
Min	2.70	2.89	2.96	2.82	2.62	2.82	2.80	2.81	3.02	2.79	2.86	2.99
Max	3.43	3.83	3.99	3.30	3.32	3.59	3.43	3.40	3.59	3.22	3.60	3.53
2s	.22	.54	2.46	.13	.07	.01	.10	.07	.11	.31	.12	.15

N - sample size

$\bar{X}$ - mean

Min - smallest measurement in sample

Max - largest measurement in sample

2s - two standard errors of the mean