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Character variation in the *Oporornis philadelphia - tolmiei* complex

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City University of New York, 1988

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**CHARACTER VARIATION IN THE
Oporornis philadelphia - tolmiei COMPLEX**

by

Jay Pitocchelli

A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy, the City University of New York.

1988

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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The City University of New York

Abstract

**CHARACTER VARIATION IN THE
Oporornis philadelphia - *tolmiei* COMPLEX**

by

Jay Pitocchelli

Adviser: Professor Wesley Lanyon

Oporornis philadelphia and *O. tolmiei* have been recognized as separate species since their first descriptions by Baird (1858). However, Chapman (1917) and Phillips (1947) questioned the specific status of these taxa. Later authors (Mayr and Short 1970, Hall 1979, Kowalski 1983) pointed to 1) the strong morphological and behavioral resemblance between these taxa, 2) the possibility of hybridization in central Alberta and 3) overlap in plumage characters and external measurements, as evidence that these taxa may not be distinct species.

I analyzed differences between these taxa for morphological and song characters from freshly collected specimens and accompanying tape recordings from the breeding ranges. I performed song playback experiments to test whether males could discriminate between *O. philadelphia* and *O. tolmiei* song types in allopatry and near the contact zones.

Most specimens can be separated using the traditional plumage characters described by Baird (1858). But, some extreme *O. philadelphia* specimens possess *tolmiei* - like characters. However, the larger overall size and smaller tail length of *O. philadelphia* separate most of these problem birds. Results of multivariate analyses of mensural characters revealed that these taxa are separate in multivariate space for external and skeletal characters.

O. tolmiei males sang higher frequency songs than *O. philadelphia* males. Frequency variables were the best discriminators of *O. philadelphia* and *O. tolmiei* OTU's in multivariate space.

Differences in primary song and morphometric variation between these taxa indicate that they are separate species. I recommend that they be treated as such, however there is no justification for the recognition of subspecies within *O. tolmiei* as recommended by Phillips (1947).

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York). I had just finished collecting and tape recording *O. philadelphia* and was bound for New York. However, after shelling out for four flat tires, plus food and fuel for the trip I was running out of money and yearning to come home when I lost the front right tire and the mooring to which it was attached while driving. The truck was stopped dead. I would have been stranded had it not been for the Mislenovich family who took me in and repaired my vehicle. At that point in time I was not exactly the type of person one let's into their house without some serious reservations. I was a complete stranger who hadn't showered or shaved in days and I was carrying two firearms and 400 skins and skeletons. However, this family saw that I needed help and they responded. These people salvaged a successful field season from near disaster and I can't thank them enough for their hospitality or their trust in me. Not only did I learn a lot about *Oporornis* warblers from this study but I also learned a lot about human nature.

TABLE OF CONTENTS

CHAPTER 1 - INTRODUCTION.....	1
CHAPTER 2 - MATERIALS AND METHODS	15
2.1 FIELD WORK.....	15
2.2 LABORATORY ANALYSES	16
CHAPTER 3 - CHARACTER CORRELATIONS.....	34
3.1 PHYSICAL PARAMETERS OF SONG.....	35
3.2 MORPHOLOGICAL VARIABLES.....	36
3.3 SUMMARY	37
CHAPTER 4 - RELATIVE VARIABILITY	41
4.1 MORPHOLOGICAL CHARACTERS	41
4.1.1 NESTED ANOVA OF MORPHOLOGICAL CHARACTERS.....	41
4.1.2 CV' FOR MORPHOLOGICAL CHARACTERS	42
4.1.3 REGRESSIONS OF CV'S OF MORPHOLOGICAL CHARACTERS ON LATITUDE AND LONGITUDE.....	44
4.1.4 CLUSTER ANALYSES OF CV'S OF MORPHOLOGICAL CHARACTERS.....	46
4.2 SONG CHARACTERS	50
4.2.1 NESTED ANOVA OF SONG PARAMETERS	50
4.2.2 CV'S FOR SONG PARAMETER CHARACTERS.....	50
4.2.3 REGRESSIONS OF CV'S OF SONG PARAMETERS ON LATITUDE AND LONGITUDE	51
4.2.4 CLUSTER ANALYSES OF CV'S OF SONG PARAMETERS	53
4.3 SUMMARY	56
CHAPTER 5 - MORPHOLOGY	81
5.1 UNIVARIATE ANALYSIS OF MORPHOLOGICAL CHARACTERS	
DIFFERENCES BETWEEN SPECIES, LOCALITIES AND REGRESSION AND CORRELATION WITH ENVIRONMENTAL VARIABLES.....	81
5.1.1 EXTERNAL CHARACTERS.....	81
5.1.2 TEMPORAL VARIATION IN EXTERNAL CHARACTERS BETWEEN POPULATIONS OF O. philadelphia AND O. tolmiei.	88
5.1.3 SKELETAL CHARACTERS	91
5.2 MULTIVARIATE ANALYSIS OF MORPHOLOGICAL CHARACTERS.....	109
5.2.1 CLUSTER ANALYSIS (CA).....	111
5.2.1.1 CA - EXTERNAL CHARACTERS.....	111
5.2.1.2 CA - SKULL COMPLEX.....	112
5.2.1.3 CA - GIRDLE COMPLEX.....	112
5.2.1.4 CA - LEG COMPLEX.....	113
5.2.1.5 CA - WING COMPLEX.....	113
5.2.1.6 CA - ALL SKELETAL COMPLEXES.....	114
5.2.2 PRINCIPAL COMPONENTS ANALYSIS (PCA)	115
5.2.2.1 PCA - EXTERNAL CHARACTERS.....	116

5.2.2.2 PCA - SKULL COMPLEX.....	117
5.2.2.3 PCA - GIRDLE COMPLEX.....	118
5.2.2.4 PCA - LEG COMPLEX.....	118
5.2.2.5 PCA - WING COMPLEX.....	119
5.2.2.6 PCA - ALL SKELETAL COMPLEXES.....	119
5.2.3 DISCRIMINANT FUNCTION ANALYSIS (DFA).....	120
5.2.3.1 DFA - EXTERNAL CHARACTERS.....	123
5.2.3.2 DFA - SKULL COMPLEX.....	123
5.2.3.3 DFA - GIRDLE COMPLEX.....	123
5.2.3.4 DFA - LEG COMPLEX.....	123
5.2.3.5 DFA - WING COMPLEX.....	124
5.2.3.6 DFA - ALL SKELETAL COMPLEXES.....	124
5.2.3.7 Mahalanobis' D2 BETWEEN BODY REGIONS.....	124
5.2.3.8 STEPWISE DFA FOR ALL SKELETAL CHARACTERS.....	125
5.3 SUMMARY.....	126
CHAPTER 6 - SONG.....	204
6.1 UNIVARIATE ANALYSIS OF PHYSICAL PARAMETERS OF SONG	
DIFFERENCES BETWEEN LOCALITIES AND REGRESSION AND CORRELATION WITH ENVIRONMENTAL VARIABLES.....	204
6.2 MULTIVARIATE ANALYSIS OF SONG PARAMETERS.....	222
6.2.1 CLUSTER ANALYSIS (CA).....	222
6.2.1.1 CA - FREQUENCY COMPLEX.....	223
6.2.1.2 CA - DURATION/INTERVAL COMPLEX.....	224
6.2.1.3 CA - SYLLABLE COMPLEX.....	224
6.2.1.4 CA - ALL COMPLEXES.....	225
6.2.2 PRINCIPAL COMPONENTS ANALYSIS (PCA).....	226
6.2.2.1 PCA - FREQUENCY COMPLEX.....	226
6.2.2.2 PCA - DURATION/INTERVAL COMPLEX.....	227
6.2.2.3 PCA - SYLLABLE COMPLEX.....	228
6.2.2.4 PCA - ALL SONG COMPLEXES.....	229
6.2.3 DISCRIMINANT FUNCTION ANALYSIS (DFA).....	229
6.2.3.1 DFA - FREQUENCY COMPLEX.....	230
6.2.3.2 DFA - DURATION/INTERVAL COMPLEX.....	231
6.2.3.3 DFA - SYLLABLE COMPLEX.....	231
6.2.3.4 DFA - ALL SONG CHARACTERS.....	231
6.2.3.5 Mahalanobis' D2 BETWEEN TAXA FOR THE SONG PARAMETER COMPLEXES.....	232
6.2.3.6 STEPWISE DFA FOR ALL SONG PARAMETERS.....	232
6.3 ANALYSIS OF GEOGRAPHIC DISTRIBUTION OF SONG SYLLABLES.....	233
6.4 RESULTS OF SONG PLAYBACK EXPERIMENTS.....	238
6.5 SUMMARY.....	239
CHAPTER 7 – DISCUSSION.....	317
7.1 MORPHOLOGY.....	317

7.1.1 SPECIES DIFFERENCES MORPHOLOGY-UNIVARIATE ANALYSIS.....	317
7.1.2 SPECIES DIFFERENCES MORPHOLOGY-MULTIVARIATE ANALYSIS.....	320
7.2 SONG.....	322
7.2.1 SPECIES DIFFERENCES SONG-UNIVARIATE ANALYSIS	322
7.2.2 SPECIES DIFFERENCES SONG-MULTIVARIATE ANALYSIS	325
7.2.3 SYLLABLE ANALYSIS AND SPECIES DIFFERENCES	327
7.3 NATURE AND STABILITY OF HYBRID CONTACT BETWEEN O. philadelphia AND O. tolmiei	328
7.4 TAXONOMIC RECOMMENDATIONS	331
7.5 IDENTIFICATION OF PROBLEM SPECIMENS.....	333
APPENDIX A.....	336
APPENDIX B.....	338
APPENDIX C	341
APPENDIX D	345
APPENDIX E.....	362
APPENDIX F.....	364
APPENDIX G	367
APPENDIX H	371
APPENDIX I	385
APPENDIX J.....	392
APPENDIX K.....	397
APPENDIX L.....	408
APPENDIX M.....	410
LITERATURE CITED	414

LIST OF TABLES

Table 1. Per Cent of the variance attributed to among taxa, among populations, and among individuals within populations from a nested ANOVA of morphological characters.....	59
Table 2. Comparison of mean coefficients of variation of morphological characters.....	60
Table 3. Per Cent of the variance attributed to among taxa, among populations, and among individuals within populations from a nested ANOVA of song characters.....	61
Table 4. Comparison of mean coefficients of variation of primary song characters.....	62
Table 5. Comparison of taxon Means (mm) per morphological character for each taxon and per cent difference between taxa.....	133
Table 6. Results of Regression Analyses of morphological characters on latitude and longitude.....	134
Table 7. Results of Correlation Analyses between morphological characters and environmental variables for <i>O. philadelphia</i>	135
Table 8. Results of Correlation Analyses between morphological characters and environmental variables for <i>O. tolmiei</i>	136
Table 9. Results of temporal comparisons of external characters between 1963 and 1985 populations of <i>O. philadelphia</i> and <i>O. tolmiei</i> from central Alberta.....	137
Table 10. Generalized Squared Distances (MAHALANOBIS' D^2) Between Taxa and Time Samples.....	138
Table 11. Loadings of External Complex Variables on Principal Components.....	139
Table 12. Loadings of Skull Complex Variables on Principal Components.....	140
Table 13. Loadings of Girdle Complex Variables on Principal Components.....	141
Table 14. Loadings of Leg Complex Variables on Principal Components.....	142

Table 15. Loadings of Wing Complex Variables on Principal Components.....	143
Table 16. Loadings of all Morphological Variables on Principal Components.....	144
Table 17. Discriminant Function Coefficients for External Complex Variables.....	145
Table 18. Discriminant Function Coefficients for Skull Complex Variables.....	146
Table 19. Discriminant Function Coefficients for Girdle Complex Variables.....	147
Table 20. Discriminant Function Coefficients for Leg Complex Variables.....	148
Table 21. Discriminant Function Coefficients for Wing Complex Variables.....	149
Table 22. Discriminant Function Coefficients for all Skeletal Complex Variables.....	150
Table 23. Results of STEPWISE DFA for Morphological Characters.....	151
Table 24. Comparison of taxon Means per song character for each taxon and per cent difference between taxa.....	248
Table 25. Results of Regression Analyses of physical parameters of primary song on latitude and longitude.....	249
Table 26. Results of Spearman Rank Order Correlation Analyses between physical parameters of primary song and environmental variables for <i>O. philadelphia</i>	250
Table 27. Results of Spearman Rank Order Correlation Analyses between physical parameters of primary song and environmental variables for <i>O. tolmiei</i>	251
Table 28. Loadings of Frequency Complex Variables on Principal Components.....	252
Table 29. Loadings of Duration/Interval Complex Variables on Principal Components.....	253
Table 30. Loadings of Syllable Complex Variables on	

Principal Components.....	254
Table 31. Loadings of all Song Complex Variables on Principal Components.....	255
Table 32. Discriminant Function Coefficients for Frequency Complex Variables.....	256
Table 33. Discriminant Function Coefficients for Duration/Interval Complex Variables.....	257
Table 34. Discriminant Function Coefficients for Syllable Complex Variables.....	258
Table 35. Discriminant Function Coefficients for all Song Parameter Variables.....	259
Table 36. Results of STEPWISE DFA for Song Parameters.....	260
Table 37. Results of Song Playback Experiments.....	261

LIST OF FIGURES

Figure 1. Breeding ranges of <i>O. philadelphia</i> and <i>O. tolmiei</i> and distribution of samples examined in this study.....	12
Figure 2. <i>O. philadelphia</i> males, females, immatures.....	13
Figure 3. <i>O. tolmiei</i> males, females, immatures.....	14
Figure 4. Song playback experiment, simultaneous presentation of <i>O. philadelphia</i> and <i>O. tolmiei</i> song.....	31
Figure 5. Skeletal characters measured in this study (adopted from Robbins and Schnell 1971).....	32
Figure 6. Song variables: A - cultural units, B - physical parameters of primary song.....	33
Figure 7. Phenogram of unstandardized correlation coefficients of song parameters.....	39
Figure 8. Phenogram of unstandardized correlation coefficients of morphological variables.....	40
Figure 9. Per Cent of the variance attributed to among taxa, among populations, and among individuals within populations from a nested ANOVA of morphological and behavioral characters.....	63
Figure 10. Variability profiles: Coefficients of Variation (CV's) plotted by morphological and behavioral variables.....	64
Figure 11. Dendrogram of <i>Oporornis philadelphia</i> populations based on CV's for SKULL CHARACTERS.....	65
Figure 12. Dendrogram of <i>Oporornis philadelphia</i> populations based on CV's for GIRDLE CHARACTERS.....	66
Figure 13. Dendrogram of <i>Oporornis philadelphia</i> populations based on CV's for LEG CHARACTERS.....	67
Figure 14. Dendrogram of <i>Oporornis philadelphia</i> populations based on CV's for WING CHARACTERS.....	68
Figure 15. Dendrogram of <i>Oporornis philadelphia</i> populations based on CV's for EXTERNAL CHARACTERS.....	69

Figure 16. Dendrogram of <i>Oporornis tolmiei</i> populations based on CV's for SKULL CHARACTERS.....	70
Figure 17. Dendrogram of <i>Oporornis tolmiei</i> populations based on CV's for GIRDLE CHARACTERS.....	71
Figure 18. Dendrogram of <i>Oporornis tolmiei</i> populations based on CV's for LEG CHARACTERS.....	72
Figure 19. Dendrogram of <i>Oporornis tolmiei</i> populations based on CV's for WING CHARACTERS.....	73
Figure 20. Dendrogram of <i>Oporornis tolmiei</i> populations based on CV's for EXTERNAL CHARACTERS.....	74
Figure 21. Dendrogram of <i>Oporornis philadelphia</i> populations based on CV's for FREQUENCY CHARACTERS.....	75
Figure 22. Dendrogram of <i>Oporornis philadelphia</i> populations based on CV's for DURATION/INTERVAL CHARACTERS.....	76
Figure 23. Dendrogram of <i>Oporornis philadelphia</i> populations based on CV's for SYLLABLE CHARACTERS.....	77
Figure 24. Dendrogram of <i>Oporornis tolmiei</i> populations based on CV's for FREQUENCY CHARACTERS.....	78
Figure 25. Dendrogram of <i>Oporornis tolmiei</i> populations based on CV's for DURATION/INTERVAL CHARACTERS.....	79
Figure 26. Dendrogram of <i>Oporornis tolmiei</i> populations based on CV's for SYLLABLE CHARACTERS.....	80
Figure 27. Geographic distribution of specimens (males and females) with eye-arcs for both taxa.....	152
Figure 28. Geographic distribution of <i>O. philadelphia</i> specimens with dark lores.....	153
Figure 29. Geographic distribution of WING means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	154
Figure 30. Bivariate plots of population means: WING, TAIL, W-T (mm), WEIGHT.....	155
Figure 31. Geographic distribution of TAIL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	156

Figure 32. Geographic distribution of W-T means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	157
Figure 33. Numbers of birds with W-T measurements (mm) lying within specified W-T intervals, <i>O. philadelphia</i>	158
Figure 34. Geographic distribution of WEIGHT means (g) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	159
Figure 35. Mahalanobis D^2 between 1963 and 1985 samples of <i>O. philadelphia</i> and <i>O. tolmiei</i> based on external measurements.....	160
Figure 36. Geographic distribution of PRL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	161
Figure 37. Bivariate plots of population means: PRL, BDEP, NASW, INORW, SKL, SKW, MANL, MAND.....	162-163
Figure 38. Geographic distribution of BDEP means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	164
Figure 39. Geographic distribution of NASW means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	165
Figure 40. Geographic distribution of INORW means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	166
Figure 41. Geographic distribution of SKL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	167
Figure 42. Geographic distribution of MAND means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	168
Figure 43. Geographic distribution of CORL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	169
Figure 44. Bivariate plots of population means: CORL, SCAPW, STERL, KEEL, KEED, SYNW, SYNMW.....	170-171
Figure 45. Geographic distribution of SCAPW means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	172
Figure 46. Geographic distribution of STERL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	173
Figure 47. Geographic distribution of KEEL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	174

Figure 48. Geographic distribution of KEED means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	175
Figure 49. Geographic distribution of FEDW means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	176
Figure 50. Bivariate plots of population means: FEDW, FEL, TIBL, TARL, TARD.....	177
Figure 51. Geographic distribution of FEL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	178
Figure 52. Geographic distribution of TARD means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	179
Figure 53. Geographic distribution of HTRL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	180
Figure 54. Bivariate plots of population means: HTRL, HDEW, HUML, ULNL, CARPL.....	181
Figure 55. Geographic distribution of HUML means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	182
Figure 56. Geographic distribution of ULNL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	183
Figure 57. Geographic distribution of CARPL means (mm) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	184
Figure 58. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on External Variables.....	185
Figure 59. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on Skull Variables.....	186
Figure 60. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on Girdle Variables.....	187
Figure 61. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on Leg Variables.....	188
Figure 62. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on Wing Variables.....	189
Figure 63. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on all Skeletal Variables.....	190
Figure 64. 3D plots of Principal Components 1, 2, 3 based on External	

variables.....	191
Figure 65. 3D plots of Principal Components 1, 2, 3 based on Skull and variables.....	192
Figure 66. 3D plots of Principal Components 1, 2, 3 based on Girdle variables.....	193
Figure 67. 3D plots of Principal Components 1, 2, 3 based on Leg variables.....	194
Figure 68. 3D plots of Principal Components 1, 2, 3 based on Wing variables.....	195
Figure 69. 3D plots of Principal Components 1, 2, 3 based on all skeletal variables.....	196
Figure 70. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for external complex variables.....	197
Figure 71. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for skull complex variables.....	198
Figure 72. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for girdle parameter complex variables.....	199
Figure 73. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for leg complex variables.....	200
Figure 74. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for wing complex variables.....	201
Figure 75. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for all skeletal complex variables.....	202
Figure 76. Mahalanobis' D^2 for each skeletal complex and for all skeletal complexes combined.....	203
Figure 77. Geographic distribution of NPSO means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	262
Figure 78. Bivariate of population means: NPSO, NSSO, NDSO, DUR, MINS, MAXS.....	263-264
Figure 79. Geographic distribution of NSSO means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	265
Figure 80. Geographic distribution of NDSO means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	266

Figure 81. Geographic distribution of DUR means (seconds) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	267
Figure 82. Geographic distribution of MINS means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	268
Figure 83. Geographic distribution of MAXS means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	269
Figure 84. Geographic distribution of NNA means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	270
Figure 85. Bivariate plots of population means: NNA, NNB, NNC, IMA, IMB, IMA, IMB, IMC, MIC, MAA, MAB, MAC.....	271-273
Figure 86. Geographic distribution of NNB means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	274
Figure 87. Geographic distribution of NNC means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	275
Figure 88. Geographic distribution of IMA means (seconds) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	276
Figure 89. Geographic distribution of IMC means (seconds) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	277
Figure 90. Geographic distribution of MIA means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	278
Figure 91. Geographic distribution of MIB means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	279
Figure 92. Geographic distribution of MIC means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	280
Figure 93. Geographic distribution of MAA means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	281
Figure 94. Geographic distribution of MAB means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	282
Figure 95. Geographic distribution of MAC means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	283
Figure 96. Geographic distribution of NFA means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	284

Figure 97. Bivariate plots of population means: NFA, NFB, IFA ,IFB, MIFA, MIFB, MAFA, MAFB.....	285-286
Figure 98. Geographic distribution of NFB means for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	287
Figure 99. Geographic distribution of IFA means (seconds) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	288
Figure 100. Geographic distribution of MIFA means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	289
Figure 101. Geographic distribution of MIFB means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	290
Figure 102. Geographic distribution of MAFA means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	291
Figure 103. Geographic distribution of MAFB means (Hz) for populations of <i>O. philadelphia</i> and <i>O. tolmiei</i>	292
Figure 104. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on Frequency Variables.....	293
Figure 105. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on Duration/interval Variables.....	294
Figure 106. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on Syllable Variables.....	295
Figure 107. Phenogram of <i>O. tolmiei</i> and <i>O. philadelphia</i> populations based on all song Variables.....	296
Figure 108. 3D plots of Principal Components 1, 2, 3 based on Frequency variables.....	297
Figure 109. 3D plots of Principal Components 1, 2, 3 based on Duration/Interval variables.....	298
Figure 110. 3D plots of Principal Components 1, 2, 3 based on Syllable variables.....	299
Figure 111. 3D plots of Principal Components 1, 2, 3 based on all song variables.....	300
Figure 112. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for frequency complex variables.....	301

Figure 113. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for duration/interval complex variables.....	302
Figure 114. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for syllable complex variables.....	303
Figure 115. Plots of Discriminant Function scores for <i>O. philadelphia</i> and <i>O. tolmiei</i> OTU's for all song parameter complex variables.....	304
Figure 116. Mahalanobis' D^2 for each song parameter complex and for all parameter complexes combined.....	305
Figure 117. Syllables shared by <i>O. philadelphia</i> and <i>O. tolmiei</i>	306
Figure 118. Graph of the number of new syllables encountered with each new individual sampled.....	307
Figure 119. Distribution of MO Syllables and Variants in the range of <i>O. philadelphia</i>	308
Figure 120. Sonographs of Newfoundland songsters.....	309
Figure 121. Sonographs of eastern continental songsters.....	310
Figure 122. Sonographs of western continental songsters.....	311
Figure 123. Dendrogram of <i>O. philadelphia</i> songsters.....	312
Figure 124. Distribution of MA Syllables and Variants in the range of <i>O. tolmiei</i>	313
Figure 125. Sonographs of Jarbidge, Nevada songsters.....	314
Figure 126. Sonographs of Oregon and Washington songsters.....	315
Figure 127. Dendrogram of <i>O. tolmiei</i> songsters.....	316

CHAPTER 1 - INTRODUCTION

The AOU Checklist (1983) currently recognizes four species in the genus *Oporornis*: *O. formosus*, *O. agilis*, *O. philadelphia* and *O. tolmiei*. *Oporornis philadelphia* and *O. tolmiei* have caused taxonomists problems because of their close morphological resemblance. They are one of many east-west species pairs or subspecific complexes which meet in the Great Plains and western Prairie Provinces (for reviews see Mengel 1964, Remington 1968 and Rising 1983b). This *Oporornis* complex presents many of the same problems that Lanyon (1978) faced prior to revising the flycatcher genus *Myiarchus*: overlap in some mensural characters, poorly understood geographic variation, and unreliable diagnostic characters (Hall 1979, Kowalski 1983). While some authors have regarded them as superspecies, sibling or crypto-species, others have considered them subspecies. In this study I will assess **specific distinctness** of *O. philadelphia* and *O. tolmiei* at the morphological and behavioral levels. The central thesis in this study is to evaluate the morphological and behavioral distinctness of these taxa and provide morphological and behavioral criteria which best separate them. These criteria could be used to identify unknown specimens.

In order to familiarize the reader early with the taxa and the characters which have been used to diagnose them I have presented these traditional characters in the introduction. I also describe the breeding ranges of each taxon and the potential contact zones. The taxonomic history section describes the problem of the status of *O. philadelphia* and *O. tolmiei* and what role traditional diagnostic characters played in these decisions.

DIAGNOSES. Baird (1858) assigned specific status to each taxon based on plumage differences. *Oporornis formosus* is much larger than *O. philadelphia* and *O. tolmiei* and lacks the gray hood characteristic of all other *Oporornis* warblers. Both sexes, immatures and adults of *O. agilis*, *O. philadelphia* and *O. tolmiei* have olive upperparts, yellow underparts and a gray hood. *Oporornis agilis*' complete eye-ring, larger size, and more pointed wing easily distinguish both sexes and immatures of this species from *O. philadelphia* and *O. tolmiei*. Traditional characters used by ornithologists to diagnose these latter two taxa are 1) broken eye-rings or eye-arcs (adults), 2) presence/absence of dark lores (adult males), 3) extent of black feathering on the throat and upper breast (adult males) and 4) Wing - Tail (W-T) measurement (all ages and sexes). Diagnoses of *Oporornis philadelphia* and *O. tolmiei* are given below.

Oporornis philadelphia, adult male: olive back, yellow underparts, gray hood, usually a sharp demarcation between black and gray feathers forming a bib or apron beneath the throat, Wing minus Tail (W-T) greater than or equal to 11mm (Figure 2).

Oporornis philadelphia, adult female: olive back, yellow underparts, gray hood, no bib or apron, throat lighter than surrounding hood, W-T greater than or equal to 11mm (Figure 2).

Oporornis philadelphia, immature male and female: similar to adult female but possess broken eye-ring or eye-arc, most birds have gray or lighter gray throats, some extreme specimens have completely yellow throats (Figure 2).

Oporornis tolmiei, adult male: similar to *Oporornis philadelphia* male but has eye-arcs, dark lores, lacks bib, W-T less than or equal to 10mm (Figure 3).

Oporornis tolmiei, adult female: similar to *Oporornis philadelphia* female but has eye-arcs, W-T less than or equal to 10mm (Figure 3).

Oporornis tolmiei, immature male and female: indistinguishable from immature *Oporornis philadelphia* birds, most birds have gray or lighter gray throats, some extreme specimens may have either brownish or yellow throats (Figure 3).

RANGE. *Oporornis philadelphia* breeds in the boreal forest north from central Michigan, Wisconsin, Minnesota and West Virginia to north-central Canada and west from Newfoundland to northeastern British Columbia. *Oporornis tolmiei* breeds in the Rocky Mountains from northern Arizona to Alaska (Figure 1). *Oporornis philadelphia* has been considered monotypic throughout its range while four subspecies of *O. tolmiei* have been described by Phillips (1947). Contact between these taxa is different than other North American east-west species pairs that overlap in broad hybrid zones (for review see Rising 1983a). Cox (1973) described **contact points** between these taxa in central Alberta along the eastern foothills of the Rocky Mountains and along the Red Deer River. Salt (1973) found a single territorial *O. tolmiei* male alongside an *O. philadelphia* male at Pigeon Lake, southwest of Edmonton. Erskine and Davidson (1976) also reported contact in the northeastern corner of British Columbia on the Liard River. In summary contact between *O. philadelphia* and *O. tolmiei* usually occurs between fewer than five individuals (based on past observations), is very localized and does not occur on an annual basis.

TAXONOMIC HISTORY. These taxa were considered specifically distinct for nearly 100 years even though 1) morphological and behavioral differences between *Oporornis philadelphia* and *O. tolmiei* are small compared to other east-west taxa considered subspecies by the 36th AOU Checklist (1983) (e.g., *Colaptes auratus*, *Icterus galbula*) and 2) little is known about the degree of behavioral isolation between these taxa in the narrow zone

of sympatry in Alberta and British Columbia. Chapman (1917) had questioned the reliability of dark lores used to separate specimens or hybrids between these taxa (see Figure 2). This was an important specific character used by Baird (1858). Taverner (1919) collected a hypothetical mixed pair (*philadelphia* male and *tolmiei* female) breeding in central Alberta, indicating a lack of species recognition in the potential contact areas. Phillips (1947) was hesitant to accept full species status of each taxon, predicting that *O. philadelphia* would be found to be an eastern subspecies of *O. tolmiei*. However, these papers did not alter the accepted specific status of these taxa. Later, a combination of close morphological resemblance and several accounts of hybridization led some modern authors to consider them dubiously distinct (Hall 1979, Hofslund 1962, Mayr and Short 1970, Mengel 1964). Hybridization between these taxa was reported in central Alberta (Cox 1973) and at least seven hybrid specimens have been described (see Hall 1979). Mayr and Short (1970) considered them subspecies and placed them in a category of hybridizing taxa of uncertain status. Hall (1979) reported finding *tolmiei* - like specimens in eastern Canada. These specimens were well within the breeding range of *O. philadelphia*, far removed from any hypothetical contact zones. He re-examined the geographic distribution of specific plumage characters from museum study skins of both taxa from each species' range. Hall (1979) found some eastern male *O. philadelphia* specimens with eye-arcs and dark lores which resembled *O. tolmiei* (see Figure 2). I also found spring female specimens with eye-arcs from Whitemouth, Manitoba (NMNH nos. 20115, 20116, 20117, Pitocchelli 1985) (see Figure 2). These traditional plumage characters are not unequivocally reliable for species diagnosis. External characters have also failed to separate

specimens of these taxa. Lanyon and Bull (1969) were able to separate 98% of *O. philadelphia* and *O. tolmiei* specimens from the allopatric portions of each taxon's range using WING minus TAIL measurements from study skins (W-T). Specimens in their study were collected far away from any potential contact zones in Alberta and British Columbia described by Cox (1973) or Erskine and Davidson (1976). Kowalski (1983) found more overlap in this measurement. He used specimens closer to the contact zones but did not publish exact localities. These studies showed that the two taxa in question are less morphologically distinct throughout each other's ranges than previously thought. Although external characters described above may be useful for diagnosing a majority of these warblers, **extreme specimens** can not reliably be identified. Recent identification problems of note include the following examples. A number of *tolmiei* - like warblers have been reported in the eastern United States by bird-banders: New Jersey (Hailman 1968) Minnesota (Peterson 1958) and North Dakota (Warner pers. comm); hypothetical first records in the form of photographs of *O. tolmiei* for some eastern states have been reported from Kansas (Patti and Meyers 1976), Minnesota (Beimborn 1977) and Missouri (Robbins, personal communication). Because traditional specific characters are not valid for extreme specimens Hall (1979) **dismissed** many reports of hypothetical hybrids or first records of *O. tolmiei* for some eastern states as variable *philadelphia* specimens. Intraspecific variation in *O. philadelphia* precludes the use of these traditional characters for the unequivocal identification of all extreme specimens of both taxa, especially hybrids.

CURRENT STUDY. I collected fresh specimens and recorded primary song from over 30 different localities in the breeding ranges of these taxa and the potential contact areas (for localities see - Figure 1, APPENDIX A) between 1982 and 1986. I made four trips across North America over this four year period - three summers in the allopatric portions of each taxon's range and one summer along the potential contact zones. Dates and states/provinces where collecting and recording occurred are listed below.

1. June, July 1983 - Maine, Quebec, Ontario.
2. June, July 1984 - Wyoming, Idaho, Nevada, California, Oregon, Washington, Montana, British Columbia.
3. June, July 1985 - Pennsylvania, New York, Minnesota, Alberta, British Columbia.
4. June 1986 - New York.

I prepared partial skins and skeletons in the field in order to 1) re-examine the geographic distribution of traditional plumage and external characters originally used to diagnose these taxa and 2) add new suites of characters (skeletal and behavioral) which might aid in separating individuals. Lanyon's (1978) study of *Myiarchus* flycatchers and Stein's (1963) work on *Empidonax* flycatchers pointed out the importance of using vocal characters in conjunction with morphological criteria when establishing species limits in taxa which are morphologically uniform. I also examined the distinctness of primary song in each *Oporornis* taxon. Breast muscle and liver tissues were collected for electrophoretic analysis. These results will be published separately.

SPECIES DIFFERENCES. Three goals of the thesis are to 1) evaluate the distinctness of each taxon at morphological and behavioral levels,

- 2) document which characters (if any) best separate individuals of each taxon,
- 3) make suggestions about the taxonomic status of these taxa.

I evaluated the distinctness of these taxa at univariate and multivariate levels for morphological and behavioral characters. For univariate analyses means per character were compared. I asked questions at two levels of this analysis. 1) What is the average difference between these taxa for morphological and behavioral characters? 2) What is the pattern of geographic variation in univariate characters and how much overlap is there between *O. philadelphia* and *O. tolmiei* populations means for each character?

At the taxon level, average per cent differences between taxa were calculated for each character and each character complex for morphological and behavioral characters.

At the geographic variation level, means for each character for all *O. philadelphia* and *O. tolmiei* populations were analyzed for significant differences. This analysis tested whether all *O. philadelphia* populations were significantly different from all *O. tolmiei* populations for each character. It was important to evaluate the amount of overlap in mensural characters (plumage and skeletal) and compare it to overlap of plumage characters.

I performed two univariate analyses of geographic variation to determine the relationship between a given character and environmental factors - regression and correlation analyses of characters with environmental data. Each character was tested for significant linear relationships with latitude or longitude using regression analyses. I performed regression analyses on characters to examine spatial patterns of variation within each taxon. Do *O. philadelphia* populations approach *O. tolmiei* in size (or in song parameters)

from east to west for morphological or behavioral characters? Do *O. tolmiei* populations approach *O. philadelphia* in size (or in song parameters) from south to north? I also tested for relationships between morphological and behavioral characters and environmental data using Spearman ranked correlation. Are large birds found in drier, warmer climates? Do songsters sing higher frequency songs in cool, moist climates?

Bivariate plots of character means for *O. philadelphia* and *O. tolmiei* populations for morphological characters served to illustrate the degree of differences between taxa for univariate characters within different morphological and song parameter complexes.

Before performing multivariate analyses of morphometric differences in multivariate space between taxa for external and skeletal characters some authors (Johnson 1980, Schnell et al. 1985) have analyzed the characters themselves to eliminate characters which can not be reliably re-measured and/or contain redundant information in relation to other characters (Baker 1985). I also analyzed morphological and behavioral characters for 1) redundancy in information yielded by each character with respect to the others using a cluster analysis (UPGMA) of a matrix correlation coefficients for different characters and 2) variability and measurement accuracy of each character using coefficients of variation and nested analysis of variance. After the character analysis I proceeded with the multivariate analyses of differences in the remaining characters between *O. philadelphia* and *O. tolmiei*.

At the multivariate level the distinctness of these taxa was analyzed using all characters simultaneously. Three multivariate techniques which assess phenetic distance between Operational Taxonomic Units (OTU's) were Cluster

Analysis (CA), Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA). The degree of discrimination of OTU's from these taxa was analyzed for each complex separately and with all character complexes combined (morphological variables were analyzed separately from behavioral variables). I also used Stepwise DFA' to find the best skeletal elements and song parameters which discriminated between these taxa.

Finally suggestions are made with regard to the taxonomic treatment of *O. philadelphia* and *O. tolmiei*. Are these separate species and what is the evidence for this determination?

Taxonomic decisions at the species level are usually based on morphological differences. However, the literature is full of descriptions of well-differentiated subspecies which freely interbreed (Fox Sparrows - *Passerella iliaca* complex, Song Sparrows - *Melospiza melodia* complex, Northern Oriole - *Icterus galbula* complex, Northern Flicker - *Colaptes auratus* complex, etc....). It is also full of cases of sibling or crypto-species who strongly resemble each other morphologically but do not interbreed (Stein 1963, Lanyon 1978, Johnson 1980, Rising and Schueler 1980). It is obvious that morphological differentiation is not necessary for reproductive isolation in all cases. In addition to morphological differences researchers (Stein 1963, Gill and Lanyon 1964, Lanyon 1978) have analyzed song characters as cues for species discrimination between morphologically similar taxa.

Lanyon (1960) pointed out the value of vocal characters in systematics, especially in cases where evidence from morphological characters was equivocal. Qualitative differences in syllables and quantitative differences in song parameters have been considered species-specific characteristics

(Lanyon 1960, Becker 1982). Playback experiments have been used to evaluate the behavioral significance of these differences. Evidence of behavioral isolation between *O. philadelphia* and *O. tolmiei* came from two sources 1) differences in song parameters (see above - univariate and multivariate analyses), qualitative differences in syllables possessed by *O. philadelphia* and *O. tolmiei* songsters, and 2) song playback experiments adopted from Lanyon (1978). The song playback experiments are an indirect measure of behavioral isolation since they only test song pattern recognition by males. It is assumed that females will discriminate similarly to males (Dilger 1956) but this should be tested in the laboratory which was beyond the scope of this thesis.

THESIS ORGANIZATION. CHAPTER 2 describes the field work and laboratory analyses used in this study. Statistical analyses and software packages are also listed in this chapter. CHAPTERS 3 and 4 present results of character analyses. CHAPTER 3 contains two separate analyses of relationships among morphological characters and relationships among behavioral characters for each taxon. In CHAPTER 4 I have summarized character variability of characters in each character set in *O. philadelphia* and *O. tolmiei* using two analyses - coefficient of variation (CV) and nested analysis of variance. I also described the spatial pattern of variability in each taxon for these characters. CHAPTERS 5 and 6 cover the results of the univariate and multivariate analyses of species differences for morphological and behavioral data respectively. CHAPTER 7 considers the results of the analyses as evidence for determining species status of each taxon. Also included are suggestions for determining status of unknown specimens based on

morphological and behavioral criteria. Tables and figures mentioned in each chapter are located at the end of that chapter.

Figure 1. Breeding ranges of *Q. philadelphica* and *Q. tolmiei*, and distribution of samples examined in this study.

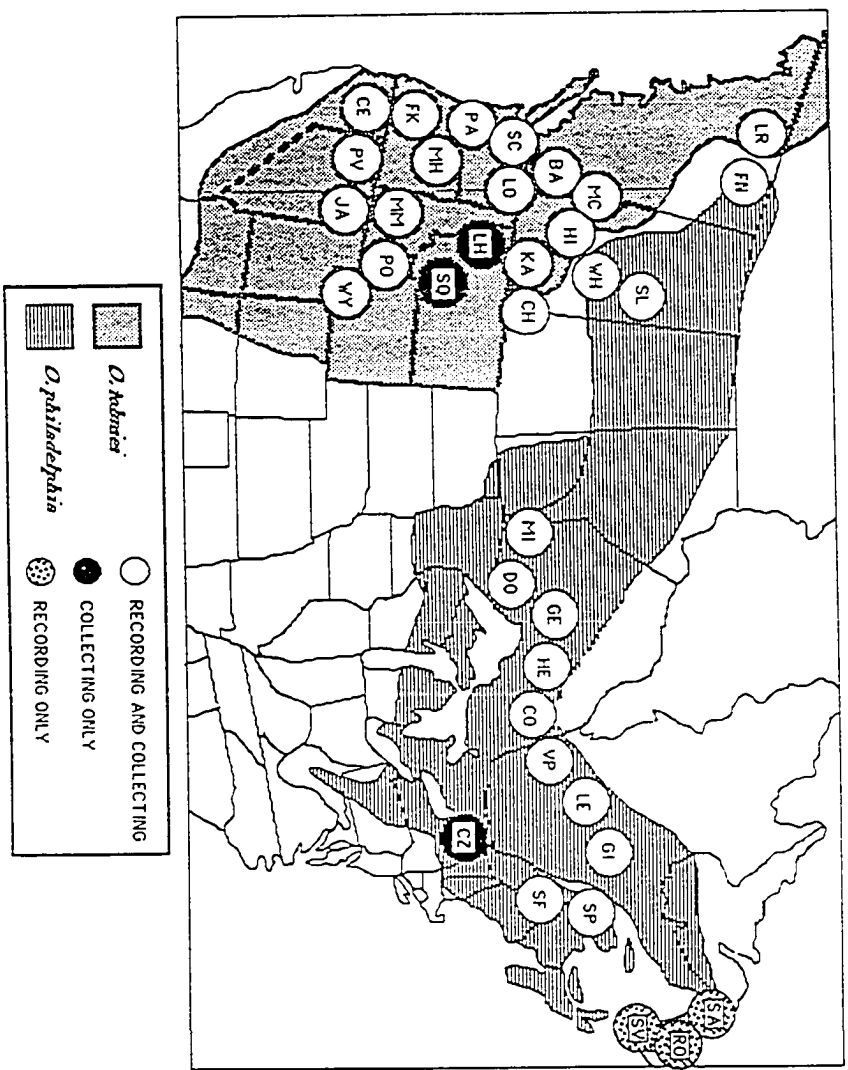


Figure 2. *O. philadelphia* males, females, immatures.



Oporornis philadelphia,
typical adult male



Oporornis philadelphia,
adult male with eye-arcs *

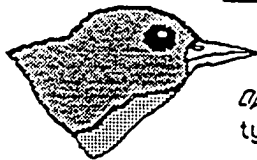


Oporornis philadelphia,
adult male with dark lores *

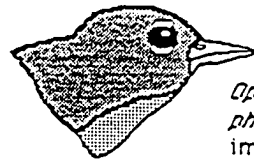


Oporornis philadelphia,
adult male with eye-arcs
and dark lores *

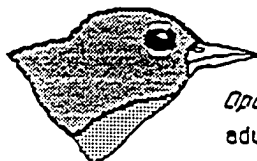
* - represent extreme specimens (uncommon to rare
in museum collections and in the field).



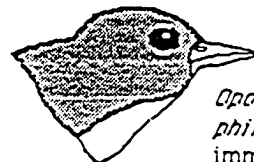
Oporornis philadelphia,
typical adult female



Oporornis philadelphia,
immature
with gray throat



Oporornis philadelphia,
adult female with eye-arcs *

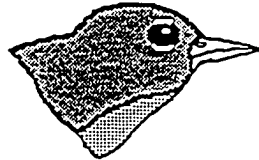


Oporornis philadelphia,
immature with
yellow throat *

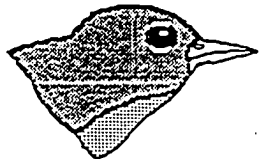
Figure 3. *O. talmiei* males, females, immatures.



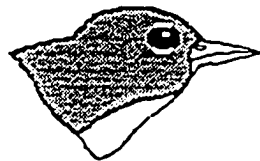
Oporornis talmiei,
adult male



Oporornis talmiei,
adult female



Oporornis talmiei,
immature with
gray throat



Oporornis talmiei,
immature with
yellow throat*

* - represent extreme specimens (uncommon to rare
in museum collections and in the field).

CHAPTER 2 - MATERIALS AND METHODS

2.1 FIELD WORK

It was necessary to collect fresh specimens from the breeding grounds in the northern United States and Canada because (1) a majority of museum collections do not contain suitable sample sizes of specimens (partial skins, skeletons and tissues) from breeding localities for meaningful statistical analyses (Zusi 1982), (2) a small series of study skin specimens from both taxa exist from the potential contact areas, and (3) museum specimens are not accompanied by voice recordings which are critical for species identification. Sample localities are listed in APPENDIX A and mapped on Figure 1.

SPECIMEN PREPARATION. Breeding birds were collected between June and July (1982-1985) with a shotgun. Every effort was made to collect birds which had previously been recorded. However, some males were disturbed during recording so not all specimens were recorded nor were all recordings represented by a specimen. Each specimen was prepared in the field as a partial skeleton and accompanying flat skin so that plumage **and** skeletal characters could be analyzed for species differences and geographic variation. Immediately upon collecting specimens I weighed the birds (nearest 0.1 gram) using Pesola scales and noted whether a given bird had an eye-arc or dark lores. The eye-arc is easily lost due to discoloring by liquids leaking from the eye blood during collecting and specimen preparation.

TAPE RECORDINGS. Song recordings were made in the field with a Uher-4000 Report recorder and Dan Gibson E.P.M. 300 microphone. For a

majority of the songsters at least 10 songs per male were recorded.

Spectrograms were prepared in the laboratory on a Kay Elemetrics 6061 Sona-Graph using wide band filter.

PLAYBACK EXPERIMENTS. Males of each taxon were subjected to song playback experiments which tested their ability to distinguish signal differences in *O. philadelphia* and *O. tolmiei* primary song patterns. I adopted Lanyon's (1978) method of simultaneous presentation of non-conspecific and conspecific songs through two speakers approximately 30m apart. Males were simultaneously exposed to five minutes of *O. philadelphia* and *O. tolmiei* song through two different speakers. After five minutes the song type for each speaker was switched (*O. philadelphia* to *O. tolmiei* and *O. tolmiei* to *O. philadelphia*, see Figure 4). Males were scored on whether they also switched their aggression towards the appropriate speakers. An *O. philadelphia* song from Ontario and an *O. tolmiei* song from Wyoming were used in these discrimination experiments. Realistic Stereo-Mate (SCPI6) recorders and Realistic/Minimus-0.6 speakers were used in the playback experiments.

2.2 LABORATORY ANALYSES

BODY MEASUREMENTS. A thorough morphometric study of a taxon should include measurements from all or most body regions (complexes) in order to adequately sample the phenome (Thorpe 1976). Measurements were taken from flat skins and skeletons. From flat skins, flattened WING (W), TAIL (T) and WING minus TAIL (W-T) measurement were used as in Phillips (1947) and Lanyon and Bull (1967). Wing measurements were made with a wing ruler (nearest mm) and tail measurements were made with Max-cal Calipers (nearest

0.1mm). External data was entered directly into a NEC Portable Computer (PC8201A) (see Marcus 1982).

Robbins and Schnell (1971) listed 50 skeletal characters used in a phenetic analysis of grassland sparrows. However Zink (1983) cautioned against using the entire suite of skeletal characters because some could not be remeasured with accuracy. I used a subset of 25 skeletal characters (Figure 5, see APPENDIX B for complete description of measurements) which could be measured reliably to nearest .05mm for this analysis. Not all specimens contained a complete set of values because of broken bones due to shotgun collecting. All skeletal measurements were made with Max-cal Calipers and data was entered into a NEC Portable Computer (PC8201A).

SONOGRAPH DATA. Twenty-six song parameter characters were taken from sonographs of *O. philadelphia* and *O. tolmiei* songsters. These included frequency, duration/interval and syllable data. A complete description of each parameter appears in Appendix F and they are also illustrated in Figure 6B. Measurements for frequency and duration/interval variables were made with Max-cal Calipers and data was entered into a NEC Portable Computer (PC8201A). Data were converted into Hz and seconds for statistical analysis.

CHARACTER ANALYSES - CHARACTER CORRELATIONS. I examined redundancy in characters in Chapter 3 using cluster analyses (UPGMA) (SAS 1985, version 5.16, PROC CLUSTER) of unstandardized correlation coefficients. A single character which represented each set or cluster was used in the ensuing multivariate analyses of species differences instead of two or three other characters which were highly correlated with it. From the pair (trio or higher) of redundant characters found by cluster analyses,

the variable which was missing more frequently among specimens was eliminated from multivariate analyses.

CHARACTER ANALYSES - CHARACTER VARIABILITY. The Coefficient of Variation, CV, has been widely used to compare the relative amounts of variation in a character across populations independent of the mean of the character (Johnson 1980, Sokal and Rohlf 1981). CV is the standard deviation (SD) expressed as a percentage of the mean. By dividing by the mean, the CV becomes independent of the unit of measurement of the character (Sokal and Rohlf 1981, however for alternative view points see - Lewontin 1966, Lande 1977, Soule 1982, Rohlf et. al. 1983, Pankakoski et. al. 1987). I calculated and compared CV's for each character for each population of *O. philadelphia* and *O. tolmiei*. I also calculated the average CV within each taxon for each character. I regressed CV's on latitude and longitude to search for the presence or absence of clinal patterns of variability in each character separately for both taxa. I also conducted Cluster Analyses on the CV's of different populations within each taxon to search for spatial patterns in variability.

A nested ANOVA was used to examine the amount of variance attributed to different sources of variation in populations of *O. philadelphia* and *O. tolmiei*. In the nested ANOVA the total variance in each character is partitioned among different levels specified by the researcher. The object of this analyses was to estimate the amount of variance which can be explained by 1) what taxon the specimen belongs to, 2) what population it belongs to and 3) how much is error or common to all specimens. The results reveal the extent of differentiation in a given character among taxa, populations and individuals (Rockwell and

Barrowclough 1987). I used PROC NESTED in SAS (1985, version 5.16) for this analysis. I compared the amount of variance in each morphological character explained by the different levels mentioned above. Percentages of the total variances attributed to each of the three levels in this analysis were graphed using Cricket Graph (version 1.1). Separate nested ANOVA's were also performed on the song parameter data.

STATISTICS: MORPHOLOGY. Skeletal and plumage data from males of each taxon were analyzed using univariate and multivariate statistical packages. UNIVARIATE. Elementary statistics such as character means, standard errors (SE), standard deviations (SD) and coefficients of variations (CV) were calculated separately each taxon and for each population sample (PROC MEANS, SAS 1985, version 5.16). I calculated the % difference for each character based on the overall means for each taxon ($\% \text{ difference} = \frac{\text{Mean}_{\text{larger}} - \text{Mean}_{\text{smaller}}}{\text{Mean}_{\text{larger}}}$) (Power 1970, Schnell et al. 1985).

The amount of overlap between populations on bivariate plots serves to indicate whether a particular combination of two characters completely discriminates between taxa. If populations overlap then the discrimination is poor but if overlap is absent then discrimination is complete. Bivariate plots were used (see Johnson 1963) in this study (CRICKET GRAPH, version 1.1) to illustrate distinctness of *O. philadelphia* and *O. tolmiei* for skeletal and external characters. For each group of skeletal (skull, girdle, leg, wing) and external (WING, TAIL, W-T and WEIGHT) elements I plotted means for all populations for a single character against population means for all other characters within each skeletal or external complex. For example, for skull measurements, PRL was plotted separately against BDEP, NASW, INORW, SKW, SKL, MANL, MAND.

CORL was plotted against KEED, KEEL, SCAPW, STERL, SYNW and SYNMW for girdle measurements. For leg bones, FEL was plotted against FEDW, TARD, TARL, and TIBL. CARPL was plotted against HTRL, HDEW, HUML, ULNL and CARPL for the wing elements. For external characters WING was plotted against TAIL, W-T and WEIGHT. Finally, I compared plots of characters based on their ability to separate populations of each taxon.

Various techniques have been used to illustrate spatial patterns of variation and overlap in character means (Baker 1985). Analysis of Variance (ANOVA) analyzes differences between samples for a particular character in the $N > 2$ samples case (Sokal and Rohlf 1981). The null hypothesis asserts no treatment differences between samples (Klockars and Sax 1986). If a significant difference between populations has been detected multiple comparisons test must be used to find where these differences between samples exist. Multiple comparisons tests find which populations are different from one another and group them into homogeneous subsets. Many different multiple comparisons test exist. I chose the Student- Newman-Keuls test which has been used with Redpolls (*Carduelis flammea* complex) (Troy 1984) and Starlings (*Sturnus vulgaris*) (Ross and Baker 1982) (PROC GLM - SNK, SAS 1985, version 5.16) (see APPENDIX D for Means, SE, N per locality for both taxa). In the SNK comparisons the critical values for rejection of the null hypothesis do not remain constant for two means being compared regardless of the number of means in the set (Klockars and Sax 1986). Critical values change for partial null hypotheses which are evaluated parallel to the original null hypothesis (Klockars and Sax 1986). Means for each character per population sampled and homogeneous subsets of populations were plotted on

maps in order to illustrate patterns of variation. Only populations with four or more birds were used in the ANOVA's.

If populations of these taxa are significantly different from each other then all *O. philadelphia* populations should be contained in homogeneous subsets separate from all *O. tolmiei* populations. If *O. philadelphia* and *O. tolmiei* populations are not significantly different from each other then homogeneous subsets will contain subsets mixed with populations from each taxon.

Geographic variation in morphological variables has been found to covary with latitude, longitude and climatic variables (James 1970, Power 1969). This has been considered evidence of morphological adaptation and selection (Gould and Johnston 1972, James 1982). Environmental selection as the primary cause of observed patterns of geographic variation was originally invoked as an explanation for the covariation with environmental data. However, alternative viewpoints exist (Gould and Lewontin 1979, predictions of vicariance model - Cracraft 1982, 1983, leapfrog model of geographic variation - Remsen 1984, phenotypic plasticity - Baker 1985). Zink and Remsen (1986, pages 32 - 33) point out that relationships between variation in morphological variables and climate "suggests but does not prove adaptation." Significant regressions are consistent with adaptation as one explanation for observed patterns of character variation but do not test it directly. More importantly the regression analyses were used to determine the direction of character variation. Does *O. tolmiei* become more like *O. philadelphia* for skeletal and plumage characters from south to north as it approaches *O. philadelphia's* breeding range? Does *O. philadelphia* become more like *O. tolmiei* from east to west

as it approaches *O. tolmiei*'s breeding range? In this study I used regression analyses to 1) test for a significant linear relationship between morphological characters and environmental variables - latitude and longitude and 2) determine how much variation in a character (dependent variable) was attributable to variation in latitude and longitude (independent variables). The coefficient of determination or R^2 was calculated by dividing the SS of the model by the total SS. In this study R^2 's have been expressed as percentages of the total character variation in relation to latitude or longitude (Power 1970).

For plumage characters, the numbers of *O. philadelphia* birds with eye-arcs and or dark lores per population were calculated and plotted on maps. I regressed these plumage characters on latitude and longitude to see if *O. philadelphia* warblers with *tolmiei* plumage characters were more common as one approached to the contact areas in the western part of *O. philadelphia*'s breeding range. Mensural characters (plumage and skeletal) were also regressed on latitude and longitude.

Correlation analyses between population means and environmental data were conducted to test for significant relationships between morphological and environmental variables as in James (1970) (PROC CORR SPEAR, SAS 1985, version 5.16). This is another approach to the study of geographic variation. Results of these analyses describe whether large birds live in cool versus warmer climates, wetter versus drier and combinations of the two. Spearman's Ranked Correlation Coefficient was used because most weather data is interval data (isophenes) and exact means for a given locality are not available. (For a list of the environmental variables and letter abbreviations see APPENDIX E). Environmental data from Canada was obtained from various Environment

Canada publications (1982a, 1982b, 1984a, 1984b). United States weather data were taken from two sources, ESSA (1968) and Visser (1954). Weather data from ESSA (1968) and Visser (1954) were converted to the metric units for use in conjunction with Canadian weather data.

MISSING DATA. Almost all skeletal specimens had at least one broken bone which was not measurable. According to Baker (1985) it is more important to increase the number of specimens used rather than use as many characters as possible. Power (1970), Johnson (1980) and others have used populations as OTU's and population means for each variable in multivariate analyses instead of the raw scores for individuals. In this type of analysis all observations have complete data sets and data from all specimens are used in computing these means. Using population means insures that all data from all specimens are used in the multivariate analyses but the within population variation component is lost. However there are some important compromises made when using means. The classification functions which are generated by the linear DFA are based on populations and are therefore better for classifying unknown samples of specimens rather than individual specimens. The use of means also inflates Mahalanobis' D^2 between populations compared to using the raw data and specimen as OTU's (Marcus, pers. comm.). This effect is minimal for *Oporornis* data since sample sizes vary from four to 25 specimens per population and both *O. philadelphia* and *O. tolmiei* OTU's have samples with large and small N 's. Characters with high CV's were also eliminated (BDEP, TARD) because of comparatively high measurement error. TIBL was broken for many specimens and it was also ignored in the multivariate analyses.

MULTIVARIATE. Morphological characters were divided into complexes: external complex (study skin measurements), and skull, girdle, leg, and wing complexes (skeletal measurements). I analyzed the ability of morphological characters (considered simultaneously) to discriminate between *O. philadelphia* and *O. tolmiei* OTU's using three multivariate techniques - cluster analysis, plots of principal component scores and discriminant function analysis. For each of the multivariate methods separate analyses were performed on each morphological complex and a single analysis of all complexes combined. I compared the ability of each complex to discriminate OTU's of each taxon. I asked several questions regarding multivariate differences between taxa. Which characters provide the best discrimination of *O. philadelphia* and *O. tolmiei* OTU's? Do intertaxon differences exist between taxa for all body regions (i.e., complexes) and are they more pronounced for some body regions versus others? Log-transformations were made on morphological data prior to all multivariate analyses to accommodate scale differences between different measurements.

I used CA's to find groups of individuals or OTU's which are more similar within groups than among groups (Neff and Marcus 1980). CA's were used in this study to find separate groups of *O. philadelphia* and *O. tolmiei* OTU's. If these taxa are distinct for each complex of morphological variables then the phenograms should contain two large clusters, one containing only *O. philadelphia* OTU's and the other only *O. tolmiei* OTU's. I used a UPGMA algorithm in SAS (version 5.16, PROC CLUSTER) to compute generalized distances between OTU's and plot (PROC TREE) dendrograms.

The purpose of using PCA is to summarize variation into a few new variables or components (Neff and Marcus 1980). PCA is an ordination technique which finds a new set of orthogonal axes in the directions of greatest variance among OTU's (Neff and Marcus 1980). These new axes are also uncorrelated. Principal components are extracted from a variance - covariance matrix. Components are new variables produced from linear combinations of the original variables. Each component accounts for a portion of the total variance. Principal component scores are obtained by solving the principal component using the original or mean-centered measurements (Neff and Marcus 1980). These scores are plotted on the appropriate component axes. Each axis is a scale against which the scores are plotted. Plots of principal component scores for OTU's illustrates the interrelationships between OTU's. I used a PCA in this study to find a new set of orthogonal axes based on morphological variables and display component scores for *O. philadelphia* and *O. tolmiei* OTU's (PROC PRINCOMP, SAS 1985, version 5.16). I analyzed each morphological complex separately and for all complexes combined using PCA's.

Classical Discriminant Function Analysis (DFA) actually describes several different DFA's which have been used to separate pre-designated groups (Neff and Marcus 1980). Discriminant analysis assigns specimens based on DF scores into pre-defined groups, designated by the investigator prior to the analysis (Neff and Marcus 1980). I used two types of DFA in this study - Canonical Variates Analysis (CVA) and Linear Discriminant Function Analysis. CVA in the two group case is a discriminant function analysis (Neff and Marcus 1980, Schnell et al 1985). The distinctness of each group is

evaluated by comparing the within versus among group "scatter" (Neff and Marcus 1980, p. 172). Mahalanobis' D^2 is the squared distance from the OTU to the group centroid and is calculated for all OTU's for all groups. Mahalanobis' D^2 is the most useful statistic for illustrating intergroup distances and the "separateness" of groups in question (Neff and Marcus 1980, p. 165). Comparisons of D^2 for each of the morphological complexes yielded information on the degree of differences between different body regions. I used SAS (1985, version 5.16, PROC DISCRIM) to calculate Mahalanobis' D^2 between *O. philadelphia* and *O. tolmiei* for all skeletal characters at once for each taxon and separately for each character complex. How well a DFA performs is also evaluated by the per cent of OTU's correctly assigned to the pre-defined groups. DFA's have been used to identify unknown specimens (Rising and Schueler 1980, Schnell et al. 1985). Classification functions are calculated for each group which compute distance of an OTU from the group centroids. These functions also can be used to compute distances for unknown specimens and assign group membership based on the values obtained from the functions (for example with California Gulls see Schnell et al. 1985, or for *Contopus* Wood Pewees see Rising and Schueler 1980). I used PROC DISCRM (SAS 1985, version 5.16) to compute these functions and classify unknown OTU's. However, because of shrinking sample sizes due to missing data, these functions are based on population means for each character and not individual specimens. The two *a priori* groups in this study were *O. philadelphia* and *O. tolmiei*, based on song type of the specimen or its neighbors in a population (OTU) which may or may not have been collected. I noted the per cent of OTU's correctly classified by the DFA's for each

morphological complex which was an indication of the similarity of *O. philadelphia* and *O. tolmiei* for each body region. I compared the assignment results of each analysis to ascertain whether degree of differences between each taxon was more pronounced for different body regions.

Standardized coefficients indicate how well individual characters effectively discriminate between the groups in the DFA. Standardized coefficients and DF scores were generated using PROC CANDISC (SAS 1985, version 5.16). I plotted DF scores generated by CANDISC for each OTU using Cricket Graph (version 1.1).

I also performed separate Stepwise DFA's on different morphological complexes and for all characters combined. Stepwise DFA's determine which of the different morphological characters provide maximum discrimination of taxa based on the amount of variability within taxa (Neff and Marcus 1980). Stepwise DFA's have been used to identify characters which best discriminated male and female California Gulls (Schnell et al. 1985) and subspecies of Redpolls (Troy 1984).

STATISTICS: SONG VARIABLES. Terminology describing bird song used in this study follows Shiovitz (1975) and Baptista (1977). The cleanest sonograph from each songster was used in subsequent analyses. Each of the variables described below can be influenced by cultural transmission as well as by genetic factors. The goals of the subsequent analyses were to describe differences between populations, not to separate cultural versus genetic influences on the differences. Two separate analyses were conducted on song variation in these taxa: 1) analysis of species differences and geographic variation in cultural units of song - song types, song

parts, and syllables (Figure 6A); 2) analysis of species differences and geographic variation in physical parameters of song - number of parts per song, number of different syllables per song, number of syllables per song, number of notes per syllable, minimum and maximum frequencies of song, minimum and maximum frequencies of individual syllables, song duration, and inter-syllable intervals (Figure 6B, see APPENDIX F for complete description of measurements taken on sonographs). Syllables from sonographs were visually inspected for similarity and entered into separate syllable catalogues (APPENDIX L - *O. philadelphia* , APPENDIX M - *O. tolmiei*) for each taxon. Physical parameters of song such as frequency and duration variables were measured from sonographs with Max-Cal calipers and data was entered directly into a NEC Portable Computer (PC8201A).

STATISTICS: SONG. Two important functions of primary song are species identification and sex identification (Van Tyne and Berger 1976). This information is sent to other conspecific males and females during territorial establishment and mating. Differences in these signals provide important isolating mechanisms between species. I investigated differences in primary song of *O. philadelphia* and *O. tolmiei* by examining differences in syllables and differences in physical parameters of song. Species differences in song occur in each character set. Two approaches to analyzing song differences between species and between populations of each taxon were taken.

1) Geographic variation in cultural units of primary song (song parts, syllables) was analyzed. I put together song syllable catalogues for each taxon and calculated the number of notes shared by these taxa as an indication of how much overlap in syllables occurred between taxa. Syllable sharing should

be minimal (or absent) if these taxa are different species. Cluster Analysis and the "isogloss method" (Mundinger 1980) were used to describe spatial patterns of variation in syllables of primary song in *O. philadelphia* and *O. tolmiei*. A similarity matrix of male songsters was created using NTSYS (SIMQUAL option with Jaccard coefficient, SAHN options). Cluster Analysis (SAHN option and UPGMA in NTSYS) was performed on the similarity matrix based on the presence/absence of song syllables in a given individual's song. The dendrogram was drawn using TREEG in NTSYS. I also mapped the distribution of different song syllables in both taxa according to Mundinger's (1980, 1982) isogloss method.

Syllables were inspected visually for differences and entered into separate song syllable catalogues for each taxon. Not all songsters sang the same syllable, note for note, as its neighbor. Variations of syllables were called variants. One type of variation involved the numbers of notes which composed the syllable. Variations might have more or less upstrokes (slash shaped notes which formed an angle with the time axis of the sonograph that was less than 90 degrees) or downstrokes (slash shaped notes which formed an angle with the time axis of the sonograph that was greater than 90 degrees), two versus three chevrons (horseshoe shaped notes), etc..., but the pattern of these notes was still shared by all variations of the original syllable. The second type of variation involved the deletion of some notes from the original syllable type while retaining the remainder of the syllable. The third type of variation involved the substitution of a note(s) by a new note type. Some of the original notes were replaced by new notes but the remainder of the syllable still identified it as a variant of the original. A new syllable was not a variant when it contained a

unique pattern of notes. Variants were scored twice in the cluster analysis, once for the original syllable and once for the variant: example MO1 (original), MO1A (variant). Tracings of the song syllables forming each catalogue are located in Appendices L (*O. philadelphia*) and M (*O. tolmiei*) and the geographic distributions of these syllables are in Appendices J (*O. philadelphia*) and K (*O. tolmiei*). These catalogues do not contain the syllable variants.

2) Physical parameters of primary song of these taxa were analyzed for a) species distinctness, b) patterns of geographic variation in population means and c) relationship with environmental variables. Physical parameters belonged to three complexes - frequency, duration/interval and syllable complexes.

Song parameter data were analyzed the same as measurement data for morphological characters. I employed the same univariate and multivariate approaches to analyzing species differences in song parameters as were applied to the morphological data. Questions raised in the morphological statistics section of this chapter also apply to song parameters.

Figure 4. Song playback experiment, simultaneous presentation of *O. philadelphia* and *O. tolmiei* song.

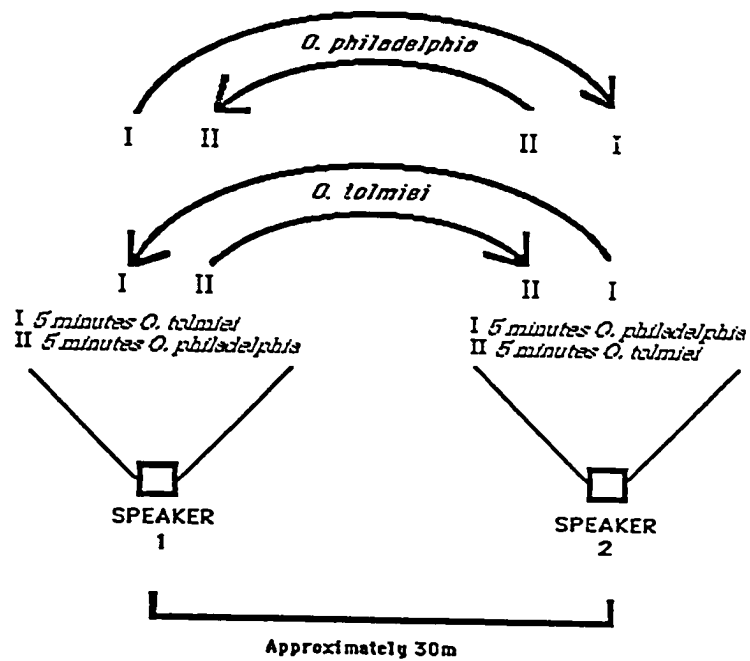


Figure 5. Skeletal characters measured in this study (adopted from Robbins and Schnell 1971).

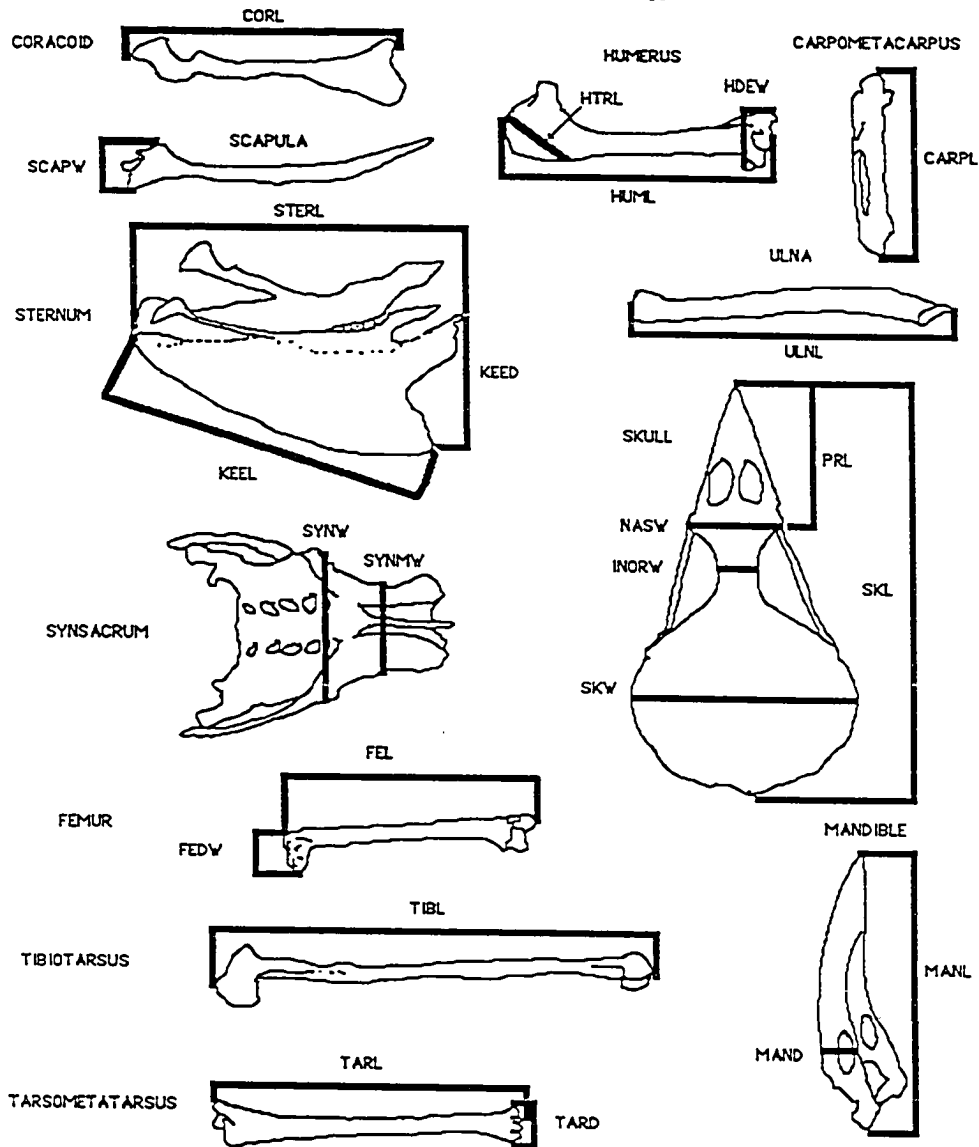
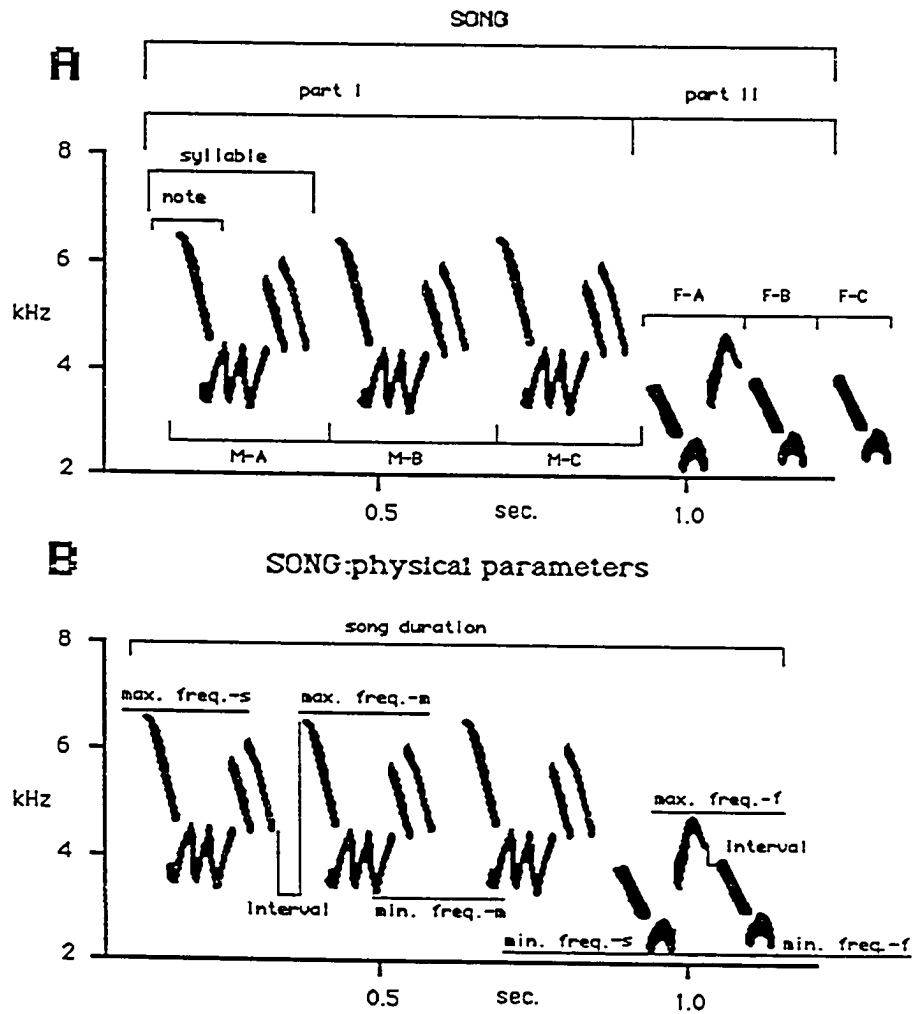


Figure 6. Song variables: A - cultural units, B - physical parameters of primary song.

SONG: parts, syllables, notes.



CHAPTER 3 - CHARACTER CORRELATIONS

Baker (1985) pointed out two problems which must be addressed prior to analyzing differences between populations - 1) how many characters should be used, 2) which characters should be used? During the 1960's and 1970's numerical taxonomists (see Sokal and Sneath 1963, Sneath and Sokal 1973) advocated using 60 or more characters from different parts of the body in order to adequately sample the entire phenome. However, the presence of highly correlated characters presents a problem of redundancy of information content. In most cases highly correlated characters represent functional complexes and convey identical information (Power 1971). Before analyzing differences between taxa, variables to be used in such analyses should be analyzed for redundancy in information content (Johnson 1980, Schnell et al. 1985). Redundant characters are eliminated from multivariate analyses because they do not add to the discrimination of taxa (Baker and Moeed 1979, Baker 1985).

In this study I analyzed morphological and song parameter characters separately for redundancy. The purpose of the analysis was to filter out characters which did not contribute to the discrimination of *O. philadelphia* and *O. tolmiei* OTU's. I performed Cluster Analyses (CA's) on unstandardized correlation coefficients to expose clusters of redundant characters. One member of a cluster was used in the multivariate analyses while the other "redundant" characters were deleted from these analyses. For the multivariate analyses I always chose the character from the cluster which had the smallest number of missing measurements across all specimens.

3.1 PHYSICAL PARAMETERS OF SONG

For *O. philadelphia* two major clusters of song variables were evident at the 0.95 distance mark (Figure 7). Clusters 1 and 2 contained a mixture of frequency, syllable and duration/interval complex variables. Within cluster 1 there are several different minor clusters. Cluster 1A is a "frequency - syllable" cluster. Cluster 1A1 is composed of syllable variables (NPSO, NDSO, NSSO). Maximum and frequency variables for Part I syllables composed cluster 1A2. This was next joined to cluster 1A3 which contained minimum frequency variables for Part I syllables, maximum frequency variables for Part II syllables and the song duration variable. Cluster 2 is a "frequency - duration/interval" cluster. Cluster 2A was composed of minimum frequency variables for Part II syllables. Cluster 2B was composed of intervals between Part I and Part II syllables.

At the 1.05 distance mark on the *O. tolmiei* dendrogram 2 major clusters emerge (Figure 7). Cluster 1 is a "minimum frequency - syllable" cluster. The second cluster is a combination of maximum frequency, interval between syllables and number of notes per syllable cluster. Cluster 1 contained three minor clusters at the 0.80 distance mark. Cluster 1A contained song syllable variables and the song duration variable. Minimum frequency variables for Part I syllables composed cluster 1B. Minimum frequency variables for Part II syllables composed cluster 1C. Four minor clusters belonging to cluster 2 were also evident at the 0.80 distance mark. Cluster 2A contained intervals between Part I and Part II variables. Maximum frequency variables joined together to form cluster 2B. Cluster 2C contained numbers of notes per Part II syllables and

next joined cluster 2D which was composed of numbers of notes per Part I syllables.

While most major clusters were mixtures of variables from different song parameter complexes (frequency, syllable and duration/interval), most minor clusters of song parameter variables for both taxa were homogeneous, composed only of variables from the same complex. Frequency variables segregated together; number of notes per syllable clustered together; number of syllables per song clustered with number of different syllables per song and number of different parts per song. There were two differences between these taxa with regard to the composition of the major clusters. In *O. philadelphia* interval variables clustered with minimum frequency variables. In contrast, interval variables clustered with maximum frequency and number of notes per syllable variables in *O. tolmiei*. In *O. tolmiei* syllable variables clustered together with minimum frequency variables instead of all frequency variables and number of notes per syllable variables as in *O. philadelphia*. However, for both taxa song parameter characters belonging to the same complex were usually more highly correlated with each other than they are with characters from different complexes.

The following characters were used in subsequent multivariate analyses of song parameters: **Frequency Complex** - MINS, MAXS, MIA, MAA, MIFA, MAFA; **Duration/Interval Complex** - DUR, IMA, IMB; **Syllable Complex** - NPSO, NSSO, NDSO, NNA, NNB, NNC.

3.2 MORPHOLOGICAL VARIABLES

At the 1.2 distance mark there are 2 major clusters of morphological variables on the *O. philadelphia* dendrogram. Six minor clusters are evident around the 0.90 distance mark (Figure 8). The first cluster is homogeneous, containing only skull characters (PRL - MANL). The remaining clusters contain mixtures of characters from different complexes. The pattern is similar for *O. tolmiei* (Figure 8). The first cluster is homogeneous while the remaining clusters are mixed. Skeletal and external characters did not cluster together by complex. Intercorrelations between skeletal characters are moderate or weak for each taxon and thus their relative information content is high.

The following characters were used in subsequent multivariate analyses of mensural characters: **External Complex** - WING, TAIL, W-T; **Skull Complex** - PRL, NASW, INORW, SKW, MANL; **Girdle Complex** - CORL, STERL, KEED, SYNW, SYNMW; **Leg Complex** - FEDW, FEL, TARL; **Wing Complex** - HTRL, HDEW, HUML, ULNL.

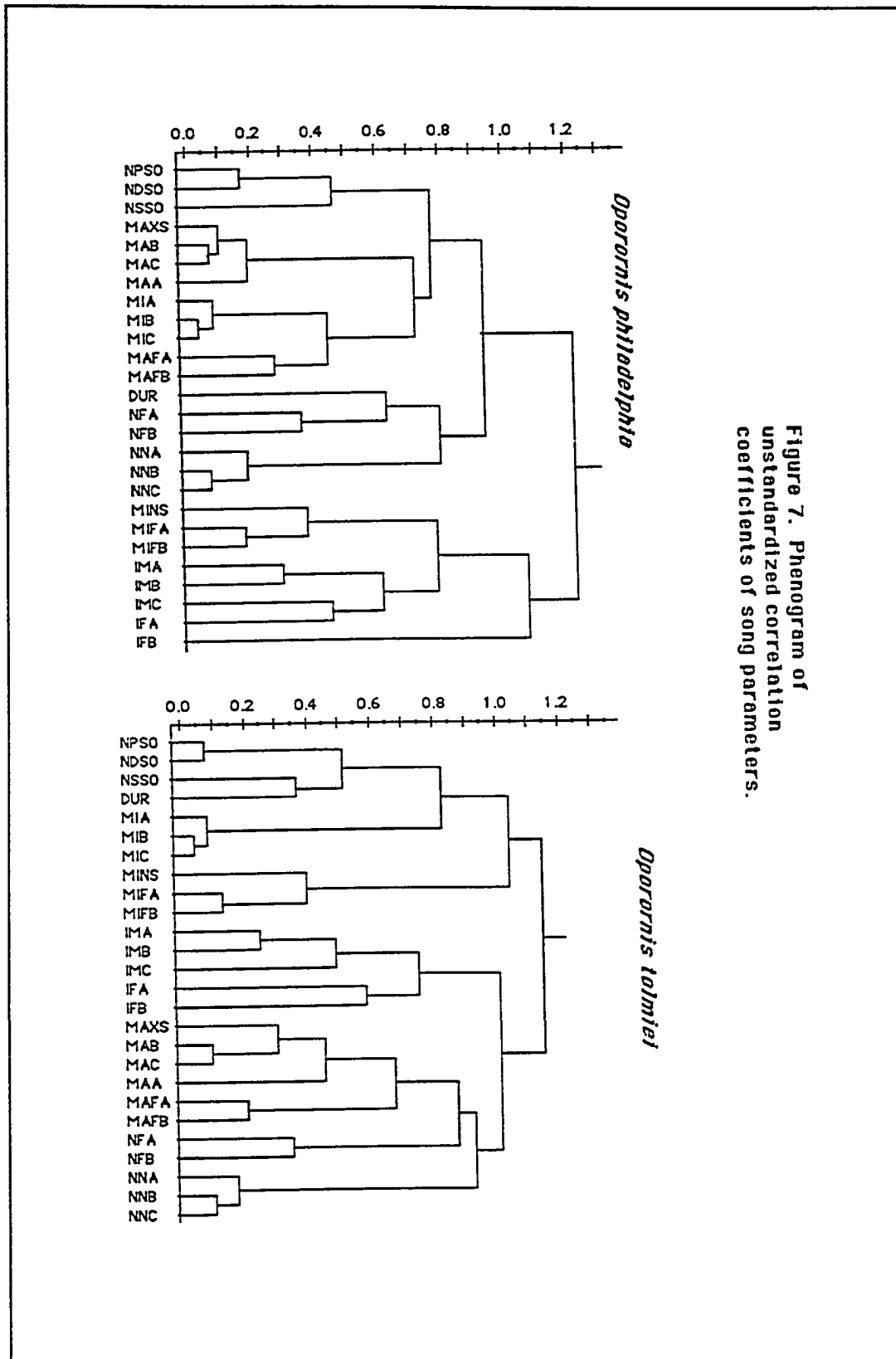
3.3 SUMMARY

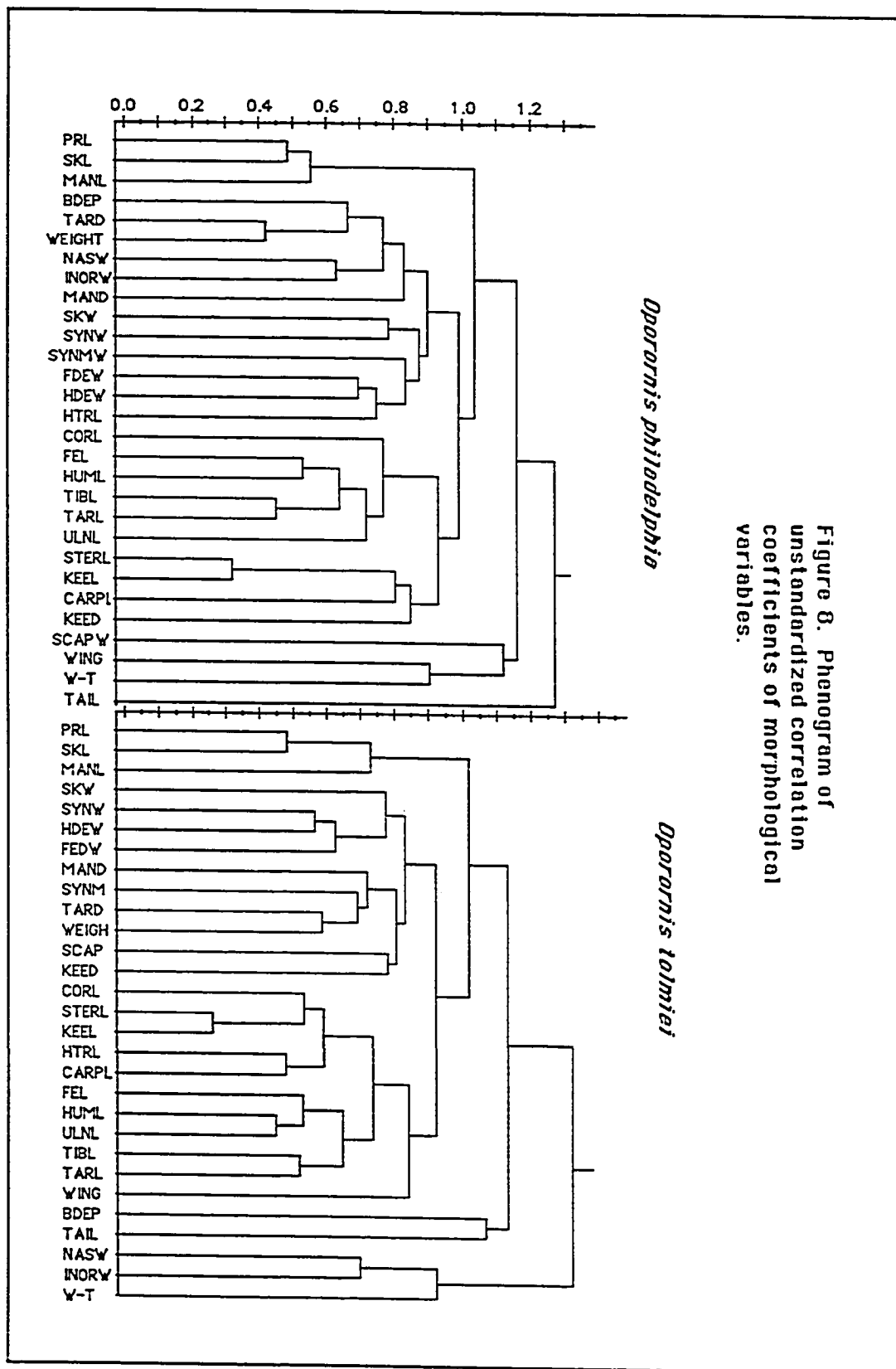
Two different patterns of correlations between variables existed between morphological and song characters. Song character variables belonging to the same complex usually clustered together. This was found in both taxa. In contrast, for morphological characters, variables belonging to the same morphological complex more often correlated with variables from different body regions than with variables from the same complex. For example in *O. tolmiei* girdle variables clustered together with wing and skull variables; external characters clustered together with leg and skull variables. Similar patterns of

clustering of variables from different body regions also existed in *O. philadelphia* .

Another major difference between morphological variable and song variable clustering is that joining of song variables into minor clusters occurred at smaller distances than joinings of morphological variables. At the 0.40 distance all song variables had joined to form a minor cluster for both taxa . Only two morphological variables in *O. tolmiei* and four in *O. philadelphia* had joined together in minor clusters at the same distance mark. Thus, individual skeletal variables provide less redundant and more new information than individual song characters.

Most song parameter variables from the same complex tended to cluster together while morphological variables from the same complex did not. These results suggest that morphological variables contain considerably more independent information than do song parameter variables. Dendrograms of skeletal measurements of California Gulls (*Larus californicus*) from Schnell et al. (1985) show a pattern similar to the results of the morphological analysis for *Oporornis* taxa. Most skeletal characters clustered together with characters from different body regions. Results of analyses of *Oporornis* song parameters agrees with Johnson's (1980) analyses of character correlations of *Empidonax* song parameter characters - most song parameters cluster together with parameter variables from the same complex (e.g., frequency with frequency, etc...).





CHAPTER 4 - RELATIVE VARIABILITY

I used two approaches to describe the relative variability of morphological and behavioral characters within each taxon: 1) nested ANOVA and 2) CV . The nested ANOVA was used to ascertain the sources of variation in each character. Variation was attributed to three sources nested in the following hierarchy: between taxa, between populations within taxa and between individuals within populations.

4.1 MORPHOLOGICAL CHARACTERS

4.1.1 NESTED ANOVA OF MORPHOLOGICAL CHARACTERS

I used the results of the nested ANOVA to separate the variance into three effects: 1) between taxa, 2) between populations within taxa and 3) between individuals within populations. By comparing the per cent of the variance attributed to each effect I was able to ascertain the amount of differentiation in each character across taxa, populations and individuals. The results for the morphological data are depicted in Figure 9 (see also Table 1). Characters with high variation between taxa are on the left of the graph and characters with low variation between taxa are on the right side of the graph. Over 70% of the variation in W-T represent variation between taxa. Other characters with a relatively high per cent (greater than 55%) of the variation attributed to which taxon the specimen belonged to were TAIL, CORL, STERL, KEEL, HUML, FEL and INORW. Characters which most of the total variance

(90% or greater) was common to all specimens (among individuals within populations effect) included SKW, TARL, SYNW, SKL, HDEW and PRL. The among population effect was small for all morphological characters.

4.1.2 CV' FOR MORPHOLOGICAL CHARACTERS

The CV has been widely used to describe and compare variability between characters and between populations for a given character (Yablokov 1974, Barnett 1977, Johnson 1980, Bird et. al. 1981, Sokal and Rohlf 1981, Pankakoski et. al. 1987). However, caution must be exercised in interpreting CV's of small traits because they are more sensitive to the affects of chance (Lande 1977, Pankakoski et. al. 1987). An inverse relationship between Mean and CV exists for many animals (Pankakoski 1987, Rohlf et. al. 1983, Yablokov 1974). Soule (1982) coined the term "allomerism" to describe the tendency for variability in traits to decrease with increasing size. I examined the relationship of variation to morphometric size by regressing character CV's on their Means separately for *O. philadelphia* and *O. tolmiei*. For both taxa there was an inverse relationship between CV's and Means which was highly significant ($p < .002$ - *O. tolmiei* and $p < .001$ - *O. philadelphia*). This pattern was also observed for song characters ($p < .001$ - *O. tolmiei* and $p < .002$ - *O. philadelphia*). Characters with small measurements had high CV's while larger characters had small CV's. Below I describe and compare variability between characters and between taxa for a given character but I do not consider the results robust for the reasons mentioned above.

The average CV for all populations within each taxon were calculated for each character (Table 2) (see APPENDIX D for CV's for all localities). External characters were less variable than skeletal characters in *O. philadelphia* and *O. tolmiei*. Exceptions include W-T and weight. W - T was the most variable character in both taxa and was much more variable in *O. tolmiei*. The smaller measurements (BDEP, SCAPW, TARD) were more variable than larger measurements (SKW, SKL, CORL, FEL, HUML etc...) in both taxa.

When all characters were compared individually between taxa, *O. philadelphia* could be considered slightly more variable than *O. tolmiei* for morphological characters (Table 2). Nine of the 25 skeletal measurements (PRL, BDEP, INORW, MANL, SCAPW, FEL, TIBL, HDEW, CARPL) were more variable in *O. philadelphia* while three measurements (MAND, KEEL, TARD) were more variable in *O. tolmiei*. Differences between taxa in CV's were not greater than .01 for all skeletal characters except INORW and TARD. The CV's of the remaining skeletal characters were equal. Wing and Tail were equally variable for *O. philadelphia* and *O. tolmiei*. The CV for W-T for *O. tolmiei* was more than three times as variable as the CV for *O. philadelphia*.

In mammals, variability in skeletal characters has been shown to be "character specific" rather than "species specific" (Yablokov 1974). I compared the amount of Relative Variability graphically to illustrate whether pattern of character variability were "species specific" or "character specific." I graphed CV's for morphological and song characters separately for both taxa following Power (1983). Figure 10 shows similar patterns for *O. philadelphia* and *O. tolmiei*. Song and morphological characters which were highly variable in *O. philadelphia* were also highly variable in *O. tolmiei*. The same holds true for

characters exhibiting low variability.

4.1.3 REGRESSIONS OF CV'S OF MORPHOLOGICAL CHARACTERS ON LATITUDE AND LONGITUDE

I performed regression analyses of CV's from *O. philadelphia* and *O. tolmiei* populations for morphological characters on latitude and longitude to determine if characters tended to vary significantly ($p < .05$) from east to west or south to north in *O. philadelphia* and *O. tolmiei*. In *O. philadelphia* seven characters showed a significant linear relationship between CV and latitude or longitude while in *O. tolmiei* three characters exhibited significant linear relationships. PRL became more variable from south to north ($p < .02$) and east to west ($p < .006$) but only 34.4% and 45.0% of the variation in CV was attributed to latitude and longitude respectively. BDEP became more variable from south to north in the range of *O. philadelphia* ($p < .03$). Only 29.3% of the variation in the CV for this character was attributed to variation in latitude. INORW became less variable from south to north ($p < .02$) and from east to west ($p < .01$). Variation in latitude accounted for 34.0% of the variation in the CV for INORW while 37.1% of the variation in the CV was longitudinal. In *O. tolmiei* MANL was the only skull measurement whose CV varied significantly with either latitude or longitude. MANL became less variable from east to west ($p < .01$) in *O. tolmiei*. Only 32.7% of the variation in the CV of MANL was attributed to longitudinal variation. KEEL became less variable from south to north ($p < .02$) and east to west ($p < .005$) in *O. philadelphia*. Variation in latitude explained 33.2% of the variation in the CV for KEEL while variation in longitude accounted for 46.6% of the variation in the CV. There were no significant linear

relationships between CV's for girdle characters and latitude or longitude for *O. tolmiei* ($p > .05$). TAIL became less variable from south to north in *O. tolmiei* ($p < .04$). No significant linear relationships between the CV's for leg characters and latitude or longitude existed for *O. philadelphia*. For wing bones only HDEW exhibited a significant negative linear relationship with longitude ($p < .02$) in *O. philadelphia*. Only 32.0% of the variation in the CV of this character was attributed to longitudinal variation. Significant linear relationships between CV's for wing characters and latitude or longitude were not found in *O. tolmiei*. WEIGHT became more variable from south to north in *O. tolmiei* ($p < .02$). Latitudinal variation accounted for 76.9% of the variation in the CV of this character. A significant positive linear relationship between the CV and longitude was also found in *O. tolmiei* ($p < .02$). Longitudinal variation accounted for 73.5% of the variation in the CV of WEIGHT. No linear relationships between CV for WEIGHT and latitude or longitude existed for *O. philadelphia*. CV's of WING and TAIL in *O. philadelphia* showed significant linear relationships with latitude ($p < .03$ and $p < .01$ respectively). Both characters became less variable from south to north. Variation in latitude attributed 28.7% of the variation in CV for WING in *O. philadelphia*. Latitudinal variation accounted for 39.0% of the variation in the CV for TAIL in *O. philadelphia*. CV for TAIL also varied significantly ($p < .02$) with longitude. TAIL became less variable from east to west in *O. philadelphia*. Longitudinal variation explained 32.8% of the variation in the CV of this character. There were no significant linear relationships between the CV's for external characters and latitude and longitude for *O. tolmiei* ($p > .05$).

4.1.4 CLUSTER ANALYSES OF CV'S OF MORPHOLOGICAL CHARACTERS

I used CA's to examine the spatial distribution of variability for different morphological complexes. I performed separate cluster analyses on the CV's of *O. philadelphia* and *O. tolmiei* populations to examine the distribution in each taxon. In the following analyses each population is an OTU and the data were the population CV's of skeletal characters. Within each taxon I performed separate CA's on different morphological complexes - skull, girdle, leg, wing, external complexes. All characters within the complex were used simultaneously.

Descriptions of geographic locations of OTU's made below are in reference to the breeding range of either *O. philadelphia* or *O. tolmiei*. For example an eastern OTU refers to an OTU from the eastern part of the breeding range, not necessarily from eastern North America. OTU's and populations are interchangeable in the following discussion.

***Oporornis philadelphia*.** There were seven clusters at the 0.70 distance mark on the phenogram for skull variables (Figure 11). Four of these contained only one OTU each (3, 4, 5, 7). Populations from clusters 1 and 2 were primarily from the eastern part of the breeding range (Ontario, Quebec, Maine, New York). Most of the remaining OTU's were from the west (except for one population from Quebec in cluster 4 - SP and one population from cluster 6 - GE from Ontario). In *O. philadelphia* there was a weak east - west pattern of variability for skull characters.

Four clusters are apparent at the 0.78 distance mark on the phenogram for girdle characters (Figure 12). Two clusters contained one population each

(3, 4). OTU's from clusters 1 and 2 were from throughout the breeding range. There was no geographic segregation of variability for girdle characters.

For leg characters there were 5 major clusters at the 0.75 distance mark (Figure 13). Two clusters had only one OTU each (2, 5). A majority of the eastern populations (Maine, New York, Ontario and Quebec) belonged to clusters 1. However SL and LP and WH from central Alberta, were also joined with eastern populations. Cluster 2 was composed of populations from eastern Quebec, western Ontario and British Columbia. Unlike other complex variables, the clusters for leg characters were geographically heterogeneous. The pattern of variability was a mosaic.

Four major clusters were evident at the 0.93 distance mark for wing characters (Figure 14). Two clusters contained one OTU each (2, 4). Most of the OTU's west of central Ontario belonged to cluster 3. However, two eastern OTU's from Quebec (LE, SP) also belonged to this western cluster. Except for one OTU from Alberta (SL), all OTU's from cluster 1 were from the east. There was weak segregation of eastern and western populations.

At the 0.70 distance mark there were 5 major clusters for external characters (Figure 15). OTU's from different clusters were distributed from throughout the breeding range. For example, OTU's from cluster 3 ranged from Alberta to Maine. Cluster 1 contained OTU's from eastern Quebec to southwestern Alberta. There was no segregation of eastern or western populations. This pattern was also a mosaic.

For some complexes there was a segregation of eastern and western populations for character variability. The western populations were along the

western boundary of the breeding range while the eastern populations are from the middle (or close to it) of the breeding range.

Oporornis tolmiei. For skull characters there were 4 major clusters at the 0.85 distance mark (Figure 16). Cluster 4 had only one OTU (from eastern Idaho - PO). Cluster 1 contains southerly populations (Nevada, Oregon, Montana) and overlaps geographically with cluster 2 to which it is joined next in the phenogram. Cluster 2 contains OTU's from northern Washington and central British Columbia. Cluster 2 overlaps geographically with cluster 3 but not with cluster 1. Cluster 3 contains OTU's from southwestern Alberta and northeastern British Columbia.

There were three major clusters of OTU's for CV's of girdle characters at the 0.85 distance mark (Figure 17). Cluster 3 contained one divergent population from Montana - SQ. Three OTU's along the eastern edge of the breeding range joined together in cluster 2. Except for three eastern OTU's (British Columbia - LR, Alberta - KA, Wyoming - WY) the rest of the populations in cluster 1 were from the southern and western parts of the breeding range (Idaho, Nevada, Oregon, Washington, British Columbia). There is a weak segregation of some eastern OTU's for the girdle complex.

Five major clusters are apparent at the 0.65 distance mark (Figure 18) for leg characters. LR from northeastern British Columbia is the only member of cluster 5. This is the most divergent member of all clusters. Cluster 1 contains OTU's from the eastern Nevada (JA), southeastern Idaho - PO, and southern Montana (SQ). this was the only cluster which showed any geographic homogeneity. OTU's from clusters 2, 3, 4, and 5 were scattered from different parts of the breeding range. Only two OTU's (KA, MC) from cluster 2 were

geographically adjacent to each other. OTU's within clusters 3 and 4 were not geographically adjacent to each other. OTU's in cluster 3 were from northern Montana and central British Columbia separated by two OTU's from Alberta and southern British Columbia. The spatial pattern of variability of in the leg complex is a mosaic with some segregation in southeastern Idaho, northeastern Nevada and southwestern Montana.

At the 0.85 distance mark there were 5 major clusters of OTU's for the wing complex (Figure 19). The geographic pattern of variability in this complex was mosaic with little or no geographic segregation of OTU's. Clusters 1, 2, and 4 each contained OTU's from different parts of the breeding range. Most geographically adjacent populations were from different clusters. However, two Idaho populations (PO, MM) were geographically adjacent to each other and belonged to cluster 2. One OTU from northern Washington (LO) and one from southeastern British Columbia (BA) were also geographically adjacent to each other and belonged to cluster 1. These were the only cases of OTU's which belonged to the same cluster and were close to each other geographically. Cluster 3 had only one OTU from northeastern California (CE). Cluster 5 also contained a single divergent population from central Washington (SC).

Four major clusters were evident at the 0.50 distance mark for external characters (Figure 20). Cluster 4 contained a single divergent population from northeastern Montana (LH). Cluster 2 also held a single populations from southwestern Idaho (MM) which was later linked to cluster 1. Members of cluster 1 were as widely distributed as Nevada and Alberta. OTU's in cluster 3 were also widely scattered from throughout the breeding range. The spatial distribution of variability in external characters was also a mosaic.

4.2 SONG CHARACTERS

4.2.1 NESTED ANOVA OF SONG PARAMETERS

As in the morphological nested ANOVA, I broke down the variance components in song parameter characters into three effects: 1) between taxa, 2) between populations within taxa, and 3) between individuals within populations. In Figure 9 the parameter characters on the left of the graph had a majority of the variance attributed to the between taxa effect while characters on the right side of the graph had a majority of the variance attributed to the between individuals effect. Characters with more than 50% of the total variance explained by between taxa effects included MAFB, MAFA, NFA, MIFB, MIFA, and MINS (Figure 9 and Table 3). The among population effect was also small for the song parameter characters. The among population effect was greatest for NNA, NNB and NNC. Characters with 80% or more of the variation attributed to between individuals were IFB, IMA and IMC.

4.2.2 CV'S FOR SONG PARAMETER CHARACTERS

CV's of physical parameters of song were averaged over localities for each taxon (Table 4) (see APPENDIX H for CV's for all localities). Considering both taxa simultaneously, the mean CV's for interval between syllable variables (IMA, IMB, IMC, IFA AND IFB) were the most variable physical parameters of song. Characters showing the least variation were maximum frequency variables (MAXS, MAA, MAB, MAC) (Table 4). There are differences between

taxa in the amount of variation in some characters (Table 4). *O. tolmiei* was more variable than *O. philadelphia* for 18 of 26 song parameter variables (Table 4). Both taxa were equally variable for DUR and MAXS song parameters. *O. philadelphia* was more variable for six of the parameter variables (MINS, MAA, MAB, MAC, MAFA, MAFB). The variability profile of song parameters showed that the characters which were highly variable in *O. philadelphia* were also highly variable in *O. tolmiei*. The same was true for characters exhibiting low variability (Figure 10). Behavioral characters were more variable than morphological characters.

4.2.3 REGRESSIONS OF CV'S OF SONG PARAMETERS ON LATITUDE AND LONGITUDE

Most song characters did not show any significant north-south or east-west patterns of increasing or decreasing variability in these taxa. *O. philadelphia* and *O. tolmiei* differed in the number and types of characters whose CV's exhibited significant linear relationships with latitude and longitude. Eight characters showed significant linear relationships in *O. philadelphia* and three characters in *O. tolmiei*. Regression of CV's of NPSO on latitude was highly significant ($p < .002$) for *O. philadelphia*. Songsters became more variable for NPSO from north to south in the range of this taxon. Latitudinal variation accounted for 45.9% of the variation in CV's of NPSO. The amount of variation in NPSO also increased significantly from east to west in *O. philadelphia* ($p < .004$). Longitudinal variation accounted for 42.9% of the in CV's of this character. A significant positive linear relationship between the CV's of NPSO and latitude ($p < .003$) was found in *O. philadelphia*. Variation in NPSO

increased from south to north in *O. philadelphia*. Variation in latitude accounted for 43.5% of the variation in CV's of NDSO in this taxon. NDSO became more variable from south to north in *O. philadelphia* ($p < .003$). Latitudinal variation accounted for 44.7% of the variation in CV's of this character in *O. philadelphia*. In *O. philadelphia* NDSO became more variable from east to west ($p < .003$). Variation in longitude accounted for 43.7% of the variation in CV's of NDSO in *O. philadelphia*. Variation in MAA decreased from south to north in *O. philadelphia* ($p < .01$). Latitudinal variation accounted for 33.7% of the variation in CV's for this character. CV's for MAA decreased from east to west in *O. tolmiei* but this relationship was barely significant ($p < .04$). Only 29.7% of the variation in this character could be attributed to longitudinal variation. In *O. tolmiei* CV's for IMA decreased significantly from east to west ($p < .002$). Variation in longitude accounted for 55.5% of the variation in the CV of this character. CV's for MIA also decreased from east to west in *O. tolmiei* ($p < .0001$). Longitudinal accounted for 82.0% of the variation in the CV of MIA. A weak but significant linear relationship ($p < .04$) existed between variability in MIFA and latitude in *O. philadelphia*. Variation in MIFA decreased from south to north. Variation in latitude accounted for 34.4% of the variation in CV's for this character. The relationship between MIFB and latitude was stronger than MIFA ($p < .02$) in *O. philadelphia* and accounted for more of the variation (46.8%) in the CV. MIFB also decreased from south to north. There was a weak but significant linear relationship between IFA and longitude ($p < .04$) in *O. philadelphia*. Variability in IFA decreased from east to west in this taxon. Longitudinal variation accounted for 36.3% of the variation in CV's of this character. In *O. tolmiei* variation in MAFB decreased east to west ($p < .0001$).

Longitudinal variation accounted for 97.0% of the variation in this character. No other significant relationships existed between CV's of song characters and latitude or longitude in *O. tolmiei*.

4.2.4 CLUSTER ANALYSES OF CV'S OF SONG PARAMETERS

I performed three separate cluster analyses on CV's to describe spatial patterns of variability for each song parameter complex - frequency, duration/interval and syllable complexes. In these analyses OTU's were the populations and CV's per song character were the data analyzed. Each taxon was analyzed separately.

***Oporornis philadelphia*.** CA's of frequency parameters revealed 5 major clusters at the 0.80 distance mark for frequency characters (Figure 21). OTU's in each of these clusters were from throughout the breeding range. There was no geographic pattern to these clusters. Cluster 1 contained populations from Maine (SF), Ontario (MI, DO, HE), Quebec (VP, GI) and Alberta (SL) and cluster 2 contained OTU's from British Columbia (FN), Newfoundland (RO, PS) and Quebec (LE). Most OTU's from cluster 1 occurred in the center of the breeding range. However, two OTU's were from Alberta, along the western boundary of the breeding range. OTU's from cluster 2 were from the periphery of the breeding range (west - British Columbia; east - Newfoundland), except for LE from Quebec. This is weak evidence for peripheral versus central patterns of variability in this taxon. Populations in close geographic proximity to each other were not necessarily clustered together. A mosaic pattern of variability in frequency complex variables exists in *O. philadelphia*.

Four major clusters were evident at the 0.65 distance mark for duration/interval variables (Figure 22). Each cluster consisted of OTU's from throughout the breeding range. OTU's from Alberta (SL, LP), Ontario (HE, DO), Maine (SF) and Newfoundland (PS) composed cluster 1. OTU's in cluster 2 were from Quebec (GI, VP, LE), eastern and central Ontario (CO and GE respectively), Alberta and British Columbia (FR). Since OTU's from these clusters were irregularly distributed throughout the breeding range there is no evidence for a peripheral versus central pattern of variability. Clusters 3 and 4 held one population each (RO and CB). OTU's from the periphery was as variable as OTU's from center of the breeding range. A mosaic pattern of variability also existed for duration/interval variables.

There were seven clusters at the 0.65 distance mark (Figure 23) for SYLLABLE characters. Clusters 2, 3, and 4 were composed of one OTU each. Other clusters did not reflect any geographic pattern. All adjacent populations belonged to different clusters except for VP and CO which were on either side of the Ontario - Quebec border. Each was composed of OTU's which were widely scattered throughout the breeding range. OTU's from the periphery were as variable as OTU's from center of the breeding range.

For each of the three song parameter complexes there was no spatial pattern of variability. Adjacent populations usually belonged to different clusters regardless of the parameter complex which was analyzed. There was also no evidence for more or less variability at the periphery or center of the breeding range. Populations from the periphery of the breeding range often belonged to clusters which included populations from the center of the breeding range and vice versa.

***Oporornis tolmiei*.** Four clusters of OTU's were evident at the 0.90 distance mark for the frequency complex (Figure 24). The most divergent, clusters 3 and 4, held one OTU each. Cluster 1 was composed of northern and southern populations in the breeding range. The southern populations were from northern Nevada (JA, PV) while the northern population was from central British Columbia (MC). These populations were at or near the southern and eastern edges of the breeding range respectively. OTU's from cluster 2 were from the center of all the sampling localities. This is also the approximate the center of the breeding range for *O. tolmiei*. However more sampling from the northern part of the breeding range (northern British Columbia) and from the south (California, Utah, Nevada, Arizona) is required to further substantiate this trend.

Three clusters were evident at the 0.80 distance mark for duration/interval characters (Figure 25). Clusters 1 and 2 were composed of populations which were both geographically distant and close to each other. However, OTU's from cluster 2 (Idaho - PO, MM; Oregon - MH, FK; Washington LO) were interior to cluster 1 OTU's (Nevada - JA, PV to the south, Washington PA and SC to the west and north, British Columbia - MC from the north). However, more sampling at the macro and microgeographic level is required from locations mentioned above to further document these patterns.

Five clusters were evident at the 0.65 distance mark for the SYLLABLE complex in *O. tolmiei* (Figure 26). Clusters 2, 4, 5 held only one cluster each. OTU's from cluster 1 were the same as cluster 1 for duration/interval complex except for LO and MH. This spatial pattern of variability was similar to the pattern for duration/interval complex variables. OTU's from the south (Nevada)

clustered with OTU's from the east and north (Washington and northern Oregon). There was no distinct segregation of variability of OTU's for this complex.

4.3 SUMMARY

NESTED ANOVA: MORPHOLOGICAL VARIABLES. The two major sources of variation in morphological characters were between taxa or between individuals within populations. The among population source was small for all characters considered.

CV: MORPHOLOGICAL VARIABLES. External characters tended to be less variable than skeletal characters except for W-T and WEIGHT. Although *O. philadelphia* was slightly more variable than *O. tolmiei* the variability profile showed that the overall pattern of variability in morphological characters was the same in each taxon. This agrees with Yablokov's findings that variability in morphological characters is character specific rather than species specific.

Only seven characters in *O. philadelphia* and three characters in *O. tolmiei* showed a significant linear relationship with either latitude or longitude. These results show that most characters do not show any spatial pattern of variability. The CA's also did not reveal any spatial patterns of variability in each of the complexes for *O. philadelphia*. Although variability in the skull and wing complexes did show some segregation of eastern and western OTU's their respective clusters were mixed with eastern and western OTU's. In *O. tolmiei* there were three major clusters which exhibited some spatial heterogeneity. Clusters 1, 2 and 3 were from the southern, middle and northern latitudes of the

breeding range respectively. CA of the girdle characters exhibited a weak segregation of eastern and western OTU's. Results of the CA's of leg and wing and external character complexes exhibited a mosaic pattern of character variability.

NESTED ANOVA: SONG PARAMETERS.

The results for song parameters were similar to the morphological results. Between taxa and between individuals within populations were the two major sources of variation for song characters. Although the among populations source of variation was larger than its counterpart for any morphological characters it was never greater than 50% of the total variation.

CV: SONG PARAMETERS. On the average most song characters were more variable than morphological characters. For both taxa duration/interval characters were the most variable characters while frequency characters were among the least variable. Although there were some slight differences in CV's between taxa the variability profile showed the pattern of variability in characters was similar in both taxa (Figure 10).

Few characters exhibited significant relationships with latitude or longitude. Only eight *O. philadelphia* song character and three *O. tolmiei* song characters showed significant relationships of variability with latitude or longitude. CA's of CV's for *O. philadelphia* song character complexes did not reveal any spatial pattern to the variability of these complexes. However, there was some segregation evident in the range of *O. tolmiei*. For the frequency complex northern and southern OTU's formed a cluster of peripheral populations while OTU's between them formed another cluster. This pattern suggests a peripheral versus central pattern of segregation of variability of this

character complex. In contrast to the lack of spatial patterns of variability in *O. philadelphia*, the frequency complex did exhibit geographic patterns in variability in *O. tolmiei's* breeding range.

Table 1. Per Cent of the variance attributed to among taxa, among populations, and among individuals within populations from a nested ANOVA of morphological characters.

MORPHOLOGICAL CHARACTER	BETWEEN TAXA	BETWEEN POPULATIONS	WITHIN POPULATIONS
PRL	8.29	27.56	64.14
BDEP	10.92	9.74	79.33
NASW	35.37	1.25	63.37
INORW	56.72	1.43	41.84
SKW	0.00	3.09	96.90
SKL	7.28	22.32	70.39
MANL	19.58	0.00	80.41
MAND	48.42	4.95	46.62
CORL	67.47	6.12	26.40
SCAPW	29.75	9.73	60.50
STERL	65.92	3.13	30.93
KEEL	60.47	5.06	34.46
KEED	49.01	2.78	48.20
SYNW	6.18	8.39	85.41
SYNMW	1.09	2.42	96.47
FEDW	30.15	4.90	64.93
FEL	57.47	4.89	37.63
TIBL	23.66	0.15	76.17
TARL	0.00	8.27	91.72
TARD	16.00	13.74	70.25
HTRL	41.57	5.67	52.74
HDEW	7.74	0.00	92.25
HUML	58.71	7.05	34.23
ULNL	34.42	4.89	60.67
CARPL	21.48	11.98	66.52
WEIGHT	53.75	15.15	31.09
WING	18.18	8.97	72.83
TAIL	69.67	7.78	22.54
W-T	80.25	5.38	14.35

Table 2. Comparison of mean coefficients of variation of morphological characters.

<i>Oporornis tolmiei</i>			<i>Oporornis philadelphia</i>	
MORPHOLOGICAL CHARACTER	MEAN CV	N	MEAN CV	N
PRL	0.16	17	0.03	15
BDEP	0.08	17	0.09	15
NASW	0.04	17	0.04	15
INORW	0.05	16	0.07	15
SKW	0.01	15	0.01	15
SKL	0.01	15	0.01	15
MANL	0.01	17	0.02	15
MAND	0.05	17	0.04	15
CORL	0.01	17	0.01	15
SCAPW	0.06	17	0.07	15
STERL	0.02	16	0.02	15
KEEL	0.04	17	0.03	15
KEED	0.04	17	0.04	15
SYNW	0.02	16	0.02	15
SYNMW	0.04	16	0.04	15
FEDW	0.02	16	0.02	15
FEL	0.01	16	0.02	15
TIBL	0.01	11	0.02	15
TARL	0.02	15	0.02	15
TARD	0.12	16	0.09	15
HTRL	0.02	16	0.02	15
HDEW	0.02	16	0.03	15
HUML	0.01	16	0.01	15
ULNL	0.02	16	0.02	15
CARPL	0.02	16	0.03	15
WEIGHT	0.04	12	0.03	15
WING	0.02	19	0.02	15
TAIL	0.03	19	0.03	15
W-T	0.42	19	0.13	15

Table 3. Per Cent of the variance attributed to among taxa, among populations, and among individuals within populations from a nested ANOVA of song characters.

SONG CHARACTER	BETWEEN TAXA	BETWEEN POPULATIONS	WITHIN POPULATIONS
NPSO	13.66	14.88	71.44
NSSO	32.52	6.11	61.36
NDSO	12.30	12.27	75.42
DUR	26.12	0.17	73.70
MINS	56.01	4.25	39.72
MAXS	21.18	23.69	55.12
NNA	0.00	32.33	67.66
NNB	0.00	40.21	59.78
NNC	0.00	42.68	57.31
IMA	1.72	8.48	89.78
IMB	0.00	6.76	93.23
IMC	0.00	29.03	70.96
MIA	14.43	19.91	65.65
MIB	18.59	17.73	63.67
MIC	20.89	18.62	60.48
MAA	8.50	19.58	71.90
MAB	8.08	22.45	69.45
MAC	11.04	25.91	63.04
NFA	51.34	13.31	35.34
NFB	62.56	10.64	26.79
IFA	15.81	32.65	51.53
IFB	11.32	0.00	88.67
MIFA	59.32	1.53	39.14
MIFB	61.70	1.36	36.93
MAFA	71.98	5.39	22.62
MAFB	74.34	5.50	20.14

Table 4. Comparison of mean coefficients of variation of primary song characters.

SONG CHARACTER	<i>Oporornis tolmiei</i>		<i>Oporornis philadelphia</i>	
	MEAN CV	N	MEAN CV	N
NPSO	0.28	13	0.19	17
NSSO	0.17	13	0.16	17
NDSO	0.31	13	0.19	17
DUR	0.15	13	0.15	17
MINS	0.12	13	0.13	17
MAXS	0.08	13	0.08	17
NNA	0.32	14	0.19	17
NNB	0.25	14	0.16	17
NNC	0.27	13	0.17	17
IMA	0.41	14	0.30	17
IMB	0.36	14	0.35	17
IMC	0.34	14	0.30	12
MIA	0.18	14	0.17	17
MIB	0.18	14	0.17	17
MIC	0.18	14	0.17	17
MAA	0.10	14	0.11	17
MAB	0.09	14	0.11	17
MAC	0.09	14	0.10	17
NFA	0.37	13	0.19	12
NFB	0.36	12	0.28	10
IFA	0.35	12	0.34	11
IFB	0.41	7	0.35	6
MIFA	0.15	12	0.14	12
MIFB	0.16	12	0.12	11
MAFA	0.11	13	0.12	12
MAFB	0.13	12	0.14	11

Figure 9. Per cent of the variance attributed to among taxa, among populations and among individuals within populations from a nested ANOVA of morphological (top) and behavioral (bottom) characters.

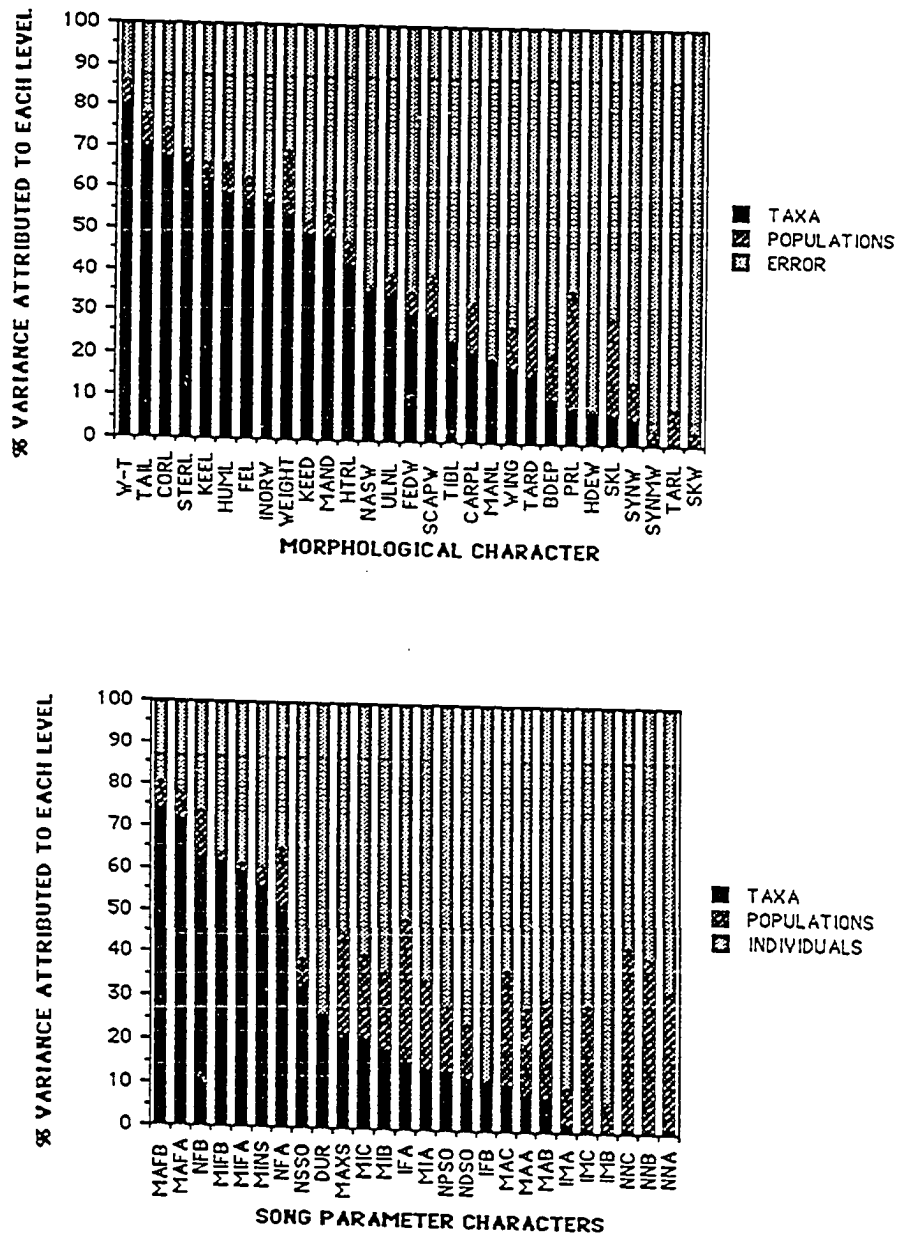


Figure 10. Variability profiles: Coefficients of Variation (CV's) plotted by morphological (A) and behavioral variables (B).

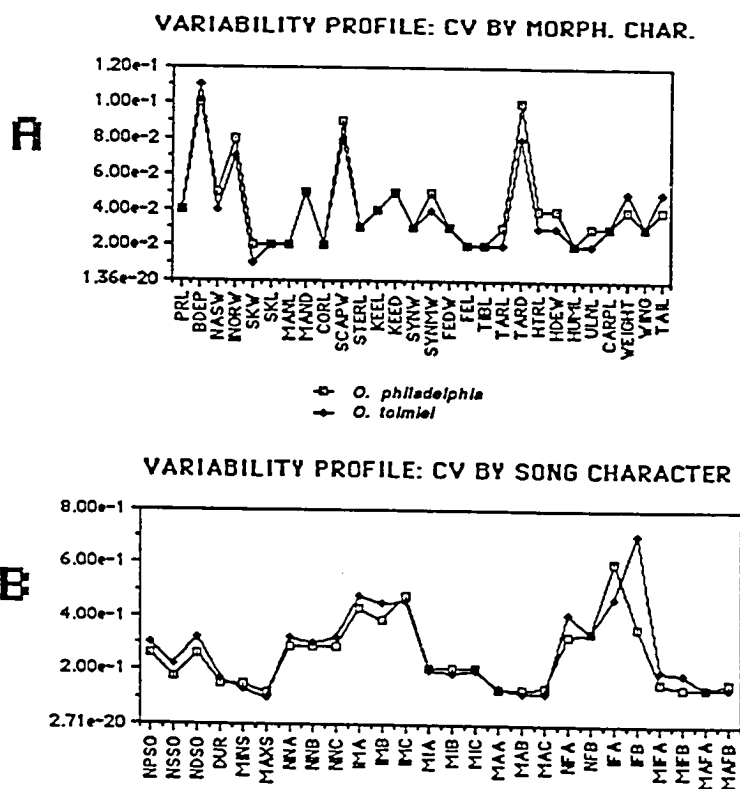


Figure 11. Dendrogram of *D. philadelphia* populations based on CV's for SKULL CHARACTERS.

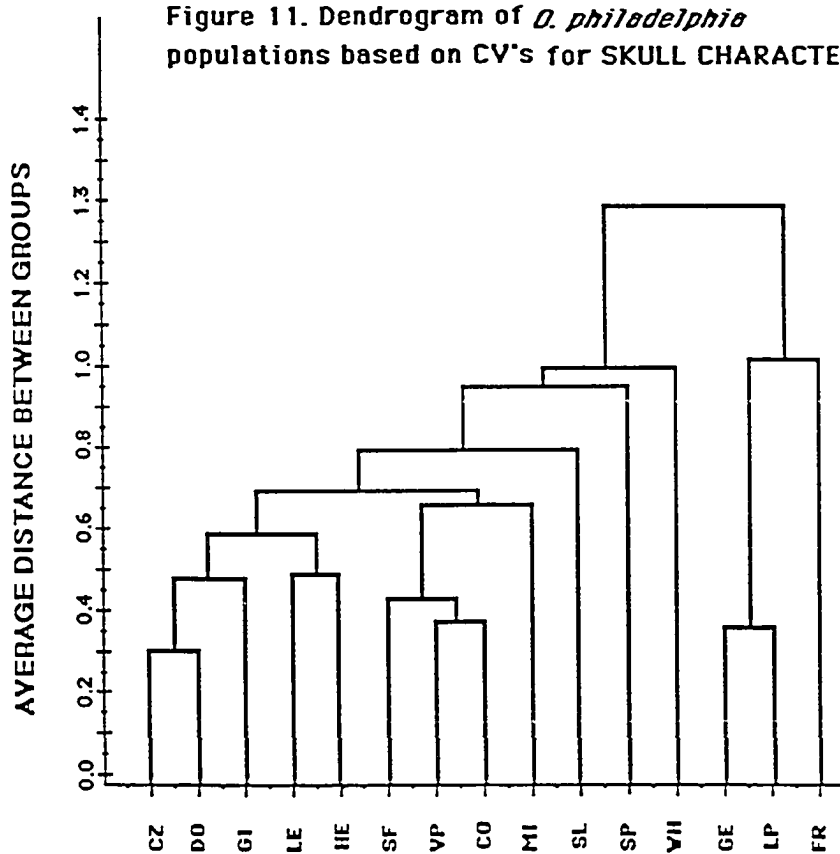
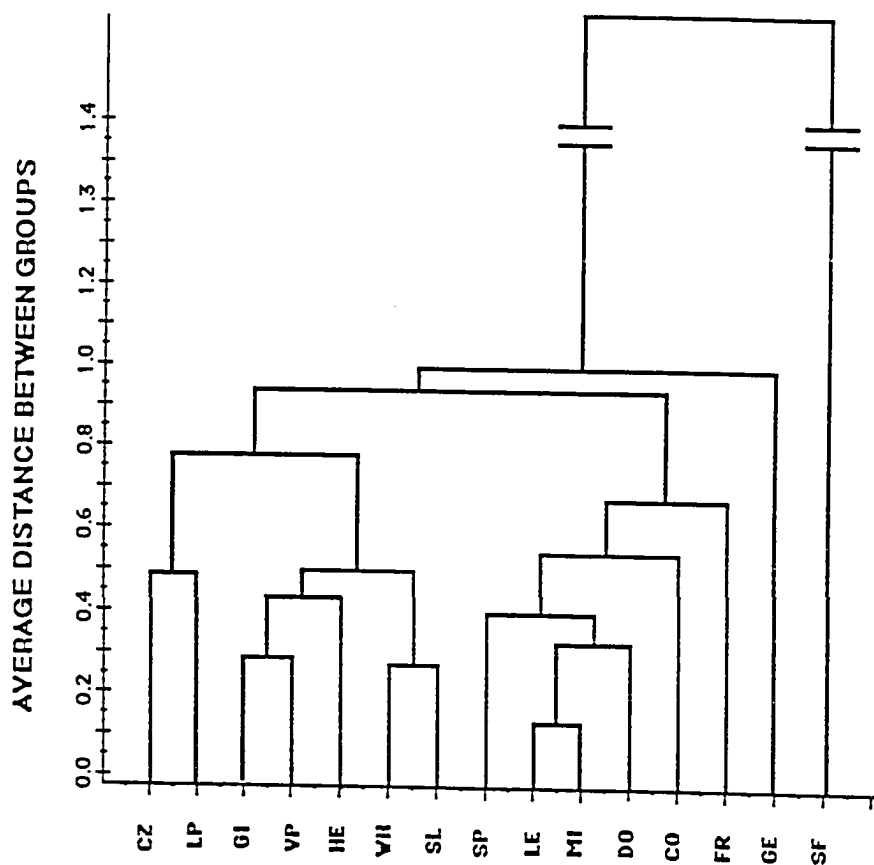


Figure 12. Dendrogram of *O. philadelphia* populations based on CV's for GIRDLE CHARACTERS



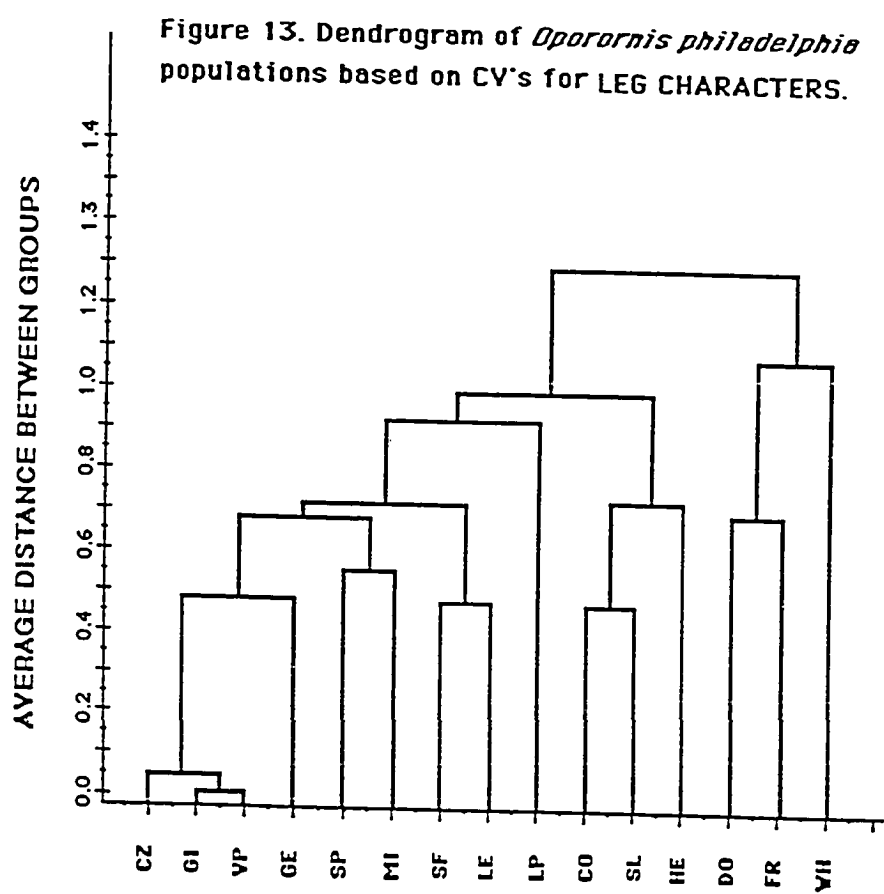
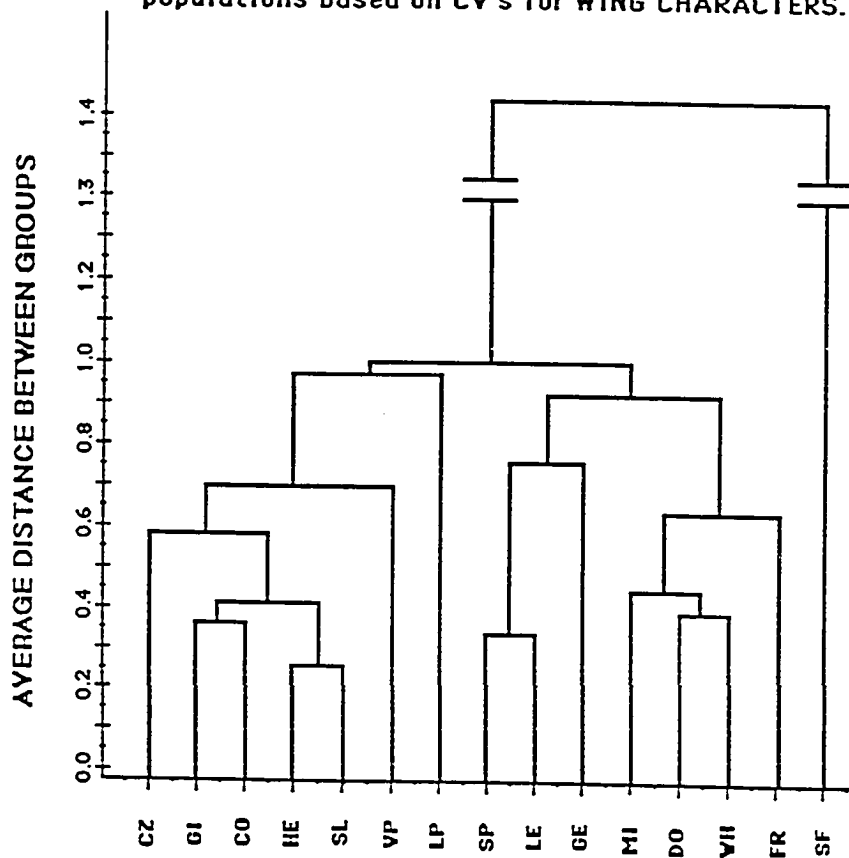


Figure 14. Dendrogram of *Oporornis philadelphia* populations based on CV's for WING CHARACTERS.



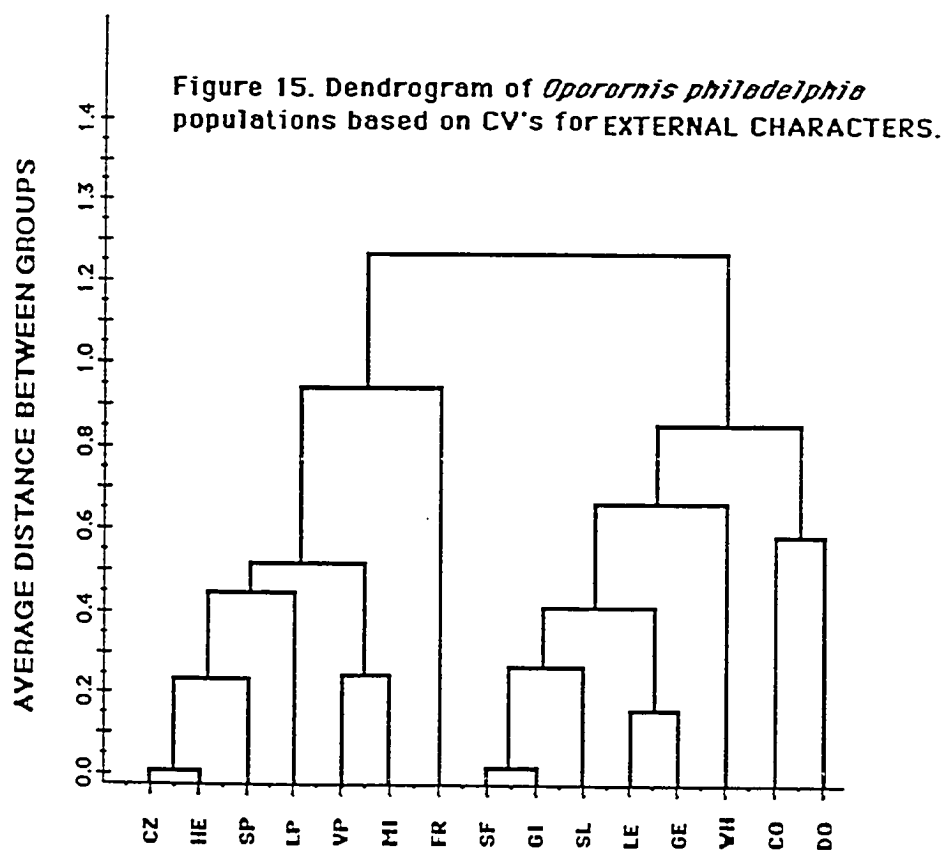
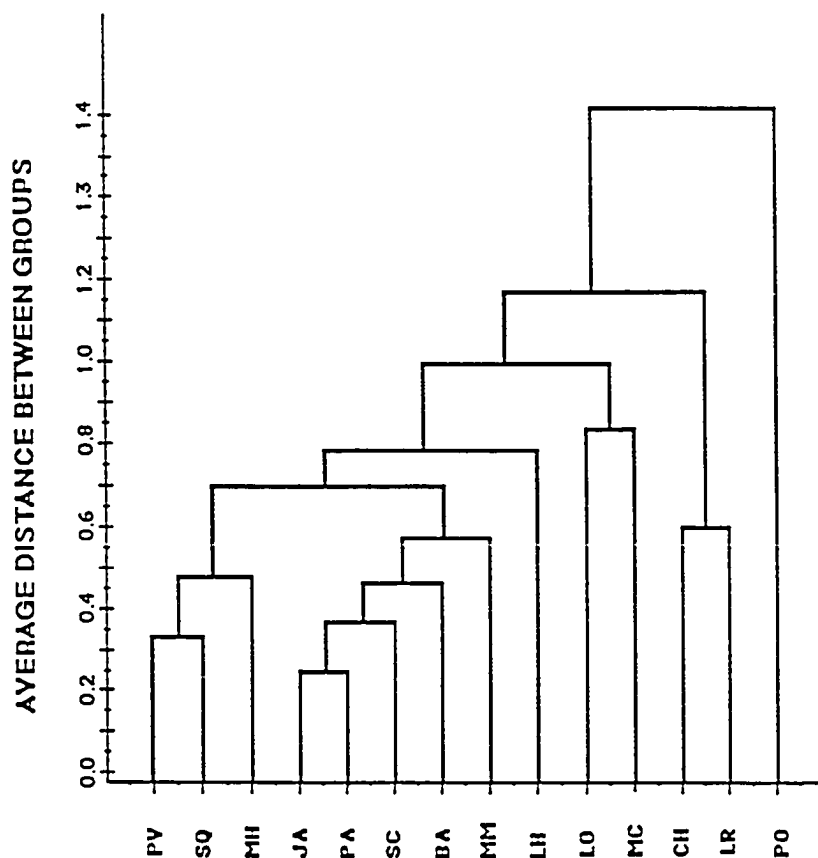
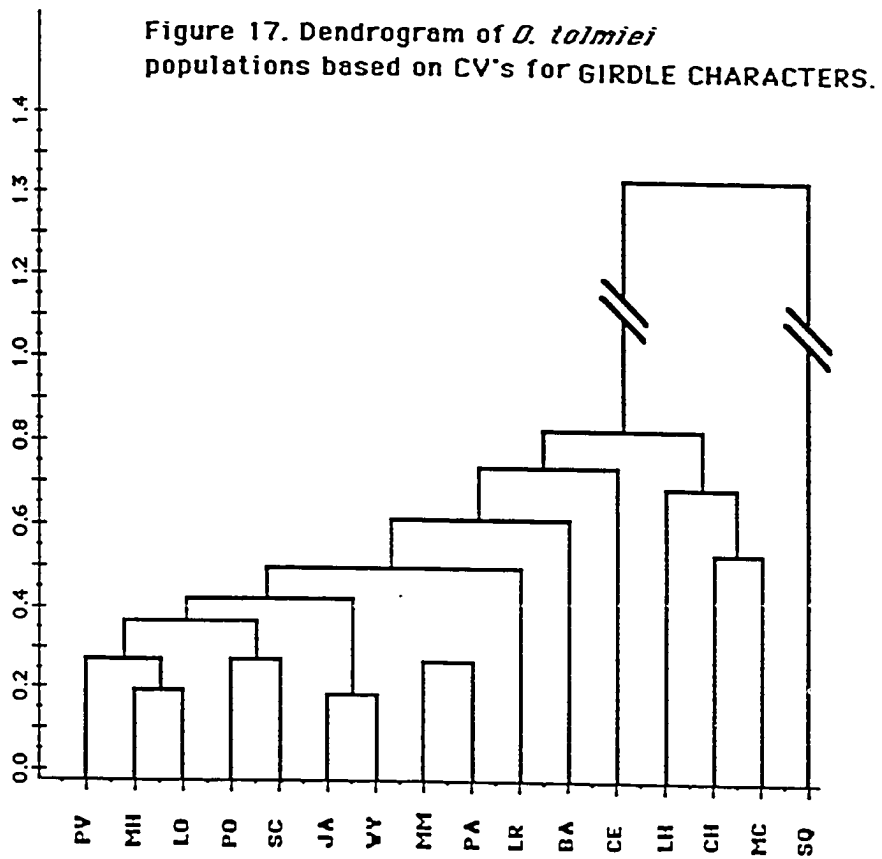


Figure 16. Dendrogram of *Oporornis tolmiei* populations based on CV's for SKULL CHARACTERS.





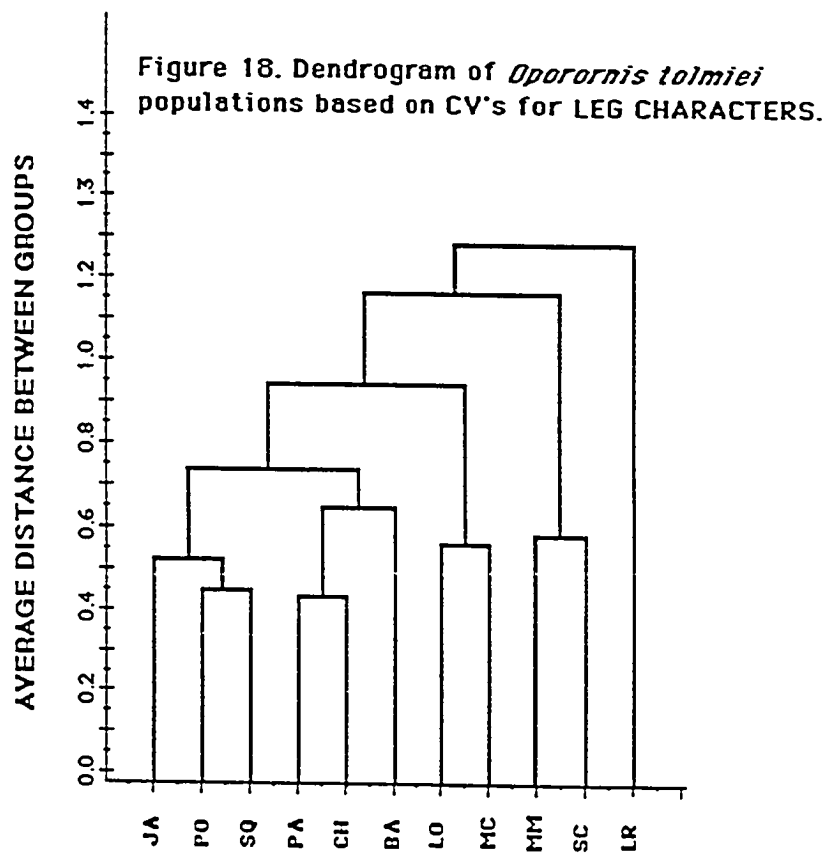
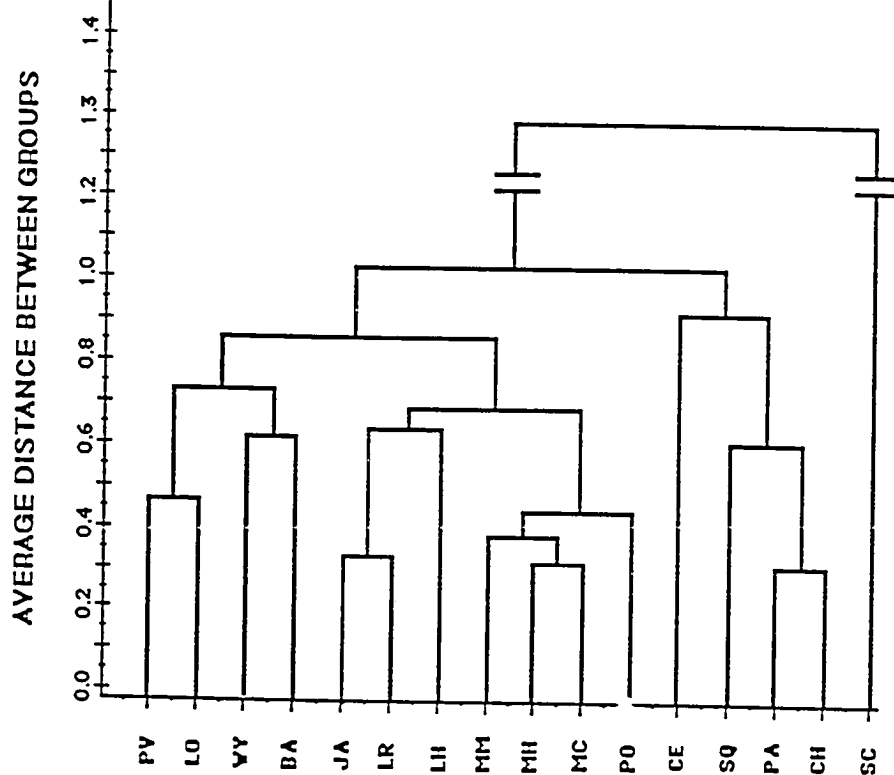


Figure 19. Dendrogram of *Oporornis tolmiei* populations based on CV's for WING CHARACTERS.



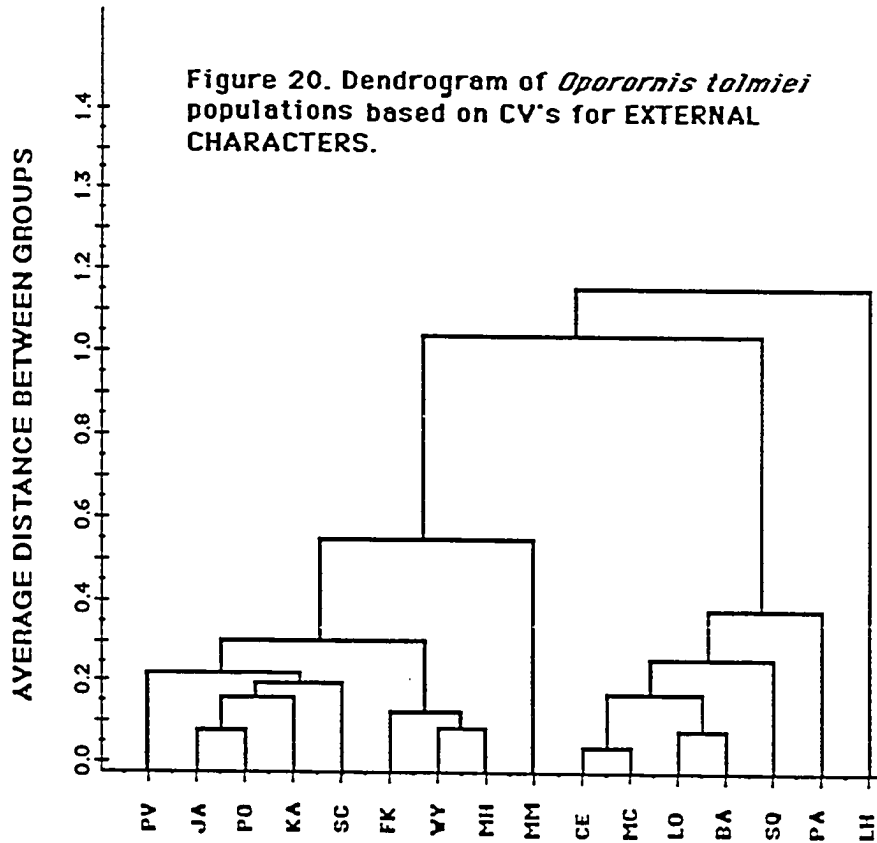


Figure 21. Dendrogram of *Oporornis philadelphia* populations based on CV's for FREQUENCY CHARACTERS.

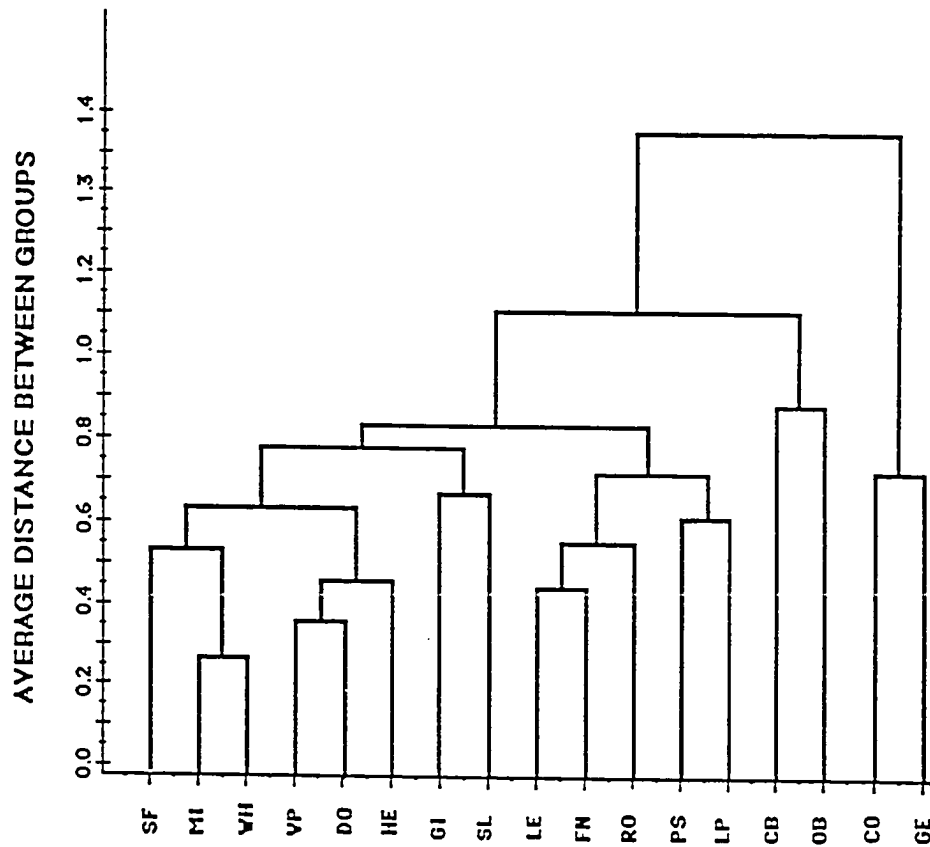
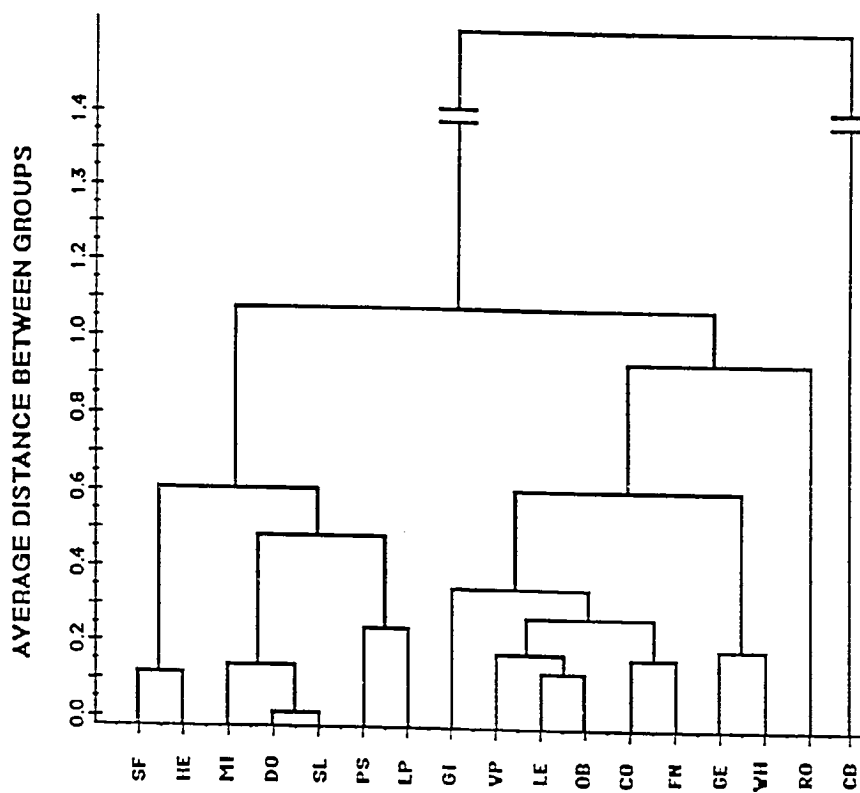


Figure 22. Dendrogram of *Oporornis philadelphia* populations based on CV's for DURATION/INTERVAL CHARACTERS.



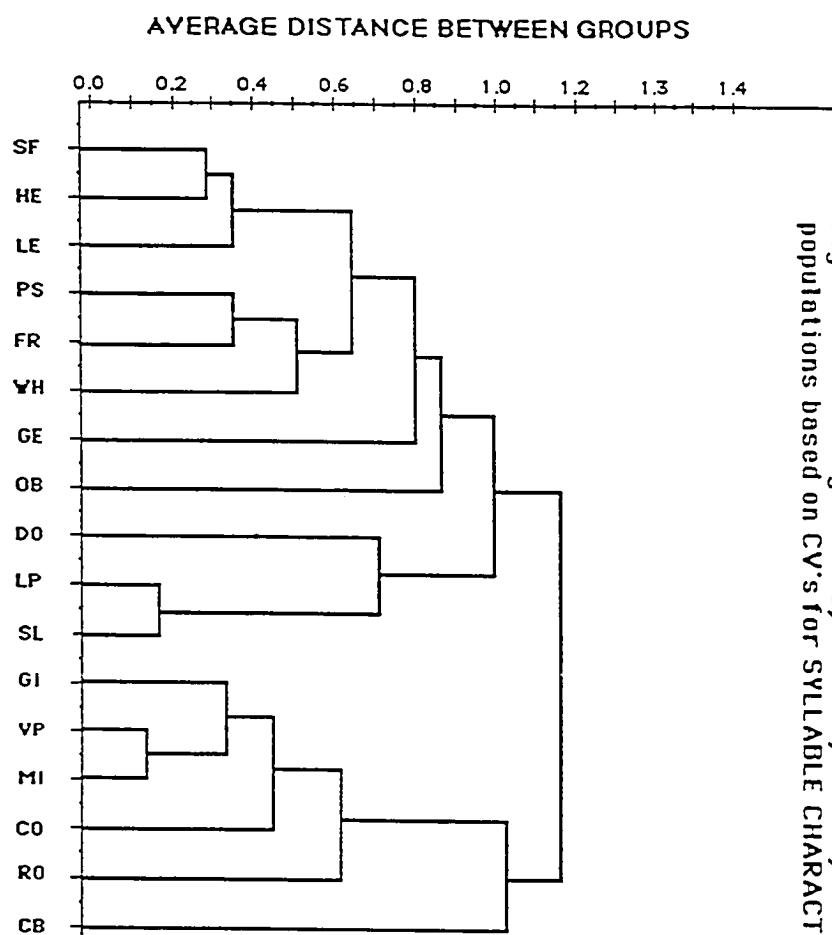


Figure 24. Dendrogram of *Oporornis tolmiei* populations based on CV's for FREQUENCY CHARACTERS.

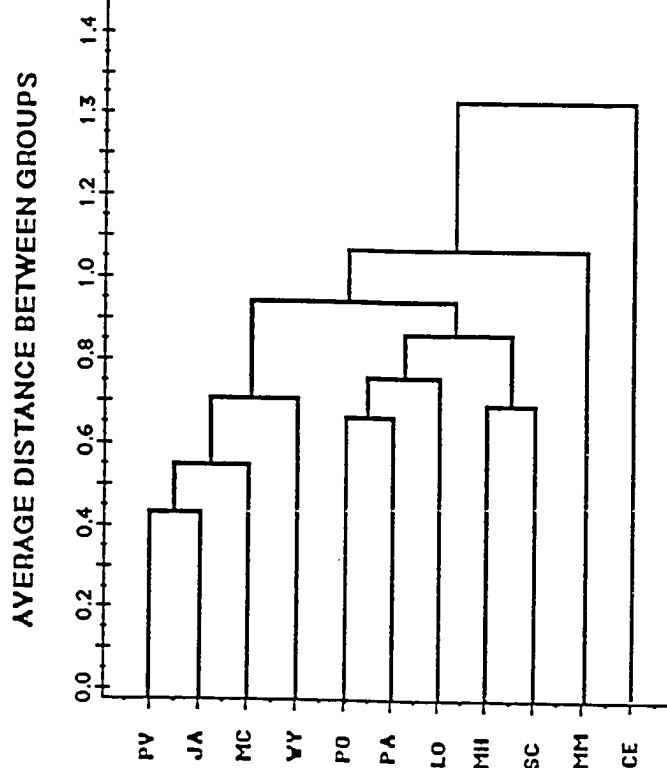


Figure 25. Dendrogram of *Oporornis tolmiei* populations based on CV's for DURATION/INTERVAL CHARACTERS.

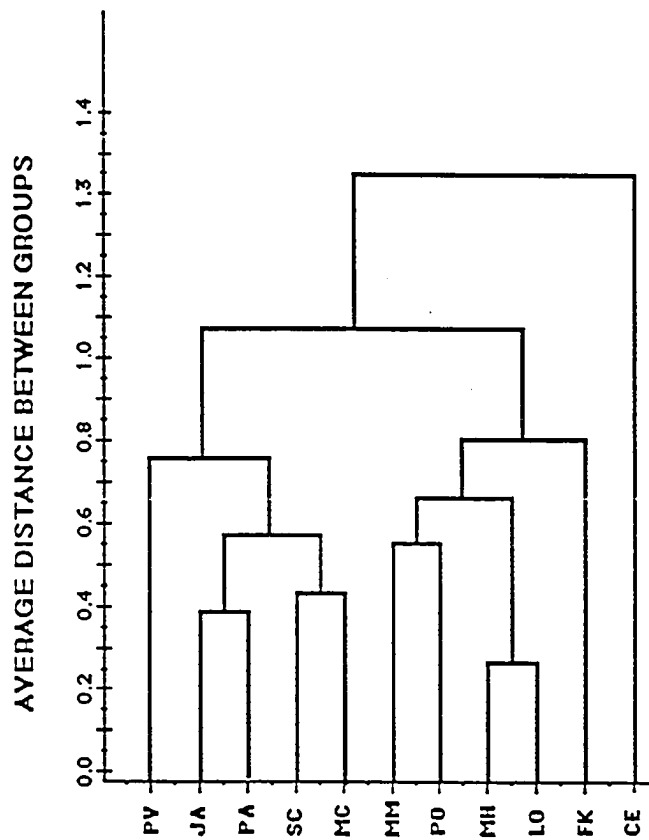
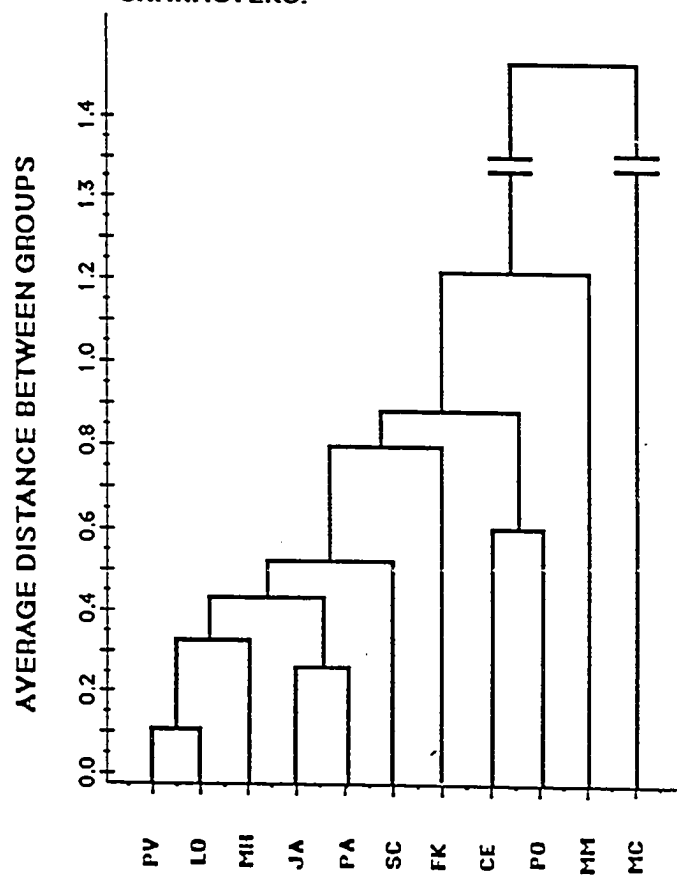


Figure 26. Dendrogram of *Oporornis tolmiei* populations based on CV's for SYLLABLE CHARACTERS.



CHAPTER 5 - MORPHOLOGY

5.1 UNIVARIATE ANALYSIS OF MORPHOLOGICAL CHARACTERS: DIFFERENCES BETWEEN SPECIES, LOCALITIES AND REGRESSION AND CORRELATION WITH ENVIRONMENTAL VARIABLES

5.1.1 EXTERNAL CHARACTERS

Plumage and external characters traditionally used to diagnose *O. philadelphia* and *O. tolmiei* can not be used to **unequivocally** separate all specimens of these taxa (Chapman 1917, Hall 1979). However they will separate all but the extreme specimens. Some *O. philadelphia* specimens have W-T measurements within the range of *O. tolmiei* or have eye-arcs or dark lores or both (Figure 2). Both Hall's (1979) and Chapman's analyses were performed on museum specimens only. Therefore, it was not possible to accurately determine the incidence and spatial pattern of occurrence of *O. philadelphia* specimens with *tolmiei*-like characters (or vice-verse) throughout its range because of inadequate sample sizes per locality and comparisons of specimens from different years. Here I present the geographic distribution of these characters based on recent collections made over a three year period. I have quantified the degree of distinctness of these taxa based on these traditional plumage and external characters by analyzing the occurrence of *tolmiei* - like characters throughout the range of *O. philadelphia* and *philadelphia* - like characters throughout the range of *O. tolmiei*.

EYE-ARCS. Hall (1979) found that 4/80 or 5% of *O. philadelphia* specimens from Quebec, Ontario and Pennsylvania which he examined had eye-arcs characteristic of *O. tolmiei*. None of the *O. tolmiei* specimens examined by Hall (1979) lacked eye-arcs. I collected birds with eye-arcs throughout the range of *O. philadelphia* during the summers of 1982, 1983, and 1984. The distribution of *O. philadelphia* specimens with eye-arcs based on this sample ranged from 0.0% in six populations to 16.6% in the Cochrane, Ontario population (Figure 27). Ontario had the largest number of birds with eye-arcs. At three localities, over 10% of the sample had eye-arcs: Dorion - 11.1%, Geraldton - 14.2%, Cochrane - 16.6%. One New York population also had a comparatively high (12.5%) incidence of birds with eye-arcs. A majority of the birds with eye-arcs were males (76.4%). Four of these 18 males were recorded and their primary songs were typical *O. philadelphia* song types (APPENDIX I). Except for a male from Slave Lake, all birds had W-T measurements within the range of typical *O. philadelphia* specimens (APPENDIX I). Individuals with eye-arcs are scarce and scattered irregularly throughout this taxon's range with no apparent pattern evident. Regression analyses of per cent of *O. philadelphia* specimens with eye-arcs on latitude and longitude did not yield significant results ($p \geq .05$). Although some specimens did possess eye-arcs, other characters for those extreme individuals such as song and W-T were typical of *O. philadelphia*. No *O. tolmiei* specimens, male or female, lacked the eye-arc character.

DARK LORES. There were no *O. tolmiei* male specimens lacking dark lores. Lores of these birds were uniformly dark throughout the range. However,

there was geographic variation in the presence or absence and darkness of this character in *O. philadelphia* males, which were classified into three groups: 1) no lores, region between eyes uniformly gray, matching rest of hood, 2) weak lores, darker between the eyes but restricted to region over the bill, 3) dark lores, black outline around proximal half of eyes and stretching over bill. Birds with dark or weak lores were lumped together as "birds with lores" for regression analyses. *Oporornis philadelphia* specimens with dark lores were far more widespread and numerous than birds with eye-arcs or W-T (Figure 28) (APPENDIX I) which agrees with Hall's (1979) results. If these taxa were hybridizing then one might expect an east - west increase in the number of *O. philadelphia* specimens with dark lores. However, there was no clinal pattern to the distribution of birds with dark lores. Regressions of the number of specimens with dark lores on latitude and longitude did not yield significant results.

The format for describing the univariate results is as follows. For external characters at the univariate level I was interested in 1) which characters showed significant differences between males of each taxon (Student's T test) (and how much larger one taxon was for each character: $\% \text{ difference per character} = \frac{\text{Mean}_{\text{larger}} - \text{Mean}_{\text{smaller}}}{\text{Mean}_{\text{larger}}}$, 2) describing the spatial pattern of individual character variation (ANOVA, SNK multiple comparison test) across the sampling range of each taxon, 3) regressing morphological characters on latitude and longitude, 4) testing for significant correlations between morphological variables environmental data. The latter two tests were used to test for evidence of climate as a selective agent on body size in these taxa (as in James 1970). I compared the results of the regression analyses with the well

known ecogeographic rules (Allen's and Bergman's rules) to see if they could be applied to two migratory taxa.

WING LENGTH (W). *Oporornis philadelphia* averaged 2.2% larger than *O. tolmiei* for this character (Table 5). Some *O. philadelphia* samples were not significantly different than some *O. tolmiei* localities (Figure 29). Three subsets contained a mixture of *O. philadelphia* and *O. tolmiei* samples. Neither taxon exhibited north-south clinal variation in this character. Bivariate plots of WING by TAIL measurements of population means from both taxa showed good separation of these taxa (Figure 30). An east-west pattern of variation was significant only for *O. tolmiei* (Table 6). Wing length decreased from east to west. Although this longitudinal relationship was highly significant ($p < .001$) it only accounted for 7.1% of the variation in this character. Correlations between W and environmental variables differed between *O. philadelphia* and *O. tolmiei*. In *O. philadelphia* there were no significant correlations with environmental variables. Correlations between W and humidity variables were highly significant for *O. tolmiei*. W was negatively correlated with RELH ($p < .005$) and positively correlated with MEJULP ($p < .006$), EVAP ($p < .001$) and JULWT ($p < .02$).

TAIL LENGTH (T). *Oporornis tolmiei* averaged 9.9% larger than *O. philadelphia* for this character (Table 5) (APPENDIX C). There was very little overlap between population means of the two taxa. However, not all *O. tolmiei* localities were significantly different from *O. philadelphia* populations. Seven subsets were composed only of *O. tolmiei* populations. Eight subsets

contained populations of both taxa (Figure 31). For information on results of Bivariate plots, see WING. Although both taxa had significant regressions of T on latitude and longitude the pattern of variation of T was different for each taxon (Table 6). Increasing T with increasing latitude was significant for *O. philadelphia* ($p < .001$) (Table 6). Only 4.5% of the variation in this character was attributed to variation in latitude. Variation in T in *O. tolmiei* was opposite to *O. philadelphia*. Tail length decreased with increasing latitude ($p < .001$). In *O. tolmiei* 20.6% of the variation in this character was attributed to latitudinal variation. This was consistent with Phillips' (1947) analysis of geographic variation in T in *O. tolmiei*. T increased from east to west in *O. philadelphia* but decreased in the same direction for *O. tolmiei*. Variation in longitude accounted for slightly more of the variation in T in *O. tolmiei* (7.7%) than in *O. philadelphia* (5.7%). T was correlated with different environmental variables in *O. philadelphia* and *O. tolmiei*. Correlation between T and MEJULT was barely significant ($p < .03$) and negative for *O. philadelphia* (Table 7). For *O. tolmiei* T was negatively correlated with MEJUNT ($p < .007$), MIJUNT ($p < .001$), MIJULT ($p < .02$), MEJUNP ($p < .001$), RELH ($p < .001$) and positively correlated with EVAP ($p < .002$) and JULWT ($p < .001$) (Table 8).

WING MINUS TAIL(W-T). *Oporornis philadelphia* averaged 56.0% larger than *O. tolmiei* for this character (Table 5) (APPENDIX C). The pattern of variation across each taxon's range was similar to variation in TAIL. Almost all *O. philadelphia* populations were significantly different from all *O. tolmiei* populations (Figure 32). Five subsets contained only *O. tolmiei* samples. One large subset was composed of only *O. philadelphia* populations. Another

subset contained a mixture of populations from each taxon. Bivariate plots of WING by W-T of population means showed perfect separation of these taxa (Figure 30). Both taxa showed significant north-south patterns of variation for this character (Table 6). Some *O. philadelphia* specimens' W-T measurements ($W-T \leq 11$ mm) fell within the range of *O. tolmiei* (according to Lanyon and Bull 1967). The number of these "tolmiei-like" individuals seemed to increase in the western part of the range of *O. philadelphia* (Figure 33) (APPENDIX I). Regression analyses revealed north-south as well as east-west patterns in this character. North-south clinal variation in W-T for *O. philadelphia* was highly significant ($p < .001$) and negative but only 5.2% of the variation in this character was attributed to latitudinal variation. Only six *O. tolmiei* specimens had W-T measurements greater than 10 mm (APPENDIX I). Four of these birds were from British Columbia within 500 km of contact with *O. philadelphia*. The other two specimens were from Washington and Oregon. This was the only external character where some *O. tolmiei* specimens resembled *O. philadelphia*. A significant positive linear relationship between W-T and latitude ($p < .001$) existed for *O. tolmiei*. Variation in latitude accounted for 25.6% of the variation in this character. Patterns of variation with longitude were different in these taxa (Table 6). W-T decreased from east to west in *O. philadelphia* ($p < .001$). Only 8.0% of the variation in this character was attributed to longitudinal variation. No significant regressions on longitude existed for *O. tolmiei*. In *O. tolmiei* significant correlations existed with almost all environmental variables (Table 8) but in *O. philadelphia* only a single temperature variable was highly correlated with W-T (Table 7). W-T was positively correlated with MAJULT ($p < .001$) for *O. philadelphia*. In *O. tolmiei*

W-T was positively correlated with MEJUNT ($p < .001$), MIJUNT ($p < .001$), MIJULT ($p < .002$), MEJUNP ($p < .001$), MEJULP ($p < .001$), RELH ($p < .001$) and negatively correlated with JULWT ($p < .001$) (Table 8).

WEIGHT. *Oporornis philadelphia* was 7.5% heavier than *O. tolmiei* for this character (Table 5) (APPENDIX C). Most *O. philadelphia* locality means were significantly heavier than *O. tolmiei* populations (Figure 34). Two of eight subsets were made up of *O. philadelphia* populations. Four subsets were comprised solely of *O. tolmiei* populations and one subset was mixed. Bivariate plots of WEIGHT by WING were able to separate almost all populations of both taxa (Figure 30). Regression analyses of WEIGHT on latitude and longitude yielded different results per taxon. Mean WEIGHT increased from south to north in the range of *O. philadelphia* ($p < .001$) (Table 6). Only 10.2% of the variation in WEIGHT was attributed to variation in latitude. No significant north-south clines were evident in *O. tolmiei*. Both taxa exhibited significant linear relationships between WEIGHT and longitude (Table 6). However, in *O. philadelphia* the relationship was positive ($p < .001$) and in *O. tolmiei* it was negative ($p < .001$). Longitudinal variation accounted for similar amounts of variation in this character for *O. philadelphia* (7.5%) and *O. tolmiei* (8.8%). Correlations between WEIGHT and most temperature variables were negative for both taxa. Correlations with precipitation were positive for *O. tolmiei* (Table 8) and negative for *O. philadelphia* (Table 7). For *O. philadelphia* WEIGHT decreased with increases in the following variables: MEJUNT ($p < .002$), MIJUNT ($p < .001$), MAJUNT ($p < .04$), MEJULT ($p < .001$), MIJULT ($p < .001$) and MEJULP ($p < .001$). Weight increased with increasing

MAJULT ($p < .001$). For *O. tolmiei* WEIGHT was negatively correlated with MEJUNT ($p < .04$) MIJULT ($p < .01$), MAJULT ($p < .03$), and positively correlated with MEJUNP ($p < .04$), MEJULP ($p < .03$) and EVAP ($p < .003$). The 98% confidence interval (Mean $\pm 2.3 \times$ SD) for W-T for *O. philadelphia* was 7.91mm - 16.51mm (compared to 9.7mm - 17.1mm obtained by Lanyon and Bull and lower limit of 10.3mm obtained by Kowalski. The confidence interval for W-T for *O. tolmiei* was -0.9mm - 11.57mm (compared to 1.7mm - 11.3mm obtained by Lanyon and Bull and upper limit of 14.6mm obtained by Kowalski). This is an overlap of 3.66mm between the two taxa for W-T which is greater than the 1mm overlap reported by Lanyon and Bull (1967) but less than 4.66mm reported by Kowalski (1983). The differences between authors is due to the fact that 1) Lanyon and Bull (1967) and Kowalski (1983) used museum skins, 2) Lanyon and Bull (1967) used only materials from the allopatric portions of the ranges of these taxa, 3) Kowalski (1983) used very small sample sizes (27 *tolmiei* and 34 *philadelphia*) from "areas closest to the area of sympatry" (Kowalski 1983, p.56).

5.1.2 TEMPORAL VARIATION IN EXTERNAL CHARACTERS BETWEEN POPULATIONS OF *O. philadelphia* AND *O. tolmiei*.

If morphological divergence is gradual over time (Bock 1979) snapshots of this process may be taken by analyzing character variation from samples separated by designated time intervals (50 year interval in Zink 1983). Until recently few neontologists have attempted to compare temporally separated populations from a given taxon. Analyses of chronological variation in morphological characters have been conducted in order to determine the

propriety of pooling specimens collected from different time periods for the purpose of studying geographic variation (Barrowclough unpublished MS, Power 1969, 1970).

Very few museums contain collections of recent animals that are more than 100 years old. However, some researchers have had limited success making temporal comparisons within a taxon. Rising (1983b) has analyzed the stability of hybrid zones of the Northern Oriole (*Icterus galbula* and *I. bullockii*) over ten year intervals; Zink (1983) was able to compare Fox Sparrow (*Passerella iliaca*) populations separated by a 50 year interval; Niethammer (1969) compared House Sparrow (*Passer domesticus*) separated by a 120 year interval. Rising (1983b) found that some hybrid zones in the Great Plains were more stable than others. Dominant phenotypes of populations from some areas (Platte and Cimarron Rivers) changed after ten years while for others it did not (western Kansas). Temporal variation in Fox Sparrows was as great as geographic variation among samples from the same time period (Zink 1983). The 50 year sampling gap was enough for significant morphological evolution to have taken place. But for House Sparrows WING and TAIL measurements were not significantly different over 120 year period.

In this study I have made temporal comparisons between specimens of *O. philadelphia* and *O. tolmiei* from the potential contact areas in central Alberta collected by Cox (1973) in the 1960's and specimens I collected from similar areas in 1985. Cox (1973) collected *O. philadelphia* specimens from Entwistle (west of Edmonton) and *O. tolmiei* specimens near the Sheep River southwest of Calgary in 1963. In 1985 I collected *O. philadelphia* specimens west and north of Entwistle (Whitecourt and Obed respectively) and *O. tolmiei*

from along the Sheep River. I measured and compared Wing (W), Tail (T) and W-T for all specimens. The reason for this analysis was to test the stability of morphological differences over a 23 year interval in the potential contact areas and determine if this is stable over time.

I tested for significant differences for each character separately using a two-way ANOVA for unbalanced samples (PROC GLM, SAS 1985 version 5.16). In this analysis the two factors are time periods when birds were collected (1963, 1985) and species differences in external measurements (*O. philadelphia* versus *O. tolmiei*) and their interaction (test the effect of species on time).

Results of the two way ANOVA shows that the only the species factor is significant (Table 9). Except for WING, neither the effect of time or the interaction between time and species is significant. The interaction between time and species was barely significant for WING (Table 9) which indicates that the relationship between time of collection and species is different for both taxa for WING in central Alberta. Species differences in TAIL and W-T characters are significant and stable over the 23 year interval between collections near the zone of contact between *O. philadelphia* and *O. tolmiei*.

I also compared Mahalanobis D^2 between each of the samples to evaluate the stability of morphological differences near the contact areas over the 22 year interval between collections (Figure 35) (PROC DISCRIM, SAS 1985, version 5.16). Figure 35 shows that Mahalanobis D^2 between taxa is larger than within taxa for 1963 and 1985 collections. Mahalanobis D^2 ranged from 5.59 - 7.73 for all intertaxon comparisons while within taxon comparisons ranged from 0.26 - 1.46 (Table 10 and Figure 35). The differences between

taxa was always greater than within taxa. This difference between taxa appears to be relatively stable over a 23 year interval.

5.1.3 SKELETAL CHARACTERS

PREMAXILLARY LENGTH (PRL). *Oporornis philadelphia* averaged 7.4% larger than *O. tolmiei* for this character (Table 5) (APPENDIX C). However, results of ANOVA showed that population Means of some localities of *O. philadelphia* were not significantly different from some *O. tolmiei* localities (Figure 36). All six subsets were composed of populations from both taxa. Populations of both taxa from Alberta and British Columbia were smaller than other populations. Bivariate plots of PRL and BDEP showed a great deal of overlap in populations means for these taxa (Figure 37). Populations from both taxa exhibited similar north-south patterns of geographic variation for this character. Regression of PRL on latitude showed that variation in PRL of *O. philadelphia* was clinal ($p < .001$), decreasing with increasing latitude but only 19.3% of this variation was attributable to latitudinal variation (Table 6). Birds with longer bills occurred in the southern portion of the breeding range of *O. tolmiei* versus birds with shorter bills from the north. Only 18.2% of the variation in PRL was attributable to latitudinal variation for this in *O. tolmiei*. Regression of PRL on longitude showed similar responses by populations from each taxon but the amount of variation attributed to longitudinal variation was different for *O. philadelphia* and *O. tolmiei* (Table 6). Variation in PRL was clinal in an east-west direction for *O. philadelphia* and *O. tolmiei*, decreasing with increasing longitude ($p < .001$). Variation in longitude accounted for 20.7%

of the variation in this character for *O. philadelphia*. Variation in PRL and longitude was also highly significant for *O. tolmiei* but accounted for only 5.4% of the variation. Each taxon seemed to respond differently to environmental variables for this character. Correlations between PRL and environmental variables were different for each taxon. PRL was significantly correlated with increasing temperature variables in *O. philadelphia*. PRL was positively correlated with the following temperature variables: MEJUNT ($p < .02$), MAJUNT ($p < .001$), MEJULT ($p < .004$) and MAJULT ($p < .002$) (Table 7). In *O. tolmiei*, PRL was correlated with precipitation variables, decreasing in length with increasing amount of precipitation (Table 8). PRL was negatively correlated with MEJUNP ($p < .006$) and MEJULP ($p < .003$).

BILL DEPTH (BDEP). *Oporornis philadelphia* averaged 5.3% larger than *O. tolmiei* for this character (Table 5) (APPENDIX C). Only two homogeneous subsets of localities were detected by the ANOVA. Both subsets were composed of populations from both taxa (Figure 38). For information on results of Bivariate plots, see PRL. Populations of both taxa responded similarly to increasing latitude. A significant linear relationship between latitude and BDEP was found in each taxon (Table 6). In *O. philadelphia*, wider bills occurred in the southern portion of the breeding range while thinner bills occurred in the north (Figure 38). However, only 4.1% of this variation could be attributed to variation in latitude. Variation in *O. tolmiei* was similar with wider bills occurring in southern populations. An even smaller portion of the variation was attributed to latitudinal variation, 2.2%. For both taxa, BDEP decreased with increasing longitude. Variation in BDEP with regard to longitude was

highly significant for *O. philadelphia* ($p < .001$) but only accounted for 5.5% of the variation in this character. Variation in *O. tolmiei* was less significant ($p < .01$). Only 3.3% of the variation in this character was attributed to variation in longitude. For both taxa BDEP increased with increasing temperature (Tables 6, 7). Temperature variables exhibiting significant correlations with BDEP included MEJUNT ($p < .02$), MAJUNT ($p < .02$), MEJULT ($p < .02$), MIJULT ($p < .02$), and MAJULT ($p < .006$) in *O. philadelphia* (Table 7). In *O. tolmiei* correlation between BDEP and MAJUNT ($p < .003$), MIJULT ($p < .003$), and MAJULT ($p < .004$) were highly significant (Table 8).

NASAL WIDTH (NASW). *Oporornis philadelphia* averaged 5.5% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). However ANOVA results showed means of some populations of *O. philadelphia* were not significantly different from some *O. tolmiei* populations (Figure 39). All five subsets were composed of populations from both taxa. Bivariate plots of PRL and NASW did not show good separation of population means of these taxa (Figure 37). Results of regression analyses of NASW on latitude were different for both taxa (Table 6). A regression of NASW on latitude was barely significant ($p < .03$) in *O. philadelphia*. Birds with wider nasal bones occurred in the south. Only 1.7% of the variation in NASW could be attributed to variation in latitude. No significant regression of NASW on latitude were found for *O. tolmiei*. There were no significant relationships between NASW and longitude in *O. philadelphia* or *O. tolmiei* ($p > .05$). Correlation analyses of NASW on environmental variables showed different responses to the environment by each taxon. For *O. tolmiei* NASW was positively correlated with MEJUNP

($p < .02$) and negatively correlated with EVAP ($p < .02$) (Table 8). There were no significant correlations between NASW and environmental variables for *O. philadelphia* ($p > .05$).

INTER-ORBITAL WIDTH (INORW). *Oporornis philadelphia* was 12.2% larger than *O. tolmiei* for this character (Table 5) (APPENDIX C). However, homogeneous subsets detected by ANOVA were composed of populations from both taxa (Figure 40). One of six subsets was composed entirely of *O. philadelphia* populations. One subset contained only *O. tolmiei* populations. Bivariate plots of PRL and INORW were able to separate most populations of these taxa (Figure 37). Results of regression analyses of INORW on latitude were different for each taxon (Table 6). For *O. philadelphia* INORW showed a significant decrease with increasing latitude ($p < .002$) but only 3.9% of the variation could be attributed to latitudinal variation. There were no north-south trends evident for *O. tolmiei* ($p > .05$). INORW decreased from east to west in *O. philadelphia* but increased in the same direction in *O. tolmiei* (Table 6). However, only 5.1% and 2.6% of the variation in INORW respectively for these taxa was attributed to longitudinal variation. Correlation between INORW and environmental variables was different in each taxon. For *O. philadelphia* INORW was not significantly correlated with any environmental variables ($p > .05$) (Table 7). However for *O. tolmiei* it was positively correlated with MEJUNP ($p < .01$), RELH ($p < .006$), and negatively correlated JULWT ($p < .01$) (Table 8).

SKULL WIDTH (SKW). *Oporornis philadelphia* averaged 0.2% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). No significant differences were found between populations of either taxon. Bivariate plots of PRL and SKW did not show good separation of populations of these taxa (Figure 37). There were no significant relationships between SKW and variation in latitude or longitude for either taxon ($p>.05$). Correlations between SKW and environmental variables were also not significant for these taxa ($p>.05$) (Tables 7, 8).

SKULL LENGTH (SKL). *Oporornis philadelphia* was 1.0% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). Some populations of *O. philadelphia* were significantly different from each other and some *O. tolmiei* populations. The same held true for populations of *O. tolmiei*. All six subsets were composed of populations from both taxa (Figure 41). Bivariate plots of PRL and SKL showed almost complete overlap between populations of these taxa (Figure 37). Regressions of SKL on latitude and longitude were similar in both taxa but the amount of variation in this character attributed to variation in latitude and longitude was different between taxa (Table 6). Birds with longer skulls were found in the northern part of the breeding range of *O. philadelphia*. The decrease in SKL from north to south was clinal ($p<.001$) but only 11.2% of this variation was attributed to variation in latitude. The same cline was less significant for *O. tolmiei* ($p<.01$). Only 5.1% of the variation in this character could be attributed to changes in latitude. SKL decreased with increasing longitude ($p<.001$). Only 10.5% of the variation in this character was attributed to variation in longitude. The same cline was evident for *O. tolmiei* but it was

barely significant and was attributed to only 3.7% of variation in longitude. Populations of *O. philadelphia* and *O. tolmiei* differed in the correlations environmental variables. For *O. philadelphia* SKL was positively correlated with the following temperature variables: MEJUNT ($p < .001$), MAJUNT ($p < .001$), MEJULT ($p < .001$), MIJULT ($p < .04$), and MAJULT ($p < .001$) (Table 7). Correlations between SKL and environmental variables were not significant for *O. tolmiei* ($p > .05$) (Table 8).

MANDIBLE LENGTH (MANL). *Oporornis philadelphia* averaged 1.9% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). However, ANOVA revealed that there were no significant differences between any populations. Bivariate plots of PRL and MANL revealed a great deal of overlap between populations of these taxa (Figure 37). There were no significant north-south or east-west linear relationships with MANL for *O. philadelphia* or *O. tolmiei* ($p > .05$). Variation in MANL was not correlated with environmental variables for these taxa.

MANDIBLE DEPTH (MAND). *Oporornis philadelphia* averaged 7.9% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). At the population level, five of seven homogeneous subsets consisted of populations from both taxa (Figure 42). Two of these subsets were composed entirely of populations of *O. philadelphia*. Bivariate plots of PRL and MAND did not separate populations of *O. philadelphia* and *O. tolmiei* (Figure 37). Results of regression analyses of MAND on latitude and longitude were different for each taxon (Table 6). Birds with deeper mandibles were found in the north,

decreasing southward through the range of *O. philadelphia*. However only 4.8% of this variation was attributed to variation in latitude. No significant north-south clines were detected in *O. tolmiei*. In *O. philadelphia* MAND decreased east to west ($p < .001$) but only 4.2% of the variation in this character was attributed to variation in longitude (Table 6). No east-west patterns of variation were evident for *O. tolmiei*. MAND was correlated with different environmental variables in *O. philadelphia* and *O. tolmiei*. MAND was highly correlated with temperature variables for *O. philadelphia*. MAND was positively correlated with MEJUNT ($p < .001$), MIJUNT ($p < .003$), MAJUNT ($p < .005$), MEJULT ($p < .006$), MIJULT ($p < .004$) (Table 7). For *O. tolmiei*, MAND was negatively correlated with MIJULT ($p < .02$) and positively correlated with MEJUNP ($p < .01$) and MEJULP ($p < .002$) (Table 8).

CORACOID LENGTH (CORL). *Oporornis philadelphia* averaged 5.3% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). However, not all *O. philadelphia* localities means were significantly different from *O. tolmiei* populations (Figure 43). One of seven homogeneous subsets contained only populations of *O. philadelphia*. Four of seven subsets contained only populations of *O. tolmiei*. Bivariate plots with KEEL showed the best separation between populations of each taxon (Figure 44). A significant positive linear relationship was found between CORL and latitude ($p < .001$) for *O. tolmiei* (Table 6). However, only 6.6% of the variation in this character was attributable to variation in latitude. No significant north-south patterns of variation were found for *O. philadelphia*. Regression of CORL on longitude was significant only for *O. tolmiei* ($p < .001$) (Table 6). Variation in longitude

accounted for only 3.5% of the variation in this character. *O. philadelphia* and *O. tolmiei* showed significant correlations with different environmental variables. For *O. philadelphia* CORL was positively correlated with ($p < .02$) with MAJUNT (Table 7). In *O. tolmiei* CORL was negatively correlated with the following temperature variables: MIJUNT ($p < .04$), MIJULT ($p < .02$), MAJULT ($p < .01$) (Table 8). Highly significant positive correlations between precipitation variables and CORL were found for *O. tolmiei*. CORL increased with increasing MEJUNP ($p < .001$), MEJULP ($p < .001$) and EVAP ($p < .002$) for *O. tolmiei* samples (Table 8).

SCAPULA WIDTH (SCAPW). *Oporornis philadelphia* was 8.2% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). However not all *O. philadelphia* populations were significantly different than *O. tolmiei* populations (Figure 45). Five of six homogeneous subsets were comprised of populations from both taxa. One subset contained one *O. philadelphia* population from Maine which was much larger than the rest. Bivariate plots of CORL and SCAPW revealed good separation of *O. philadelphia* and *O. tolmiei* populations (Figure 44). This character varied differently with respect to latitude and longitude for these taxa (Table 6). In *O. philadelphia* SCAPW became thinner from south to north ($p < .001$). In *O. tolmiei* the regression was less significant ($p < .01$) but the pattern was an increase in SCAPW from south to north. In each case only a small portion of the variation in SCAPW was due to latitudinal variation, 4.2% for *O. philadelphia* and 3.3% for *O. tolmiei*. Regression of SCAPW was significant for *O. philadelphia* but not for *O. tolmiei*. SCAPW became thinner from east to west ($p < .001$). Only 4.6% of the variation

in this character was attributed to variation in longitude. Significant correlations of SCAPW with temperature variables were found for both taxa. SCAPW was positively correlated with MEJULT ($p < .03$) and MIJULT ($p < .004$) (Table 7) for *O. philadelphia*. For *O. tolmiei* MEJUNT ($p < .002$), MIJUNT ($p < .01$), MAJUNT ($p < .007$), MEJULT ($p < .01$), MEJUNP ($p < .006$), MEJULP ($p < .001$) were positively correlated with SCAPW (Table 8). Wider scapulae were found in warmer climates with more precipitation.

STERNUM LENGTH (STERL). *Oporornis philadelphia* averaged 6.5% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). Not all *O. philadelphia* populations were significantly different than *O. tolmiei* populations. Two of five subsets were composed exclusively of *O. philadelphia* populations while three were composed only of *O. tolmiei* populations (Figure 46). Bivariate plots of CORL and STERL showed complete separation of *O. philadelphia* and *O. tolmiei* populations (Figure 44). There were no significant linear relationships between variation in STERL and latitude for either taxon ($p > .05$). Only *O. tolmiei* showed a significant linear relationship between STERL and longitude. STERL decreased with increasing longitude (Table 6). Only 4.7% of the variation in this character was attributed to longitudinal variation. Correlations with environmental variables and STERL differed between taxa. For *O. tolmiei* STERL was positively correlated with MEJUNP ($p < .001$) and MEJULP ($p < .001$) (Table 8). Populations with longer STERL's were found in wetter climates. In *O. philadelphia* STERL did not show significant correlations with any environmental variables.

KEEL LENGTH (KEEL). *Oporornis philadelphia* averaged 7.6% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). At the population level, *O. philadelphia* was not significantly different from some *O. tolmiei* populations (Figure 47). Four of ten subsets were composed exclusively of *O. tolmiei* populations. Six subsets were composed of a mixture of *O. philadelphia* and *O. tolmiei* populations. Populations of *O. philadelphia* and *O. tolmiei* were best separated on Bivariate plots of CORL and KEEL (Figure 44). Regression analyses of KEEL on latitude and longitude yielded different results for each taxon (Table 6). KEEL showed a positive regression with latitude ($p < .001$) but only 6.7% of the variation in this character was attributed to latitudinal variation for *O. tolmiei* ($p < .001$). A significant north-south cline was not evident for *O. philadelphia*. For *O. tolmiei* variation in KEEL was significantly related to variation in longitude ($p < .04$). Only 2.4% of the variation in KEEL was attributed to variation in longitude. There was no significant linear relationship between longitude and KEEL for *O. philadelphia* ($p > .05$). Correlations between KEEL and environmental variables were different for *O. philadelphia* and *O. tolmiei*. KEEL was not correlated with these variables for *O. philadelphia* ($p > .05$). For *O. tolmiei* KEEL was negatively correlated with MAJULT ($p < .02$) (Table 8). KEEL was positively correlated with precipitation variables. KEEL increased with increasing MEJUNP ($p < .002$) and MEJULP ($p < .001$) (Table 8).

KEEL DEPTH (KEED). *Oporornis philadelphia* averaged 7.2% deeper than *O. tolmiei* for this character (Table 5) (APPENDIX C). However, many *O. philadelphia* populations were not significantly different from *O. tolmiei*

populations (Figure 48). Nine of ten subsets were composed of populations from both taxa. Only one subset was composed entirely of *O. tolmiei* populations. For results on Bivariate plots, see CORL. Regression analyses of KEED on latitude yielded different results for each taxon (Table 6). No significant north-south clines in KEED existed for *O. philadelphia*. KEED showed a significant increase with increasing latitude ($p < .006$) in *O. tolmiei*. Only 4.3% of the variation in this character was attributed to variation in latitude. Neither taxon exhibited a significant east-west pattern of variation for this character ($p > .05$) (Table 6). Results of correlation analyses of KEED with environmental variables were different for each taxon. For *O. philadelphia* KEED was positively correlated with MAJUNT ($p < .02$) (Table 7). In *O. tolmiei* the correlation with MIJULT ($p < .03$) was negative (Table 8). KEED increased with increasing temperature for *O. philadelphia* but decreased with increasing temperature in *O. tolmiei*. For *O. tolmiei* KEED was also highly correlated with MEJUNP ($p < .001$) and MEJULP ($p < .001$) (Table 8). KEED increased with increasing precipitation.

MAXIMUM SYNSACRUM WIDTH (SYNW). *Oporornis philadelphia* averaged 1.2% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). At the population level, no significant differences between any localities were observed. However, Bivariate plots of CORL and SYNW revealed good separation of *O. philadelphia* and *O. tolmiei* populations (Figure 44). Regression analyses of SYNW for both taxa were similar except for respect to longitude. SYNW did not vary clinally from north-south or east-west in either taxon (Table 6). There was no significant relationship between SYNW and

longitude in *O. philadelphia*. For *O. tolmiei* a positive linear relationship existed between SYNW and longitude ($p < .006$). However, only 4.9% of the variation in this character was attributed to variation in longitude. SYNW was correlated with different environmental variables in *O. philadelphia* and *O. tolmiei*. In *O. philadelphia* SYNW decreased with increasing MEJULT ($p < .04$) (Table 7). A strong positive correlation existed between SYNW and MEJULP ($p < .001$) for *O. tolmiei* (Table 8).

MINIMUM SYNSACRUM WIDTH (SYNMW). *Oporornis philadelphia* averaged 0.9% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). ANOVA revealed that there were no significant differences between populations of both taxa. Bivariate plots of CORL and SYNMW showed good separation of populations of each taxon (Figure 44). There were no significant north-south or east-west patterns of variation in either taxon ($p > .05$). Both taxa showed correlations with different environmental variables. For *O. philadelphia* SYNMW increased with increasing MAJULT ($p < .03$) (Table 7). SYNMW increased with increasing MEJULP in *O. tolmiei* ($p < .009$) (Table 8).

FEMUR DISTAL END WIDTH (FEDW). *Oporornis philadelphia* averaged 3.0% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). However, not all populations of *O. philadelphia* were significantly different from *O. tolmiei* populations. All six homogeneous subsets were composed of populations from *O. philadelphia* and *O. tolmiei* (Figure 49). Bivariate plots of

FEL and FEDW revealed good separation of *O. philadelphia* and *O. tolmiei* populations (Figure 50). Regression analyses revealed that neither taxon showed any significant latitudinal variation in this character (Table 6). *O. tolmiei* showed a significant linear relationship with longitude ($p < .001$), decreasing from east to west. Only 10.9% of the variation in this character was attributed to longitudinal variation. While *O. philadelphia* exhibited no significant correlations with environmental variables, FEDW was significantly correlated with MEJULP ($p < .005$) and EVAP ($p < .002$) for *O. tolmiei* (Table 8). Both correlations were positive.

FEMUR LENGTH (FEL). Mean femur length was larger for *O. philadelphia* specimens (APPENDIX C). *Oporornis philadelphia* was 4.6% longer than *O. tolmiei* for this character (Table 5). However, some means of *O. tolmiei* populations were not significantly different from *O. philadelphia* populations (Figure 51). Six subsets contained a mixture of *O. philadelphia* and *O. tolmiei* populations. One subset contained only *O. philadelphia* populations and one subset contained only *O. tolmiei* populations. For results of Bivariate plots, see FEDW. Regressions of FEL on latitude were different for each *O. philadelphia* and *O. tolmiei*, but both taxa exhibited negative relationships with longitude (Table 6). A negative significant linear relationship was found between FEL and latitude for *O. philadelphia*. Only 3.7% of the variation in this character was attributable to latitudinal variation. A significant north-south cline was not found in *O. tolmiei*. FEL decreased from east to west in *O. philadelphia* ($p < .003$) and *O. tolmiei* ($p < .002$). However, only a small portion of the variation in this character was attributed to longitudinal variation,

5.6% and 5.4% respectively for these taxa. Positive correlations with temperature variables existed for both taxa. However the relationship between FEL and increasing temperature was stronger in *O. philadelphia*. For *O. philadelphia* FEL was significantly correlated with MEJUNT ($p < .005$), MAJUNT ($p < .01$), MEJULT ($p < .03$), MIJULT ($p < .04$), and MAJULT ($p < .03$) (Table 7). FEL was showed a strong correlation with MEJULT ($p < .005$) for *O. tolmiei* (Table 8).

TIBIOTARSUS LENGTH (TIBL). The tibiotarsus was larger on the average for *O. philadelphia* specimens (APPENDIX C). *Oporornis philadelphia* was 2.2% longer than *O. tolmiei* for this character (Table 5). There was only one subset found for this character. No localities were significantly different from each other. However, Bivariate plots of FEL and TIBL showed good separation of *O. philadelphia* and *O. tolmiei* populations (Figure 50). There were no north-south clines evident for this character for either taxon ($p > .05$). Only *O. tolmiei* exhibited a significant regression of TIBL on longitude ($p < .003$) (Table 6). TIBL decreased with from east to west. Variation in longitude accounted for 18.3% of the variation in this character. TIBL was not correlated with any environmental variables for *O. philadelphia* or *O. tolmiei*.

TARSOMETATARSUS LENGTH (TARL). *Oporornis tolmiei* averaged 0.1% longer than *O. philadelphia* for this character (Table 5) (APPENDIX C). There were also no significant differences between any of the localities. However Bivariate plots showed moderate separation of *O. philadelphia* and *O. tolmiei* populations (Figure 50). TARL exhibited a

negative slope with respect to latitude ($p < .03$) for *O. tolmiei* but variation in latitude accounted for only 3.0% of the variation in this character (Table 6). No significant north-south patterns were found in *O. philadelphia* for TARD. Absence of longitudinal variation in this character was common to both taxa. In *O. philadelphia* correlations existed between TARD and temperature variables while in *O. tolmiei* correlations were with humidity variables. For *O. philadelphia* TARD increased with increasing MEJUNT ($p < .01$), MAJUNT ($p < .003$), and MAJULT ($p < .004$). TARD decreased with increasing RELH ($p < .001$) but increased with EVAP ($p < .02$) and JULWT ($p < .001$).

TARSOMETATARSUS DEPTH (TARD). *Oporornis philadelphia* averaged 6.3% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). Most *O. philadelphia* and *O. tolmiei* localities were not significantly different from each other for this character (Figure 52). None of the four subsets were comprised solely of localities belonging to one taxon or the other. Bivariate plots of TARD and FEL revealed little overlap between populations of these taxa (Figure 50). A significant north-south cline in TARD was observed in *O. philadelphia* ($p < .001$) but not for *O. tolmiei* (Table 6). Populations of *O. philadelphia* showed an increase in the width of this character from north to south. Only 10.6% of the variation in this character could be attributed to variation in latitude. A highly significant linear relationship between TARD and longitude was found for *O. philadelphia* ($p < .001$). TARD decreased from east to west but only 12.1% of the variation in this character was attributed to longitudinal variation. No significant linear relationship between TARD and longitude existed for *O. tolmiei*. TARD was positively correlated with

temperature variables for *O. philadelphia* (Table 7) while in *O. tolmiei* it was negatively correlated with a single temperature variable, MIJUNT ($p < .04$) (Table 8). For *O. philadelphia* strong positive correlations were found with MEJUNT ($p < .001$), MIJUNT ($p < .001$), MAJUNT ($p < .001$), MEJULT ($p < .001$), MIJULT ($p < .001$), MAJULT ($p < .04$), and a precipitation variable MEJUNP ($p < .001$) (Table 7).

HUMERUS TROCHANTER LENGTH (HTRL). *Oporornis philadelphia* averaged 4.3% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). However, at the population level there were significant differences between locality means (Figure 53). All seven subsets contained a mixture of *O. philadelphia* and *O. tolmiei* localities. Bivariate plots of HTRL and CARPL showed moderate separation of *O. philadelphia* and *O. tolmiei* populations (Figure 54). Each taxon exhibited different linear relationships with latitude and longitude for HTRL (Table 6). For *O. philadelphia* a negative relationship between HTRL and latitude was barely significant ($p < .01$). Only 2.4% of the variation in this character could be attributed to latitudinal variation. *O. tolmiei* did not show a significant north-south cline in this character. For *O. tolmiei* HTRL decreased from east to west ($p < .01$) but only 3.3% of the variation could be attributed to longitudinal variation (Table 6). In *O. philadelphia* correlations between HTRL and temperature variables were significant while precipitation variables showed significant correlations with HTRL for *O. tolmiei*. HTRL was positively correlated with MEJUNT ($p < .02$), MAJUNT ($p < .03$), and MEJULT ($p < .01$) for *O. philadelphia* (Table 7). HTRL increased with increasing temperature in this taxon. Highly significant correlations existed for MEJUNP

($p < .007$), and MEJULP ($p < .001$) in *O. tolmiei* (Table 8). HTRL increased with increasing precipitation.

HUMERUS DISTAL END WIDTH (HDEW). *Oporornis philadelphia* averaged 1.8% wider than *O. tolmiei* for this character (Table 5) (APPENDIX C). However, there were no significant differences between localities of *O. philadelphia* or *O. tolmiei*. Bivariate plots of HTRL and HDEW showed overlap in HDEW but *O. philadelphia* had longer HTRL's on the average which separated most populations of these taxa (Figure 54). There were no significant north-south clines in this character for either taxon ($p > .05$). Longitudinal variation in this character was different in each taxon. Longitudinal variation in HDEW in *O. philadelphia* was not significant ($p > .05$). A linear relationship with longitude was barely significant for *O. tolmiei* ($p < .01$) and accounted for only 3.8% of the variation in this character (Table 6). There were no significant correlations between HDEW and the climatic variables for either taxon ($p > .05$).

HUMERUS LENGTH (HUML). *Oporornis philadelphia* averaged 3.9% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). Not all *O. tolmiei* localities were significantly different from all *O. philadelphia* localities (Figure 55). Three subsets contained only *O. tolmiei* localities. Six subsets were comprised of a mixture of *O. philadelphia* and *O. tolmiei* localities. HUML did not exhibit north-south clines for either taxon. Bivariate plots of HTRL and HUML showed complete separation of *O. philadelphia* and *O. tolmiei* populations (Figure 54). Variation in HUML with respect to longitude was only significant for *O. tolmiei*. HUML decreased from east to west in the range of *O.*

tolmiei ($p < .001$) (Table 6). Only 10.8% of the variation in this character was attributed to variation in longitude. Correlations between HUML and environmental variables were different in each taxon. For *O. philadelphia* HUML was positively correlated with MAJUNT ($p < .02$) (Table 7). HUML was negatively correlated with RELH ($p < .01$), and was positively correlated with MEJULP ($p < .004$), EVAP ($p < .001$), and JULWT ($p < .006$) (Table 8).

ULNA LENGTH (ULNL). *Oporornis philadelphia* averaged 3.0% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). Not all *O. philadelphia* samples were significantly different from *O. tolmiei* samples (Figure 56). The four subsets contained both *O. philadelphia* and *O. tolmiei* populations. Bivariate plots of HTRL and ULNL also showed near complete separation of *O. philadelphia* and *O. tolmiei* populations (Figure 54). ULNL did not show any north-south clines for *O. philadelphia* or *O. tolmiei*. Clinal variation with respect to longitude was significant in both taxa. ULNL decreased from east to west in *O. philadelphia* ($p < .02$) and *O. tolmiei* ($p < .005$) (Table 6). However, only 2.7% and 6.0% respectively of the variation in ULNL was attributed to longitude in these taxa. ULNL was highly correlated with temperature variables in *O. philadelphia* and a single humidity variable for *O. tolmiei*. For *O. philadelphia* ULNL increased with corresponding increases in the following temperature variables: MEJUNT ($p < .006$), MAJUNT ($p < .001$), and MEJULT ($p < .02$) (Table 7). ULNL was positively correlated with EVAP ($p < .01$) in *O. tolmiei* (Table 8).

CARPOMETACARPUS LENGTH (CARPL). *Oporornis philadelphia* averaged 2.7% longer than *O. tolmiei* for this character (Table 5) (APPENDIX C). Most *O. philadelphia* samples were not different from *O. tolmiei* populations (Figure 57). For results of Bivariate plots, see HTRL. Regressions on latitude and longitude were different in these taxa (Table 6). Variation in CARPL was significant only for latitude in *O. tolmiei*. CARPL increased with increasing latitude in *O. tolmiei* ($p < .02$). However, only 3.6% of the variation in this character was attributed to variation in latitude (Table 6). Correlations between CARPL and environmental variables differed between taxa. No significant relationships between CARPL and environmental variables were evident for *O. philadelphia*. In *O. tolmiei*, significant positive correlations were observed with MAJUNT ($p < .02$), MEJUNP ($p < .001$) and MEJULP ($p < .001$) (Table 8). This was the only skeletal variable which increased with increasing temperature in *O. tolmiei*.

5.2 MULTIVARIATE ANALYSIS OF MORPHOLOGICAL CHARACTERS

INTRODUCTION. Thorpe (1976) advocated the use of multivariate analyses in conjunction with univariate analyses because of 1) the importance of correlations among measurement variables; 2) that univariate measurements are only part of an "overall size measurement" therefore all characters should be examined "simultaneously" in multivariate space.

Multivariate analyses have been used by taxonomists to discriminate between groups or populations of organisms based on morphological characters. Each multivariate analysis has its own algorithm which

distinguishes it from the others. Investigations of geographic variation (Gould and Johnston 1973, Johnson 1980, Power 1969, Sneath and Sokal 1973, Thorpe 1976, Zink and Remsen 1986) have used Cluster Analyses (CA's), Discriminant Function Analyses (DFA's) and Principal Component Analyses (PCA's) to assess the phenotypic similarity of populations. I used the three methods above to measure distances between populations, partition samples into groups based on similarity and display these patterns. OTU's in these analyses were the populations and data were the means per population for each character. It is important to stress that sample sizes ranged from four to twenty-five individuals. CA's and PCA's were used to explore the data - 1) What are the relationships (distances) between populations from each taxon based on many characters simultaneously (description of phenetic resemblances between populations, projections of OTU's in three dimensions)? Is there good separation between OTU's of each taxon based on analysis each of the different morphological complexes? PCA's - 1) Is PC1 a "size component" as in studies of other taxa? 2) What are the loadings of the individual characters (highest to lowest) on each component and how do they change from one component to another? DFA - 1) How well are specimens of known voice recordings classified into primary song groups based on their skeletal and external measurements? Are specimens separable on discriminant function axes? The above analyses were performed on all characters simultaneously and individually for each complex (skull, girdle, leg, wing, external complexes). I computed Mahalanobis' D^2 for each morphological complex to compare the degree of differentiation between complexes in these taxa. I also compared the

results from PCA's, CA's, and DFA's to examine the degree of concordance among these analyses.

5.2.1 CLUSTER ANALYSIS (CA)

For each of the CA's mentioned below OTU's were populations from each taxon. Data for each of the OTU's were the population means for the morphological characters. I performed separate CA's on OTU's for each set of morphological characters - external, skull, girdle, leg, wing complexes. I also performed a CA with all skeletal characters combined. I conducted CA's for different complexes to reveal the amount of underlying distinctness between tax at each of these morphological levels.

5.2.1.1 CA - EXTERNAL CHARACTERS

Two major homogeneous clusters emerge at the 0.75 distance mark (Figure 58). All *O. tolmiei* populations composed cluster 1 while all *O. philadelphia* populations composed cluster 2. In cluster 2 eastern, western northern and southern populations were mixed together in several minor clusters. However, in cluster 1 some spatial patterns existed. Southern populations (PV, WY, MM, JA) joined together in cluster 1A; more northerly populations joined in 1B.

When analyzed simultaneously external complex variables provided good separation of populations of each taxon. All populations of *O. philadelphia* and *O. tolmiei* were sorted into two major clusters.

5.2.1.2 CA - SKULL COMPLEX

Phenogram of skull variables revealed three major clusters at the 1.20 distance mark (Figure 59). *O. tolmiei* populations composed cluster 1. There was no spatial pattern to the minor clusters of *O. tolmiei* populations in cluster 1. Cluster 2 was composed of *O. philadelphia* populations and one *O. tolmiei* population (KA). An east - west pattern of population segregation occurred in cluster 2. Cluster 2A contained western populations of *O. philadelphia* and one eastern population of *O. tolmiei* (KA). All eastern *O. philadelphia* populations were joined in cluster 2B. A third cluster contained one divergent *O. tolmiei* population from northern Oregon (MH).

When analyzed simultaneously skull characters are good discriminators of *O. philadelphia* and *O. tolmiei* populations. However CA has some problems with *O. tolmiei* populations from central Alberta near the hypothetical contact areas. Although no geographic pattern emerged for *O. tolmiei*, an east - west pattern was evident within the *O. philadelphia* cluster.

5.2.1.3 CA - GIRDLE COMPLEX

Two major clusters are evident at the 0.85 mark (Figure 60). All *O. tolmiei* populations join together in cluster 1. Within this cluster two minor clusters are apparent at the 0.65 distance mark. These represent weak east -west divisions of *O. tolmiei* populations. Cluster 1A contains one southern 3 western populations (except for LO) and cluster 1B is composed of southern, eastern

and northern populations (except for SC). Cluster 2 contains only *O. philadelphia* populations. Within cluster 2 geographically distant populations are clustered together and no spatial pattern is evident.

Considered simultaneously, girdle characters are good discriminators of *O. tolmiei* and *O. philadelphia* populations. *O. philadelphia* populations joined together only with *O. philadelphia* populations. The same held true for *O. tolmiei* populations which clustered together with each other.

5.2.1.4 CA - LEG COMPLEX

At the 0.95 distance mark there are two well defined clusters (Figure 61). Cluster 2 is composed exclusively of *O. philadelphia* populations but is missing SL from central Alberta. SL joined with the *O. tolmiei* populations in cluster 1. There is no spatial pattern to populations joined within either of the major clusters. Eastern, western, southern and northern populations are mixed together in both clusters.

CA's of all leg variables considered simultaneously will discriminate most populations of *O. philadelphia* and *O. tolmiei* but has trouble with some *O. philadelphia* populations from central Alberta, near the hypothetical contact areas for these taxa. OB and LP are closer to contact with *O. tolmiei* in Alberta but were clustered with other *O. philadelphia* populations (Figure 61, see cluster 2).

5.2.1.5 CA - WING COMPLEX

Two major clusters emerge at the 1.05 mark (Figure 62). Cluster 1 is composed exclusively of *O. tolmiei* populations while cluster 2 contains only *O. philadelphia* populations (Figure 62). In both major clusters northern and southern populations were clustered separately from each other. Cluster 1A was composed primarily of southern populations (except for LR) while 1B contained northern populations. The two most southerly populations of *O. philadelphia* (CZ and SF) composed cluster 2A. Cluster 2B contained northern populations.

Simultaneous analysis of all wing variables provided good discrimination of populations from both taxa. Furthermore, within both taxa southern and northern populations were also separated.

5.2.1.6 CA - ALL SKELETAL COMPLEXES

When skeletal characters from all the complexes are considered simultaneously there are 2 major clusters at the 1.10 distance mark (Figure 63). All but one OTU from central Alberta (OB) in cluster 1 are *O. tolmiei* populations. One *O. tolmiei* OTU from southwestern Alberta (KA) belonged to cluster 2 which contained the *O. philadelphia* populations. OTU's joined in cluster 1A were also close to each other geographically, northwestern Nevada and southeastern Idaho. Except for JA from northeastern Nevada and MM from southwestern Idaho, cluster 2 contained populations from southern, central and northeastern Washington. OTU's in cluster 2C were from or near the eastern edge of the breeding range of *O. tolmiei*, including two populations which were geographically adjacent to each other in eastern Montana. Segregation of

geographically adjacent OTU's was also apparent in *O. philadelphia* clusters. OTU's from clusters 2A and 2C were from the eastern part of the breeding range while clusters from 2B were from the west. All OTU's in cluster 2A except for SF from northern Maine were from Ontario. Except for CZ from northern New York and MI from western Ontario, all OTU's in cluster 2C were from Quebec.

When skeletal characters from the different body regions are considered simultaneously they provide good discrimination of *O. philadelphia* and *O. tolmiei* OTU's except for some populations near the contact zones from central and southern Alberta. Both of these were the last OTU joined to either cluster 1 or 2 indicating that they were the most divergent members of their respective clusters. Larger sample sizes from these areas may be part of the problem. Both OTU's had less than 10 specimens compared to other OTU's near the contact zones with larger sample sizes that were correctly placed in their appropriate clusters (e.g., *O. philadelphia* OTU in cluster 2 - SL from Alberta; *O. tolmiei* OTU in cluster 1 - MC from east-central British Columbia). A majority of the minor clusters in each taxon were geographically homogeneous, containing OTU's which were geographically adjacent to each other. Populations which were close to each other geographically were more similar to each other in size.

5.2.2 PRINCIPAL COMPONENTS ANALYSIS (PCA)

Only the first three Principal Components were extracted from variance-covariance matrices. In almost all cases these principal components explained at least 85% or more of the total variance. As in the CA's, the OTU's were *O. philadelphia* and *O. tolmiei* populations and the data were means for the

morphological characters for that population. OTU's were projected onto 3 dimensional plots, each axis corresponding to one of the three principal components. Character loadings for each complex were the correlations of the characters with the principal components. Six separate PCA's were performed on the data. Each analysis was conducted for a different morphological complex - external, skull, girdle, leg, wing and all skeletal complexes combined. These PCA's were conducted to reveal the morphological distinctness of each taxon for each body region.

5.2.2.1 PCA - EXTERNAL CHARACTERS

Plots of the first three principal components showed complete separation *O. tolmiei* and *O. philadelphia* populations (Figure 64). The larger birds are in the upper right of the plot and the smaller birds in the lower left of the plot. *O. philadelphia* and *O. tolmiei* populations closest to each other in 3D space (middle of the plot) were from Alberta and British Columbia (*O. philadelphia* - OB, FR, SL; *O. tolmiei* - KA, MC, BA, LR). *O. philadelphia* and *O. tolmiei* populations from the potential contact areas in these two provinces were more similar to each other based on external characters.

The first principal component explained 99.8% of the total variation (Table 11). T was negatively correlated with PRIN1. W-T was the most highly correlated external variable with PRIN1 (Table 11). Correlation between WING and the PRIN1 was slightly positive. W-T swamps the effects of the other variables with its high loading. All characters varied positively with PRIN2. WING and TAIL contributed the highest loadings on PRIN2. PRIN2 was a

"WING, TAIL" factor due to the high loadings on this component. PRIN3 explained 0.1% of the total variation. It was negatively correlated with WING and positively correlated with TAIL and W-T. WING and TAIL also loaded heavily on PRIN3.

PRIN1 explained almost all of the variation in the external measurements and W-T had the highest loading on this component. PRIN1 is a "W-T" factor due to high loading of this variable on PRIN1. W-T is one of the best morphological characters for separating these taxa.

5.2.2.2 PCA - SKULL COMPLEX

O. philadelphia and *O. tolmiei* populations were separated on 3D plots of the first three principal components scores (Figure 65). The larger birds for these characters are in the upper right of the plot and the smaller birds in the lower right. *O. philadelphia* populations from central Alberta and British Columbia (LP, OB, FR, SL, and one from western Ontario - MI) were the closest *O. philadelphia* populations to any *O. tolmiei* OTU's. *O. tolmiei* populations close to *O. philadelphia* were KA and BA from Alberta and British Columbia respectively. Populations from the contact areas were the closest OTU's to the other taxon in 3D space for both taxa.

PRIN1 explained 74.3% of the total variation (Table 12). SKW was the only variable which had a negative correlation with PRIN1. INORW had the highest loading on PRIN1, making it an "INORW" factor. PRIN2 explained 14.1% of the variation. PRL and NASW had higher loadings on PRIN2. Only

10.1% of the total variation was explained by PRIN3. NASW had the highest loading on PRIN3.

5.2.2.3 PCA - GIRDLE COMPLEX

O. philadelphia and *O. tolmiei* populations were separated when PCA scores were plotted along the first three principal components based on girdle variables. Larger birds are on the top of the plot and smaller birds are on the bottom (Figure 66). KA and MC from Alberta and British Columbia were the closest *O. tolmiei* populations to *O. philadelphia* OTU's. However *O. philadelphia* populations from these provinces were not close to the *O. tolmiei* OTU's. The closest *O. philadelphia* OTU's to *O. tolmiei* populations were from Ontario (CO, DO) and Maine (SF).

PRIN1 explained 86.2% of the total variation (Table 13). All girdle characters were positively correlated with PRIN1. KEED had the highest loading on this component. PRIN2 and PRIN3 combined only explained about 10.0% of the total variation. SYNMW had the highest loading on PRIN2. PRIN2 is a "SYNMW" factor. KEED and SYNW loaded the highest on PRIN3.

5.2.2.4 PCA - LEG COMPLEX

Plots of the first three principal components for the leg complex revealed good separation of *O. philadelphia* and *O. tolmiei* populations (Figure 67). The closest *O. tolmiei* population to any of the *O. philadelphia* OTU's was BA, from central British Columbia and LH from Montana. Eastern *O. philadelphia*

populations (SF, SP, DO) and SL from central Alberta were closest to any *O. tolmiei* OTU's.

PRIN1 accounted for 78.5% of the total variation (Table 14). All leg variables were positively correlated with PRIN1. The heaviest loading on PRIN1 was from FEDW. Only 13.1% of the total variation was explained by PRIN2. TARL had the highest loading on PRIN2. PRIN3 explained 8.4% of the total variation. The highest loading was from FEDW.

5.2.2.5 PCA - WING COMPLEX

O. philadelphia and *O. tolmiei* populations were completely separated when PCA scores were plotted using the first three principal components for wing characters (Figure 68). Larger birds are on the left of axes PRIN2 and PRIN3 while smaller birds are on the right these axes. The closest *O. tolmiei* OTU's to *O. philadelphia* populations were from Montana (LH) and central Alberta (KA). One *O. philadelphia* population from central Alberta (OB) and other eastern populations (SP - Quebec, DO - Ontario, and CZ - New York) came closest to any *O. tolmiei* OTU's.

PRIN1 accounted for 85.7% of the total variation (Table 15). Each of the wing characters was positively correlated with PRIN1. HTRL had the highest loading on PRIN1. PRIN2 and PRIN3 combined accounted for less than 14.0% of the total variation. HTRL contributed the most to PRIN2 while HDEW had the highest loading on PRIN3.

5.2.2.6 PCA - ALL SKELETAL COMPLEXES

When all skeletal variables are considered simultaneously plots of PCA scores of the first three PC's showed complete separation of *O. philadelphia* and *O. tolmiei* OTU's (Figure 69). Larger birds are depicted on the left half of the plot while smaller populations are in the lower right part of the plot. Montana (LH) and Alberta (KA) *O. tolmiei* populations are closest to any *O. philadelphia* OTU's. One Alberta (LP) and other eastern (Ontario - HE, CO, MI; Quebec - LE) *O. philadelphia* populations came closest to *O. tolmiei*.

PRIN1 explained 62.1% of the total variation (Table 16). This is probably an overall size factor because of all the positive correlations with the skeletal characters. It is normally regarded as such in the literature (Johnston and Selander 1972, Troy 1984, Schnell et al. 1985). TARD had the highest loading on PRIN1. PRIN2 accounted for 15.2% of the total variation. PRIN2 is a contrast among some skull and leg elements (which are weighted negatively - PRL, BDEP, SKW, SKL, TARL, TARD) and the remainder of the body regions (which are weighted positively). TARD also had the highest loading on this component. Only 9.3% of the total variation was accounted for by PRIN3. PRIN3 is also a contrast among elements from different regions of the skeleton. Some skull, girdle and one leg character were weighted negatively on PRIN3 while all others were weighted positively. BDEP contributed the most to PRIN3.

5.2.3 DISCRIMINANT FUNCTION ANALYSIS (DFA)

I used DFA's to test for additional possible differences between *O. philadelphia* and *O. tolmiei*. In a DFA group membership is specified *a priori*

to the analysis in contrast to PCA where group membership is not specified. I pooled samples into two groups based on dominant song types for those populations. Populations where males sang *O. philadelphia* songs types were labeled *O. philadelphia* and populations where males sang *O. tolmiei* song types were labeled *O. tolmiei* prior to the DFA. The question I asked was whether populations with an *O. philadelphia* or *O. tolmiei* song type could be accurately classified as belonging to that song type based on morphological variables. Groups designated prior to the analysis were *O. philadelphia* song type or *O. tolmiei* song types. DFA's were similar to the two multivariate techniques above. OTU's were populations of *O. tolmiei* and *O. philadelphia* and the data were means for each morphological character for a given population.

I performed five separate DFA's on these data, one for each morphological complex (external, skull, girdle, leg, wing) and another DFA was performed on data from all the skeletal regions analyzed simultaneously. For each of the DFA's I have presented the classification functions and the standardized coefficients in Table . Classification functions are used to calculate the distance of each specimen from each group centroid (Neff and Marcus 1980). I used SAS (version 5.16, PROC DISCRIM) to compute classifications for *O. philadelphia* and *O. tolmiei* . For each specimen the original measurements are multiplied by the coefficients and added to the constant. The calculations are made for both functions and the OTU is assigned to that taxon for which the resulting value is the greatest (Schnell et al 1984). The per cent of correctly classified OTU's is an indication of how well the characters discriminate between groups. However, in order to include data

from as many specimens as possible these functions were generated based on character means per locality and not raw scores for each specimen. Therefore caution must be exercised when using these functions to classify unknown specimens.

Canonical Variates Analysis (CVA) is a form of DFA used primarily to plot scores for OTU's onto the DF axis. The raw data is multiplied by the canonical variate coefficients to compute the canonical variate scores (Neff and Marcus 1980). These are plotted on the canonical axes which in the two group case is the discriminant function axis. Canonical variate scores (also called DF scores in this discussion) and Standardized Coefficients were computed using PROC CANDISC in SAS (1985, version 5.16). Standardized coefficients are obtained by multiplying the original canonical variate coefficient by the standard deviation (SD - pooled within groups) for each variable (Neff and Marcus 1980). "They are the amount that the canonical variate score will change for each change of an original variable by one standard deviation" (Neff and Marcus 1980, p. 158). These new coefficients indicate the relative importance of each character in discriminating between groups (regardless of sign) (Johnson 1980, Rising and Schueler 1980).

Zink (unpublished MS cited in Zink and Remsen 1986) estimated intertaxon phenetic distances for several body regions in the *Pipilo fuscus* complex and found that different body regions had "undergone relatively greater differentiation than other body regions" (Zink and Remsen 1986, p. 6). I also calculated Mahalanobis' D^2 between *O. philadelphia* and *O. tolmiei* for each of the different morphological complexes to determine and compare the amount of differentiation of the different body regions in these taxa.

5.2.3.1 DFA - EXTERNAL CHARACTERS

TAIL followed by W-T were the best discriminators from this complex (Table 17). Projections of OTU scores are completely separated on the discriminant function axis (Figure 70).

5.2.3.2 DFA - SKULL COMPLEX

INORW was the best discriminator while SKL was the least in the skull complex (Table 18). Plots of canonical variate scores on the discriminant function axis showed complete separation of *O. philadelphia* and *O. tolmiei* OTU's.

5.2.3.3 DFA - GIRDLE COMPLEX

SCAPW discriminated least effectively between *O. philadelphia* and *O. tolmiei* (Table 19). Plots of DF scores on the discriminant function axis showed complete separation of *O. philadelphia* and *O. tolmiei* OTU's (Figure 72).

5.2.3.4 DFA - LEG COMPLEX

FEDW and FEL were the best discriminating characters while TIBL and TARL least effectively discriminated between *O. philadelphia* and *O. tolmiei* (Table 20). When canonical variate scores were plotted on the discriminant

axis SQ from Montana was the only *O. tolmiei* OTU misclassified as *O. philadelphia* (Figure 73).

5.2.3.5 DFA - WING COMPLEX

HTRL and HUML were the most effective discriminators among the WING characters measured. HDEW and CARPL were the poorest discriminators (Table 21). Plots of canonical variate scores on the discriminant function axis revealed complete discrimination of *O. philadelphia* and *O. tolmiei* OTU's (Figure 74).

5.2.3.6 DFA - ALL SKELETAL COMPLEXES

Plots of DF scores on the discriminant function axis also showed complete separation of *O. philadelphia* and *O. tolmiei* OTU's when all skeletal characters were used (Figure 75). Characters which contributed the most to the discrimination of *O. philadelphia* and *O. tolmiei* OTU's included KEEL, STERL and HUML (Table 22). Characters which least effectively discriminated between taxa were MANL and FEDW (Table 22).

5.2.3.7 Mahalanobis' D^2 BETWEEN BODY REGIONS

Distance between taxa for LEG complex characters was only slightly greater than WING characters. Differentiation between taxa was less for WING and LEG characters. EXTERNAL, GIRDLE, and SKULL character complexes

exhibited the greatest differentiation between taxa. However morphological distance between taxa was greatest when characters from each of the body regions were used in the DFA. Mahalanobis' D^2 between taxa ranged from 12.55 for WING complex to 87.26 when all characters from each complex were analyzed simultaneously (Figure 76).

5.2.3.8 STEPWISE DFA FOR ALL SKELETAL CHARACTERS

I used STEPWISE DFA to determine which of the skeletal elements provided maximum discrimination of OTU's from these taxa with respect to the variability within each taxon. Variables were entered into the analysis one at a time (forward selection) based on the level of an F test from analysis of covariance. Since the probability of rejecting a true null hypothesis at the 0.05 level increases with the number of significance tests performed an overall significance level of 15% was used in this analysis. The stepwise selection stops when all the variables in the model meet the criterion to stay and all the remaining variables do not meet the criterion to enter the analysis. Wilk's Lambda is close to 0.00 when the OTU's from the predesignated groups can be discriminated and near 1.00 when they can not be discriminated (SAS 1985).

The STEPWISE DFA proceeded for seven steps in the morphological analysis. According to the results of this procedure the six variables which best separated *O. philadelphia* and *O. tolmiei* OTU's were (in order): INORW, FEL, CORL, SKW, SCAPW, HTRL (Table 23). In each case Wilk's Lambda is close to 0.00 (Table 23) indicating good separation of OTU's. At each step the class means are significantly different from each other ($p < .0001$, based on the

approximation of Wilk's Lambda). These results suggest that a combination of skeletal elements from different body regions - skull, leg, girdle and wing regions, are necessary to provide the best separation of *O. philadelphia* and *O. tolmiei* OTU's.

5.3 SUMMARY

SPECIES DIFFERENCES - AVERAGE Per Cent DIFFERENCES BETWEEN TAXA FOR MORPHOLOGICAL

CHARACTERS. Size differentiation exists for all morphological characters. *Oporornis philadelphia* was significantly different from *O. tolmiei* for 22 of 29 morphological characters (APPENDIX C). However, for almost every character the 95% confidence intervals showed overlap between taxa and specimens could not be separated based on individual characters. W-T was the best morphological character used to separate specimens of these taxa.

Species differences between skeletal complexes ranged from 3.14% (WING) - 5.27% (GIRDLE) (Table 5). The average per cent difference between taxa for the skull complex was 5.17%; girdle complex- 5.27%; leg complex - 3.24%; wing complex - 3.14%; external characters combined - 22.7% (Table 5). The greatest difference between taxa were in external characters. When characters were analyzed individually *O. philadelphia* averaged larger size than *O. tolmiei* for all morphological characters except four (SKW, KEED, TARL, TAIL) (Table 5). The largest per cent difference between taxa was 56.0% larger W-T in *O. philadelphia* while the smallest per cent difference (0.1%) occurred for TARL. At the univariate level for all specimens combined there has been

greater size differentiation between these taxa for external characters (22.7%) than for skeletal characters (3.0% - 6.0%).

SPECIES DIFFERENCES - BIVARIATE PLOTS. Bivariate plots convey information on the degree of separation of taxa in two dimensional character space. Plots of different pairs of characters yielded conflicting results on the degree of differentiation between populations of each taxon. **EXTERNAL CHARACTERS.** Bivariate plots of external characters revealed good separation for characters plotted against WING (Figure 30). **SKULL CHARACTERS.** Except for PRL x INORW, bivariate plots of skull elements plotted against PRL showed poor separation of populations from each taxon (Figure 37). **GIRDLE CHARACTERS.** All plots of girdle elements against CORL showed good separation of populations of each taxon (Figure 44). Plots of CORL by KEEL, STERL, and KEED were best at separating these taxa. **LEG CHARACTERS.** Leg characters plotted against FEL revealed good separation of *O. philadelphia* and *O. tolmiei* populations (Figure 50). **WING CHARACTERS.** Plots of wing elements by HTRL also separated populations from these taxa. The best separation was HTRL x HUML (Figure 54).

According to bivariate plots differentiation between these taxa was greatest for EXTERNAL, GIRDLE, LEG and WING complexes and poorest for skull complexes.

GEOGRAPHIC VARIATION - UNIVARIATE ANALYSES. Taxon versus taxon means comparison leaves out the geographic component of morphological variation. Results from ANOVA's showed that many *O. philadelphia* and *O. tolmiei* population means were not significantly different

from each other for external and skeletal characters. Most *O. philadelphia* populations were significantly different from *O. tolmiei* populations for W-T.

GEOGRAPHIC VARIATION - REGRESSION ANALYSES.

Patterns of north-south and east-west clinal variation in morphological characters differed between characters and also between taxa (Table 6). For *O. philadelphia* 25 morphological characters exhibited significant linear relationships with latitude or longitude while 28 were found for *O. tolmiei* (Table 6). In *O. philadelphia* 10 characters decreased with increasing latitude and 3 increased with increasing latitude. This disparate trend was not observed in *O. tolmiei*. In *O. tolmiei* five characters decreased with increasing latitude and six increased with increasing latitude. Variation in longitude was similar in both taxa. Ten characters were negatively related with longitude in *O. philadelphia* and 16 characters in *O. tolmiei*. Only one and two characters were positively related with latitude for *O. tolmiei* and *O. philadelphia* respectively.

Within taxa not all characters within a skeletal complex varied together with latitude or longitude in both taxa. For example in the leg complex of *O. philadelphia* only FEL and TARD showed significant regressions while TIBL and TARL regressions were not significant. In both taxa some characters in the same complex increased while others decreased from north-south or east-west - reverse variation. There were three cases of reverse variation 1) In *O. tolmiei* TAIL decreased and W-T increased with increasing latitude and 2) In *O. tolmiei* PRL, BDEP, decreased from east to west while INORW increased in that same direction. 3) TAIL increased from east to west while W-T decreased in that direction in *O. philadelphia*. In *O. philadelphia* WEIGHT, TAIL, and W-T

increased with increasing latitude while all other characters ("from different complexes") decreased in the same direction.

Although many significant regressions on latitude and longitude were found in both taxa, R^2 's were very small for these regressions (usually less than 25%), accounting for little of the variation in these characters.

GEOGRAPHIC VARIATION - CORRELATION ANALYSES. A majority of morphological characters of *O. philadelphia* were highly correlated with Temperature variables while a majority of morphological characters of *O. tolmiei* were highly correlated with Precipitation variables (Tables 7, 8). There were 46 positive and eight negative significant correlations between morphological characters and Temperature variables and only one (negative) significant correlation with a Precipitation variable for *O. philadelphia*. Only WEIGHT was correlated with a precipitation variable in *O. philadelphia*. The positive correlations between morphological characters and temperature data indicates that larger birds are found in warmer climates and smaller birds in cooler areas in the breeding range of *O. philadelphia*. This contradicts Bergman's rule that predicts larger body size in cooler climates. In contrast to *O. philadelphia* 42 positive and 9 negative correlations between morphological characters and precipitation variables existed in *O. tolmiei*. For *O. tolmiei* only 12 positive and 13 negative correlations existed between morphological characters and Temperature variables. In *O. tolmiei*'s breeding range the larger birds are found in wetter climates and smaller birds in drier areas.

If strong correlations between morphological elements and environmental variables are evidence of natural selection then *O. philadelphia* seems more sensitive to temperature and *O. tolmiei* to precipitation variables.

MULTIVARIATE ANALYSES. Results of CA's of each morphological complex and all complexes combined showed good separation of *O. philadelphia* and *O. tolmiei* OTU's. *O. philadelphia* OTU's were completely separated from *O. tolmiei* OTU's in the CA's of EXTERNAL, GIRDLE and WING COMPLEXES. SKULL and LEG COMPLEXES were not as successful in discriminating taxa in the CA. One *O. philadelphia* and one *O. tolmiei* population from central Alberta were misclassified by the CA's for these two complexes. When components of all complexes were considered simultaneously one *O. philadelphia* population from central Alberta was misclassified as *O. tolmiei*.

Separate plots of PCA scores from analyses of EXTERNAL, SKULL, GIRDLE, LEG and WING COMPLEXES showed complete separation of *O. philadelphia* and *O. tolmiei* OTU's. Complete separation of *O. philadelphia* and *O. tolmiei* OTU's was also achieved plotting PCA scores when elements from each of the complexes were used simultaneously. Except for the GIRDLE and LEG COMPLEXES, *O. philadelphia* and *O. tolmiei* OTU's closest to each other in the 3D plots were from the Alberta and British Columbia. In PCA's of the GIRDLE and LEG COMPLEXES the closest *O. tolmiei* OTU's to any *O. philadelphia* OTU's were from Alberta and British Columbia but the closest *O. philadelphia* OTU's were from Ontario, Quebec and Maine. Not all OTU's from the contact areas were closest to each other on the 3D plot when all skeletal characters were evaluated simultaneously.

One-hundred per cent of *O. philadelphia* and *O. tolmiei* OTU's were correctly assigned to their respective taxa by DFA's of EXTERNAL, SKULL, GIRDLE, LEG and WING COMPLEXES. Projections of OTU's on the DF axis by

the Canonical Variates Analysis of EXTERNAL, SKULL, GIRDLE and WING COMPLEXES also showed complete separation of *O. philadelphia* and *O. tolmiei* OTU's. Results of DFA and CVA of all skeletal characters also completely discriminated *O. philadelphia* and *O. tolmiei* OTU's. CVA of the LEG COMPLEX misclassified one *O. tolmiei* OTU from central Montana.

The multivariate analyses of morphological variables were all in general agreement with one another - nearly complete or complete separation of *O. philadelphia* and *O. tolmiei* OTU's based on the different skeletal complexes. Separation using DFA's was more complete than with CA's or PCA's. Problem OTU's which were misclassified by CA's and DFA' or closest in 3D space in PCA's to OTU's from the other taxon were primarily from Alberta and British Columbia.

Inconsistencies in the pattern of differentiation between taxa for different complexes might imply different selective or stochastic forces operating on these complexes (Zink and Remsen 1986). Comparisons of Mahalanobis D^2 between different skeletal complexes revealed different amounts of morphometric variation between taxa for each complex. For *O. philadelphia* and *O. tolmiei* Mahalanobis D^2 was greatest when elements from each of the different complexes were analyzed simultaneously, followed by SKULL, GIRDLE, EXTERNAL, LEG and WING COMPLEXES. Leg and wing bones show the least amount of differentiation compared to skull and girdle bones.

Results of STEPWISE DFA indicated that a combination of skeletal elements from the different body regions provided the best separation of *O. philadelphia* and *O. tolmiei* OTU's. In this analysis the best combination included seven morphological characters - INORW, SKW (SKULL Complex),

CORL, SCAPW (GIRDLE Complex), FEL (LEG Complex), and HTRL (WING Complex) (Table 23).

Table 5. Comparison of taxon Means (mm) per morphological character for each taxon and per cent difference between taxa.

MORPH. CHARACTERS*	<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	Per Cent Difference	Taxon Difference
PRL	13.72	13.43	7.4%	<i>philadelphia>tolmiei</i>
BDEP	1.12	1.06	5.3%	<i>philadelphia>tolmiei</i>
NASW	5.95	5.62	5.5%	<i>philadelphia>tolmiei</i>
INORW	3.03	2.66	12.2%	<i>philadelphia>tolmiei</i>
SKW	13.35	13.38	0.2%	<i>tolmiei>philadelphia</i>
SKL	30.74	30.42	1.0%	<i>philadelphia>tolmiei</i>
MANL	22.32	21.89	1.9%	<i>philadelphia>tolmiei</i>
MAND	1.51	1.39	7.9%	<i>philadelphia>tolmiei</i>
SKULL COMPLEX AVERAGE			5.17%	<i>philadelphia>tolmiei</i>
CORL	14.59	13.81	5.3%	<i>philadelphia>tolmiei</i>
SCAPW	1.94	1.78	8.2%	<i>philadelphia>tolmiei</i>
STERL	16.44	15.37	6.5%	<i>philadelphia>tolmiei</i>
KEEL	14.71	13.58	7.6%	<i>philadelphia>tolmiei</i>
KEED	6.32	5.84	7.2%	<i>tolmiei>philadelphia</i>
SYNW	8.90	8.79	1.2%	<i>philadelphia>tolmiei</i>
SYNMW	5.04	4.99	0.9%	<i>philadelphia>tolmiei</i>
GIRDLE COMPLEX AVERAGE			5.27%	<i>philadelphia>tolmiei</i>
FEDW	2.61	2.53	3.0%	<i>philadelphia>tolmiei</i>
FEL	15.48	14.76	4.6%	<i>philadelphia>tolmiei</i>
TIBL	28.14	27.51	2.2%	<i>philadelphia>tolmiei</i>
TARL	20.57	20.60	0.1%	<i>tolmiei>philadelphia</i>
TARD	2.21	2.07	6.3%	<i>philadelphia>tolmiei</i>
LEG COMPLEX AVERAGE			3.24%	<i>philadelphia>tolmiei</i>
HTRL	3.64	3.48	4.3%	<i>philadelphia>tolmiei</i>
HDEW	3.30	3.24	1.8%	<i>philadelphia>tolmiei</i>
HUML	14.50	13.93	3.9%	<i>philadelphia>tolmiei</i>
ULNL	16.53	16.03	3.0%	<i>philadelphia>tolmiei</i>
CARPL	9.46	9.20	2.7%	<i>philadelphia>tolmiei</i>
WING COMPLEX AVERAGE			3.14%	<i>philadelphia>tolmiei</i>
WEIGHT	14.24	13.17	7.5%	<i>philadelphia>tolmiei</i>
WING	61.56	60.15	2.2%	<i>philadelphia>tolmiei</i>
TAIL	49.32	54.78	9.9%	<i>tolmiei>philadelphia</i>
W-T	12.21	5.37	56.0%	<i>philadelphia>tolmiei</i>
EXTERNAL COMPLEX AVERAGE			22.7%	<i>philadelphia>tolmiei</i>

Bold face type - indicates that *O. tolmiei* is greater than *O. philadelphia* for that character.

Table 6. Results of Regression Analyses of morphological characters on latitude and longitude.

MORPH. CHAR.	LATITUDE		LONGITUDE	
	<i>O. philadelphia</i>		<i>O. tolmiei</i>	
	Signif. Level	R ²	Signif. Level	R ²
PRL	.001(-)19.3		.001(-)18.2	
BDEP	.001(-) 4.1		.04(-) 2.2	
NASW	.03(-) 1.7			
INORW	.002(-) 3.9		.001(-) 5.1	
SKW				
SKL	.001(-)11.2		.01(-) 5.1	
MANL			.001(-)10.5	
MAND	.001(-) 4.8			
CORL			.001(-) 4.2	
SCAPW	.001(-) 4.2		.001(-) 6.6	
STERL				
KEEL			.001(+).6.7	
KEED	.001(+).4.3			
SYNW				
SYNMW				
FEDW				
FEL	.003(-) 3.7		.001(-) 5.6	
TIBL				
TARL				
TARD	.001(-)10.6		.001(-)12.1	
HTRL	.01(-) 2.4			
HDEW				
HUML				
ULNL			.02(-) 2.7	
CARPL				
WEIGHT	.001(+).10.2		.001(+).7.5	
WING				
TAIL	.001(+).4.5		.001(+).5.7	
W-T	.001(-) 5.2		.001(-) 8.0	

Table 7. Results of Spearman Rank Order Correlation Analyses between morphological characters and environmental variables for *O. philadelphia*.

	MORPH.	MEJUNT	MJUNT	MAJUNT	MEULT	MULT	MAULT	MEJUNP	MEJULP	REH	EVAP	JULWT
CHAR.												
PRL	.02(+)		.001(+)	.004(+)		.002(+)						
BDEP	.02(+)		.02(+)	.02(+)	.02(+)	.006(+)						
NASW												
NORW												
SKV												
SKL	.001(+)		.001(+)	.001(+)	.04(+)	.001(+)						
MANL												
MAND	.001(+)		.003(+)		.005(+)	.006(+)	.001(+)					
CORL			.02(+)									
SCAPW				.03(+)	.004(+)							
STERL												
KEEL			.02(+)									
KEED				.04(-)								
SYMW						.03(+)					.003(-)	
SYNAM												
FEDW												
FEL	.005(+)		.01(+)	.03(+)	.04(+)	.03(+)						
TBL												
TARL	.01(+)		.003(+)			.004(+)						
TARD	.001(+)		.001(+)		.001(+)	.001(+)	.001(+)					
HTRL	.02(+)		.03(+)	.01(+)						.04(+)	.001(+)	
HDEW												
HUML			.02(+)									
ULNL	.006(+)		.001(+)	.02(+)								
CARPL												
WEIGHT	.002(-)	.001(-)	.04(-)	.001(-)	.001(-)	.001(+)		.001(-)				
WING												
TAIL												
WLT			.03(-)			.001(+)						

Table 8. Results of Correlation Analyses between morphological characters and environmental variables for *O. tolmiei*.

	MOEPL	MEJUNT	MJUNT	MAJUNT	MEJULT	MJULT	MAJULT	MEJUP	MEJUP	RELH	EVAP	JULWT
CHAR.												
PRL												
BDEP												
NASW			.003(+)		.003(+)	.004(+)	.006(-)	.003(-)				
MOFW							.02(+)		.02(-)			
SKV							.01(+)		.006(+)		.01(-)	
SKL												
MANL												
MAND												
CORL												
SCAPW	.04(-)	.007(+)	.01(+)		.02(-)	.01(-)	.01(+)	.002(+)	.001(+)	.002(+)		
STERL												
KEEL	.002(+)	.01(+)			.02(-)	.01(-)	.006(+)	.001(+)	.001(+)			
KEED							.001(+)		.001(+)			
SYAW							.001(+)		.001(+)			
SYMMW							.001(+)		.001(+)			
FEDW							.009(+)		.009(+)			
FEL							.005(+)		.005(+)			
TERL												
TARL												
TARD												
HTFL												
HDEW	.04(-)						.007(+)	.001(+)	.001(-)	.02(+)	.001(+)	
HJUL												
UJUL												
CARPL												
WEIGHT	.04(-)	.02(+)			.01(-)	.03(-)	.001(+)	.001(+)	.003(+)	.001(+)	.02(+)	
WING							.04(+)	.006(+)	.005(-)	.001(-)	.002(+)	
TAL	.007(-)	.001(-)			.02(-)	.002(+)	.001(-)	.001(-)	.001(-)	.002(+)	.001(+)	
W-T	.001(+)	.001(+)			.002(+)		.001(+)	.001(+)	.001(+)	.001(+)	.001(-)	

Table 9. Results of temporal comparisons of external characters between 1963 and 1985 populations of *O. philadelphia* and *O. tolmiei* from central Alberta.

TAXON	WING* Means		
	1963	1985	
<i>O. philadelphia</i>	61.92	61.58	
<i>O. tolmiei</i>	61.37	59.40	
TAXON	TAIL* Means		
	1963	1985	
<i>O. philadelphia</i>	51.80	50.79	
<i>O. tolmiei</i>	53.16	53.94	
TAXON	W-T* Means		
	1963	1985	
<i>O. philadelphia</i>	10.12	10.70	
<i>O. tolmiei</i>	6.09	7.42	
Completed ANOVA		Probability levels	
Source of variation	WING	TAIL	W-T
Taxon	.100	.001	.001
Time of collection	.690	.723	.505
Taxon x Time	.049	.064	.863

* - measurements in mm.

Bold face type indicates $p < .05$.

Table 10. Generalized Squared Distances (MAHLANOBIS D²)
Between Taxa and Time Samples.

GROUP	<i>Oporornis philadelphia</i>		<i>Oporornis tolmiei</i>	
	1963	1985	1963	1985
<i>O. philadelphia</i> 1963 N=15	0.000	0.266	7.394	5.593
<i>O. philadelphia</i> 1985 N=15		0.000	7.733	6.701
<i>O. tolmiei</i> 1985 N=4			0.000	1.465
<i>O. tolmiei</i> 1985 N=7				0.000

Table 11. Loadings of External Complex Variables on Principal Components.

External Character	PC1	PC2	PC3
WING	0.019	0.672	-0.739
TAIL	-0.111	0.736	0.666
WT	0.993	0.069	0.089
% Variance ¹	99.8%	0.1%	0.1%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 12. Loadings of Skull Complex Variables on Principal Components.

Skull Character	PC1	PC2	PC3
PRL	0.161	0.853	0.493
NASW	0.420	-0.510	0.748
INORW	0.884	0.092	-0.438
SKW	-0.011	0.033	-0.018
MANL	0.122	-0.038	-0.591
% Variance ¹	74.3%	14.1%	10.1%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 13. Loadings of Girdle Complex Variables on Principal Components.

Girdle Character	PC1	PC2	PC3
CORL	0.448	-0.228	0.152
STERL	0.566	-0.226	0.378
KEED	0.668	0.235	-0.603
SYNW	0.153	-0.037	0.609
SYNMW	0.086	0.916	0.311
% Variance ¹	86.2%	5.8%	5.0%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 14. Loadings of Leg Complex Variables on Principal Components.

Leg Character	PC1	PC2	PC3
FEDW	0.572	0.415	-0.706
FEL	0.187	-0.358	0.451
TARL	0.065	0.835	0.545
% Variance ¹	78.5%	13.1%	8.4%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 15. Loadings of Wing Complex Variables on Principal Components.

Wing Character	PC1	PC2	PC3
HTRL	0.667	-0.655	-0.347
HDEW	0.297	-0.155	0.785
HUML	0.535	0.431	0.315
ULNL	0.422	0.599	-0.404
% Variance ¹	85.7%	7.1%	4.6%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 16. Loadings of All Skeletal Variables on Principal Components.

Skeletal Character	PC1	PC2	PC3
PRL	0.101	-0.164	0.198
BDEP	0.218	-0.121	0.866
NASW	0.141	0.046	-0.217
INORW	0.352	0.287	-0.128
SKW	0.000	-0.023	-.024
SKL	0.050	-0.068	0.071
MANL	0.057	0.043	-0.010
MAND	0.245	0.154	0.012
CORL	0.137	0.212	-0.038
SCAPW	0.243	0.243	0.182
STERL	0.190	0.222	-0.053
KEEL	0.222	0.291	-0.047
KEED	0.220	0.257	-0.084
SYNW	0.052	0.038	-0.039
SYNMW	0.033	0.051	0.068
FEDW	0.103	0.089	0.049
FEL	0.136	0.114	0.036
TIBL	0.063	0.086	0.061
TARL	0.025	-0.045	0.076
TARD	0.664	-0.659	-0.255
HTRL	0.119	0.173	0.012
HDEW	0.056	0.056	0.007
HUML	0.103	0.123	0.051
ULNL	0.085	0.086	0.043
CARPL	0.070	0.103	0.047
% Variance ¹	62.1%	15.2%	9.3%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 17. Discriminant Function Coefficients for External Complex Variables.

External Complex	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
CONSTANT	-2538.94	-2504.46	
WING	-19.27	-24.78	-1.4751
TAIL	77.84	75.76	4.4952
WT	11.30	14.53	2.6321

Table 18. Discriminant Function Coefficients for Skull Complex Variables.

	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
Skull Complex			
CONSTANT	-181253.12	-180505.97	
PRL	2348.40	2345.20	-0.246
NASW	-3684.26	-3650.82	-0.402
INORW	-1477.67	-1404.29	2.252
SKW	1387.81	1157.05	-0.689
SKL	8718.64	9300.87	-0.036
MANL	33933.31	33854.54	0.700
MAND	69160.20	68557.84	0.797

Table 19. Discriminant Function Coefficients for Girdle Complex Variables.

	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
Girdle Complex			
CONSTANT	-34770.79	-34048.58	
CORL	-4033.54	-4098.32	0.6460
SCAPW	19331.29	19246.31	0.0152
STERL	1502.58	1513.39	2.9220
KEEL	16000.25	15631.71	-1.1327
KEED	-16924.86	-16829.27	0.6905
SYNW	653.84	582.91	-0.5125
SYNMW	8180.79	8371.19	0.0481

Table 20. Discriminant Function Coefficients for Leg Complex Variables.

Leg Complex	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
CONSTANT	-55135.92	-54145.78	
FEDW	2794.46	2769.52	11.58
FEL	-7955.41	-8028.50	12.83
TIBL	15303.58	15057.01	-1.937
TARL	21403.31	21339.84	-0.042

Table 21. Discriminant Function Coefficients for Wing Complex Variables.

Wing Complex	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
CONSTANT	-35027.90	-34364.73	
HTRL	-808.25	-822.36	1.2098
HDEW	-2686.14	-2836.60	-0.4742
HUML	-837.10	-682.69	1.0701
ULNL	9580.36	9430.28	0.5014
CARPL	17661.86	17573.81	-0.3176

Table 22. Discriminant Function Coefficients for all Skeletal Complex Variables.

Morphological Character	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
CONSTANT	-1373783.44	-1357045.49	
PRL	-10125.26	-9965.33	2.565
NASW	-48867.37	-48602.21	2.277
INORW	13167.56	13352.92	5.275
SKW	39185.53	37894.04	1.407
SKL	218783.19	220346.52	-2.368
MANL	-4230.33	-3164.60	0.512
MAND	388734.26	385005.97	-3.850
CORL	-101720.05	-101380.98	-7.494
SCAPW	4359.59	5496.20	-3.288
STERL	17650.24	18438.06	10.572
KEEL	355347.00	350917.06	-13.530
KEED	-401779.39	-398005.10	8.459
SYNW	52382.03	52079.51	-1.012
SYNMW	-184526.42	-183717.79	1.412
FEDW	163706.34	162050.75	-0.749
FEL	71538.35	72682.81	-1.034
TIBL	212731.67	211070.44	8.115
TARL	198852.08	196969.03	-2.874
HTRL	-29641.96	-29313.60	6.155
HDEW	9512.17	7539.23	-3.841
HUML	-211835.53	-209604.33	12.655
ULNL	261223.42	257405.09	-4.290
CARPL	-225336.84	-222866.29	-1.926

Table 23. Results of STEPWISE DFA for Morphological Characters.

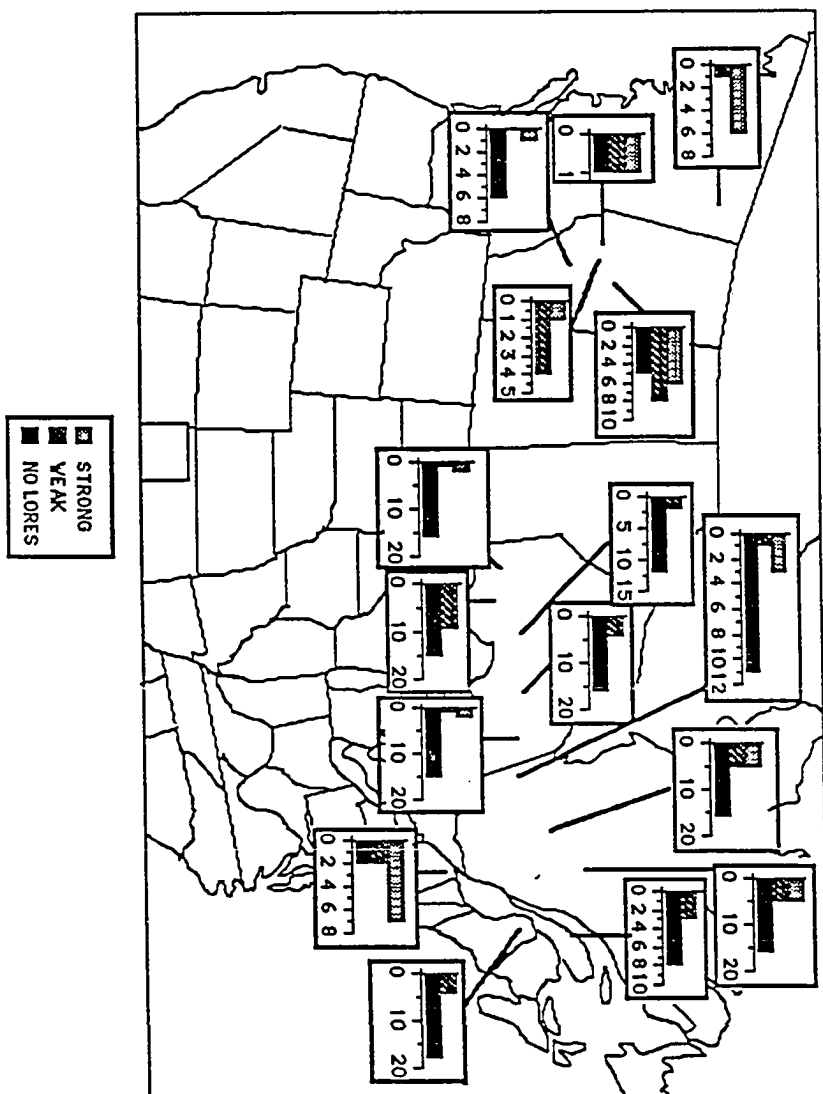
VARIABLE	STEP	F STATISTIC	PROB > F *	WILKS' LAMBDA**	PROB > LAMBDA***
INORW	1	141.467	0.0001	0.160	0.0001
FEL	2	20.992	0.0001	0.088	0.0001
CORL	3	5.486	0.0274	0.072	0.0001
SKW	4	8.093	0.0089	0.054	0.0001
SCAPW	5	2.359	0.1380	0.049	0.0001
HTRL	6	3.828	0.0632	0.042	0.0001

* - probability level after the variable has been entered.

** - likelihood ratio statistic for testing whether the taxon means are significantly different.

*** - probability level based on the F approximation to Wilk's Lambda.

Figure 28. Geographic distribution of *A. philadelphica* specimens with dark lores.



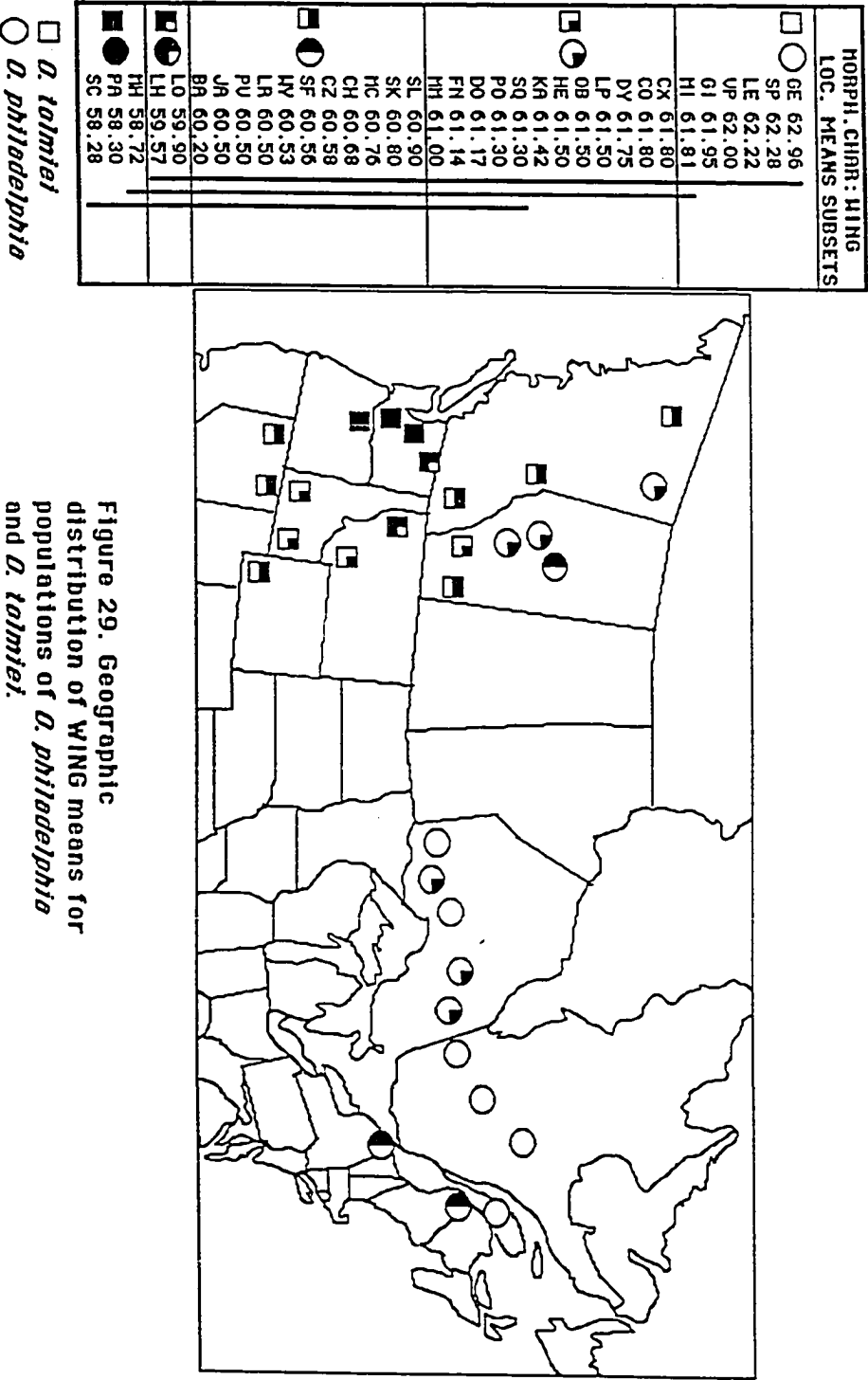
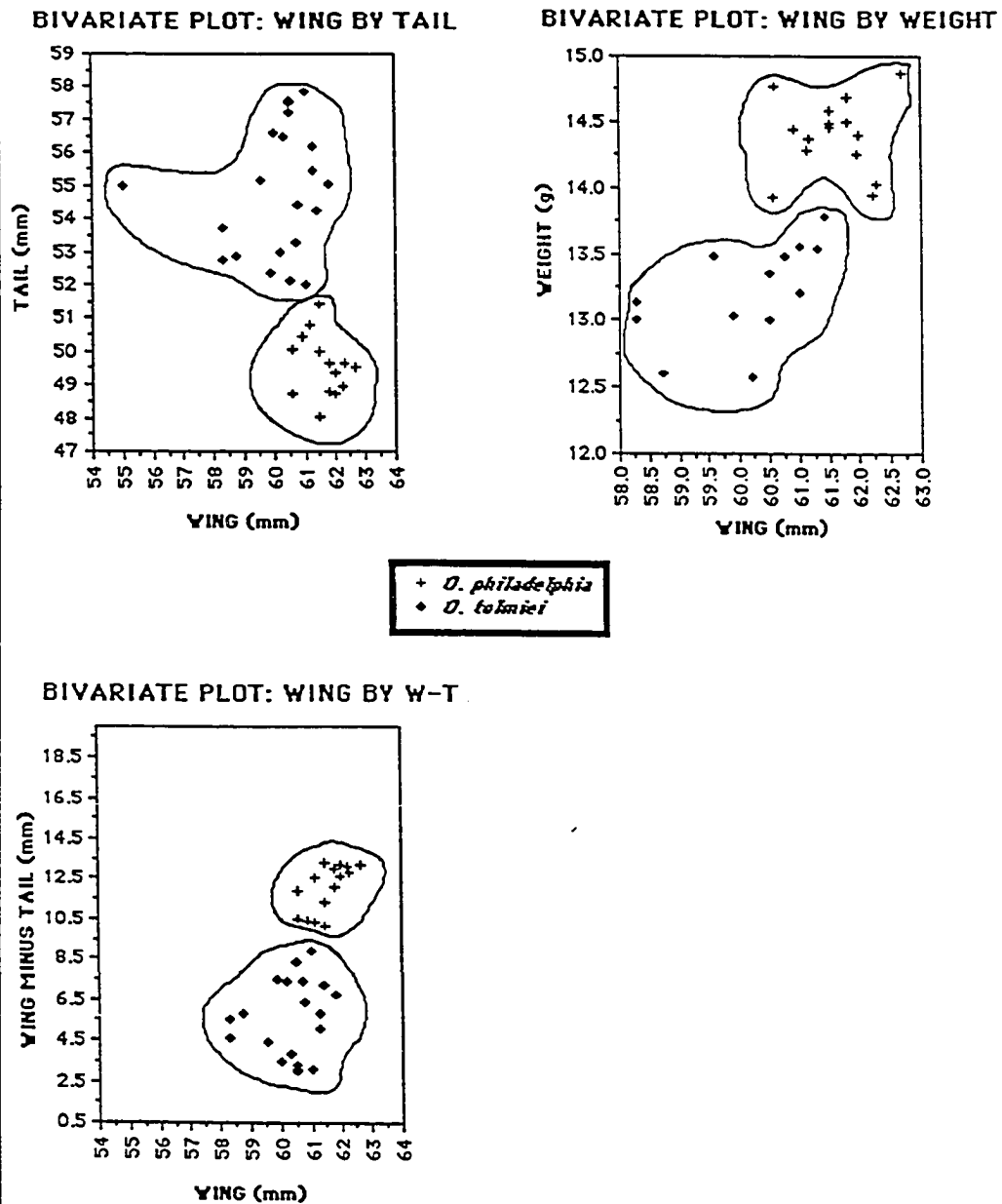
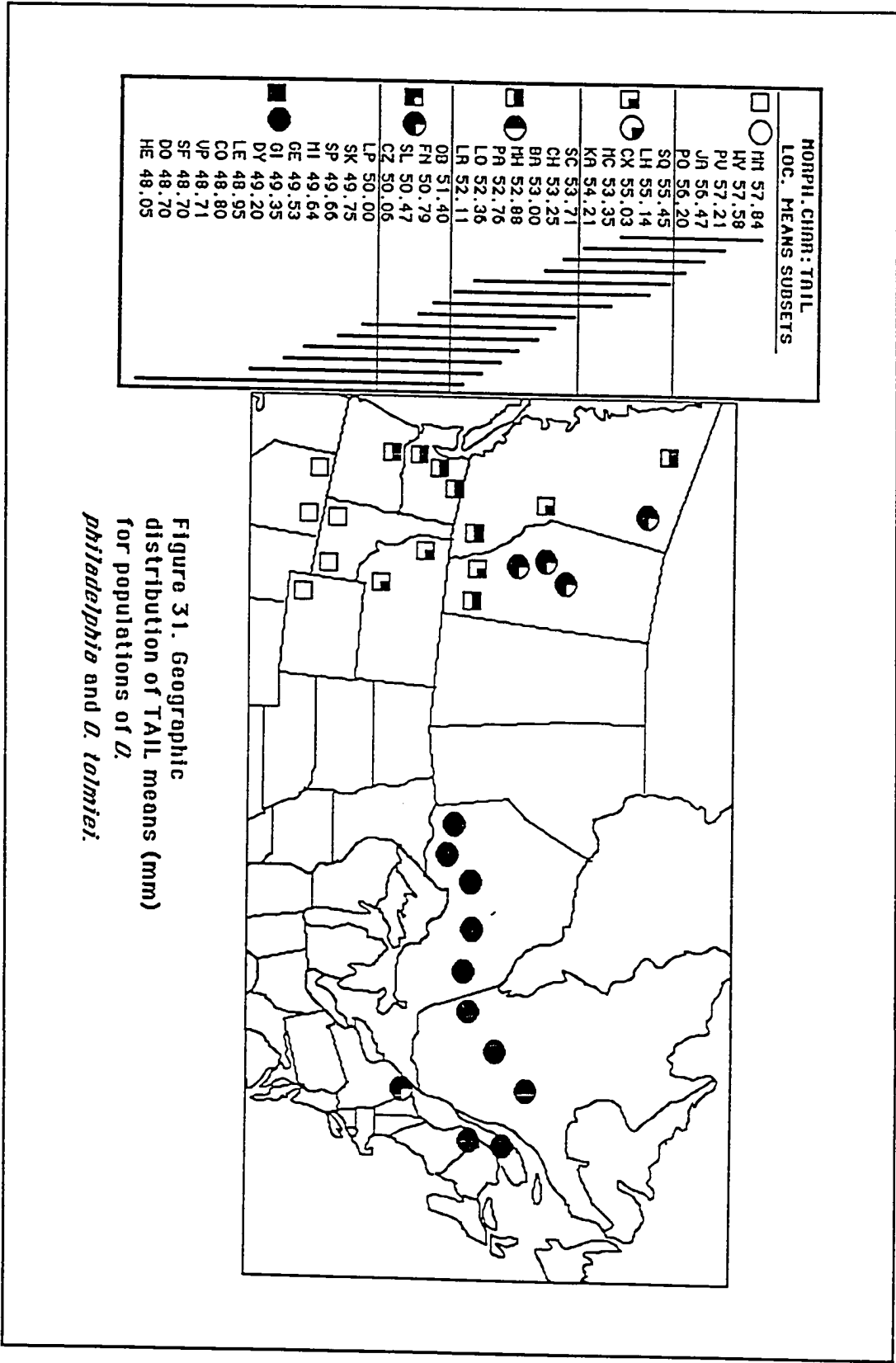
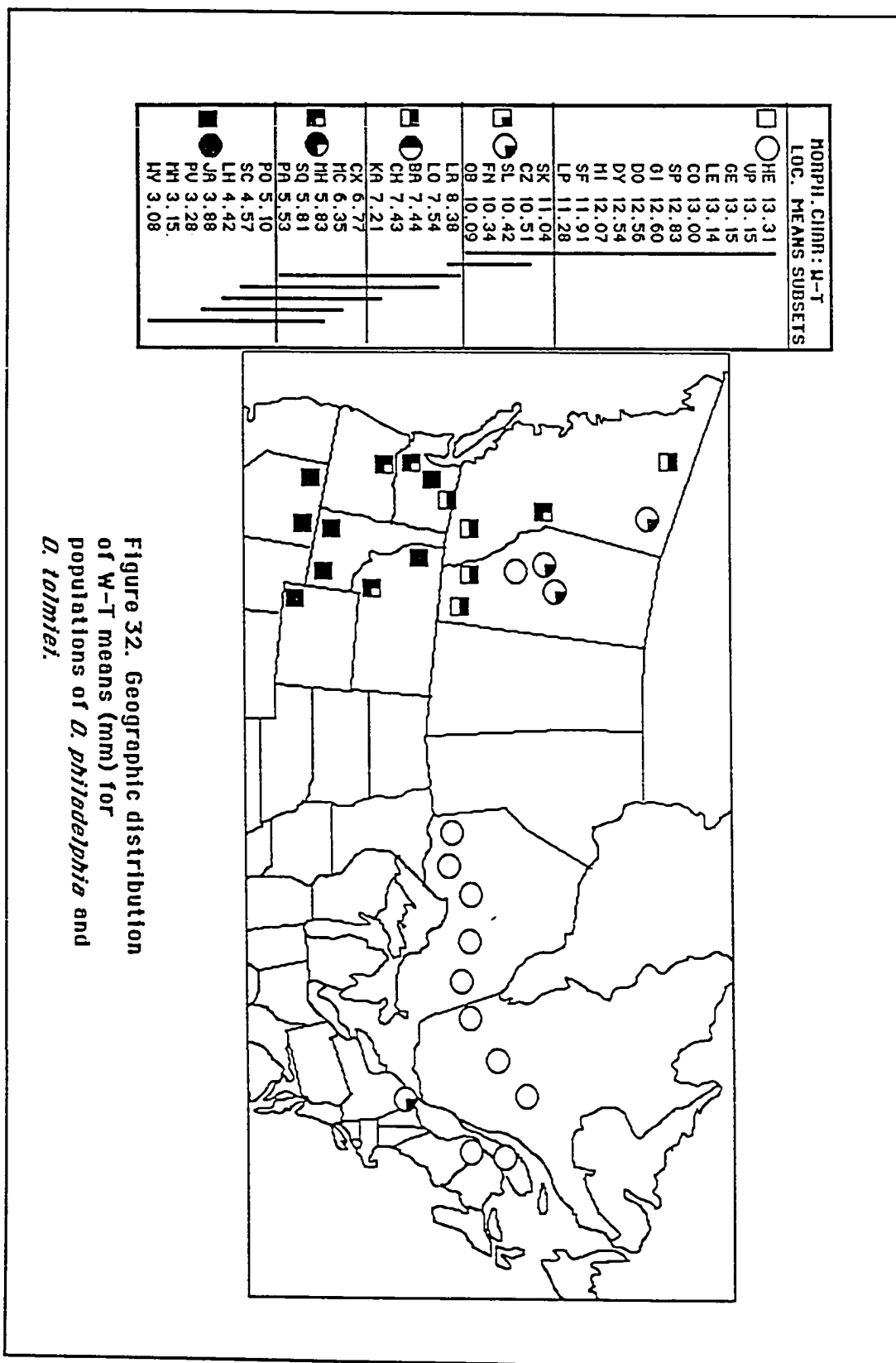


Figure 30. Bivariate plots of population means: WING, TAIL, W-T (mm), WEIGHT.







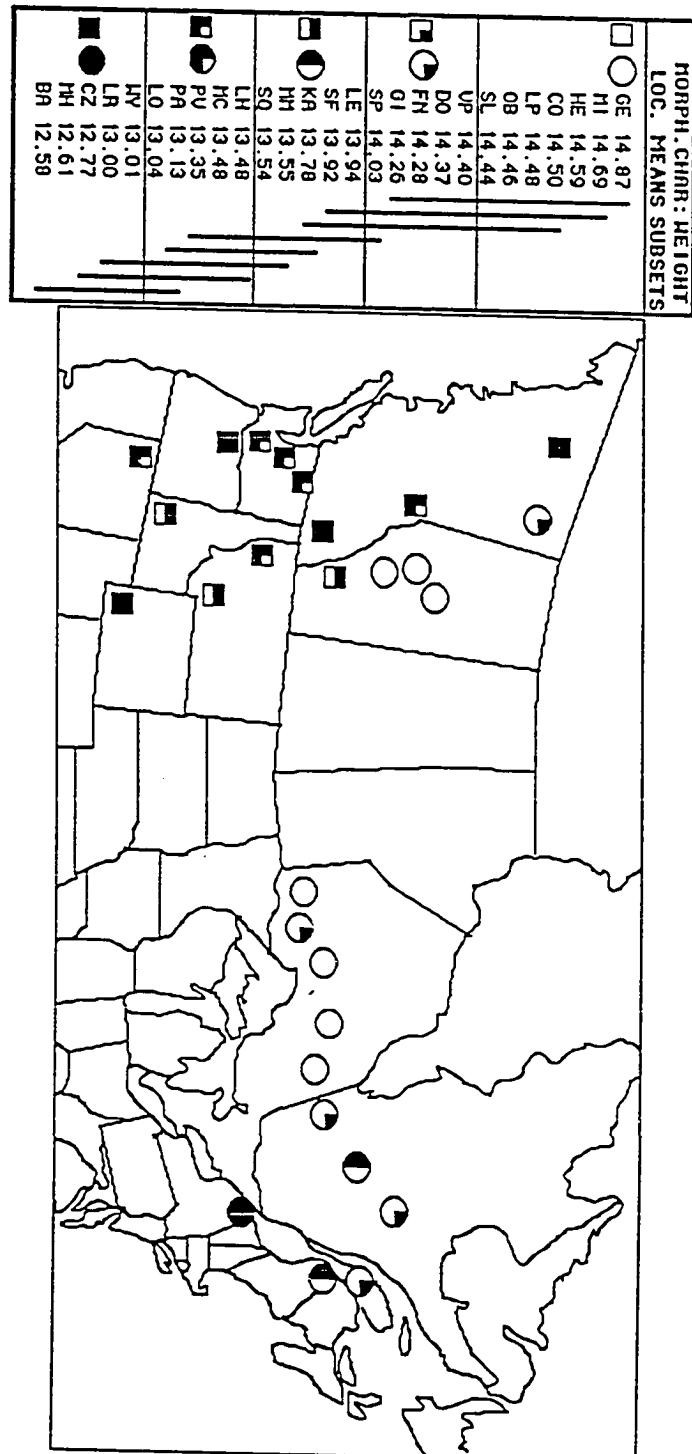
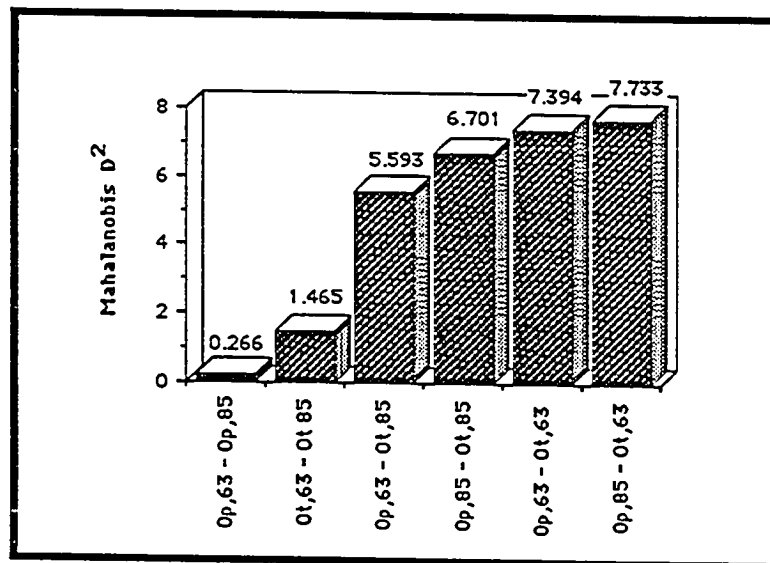


Figure 34. Geographic distribution of WEIGHT means (g) for populations of *D. philadelphia* and *D. tolmiei*.

Figure 35. Mahalanobis D² between 1963 and 1985 samples of *O. philadelphia* and *O. tolmiei* based on external measurements.



O. philadelphia - Op
O. tolmiei - Ot
 1963 - 63
 1985 - 85

MORPH. CHNR: PRL	
LOC. MEANS SUBSETS	
□	HE 14.18
○	UP 14.02
	CZ 13.99
	DO 13.85
	GE 13.84
	LE 13.82
	CO 13.81
	O1 13.80
	SP 13.80
◐	PO 13.77
	M1 13.74
	SF 13.72
	JA 13.68
	MH 13.67
	SQ 13.64
	HY 13.63
	SC 13.62
	PU 13.52
	LO 13.49
◑	MH 13.39
◐	PH 13.38
	LH 13.37
	BR 13.34
	SL 13.21
	LR 12.87
	LP 12.80
■	MC 12.79
●	FN 12.74
	KA 12.57
	OB 12.56

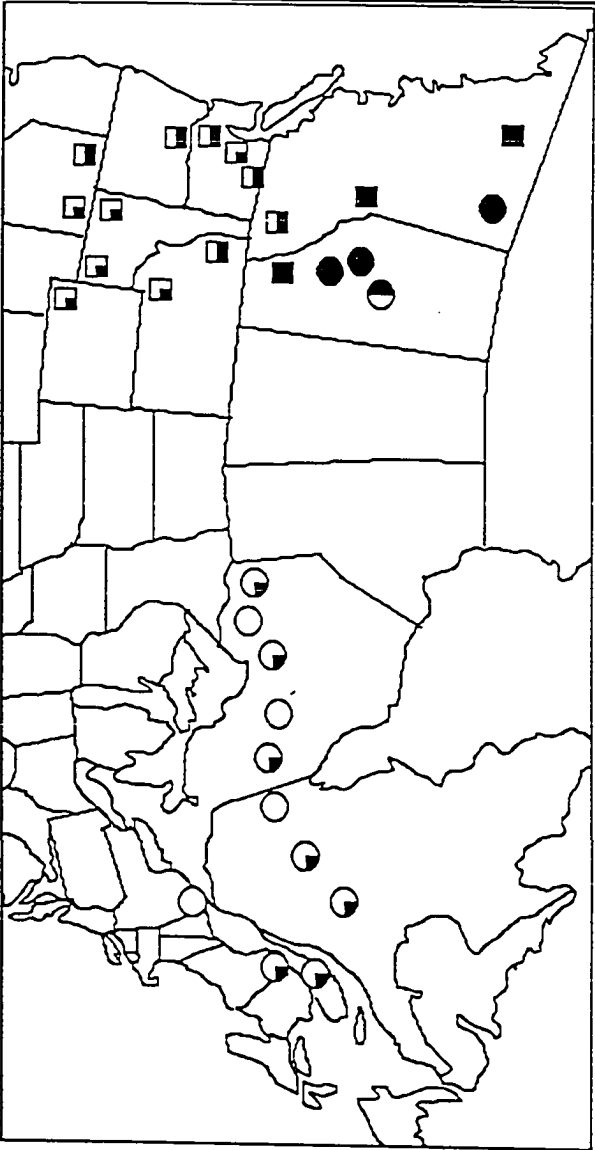


Figure 36. Geographic distribution of PRL means (mm) for populations of *D. philadelphia* and *D. tolmiei*.

Figure 37. Bivariate plots of population means: PRL, BDEP, NASW, INORW, SKL, SKW, MANL, MAND.

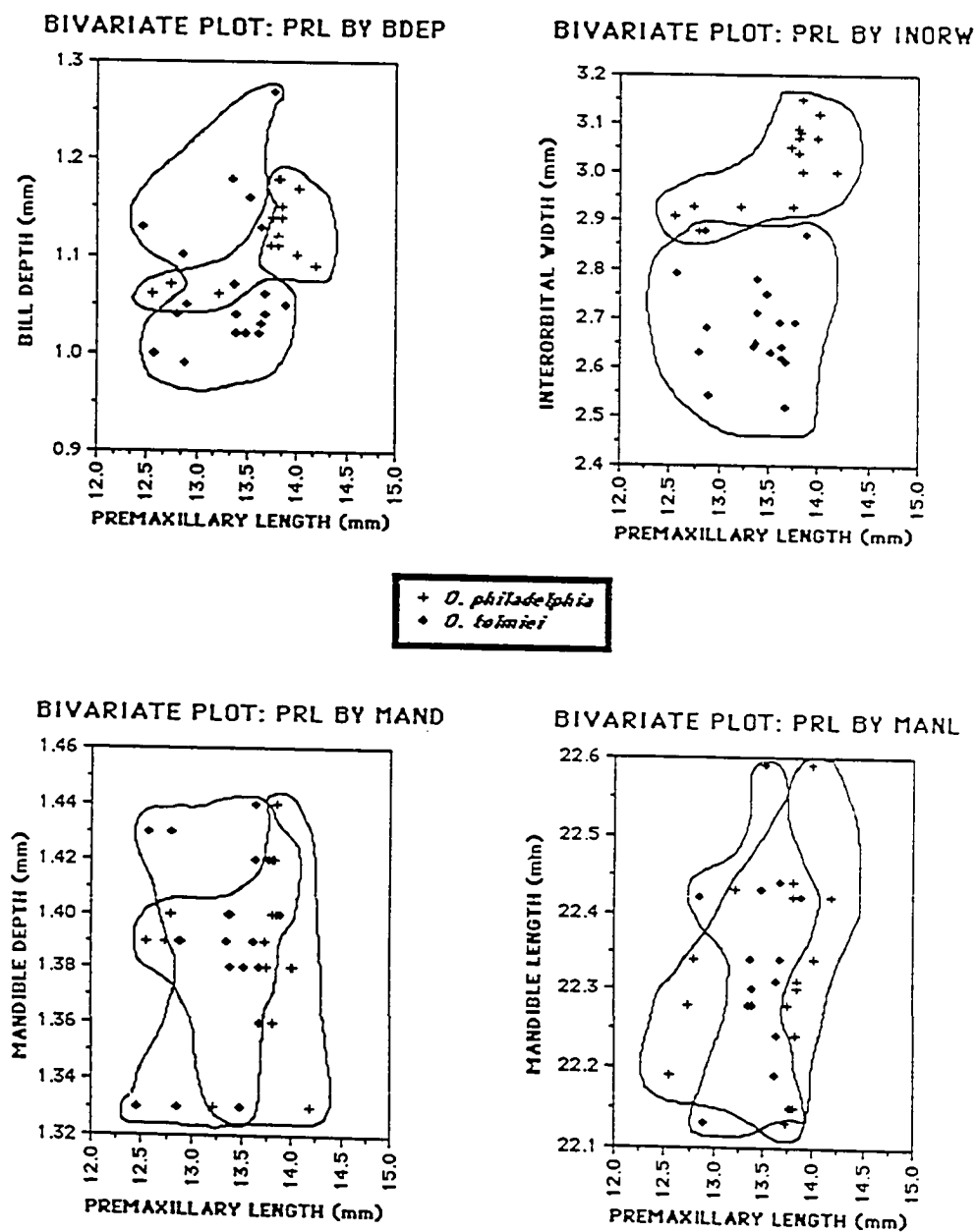
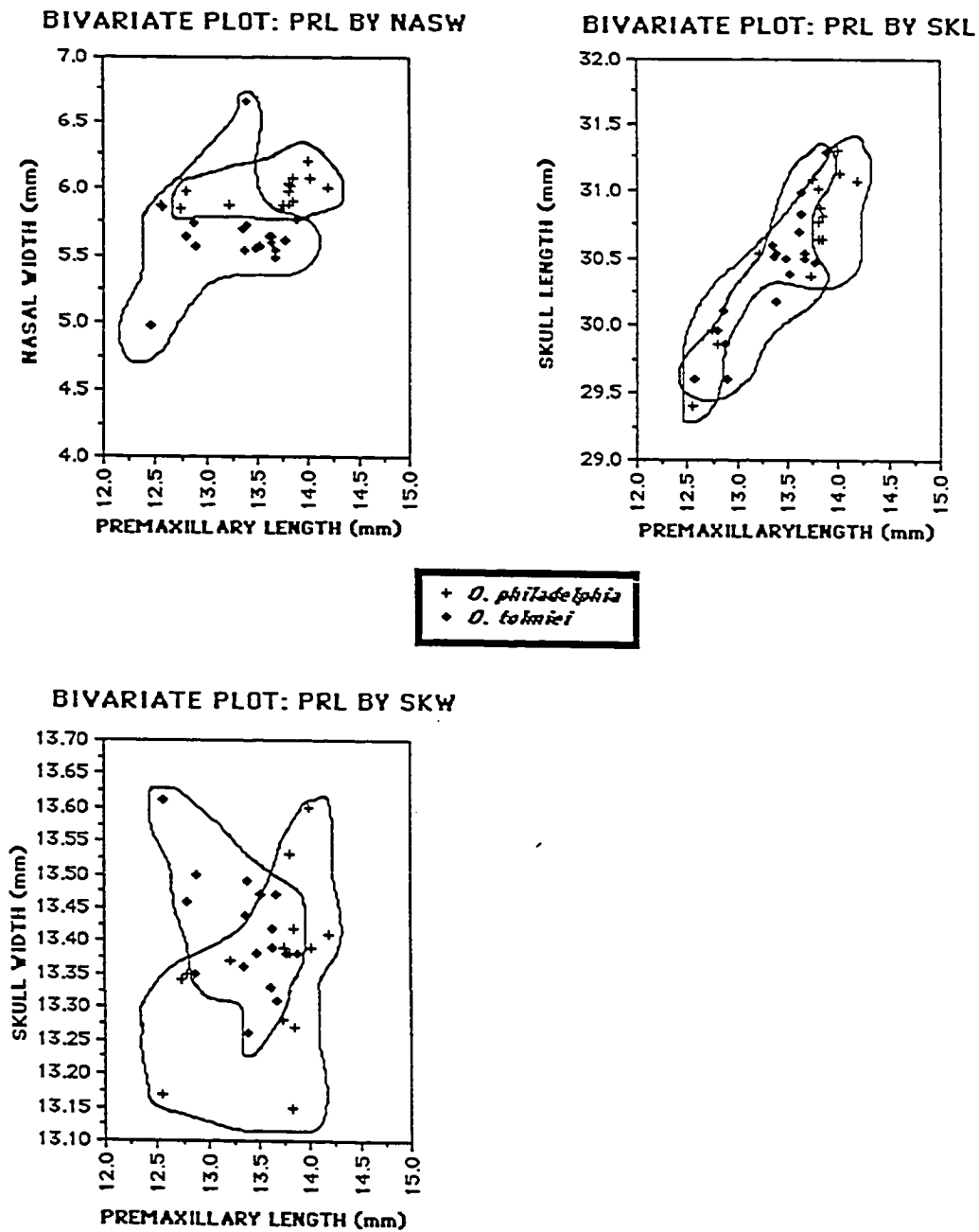


Figure 37. Bivariate plots of population means: PRL, BDEP, NASW, INORW, SKL, SKW, MANL, MAND (cont'd).



MORPH. CLIM.: BDEP		LOC. MEANS SUBSETS
LOC.	MEANS SUBSETS	
LE 1.18		
GI 1.18		
BA 1.18		
UP 1.17		
PU 1.16		
GE 1.15		
HI 1.14		
DO 1.14		
SQ 1.13		
CO 1.12		
PO 1.12		
SP 1.11		
SF 1.11		
CZ 1.10		
HE 1.09		
FN 1.07		
LH 1.07		
JN 1.06		
SL 1.06		
OB 1.06		
HH 1.04		
MC 1.04		
HC 1.04		
LP 1.04		
HY 1.03		
PR 1.02		
LO 1.02		
SC 1.02		
KA 1.00		
LR 0.99		

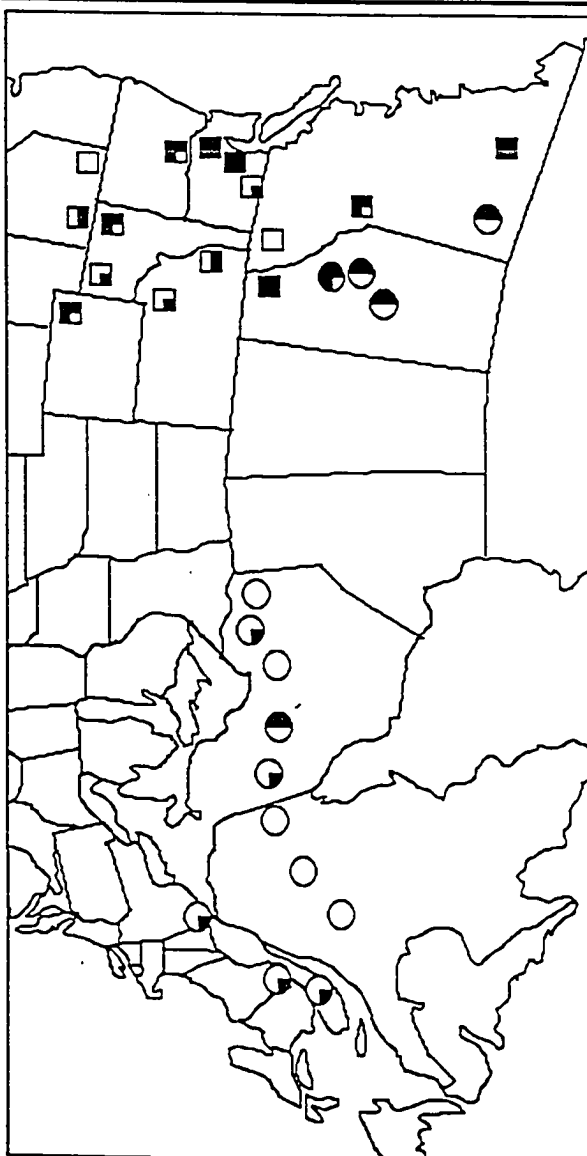


Figure 38. Geographic distribution of BDEP means (mm) for populations of *Q. philadelphia* and *Q. tolmiei*.

HORPH. CHART: NASW	
LOC. MEANS SUBSETS	
□ ○	CZ 6.20
□ ○	UP 6.07
□ ○	GE 6.06
□ ○	SP 6.03
□ ○	LE 6.01
□ ○	HE 6.00
□ ○	OI 5.96
□ ○	LP 5.96
□ ○	DO 5.90
□ ○	CO 5.87
□ ○	MI 5.87
□ ○	SL 5.86
□ ○	OS 5.86
□ ○	KA 5.85
□ ○	FN 5.84
□ ○	SF 5.84
□ ○	LR 5.73
□ ○	PA 5.72
□ ○	BA 5.69
□ ○	HI 5.65
□ ○	SQ 5.64
□ ○	SC 5.64
□ ○	HC 5.63
□ ○	PO 5.61
□ ○	HY 5.60
□ ○	PU 5.56
□ ○	LO 5.55
□ ○	LH 5.54
□ ○	JR 5.54
□ ○	HI 5.48

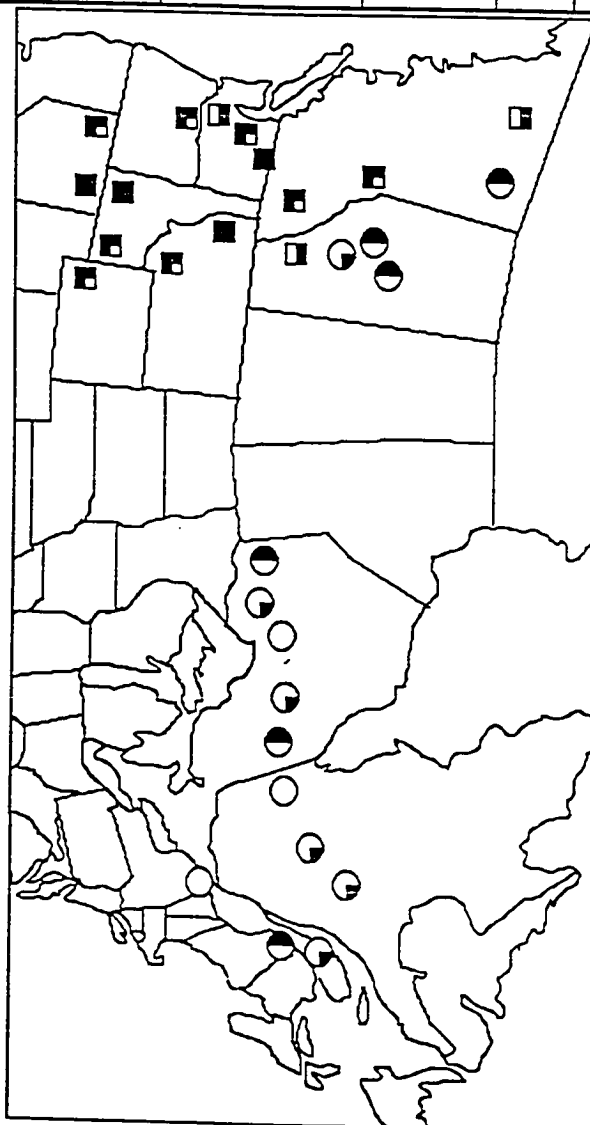


Figure 39. Geographic distribution of NASW means (mm) for populations of *O. philadelphia* and *O. talpiae*.

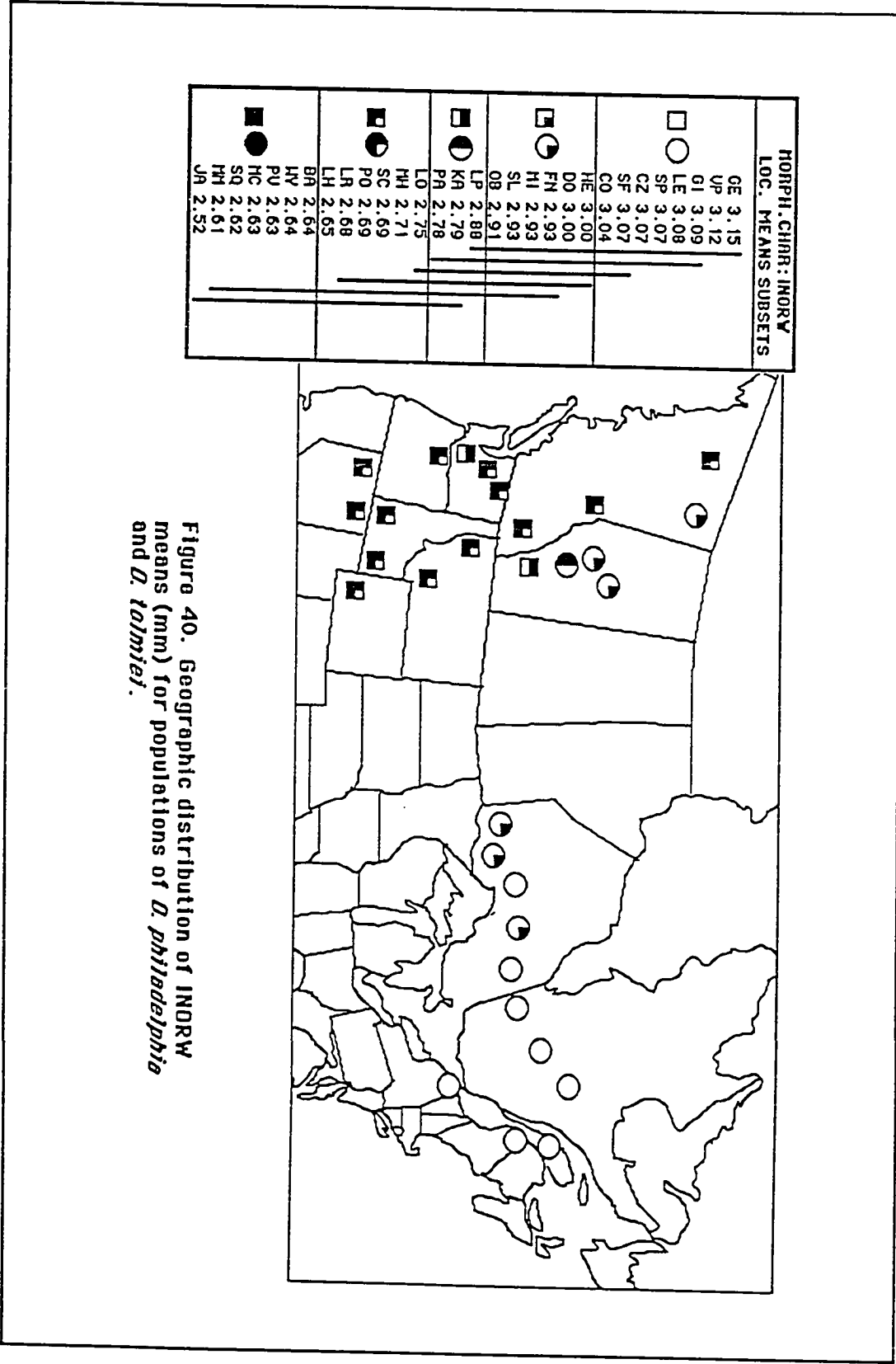


Figure 40. Geographic distribution of INDRY means (mm) for populations of *A. philadelphia* and *A. tolmiei*.

HONPHI, CHNH: SKL	
LOC. MEANS SUBSETS	
□	CZ 31.29
○	UP 31.13
●	HI 31.08
●	HE 31.06
●	GI 31.01
●	SQ 30.98
●	LE 30.87
●	HY 30.82
●	GE 30.81
●	CO 30.77
●	SC 30.70
●	DO 30.64
●	SP 30.63
●	BA 30.60
●	JA 30.54
●	PA 30.54
●	SL 30.53
●	LH 30.51
●	LO 30.50
●	MH 30.49
●	PO 30.47
●	PV 30.38
●	SF 30.37
●	HH 30.18
●	FN 29.96
●	MC 29.96
●	LR 29.86
●	LP 29.86
●	KA 29.61
●	OB 29.40

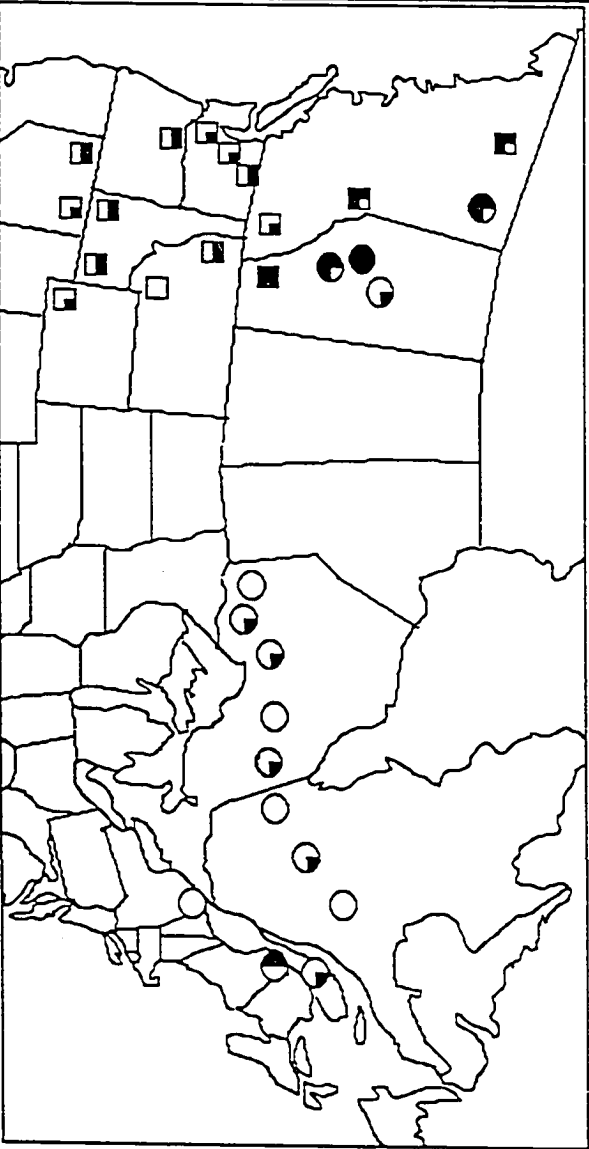


Figure 41. Geographic distribution of SKL means (mm) for populations of *D. philadelphia* and *D. tolmiei*.

MORPH. CLIM.: MAND		LOC. MEANS SUBSETS	
□	○	MI 1.57	
		CZ 1.56	
		SP 1.54	
		UP 1.53	
		GI 1.52	
		SF 1.51	
		DO 1.51	
		GE 1.51	
▣	●	LE 1.50	
		FN 1.49	
		SL 1.49	
		HE 1.48	
		CO 1.48	
		SO 1.44	
		OB 1.43	
		HC 1.43	
▣	●	KN 1.43	
		LP 1.43	
		HY 1.42	
		PO 1.42	
		LH 1.40	
		PA 1.40	
		SC 1.39	
▣	●	LR 1.39	
		BR 1.39	
		PU 1.38	
		MH 1.38	
■	●	JA 1.36	
		LO 1.33	

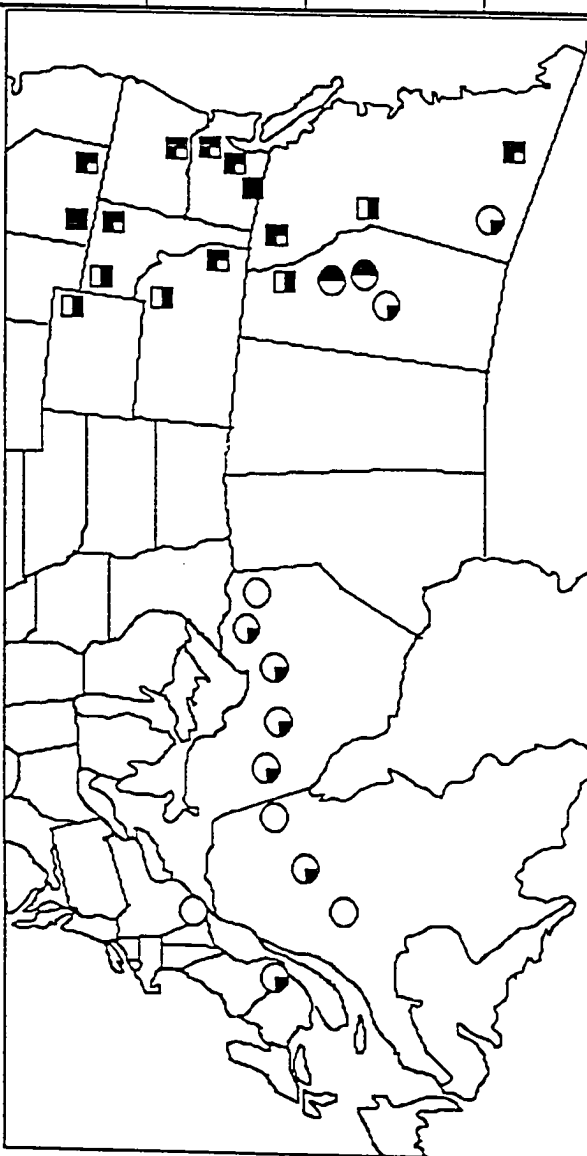


Figure 42. Geographic distribution of MAND means (mm) for populations of *Q. philadelphica* and *Q. tolmiei*.

MORPH. CHAR. : CORL	
LOC. MEANS SUBSETS	
□ ○	CZ 14.91
	FN 14.77
	GI 14.77
	OB 14.65
	SL 14.65
	HE 14.62
	GE 14.62
	LP 14.57
	SP 14.56
	LE 14.56
□ ○	UP 14.51
	CO 14.51
	SF 14.50
	HI 14.42
	DO 14.42
	KA 14.37
□ ○	HC 14.18
	LH 14.13
	LR 13.99
	SQ 13.99
	BA 13.91
	PO 13.88
□ ○	PV 13.82
	SC 13.80
	JN 13.78
	HY 13.77
	HH 13.72
■ ●	LO 13.61
	PA 13.57
	HH 13.40

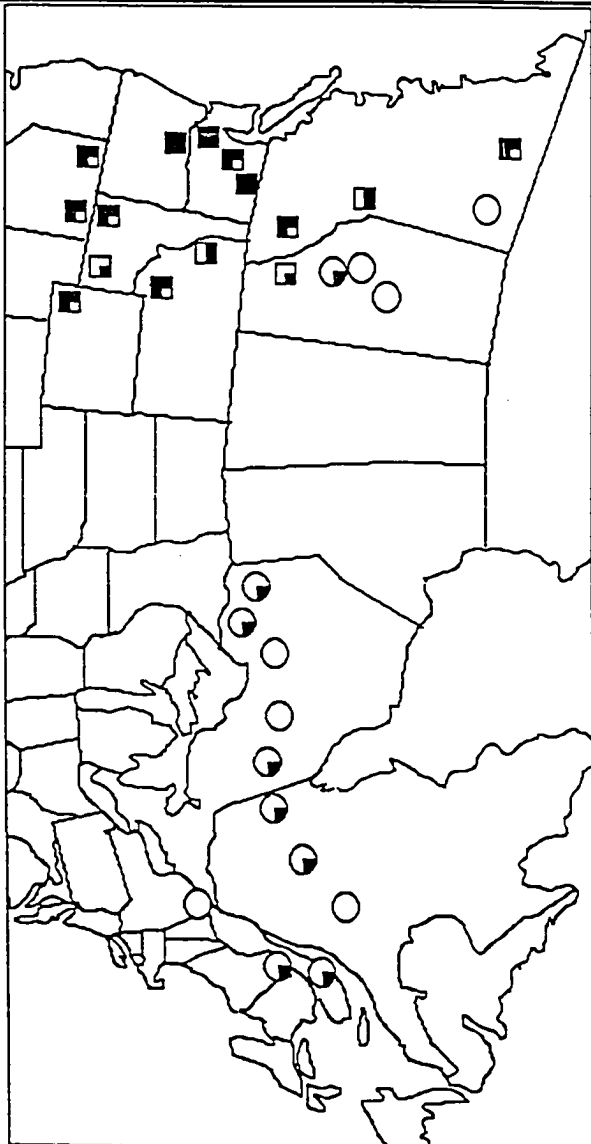


Figure 43. Geographic distribution of CORL means (mm) for populations of *Q. philadelphia* and *Q. tolmiei*.

Figure 44. Bivariate plots of population means: CORL, SCAPW, STERL, KEEL, KEED, SYNW, SYNMW.

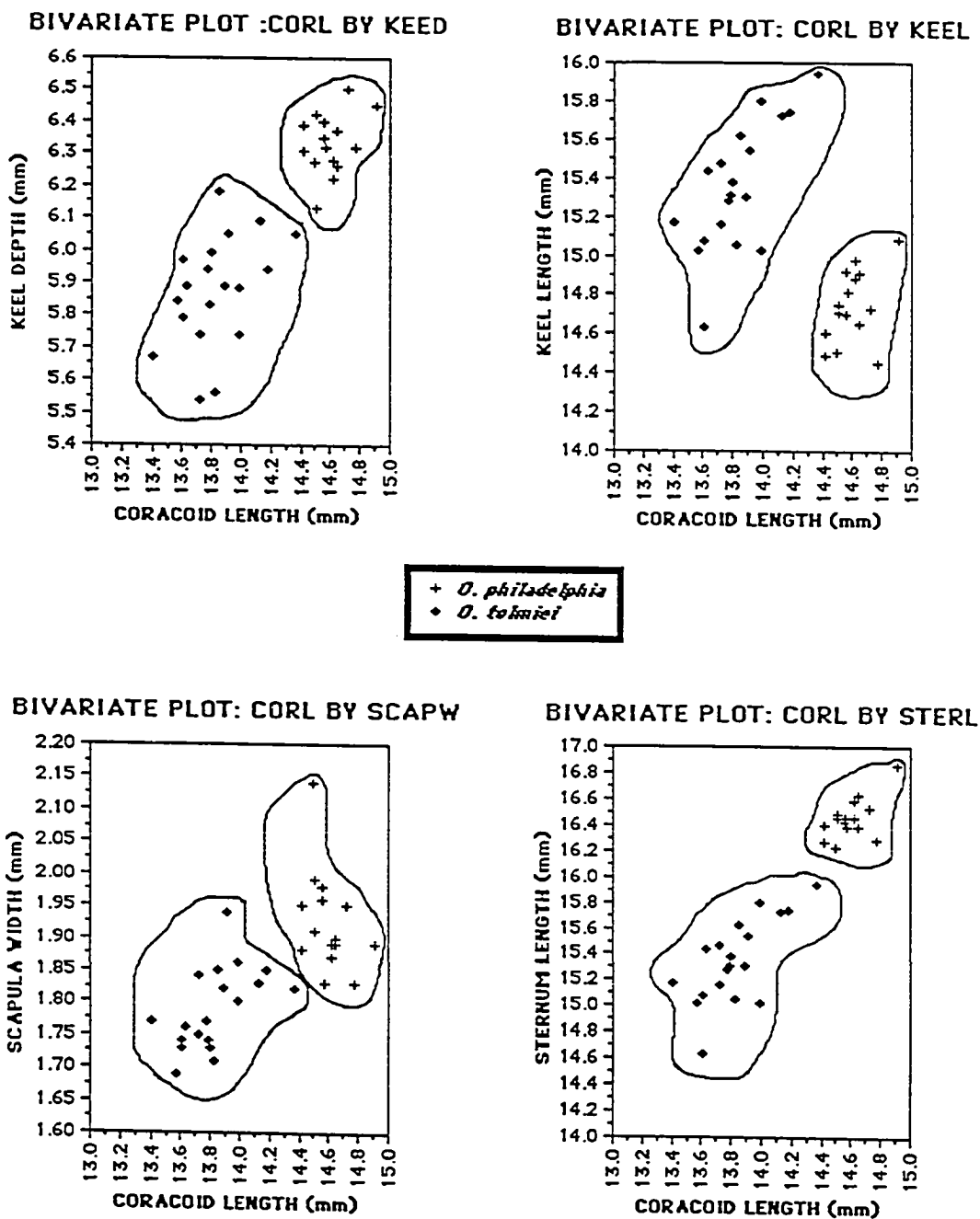
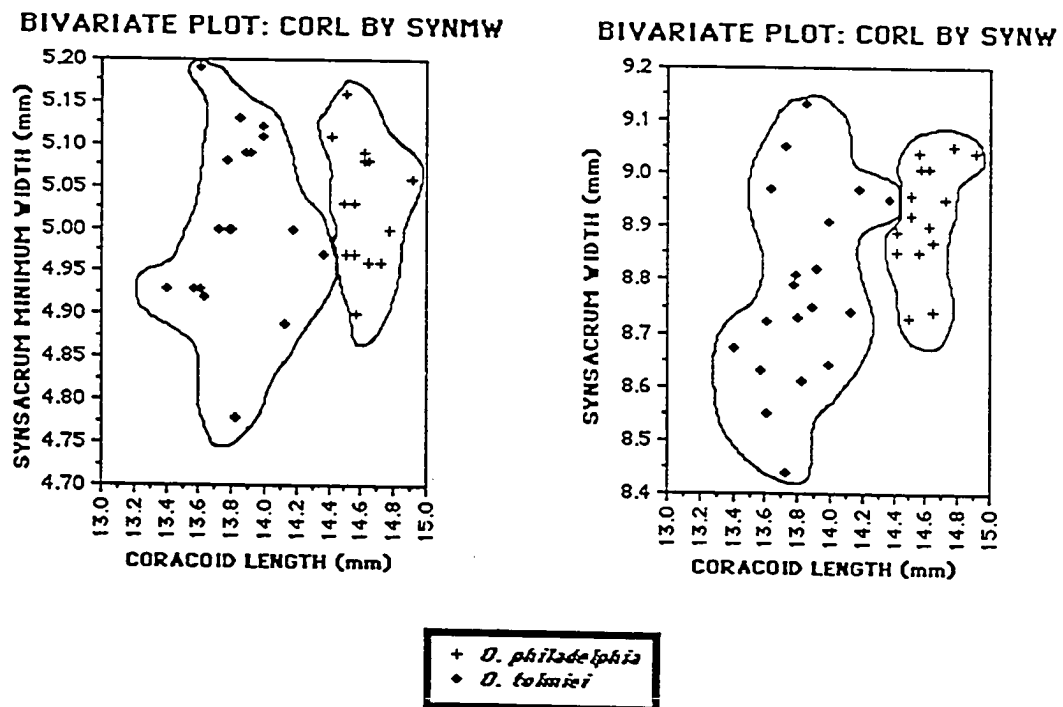


Figure 44. Bivariate plots of population means: CORL, SCAPW, STERL, KEEL, KEED, SYNW, SYNMW (cont'd).



MORPH. CHIM: SCAPW		LOC. MEANS SUBSETS	
□	SF 2.14	○	UP 1.99
◐	LE 1.98	◑	LE 1.98
◒	SP 1.96	◓	SP 1.96
◔	DO 1.95	◕	BA 1.94
◖	BA 1.94	◗	OI 1.94
◘	CO 1.91	◙	CO 1.91
◚	SL 1.90	◛	SL 1.89
◜	GE 1.89	◝	CZ 1.89
◞	HI 1.88	◟	HE 1.87
◠	SQ 1.86	◡	MC 1.85
◢	LH 1.83	◣	LP 1.83
◤	FN 1.83	◥	KA 1.82
◦	PO 1.82	◧	LR 1.80
◨	LV 1.77	◩	MH 1.77
◪	JH 1.75	◫	JA 1.74
◬	SC 1.73	◭	LO 1.71
◮	PV 1.71	◯	PR 1.69

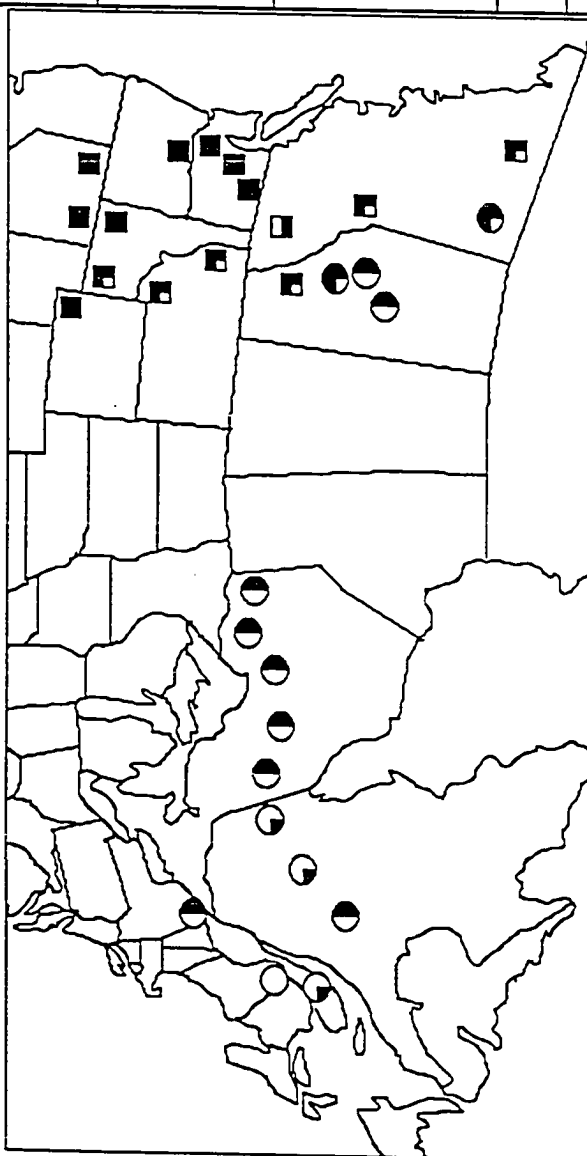


Figure 45. Geographic distribution of SCAPW means (mm) for populations of *D. philadelphia* and *D. tolmiei*.

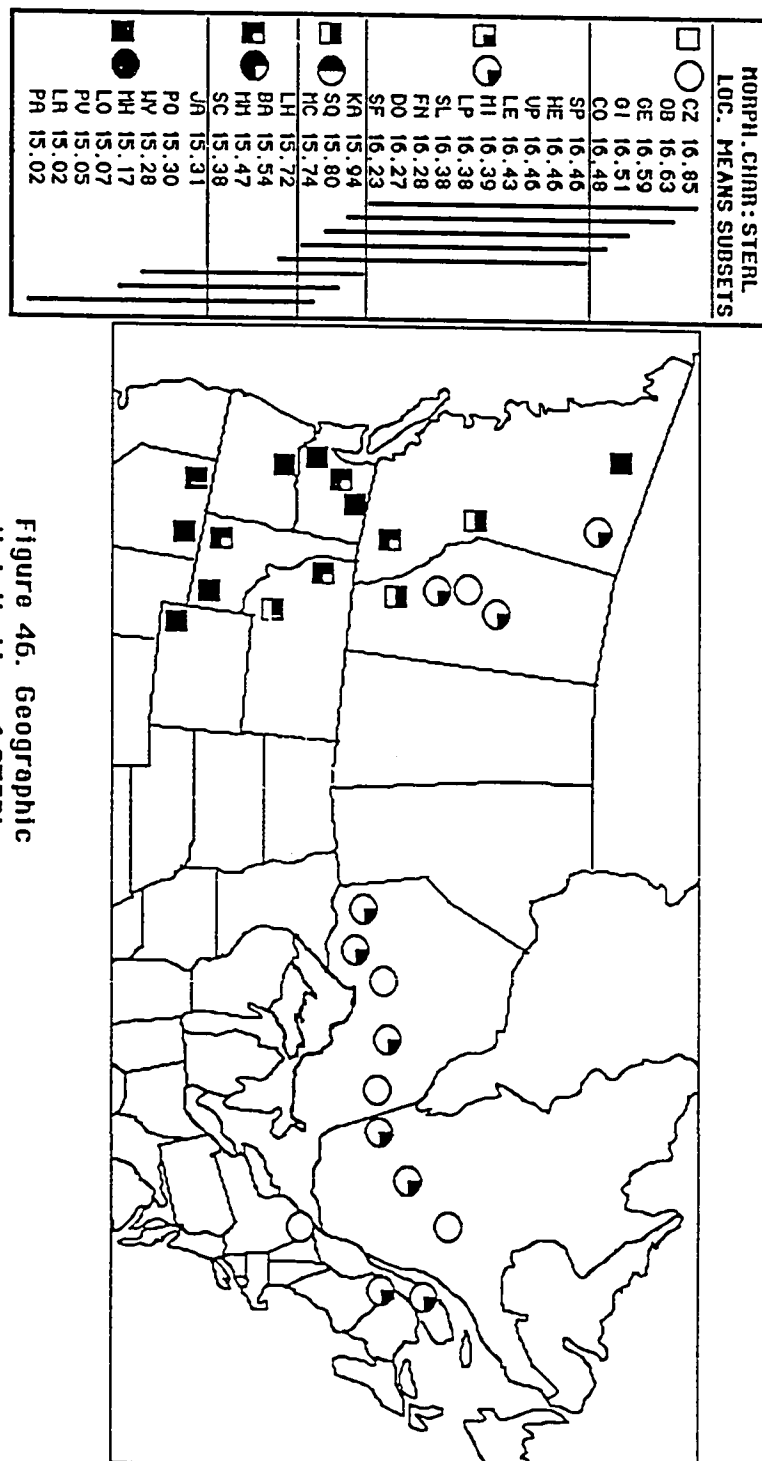


Figure 46. Geographic distribution of STERL means (mm) for populations of *Q. philadelphica* and *Q. tolmiei*.

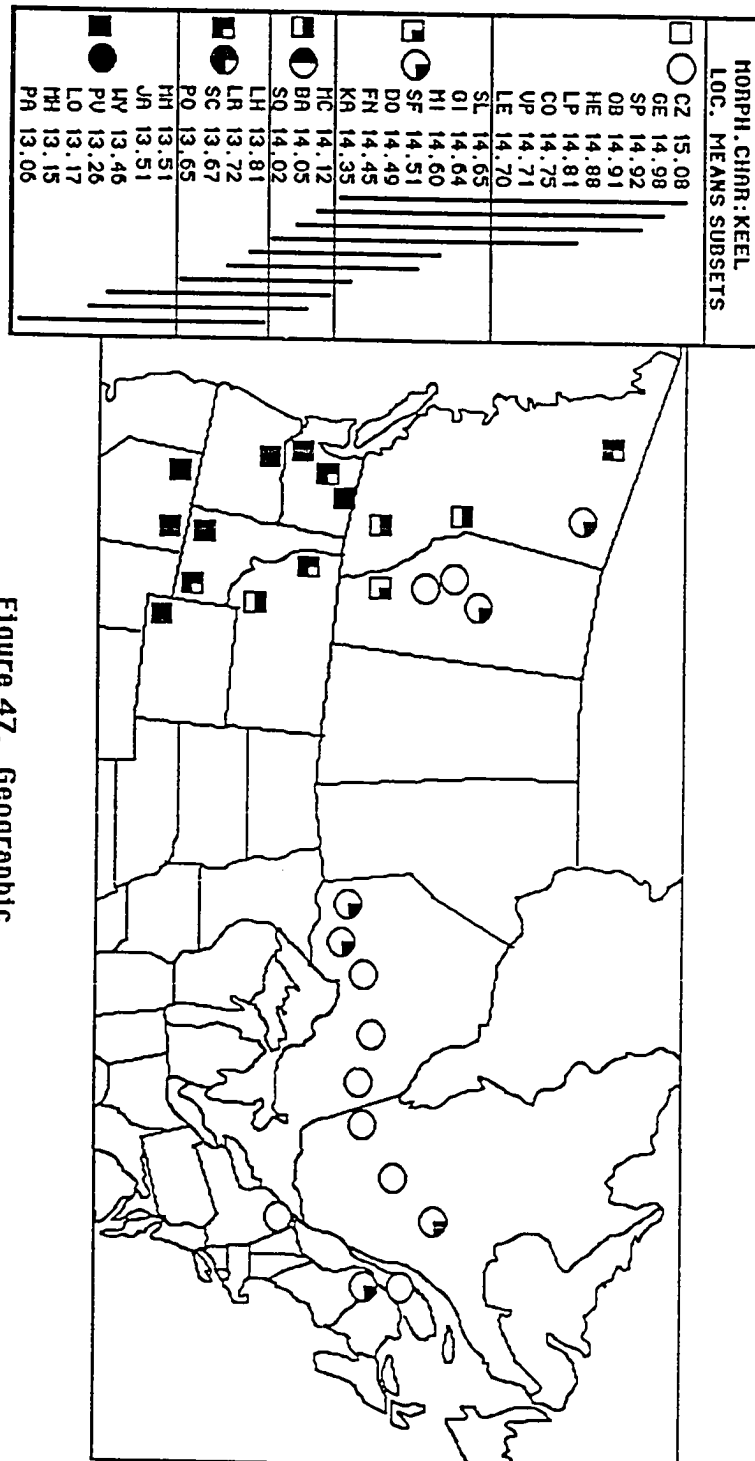


Figure 47. Geographic distribution of KEEL means (mm) for populations of *Q. philadelphica* and *Q. tolmiei*.

MORPH. CHAR. : KEED	
LOC. MEANS SUBSETS	
□	01 6.51
○	CZ 6.45
	UP 6.42
	SP 6.40
	H1 6.39
	OB 6.37
	LE 6.35
	LP 6.32
	FN 6.32
	DO 6.31
	HE 6.28
	SF 6.27
◐	SL 6.26
	GE 6.22
	CO 6.13
	LH 6.09
	KA 6.05
	BA 6.05
◑	SC 5.99
	UY 5.94
	MC 5.94
	PO 5.89
◒	LR 5.88
	PA 5.84
	JH 5.83
	LO 5.79
	NH 5.74
◓	SQ 5.74
●	NH 5.67
■	PV 5.56

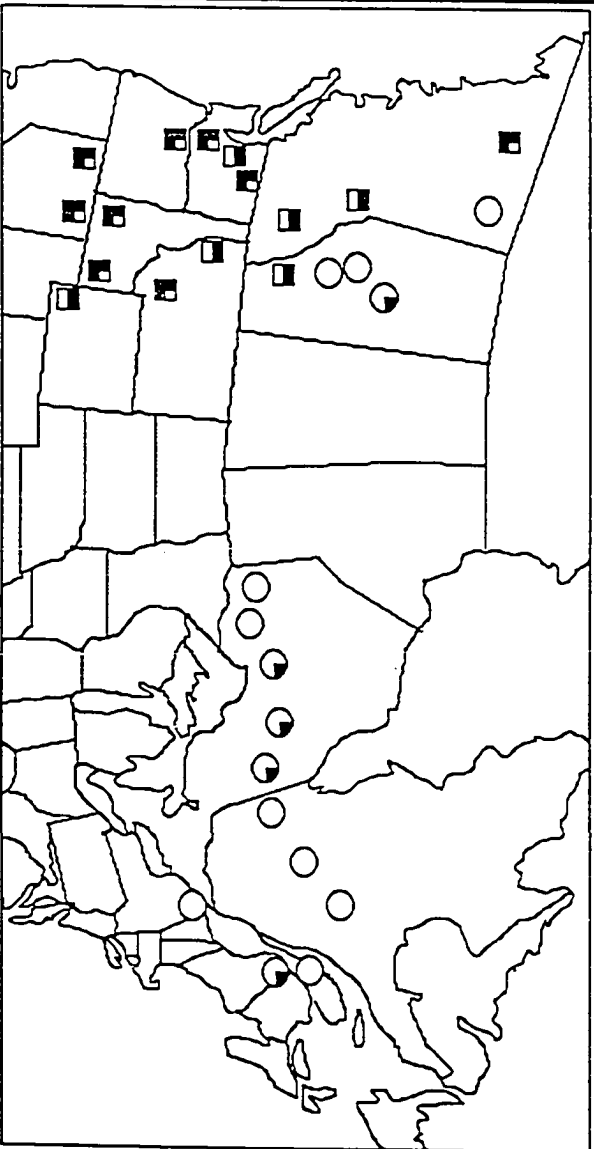


Figure 4B. Geographic
distribution of KEED means (mm)
for populations of *Q.*
philadelphica and *Q. tolmiei*.

MORPH. CHAR.: FEDW		LOC. MEANS SUBSETS	
□	○	CZ 2.66	
		GE 2.65	
		UP 2.62	
		HI 2.62	
		LE 2.62	
		GI 2.61	
		OB 2.61	
		CO 2.61	
		FN 2.60	
		HE 2.60	
□	●	SP 2.59	
		DO 2.59	
		SL 2.59	
		SF 2.59	
		SQ 2.58	
		HC 2.58	
		HY 2.57	
		LP 2.56	
		HM 2.56	
□	●	PO 2.56	
		KN 2.56	
		LH 2.55	
		BA 2.53	
		PV 2.52	
□	●	SC 2.52	
		LO 2.51	
		JA 2.15	
■	●	HH 2.47	
		PA 2.46	
		LR 2.45	

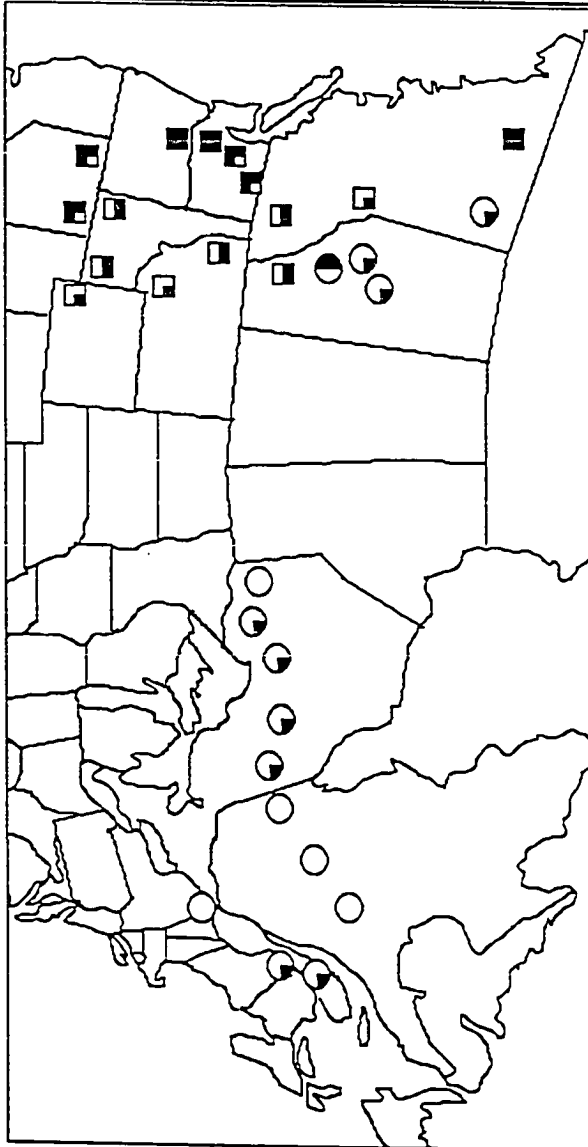
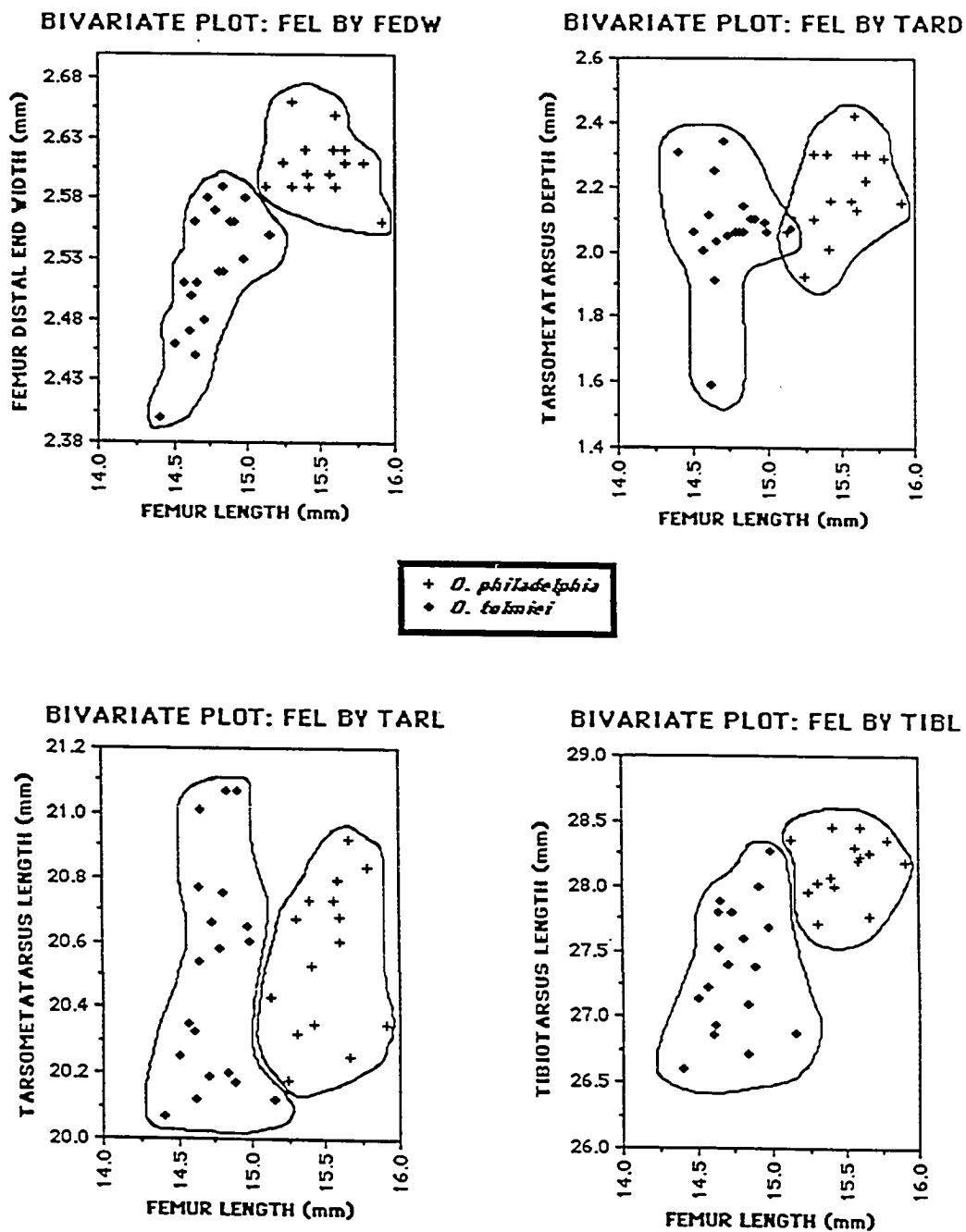


Figure 49. Geographic distribution of FEDW means (mm) for populations of *D. philadelphia* and *D. talpae*.

Figure 50. Bivariate plots of population means: FEDW, FEL, TIBL, TARL, TARD.



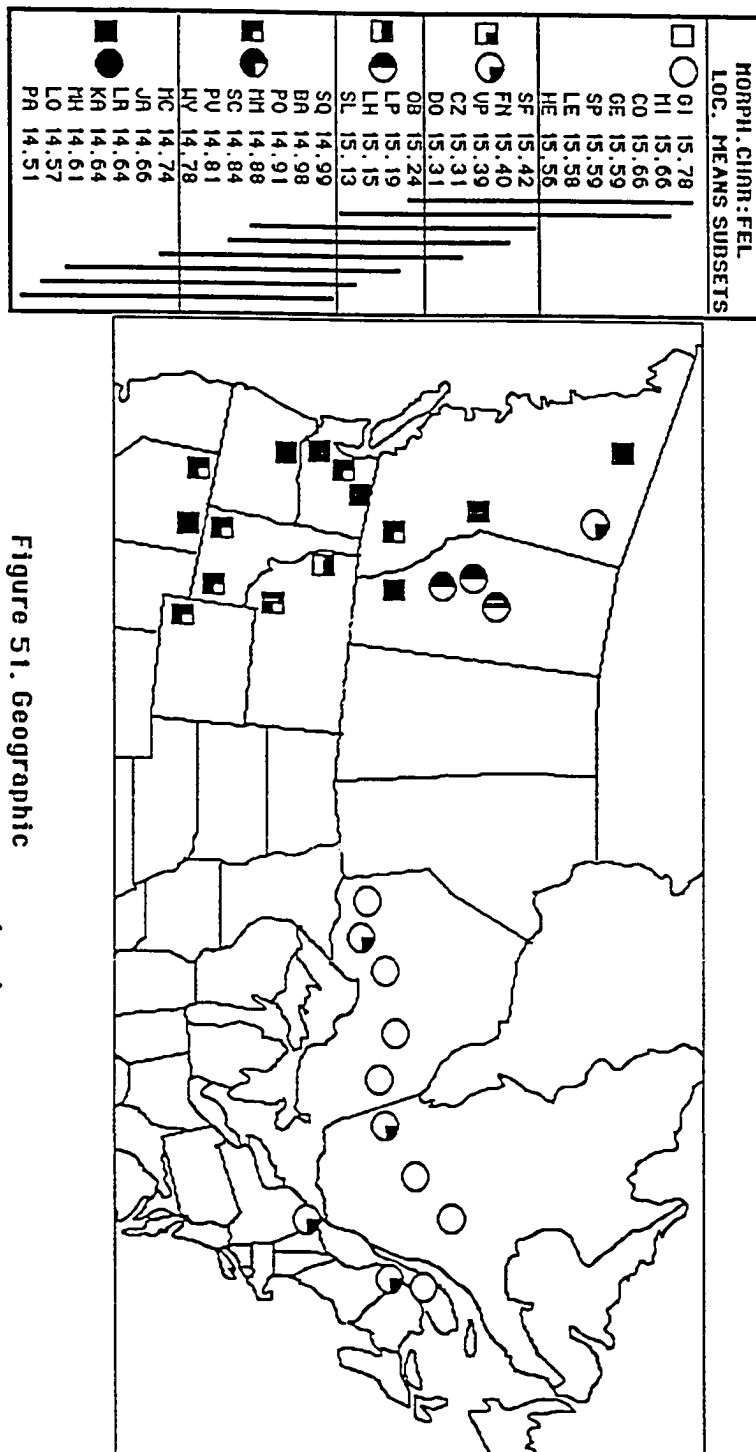


Figure 51. Geographic distribution of FEL means (mm) for populations of *D. philadelphica* and *D. tolmiei*.

MORPH. CHAR. : TARD		LOC. MEANS SUBSETS
LOC. MEANS SUBSETS		
□	○	LE 2.42
		SP 2.30
		H1 2.30
		UP 2.30
		C2 2.30
		G1 2.29
	●	KA 2.25
		CO 2.22
		HE 2.16
		SF 2.16
		LP 2.15
		SC 2.14
■	●	GE 2.13
		MH 2.11
		MH 2.10
		PO 2.10
		DO 2.10
		BA 2.09
		LH 2.07
		PA 2.06
		HY 2.06
■	●	SL 2.06
		PU 2.06
		SQ 2.06
		HC 2.05
		JA 2.03
		FN 2.01
		LO 2.00
■	●	OB 1.92
		LR 1.91

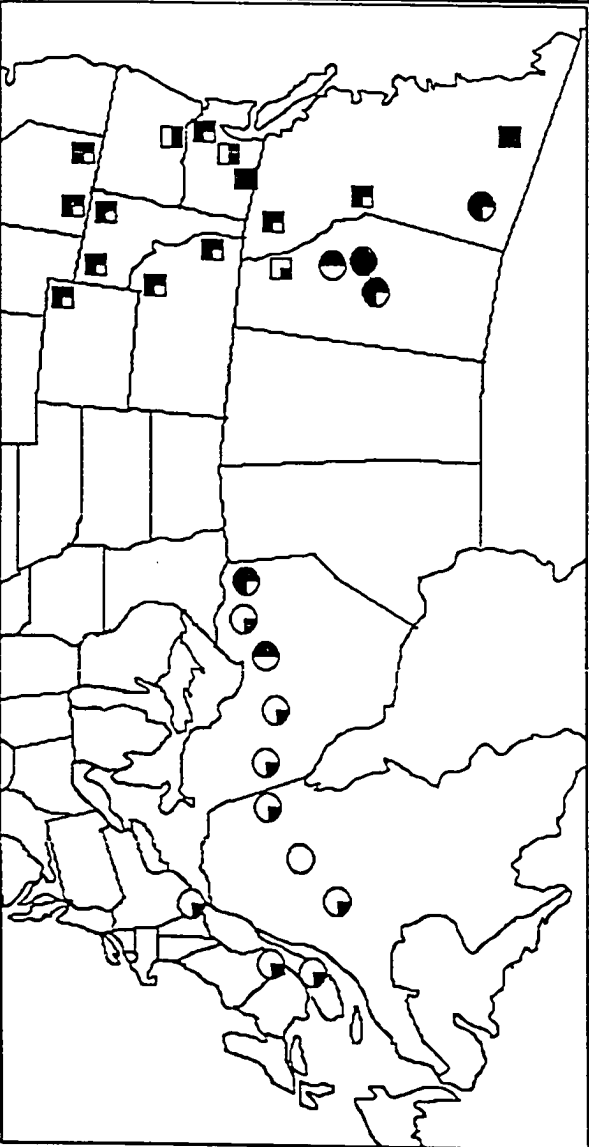


Figure 52. Geographic distribution of TARD means (mm) for populations of *Q. philadelphica* and *Q. tolmiei*.

MORPH. CHR.: HTL	
LOC. MEANS SUBSETS	
□	SF 3.75
○	CZ 3.75
	GI 3.67
	OB 3.66
	CO 3.64
	UP 3.64
	HE 3.64
◐	HI 3.63
	LP 3.63
	SL 3.62
	DO 3.62
	LE 3.61
	FN 3.60
	GE 3.59
	SQ 3.59
◑	HC 3.58
	SP 3.56
	BA 3.56
	LH 3.56
	KA 3.52
◒	HM 3.50
	SC 3.48
■	PO 3.46
	LR 3.46
●	PV 3.45
	JA 3.44
	HY 3.44
	LO 3.43
	PA 3.42
	HH 3.41

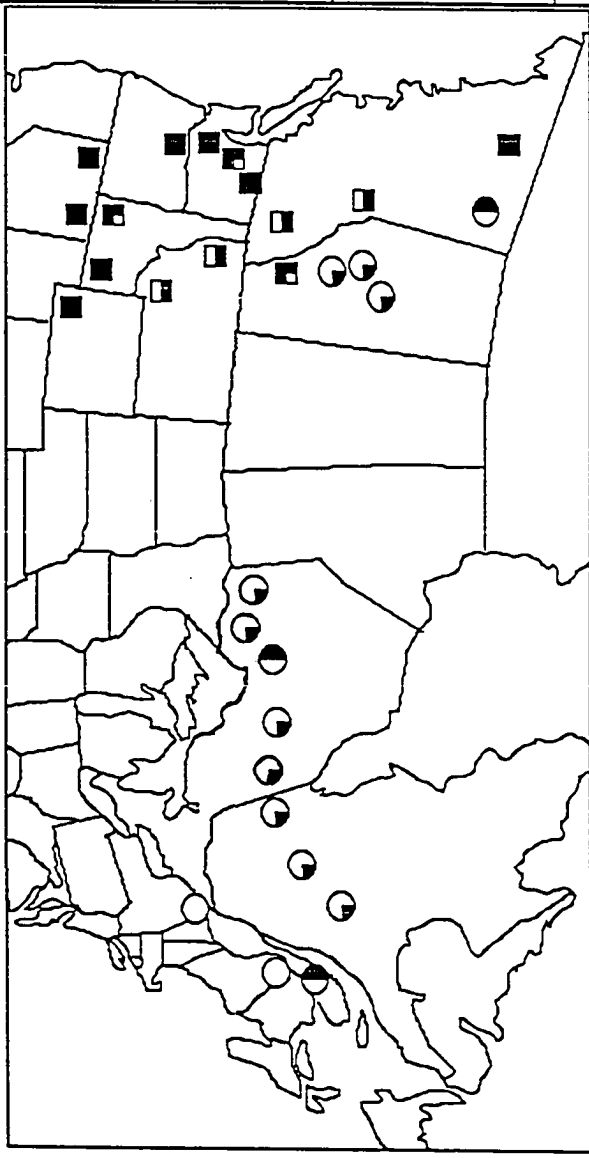
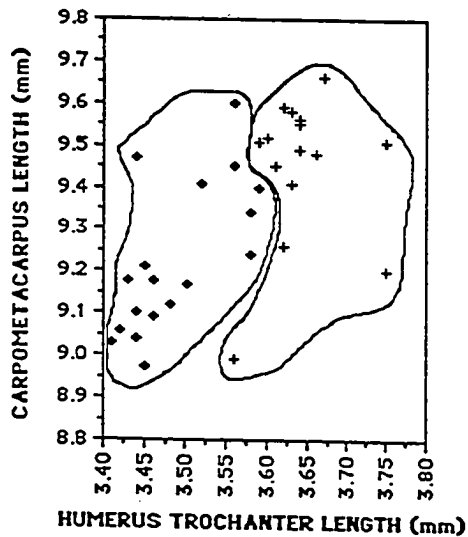


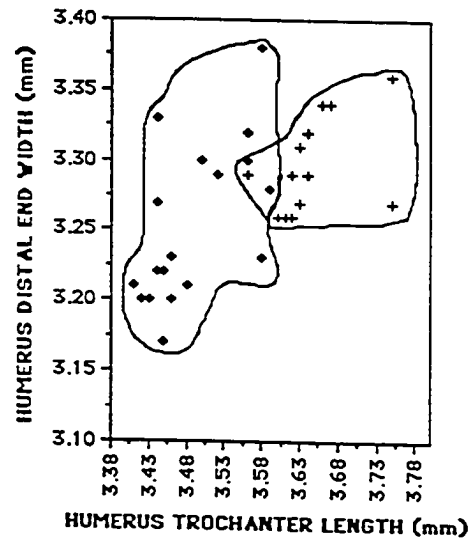
Figure 53. Geographic distribution of HTL means (mm) for populations of *D. philadelphica* and *D. tolmiei*.

Figure 54. Bivariate plots of population means: HTRL, HDEW, HUML, ULNL, CARPL.

BIVARIATE PLOT: HTRL BY CARPL

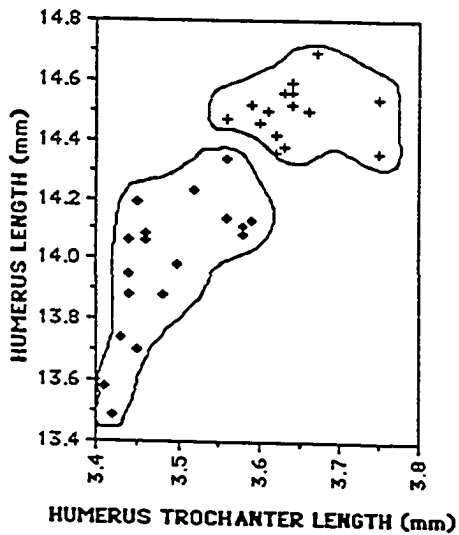


BIVARIATE PLOT: HTRL BY HDEW

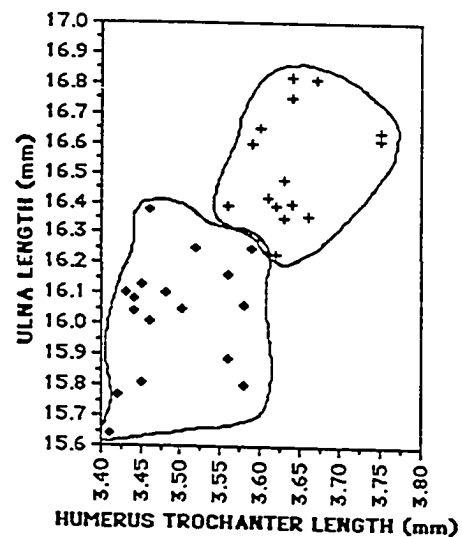


+ *O. philadelphia*
• *O. tolmiei*

BIVARIATE PLOT: HTRL BY HUML



BIVARIATE PLOT: HTRL BY ULNL



MORPH. CHAR: HUML	
LOC. MEANS SUBSETS	
□	01 14.69
○	CO 14.59
	HI 14.56
	HE 14.56
	CZ 14.54
	GE 14.52
	UP 14.52
	LE 14.50
	OB 14.50
	SP 14.47
	FN 14.46
	SL 14.42
◐	LP 14.38
	SF 14.36
	DO 14.36
	LH 14.34
	KA 14.23
	PV 14.19
	BA 14.14
	SQ 14.13
◑	HC 14.11
	PQ 14.08
	HY 14.06
	LR 14.06
	JH 13.98
◒	JA 13.95
	SC 13.88
	LO 13.74
●	HH 13.58
■	PA 13.49

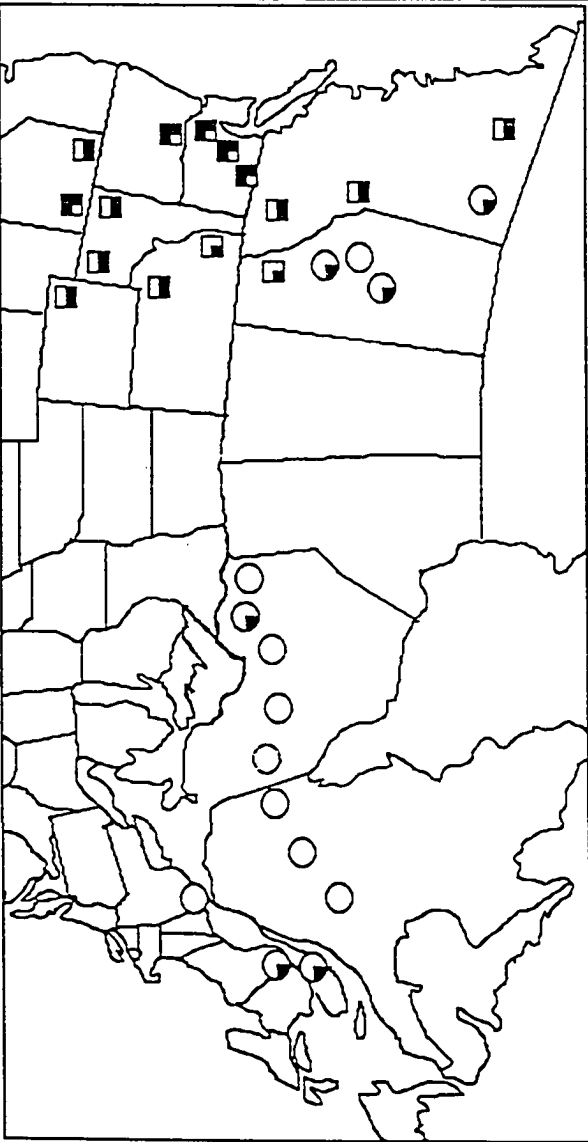


Figure 55. Geographic distribution of HUML means (mm) for populations of *Q. philadelphia* and *Q. tolmiei*.

MORPH. CHAR. : ULNL.	
LOC. MEANS SUBSETS	
□	UP 16.82
○	G1 16.81
	HE 16.75
	FN 16.65
	SF 16.64
	CZ 16.61
	GE 16.60
	HI 16.48
	LE 16.42
	CO 16.40
◐	SL 16.39
◑	SP 16.39
	PO 16.38
	OB 16.36
	LP 16.35
	KA 16.25
	SQ 16.25
◒	DO 16.23
◓	LH 16.16
	PV 16.13
	LO 16.10
	SC 16.10
	AY 16.08
◔	HC 16.06
◕	HI 16.05
	JA 16.04
	LR 16.01
	BA 15.89
◖	PA 15.77
◗	PH 15.64

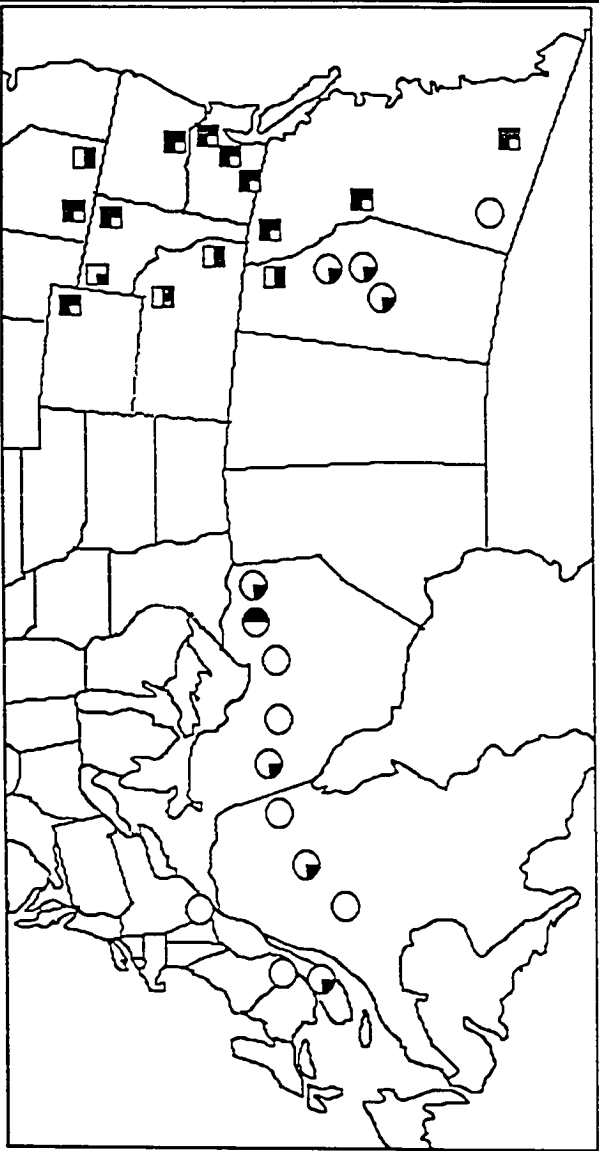


Figure 56. Geographic distribution of ULNL means (mm) for populations of *Q. philadelphica* and *Q. tolmiei*.

MORPH. CHAR.: CARPL		LOC. MEANS SUBSETS	
□	GI 9.66		
○	BA 9.60		
	SL 9.59		
	HI 9.58		
	CO 9.56		
	HE 9.55		
	FN 9.52		
	GE 9.51		
	CZ 9.51		
□	UP 9.49		
○	OB 9.48		
	LE 9.45		
	LH 9.45		
	LP 9.41		
	KA 9.41		
	SQ 9.40		
	HC 9.34		
□	DO 9.26		
	PV 9.21		
	SF 9.20		
□	LO 9.18		
○	PO 9.18		
	HH 9.17		
	SC 9.12		
	HY 9.10		
	LR 9.09		
■	PA 9.06		
●	JH 9.04		
	MH 9.03		
	SP 8.99		

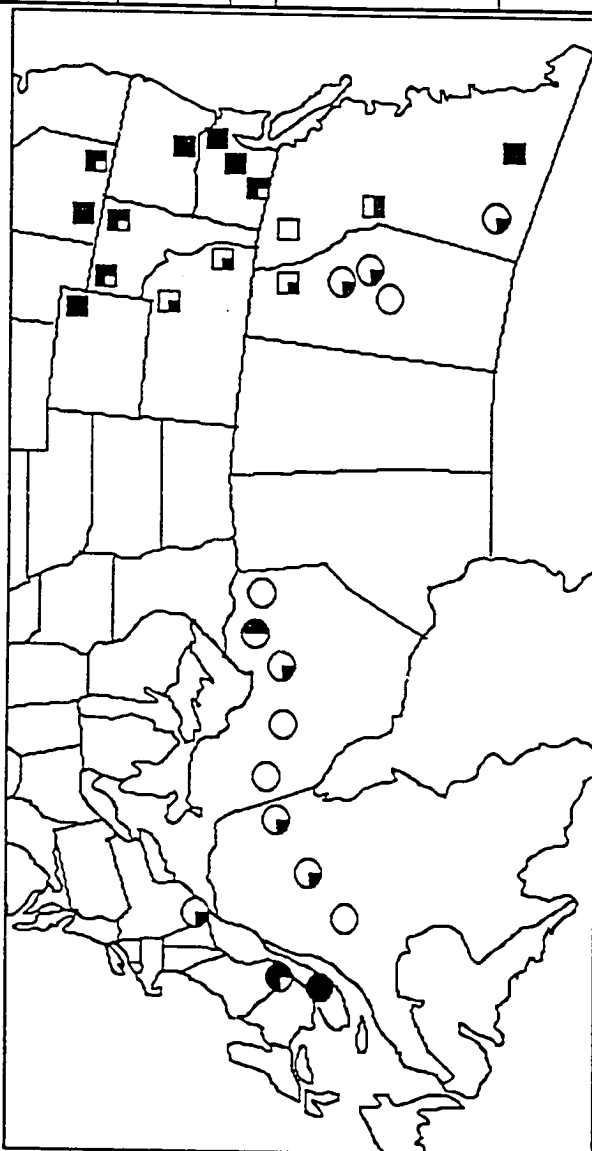


Figure 57. Geographic distribution of CARPL means (mm) for populations of *Q. philadelphica* and *Q. tolimiei*.

Figure 58. Phenogram of *D. tolmiei* and *D. philadelphia* populations based on External Variables.

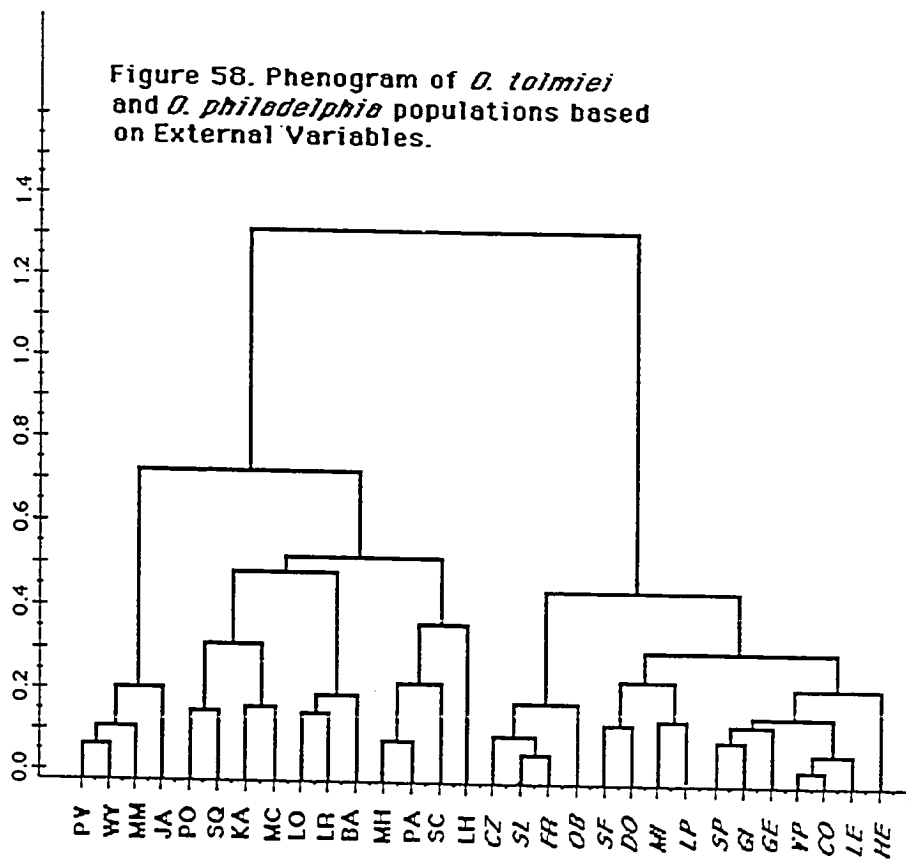


Figure 59. Phenogram of *D. tolmiei* and *D. philadelphia* populations based on Skull Variables.

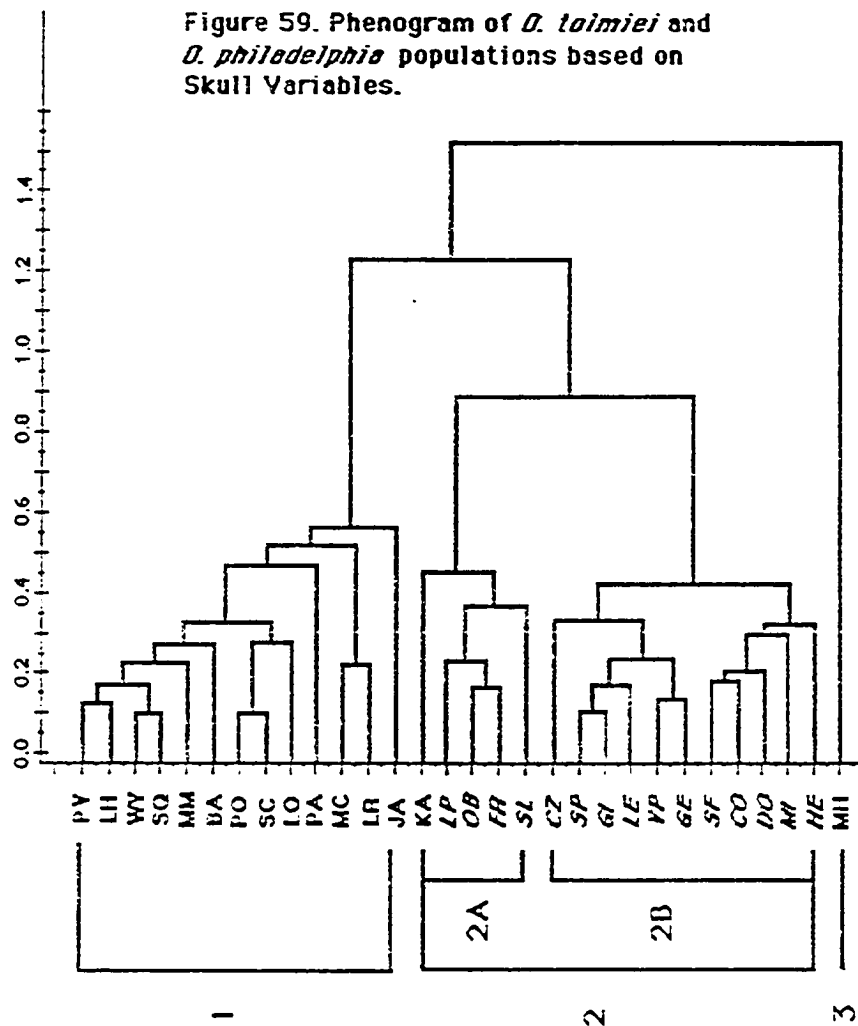


Figure 60. Phenogram of *O. tolmiei* and *O. philadelphia* populations based on Girdle Variables.

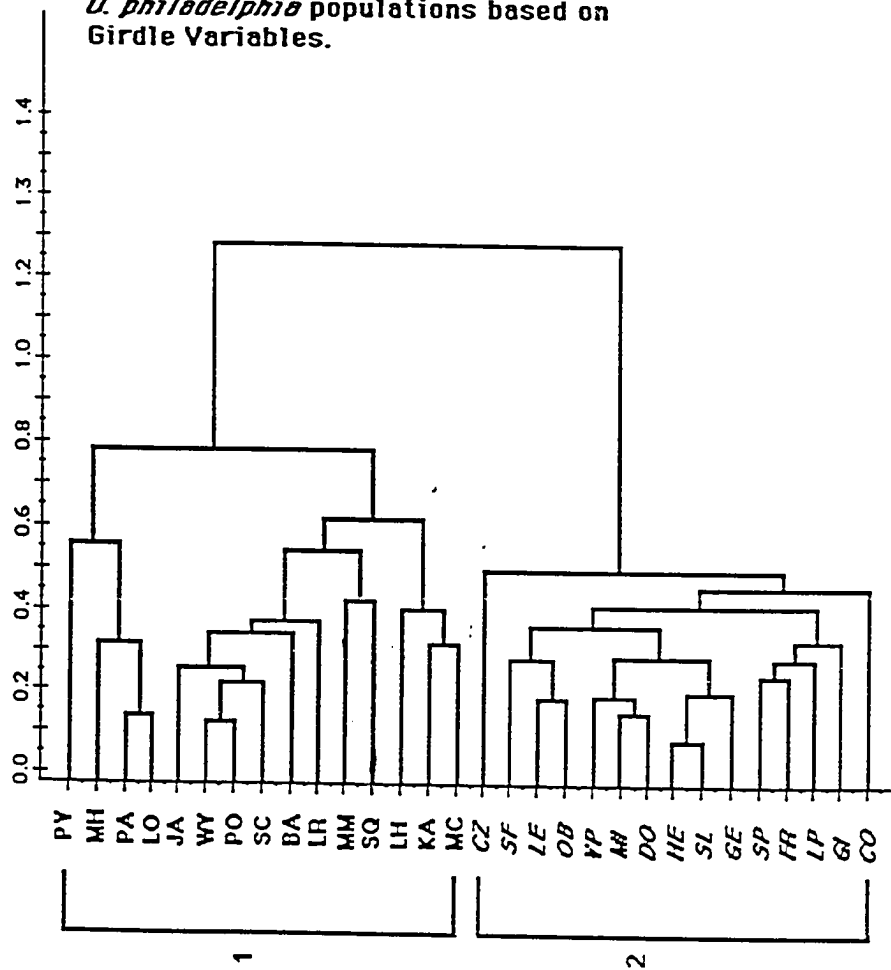
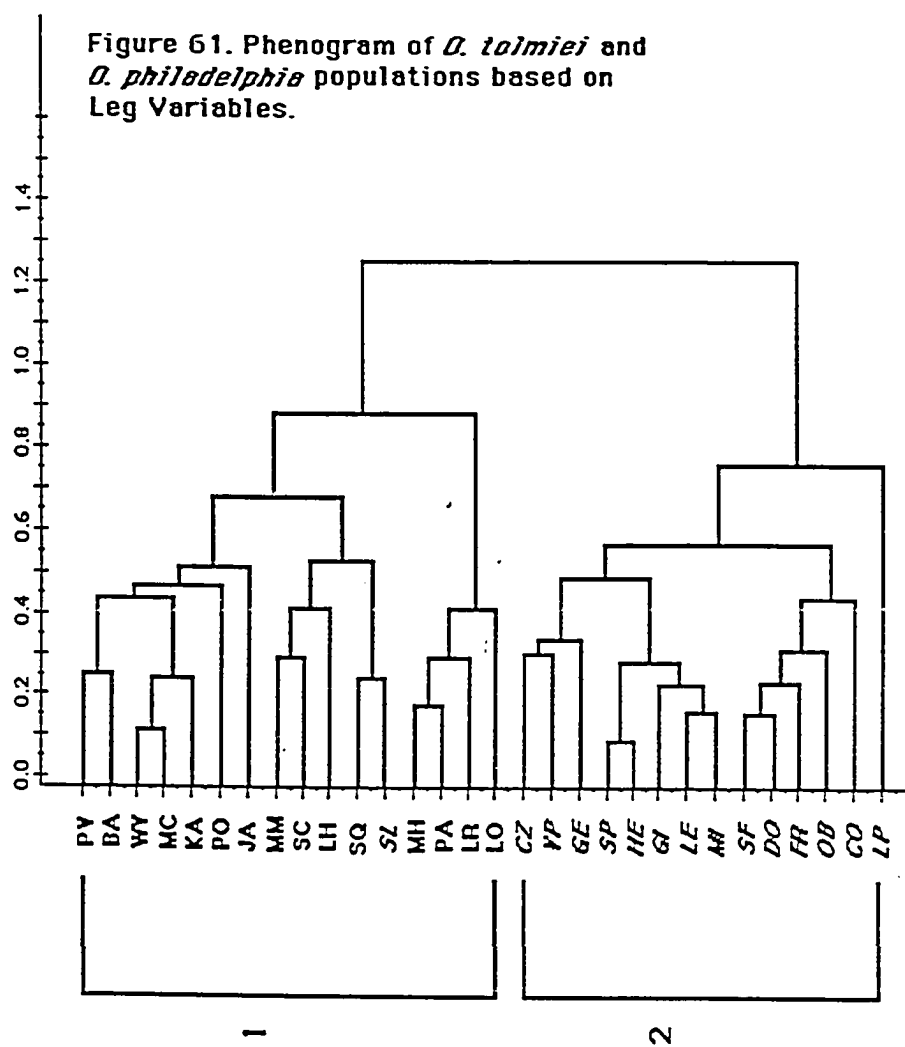


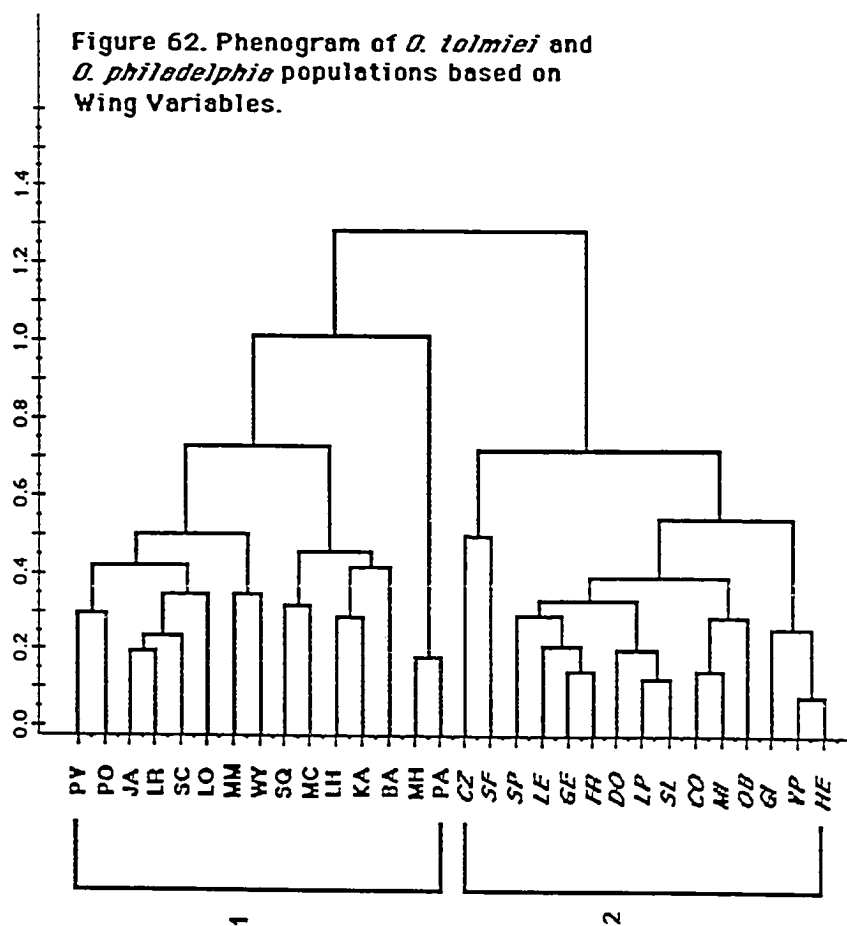
Figure 61. Phenogram of *O. talmiei* and *O. philadelphia* populations based on Leg Variables.



1

2

Figure 62. Phenogram of *O. tolmiei* and *O. philadelphia* populations based on Wing Variables.



1

2

Figure 63. Phenogram of *O. tolmiei* and *O. philadelphia* populations based on all Skeletal Variables.

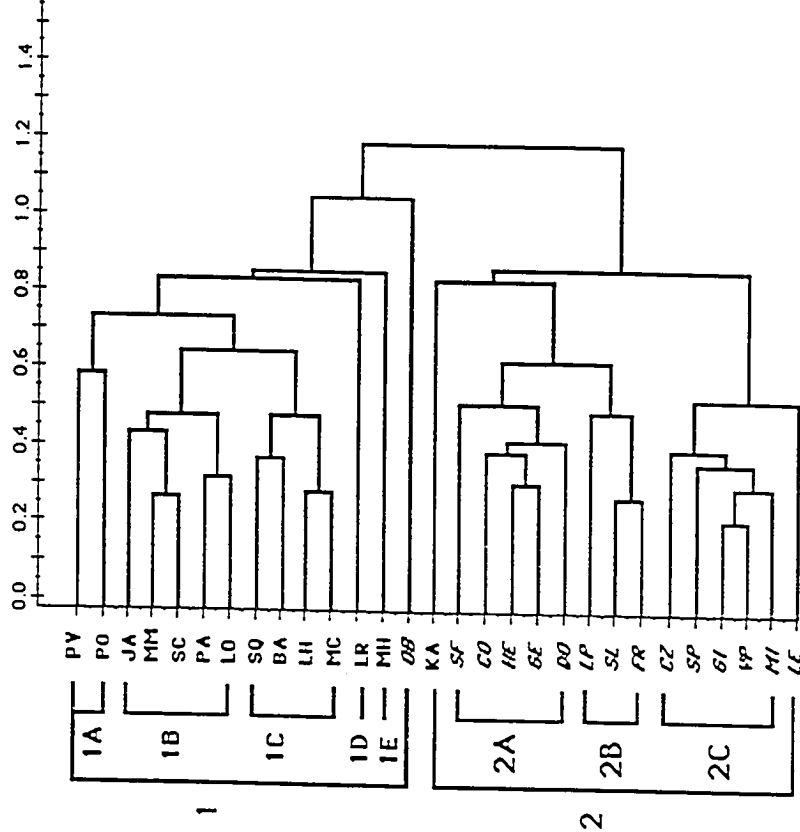


Figure 64. 3D plots of Principal Components 1, 2, 3 based on External variables.

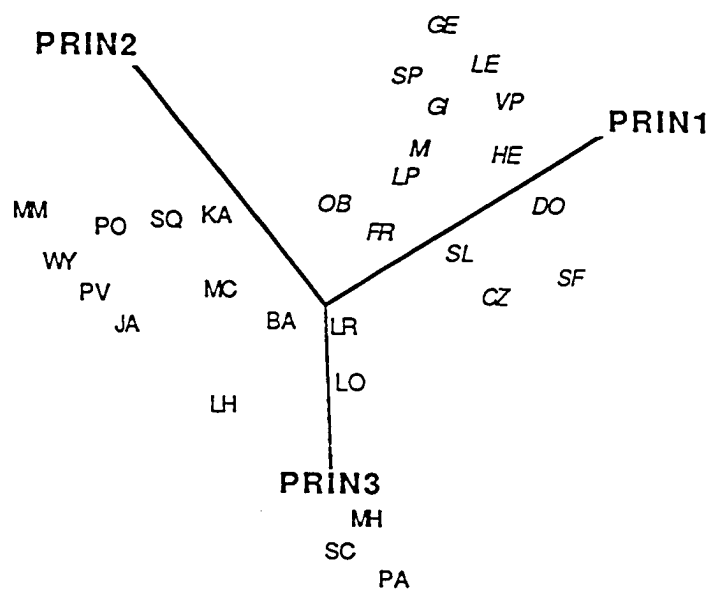


Figure 65. 3D plots of Principal Components 1, 2, 3 based on Skull and variables.

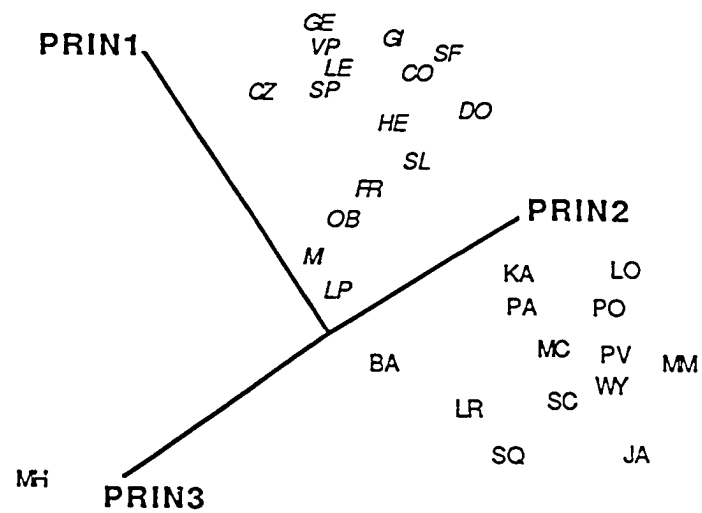


Figure 66. 3D plots of Principal Components 1, 2, 3 based on Girdle variables.

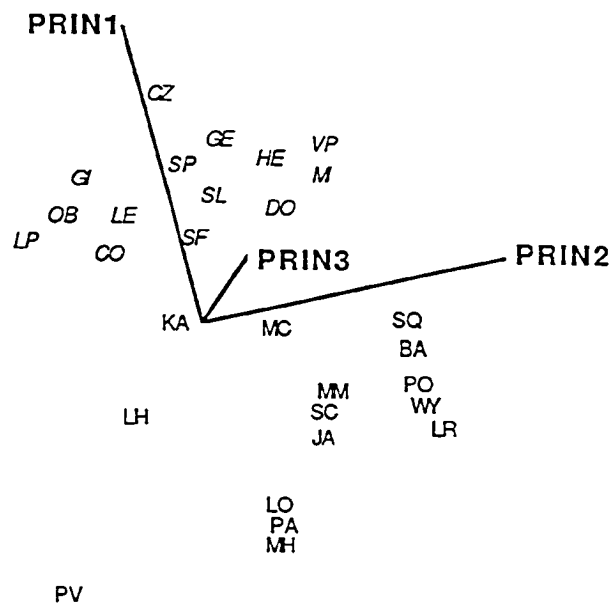


Figure 67. 3D plots of Principal Components 1, 2, 3 based on Leg variables.

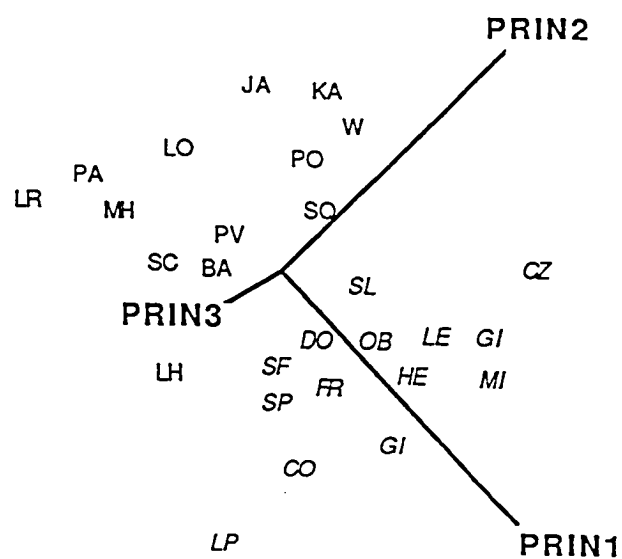


Figure 68. 3D plots of Principal Components 1, 2, 3 based on Wing variables.

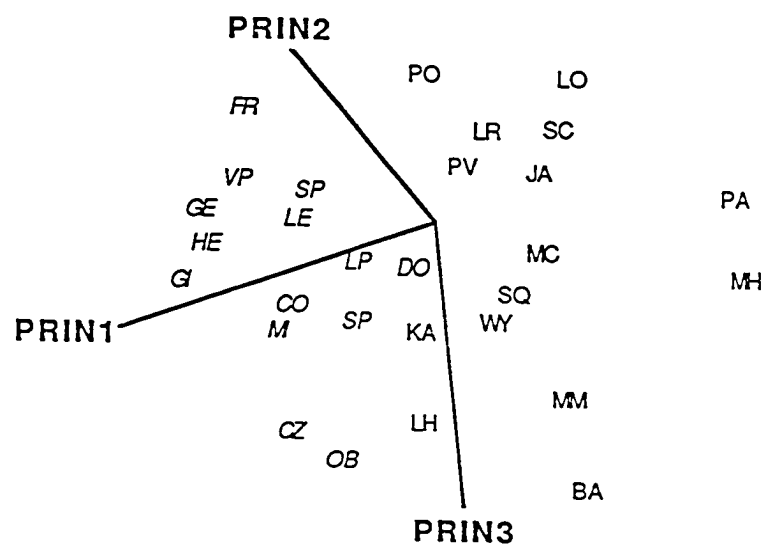


Figure 69. 3D plots of Principal Components 1, 2, 3 based on all skeletal variables.

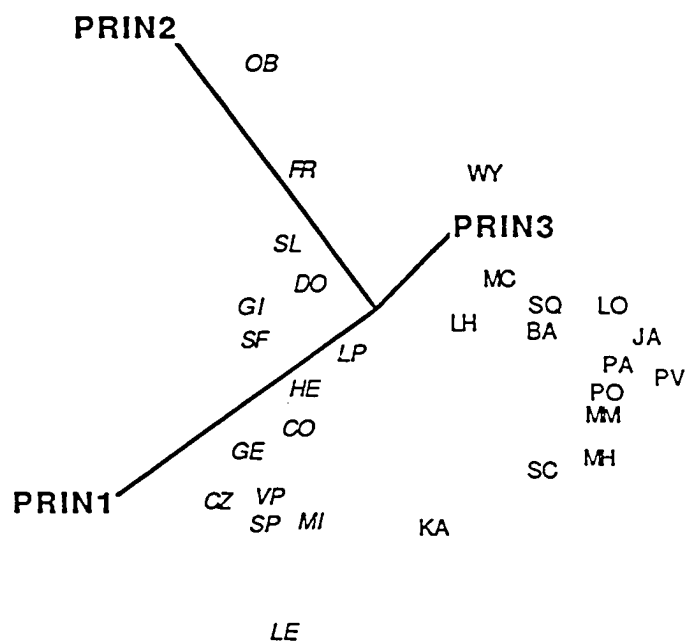


Figure 70. Plots of Discriminant Function scores for *O. philadelphia* and *O. tolmiei* OTU's for external complex variables.

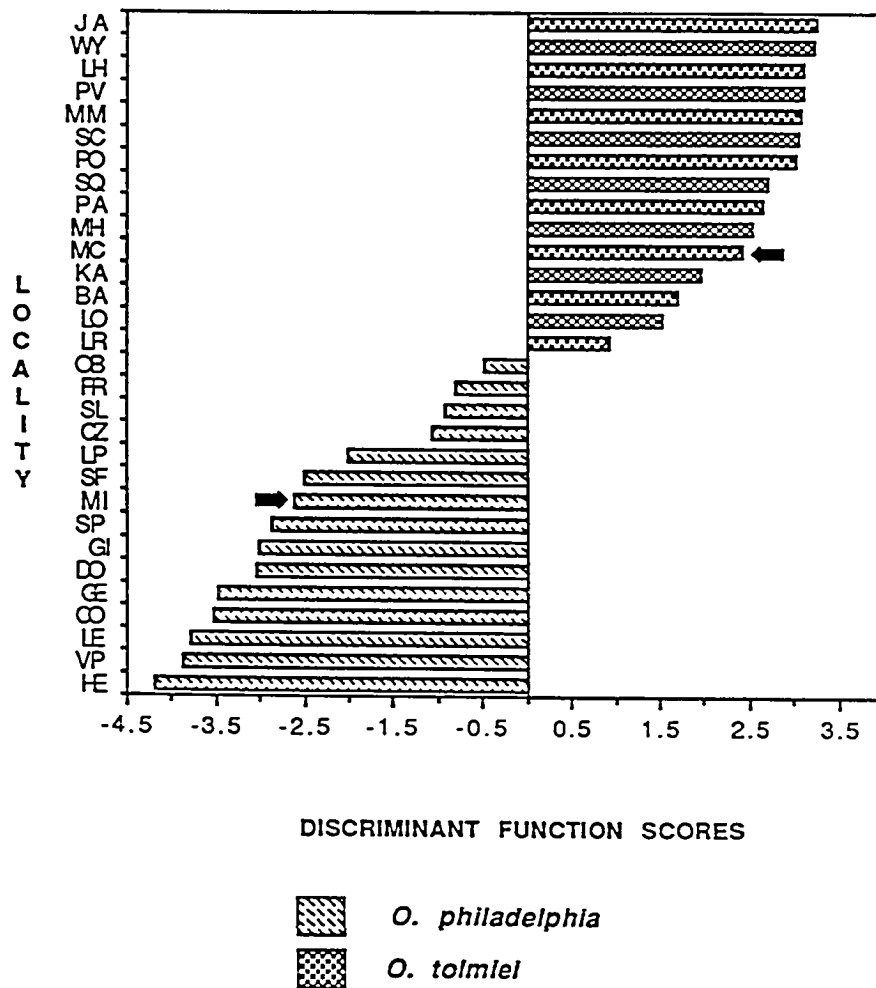


Figure 71. Plots of Discriminant Function Scores for *O. philadelphia* and *O. tolmiei* skull complex variables.

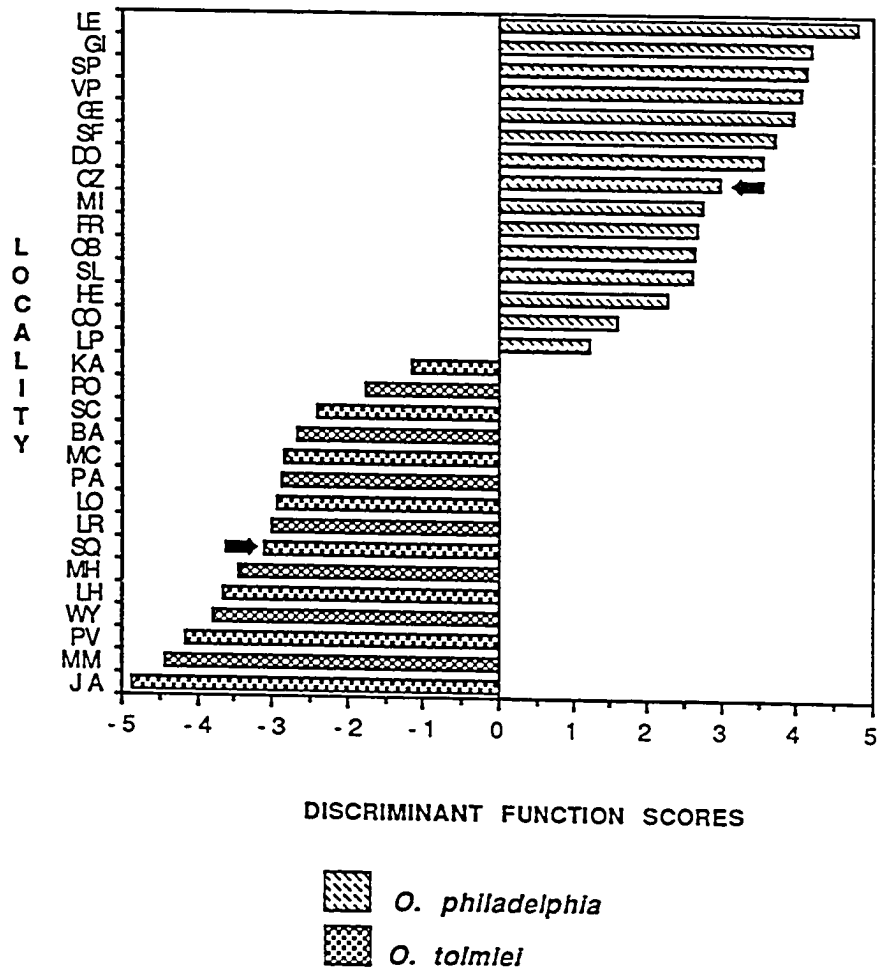


Figure 72. Plots of Discriminant Function Scores for *O. philadelphia* and *O. tolmiei* OTU's for girdle complex variables.

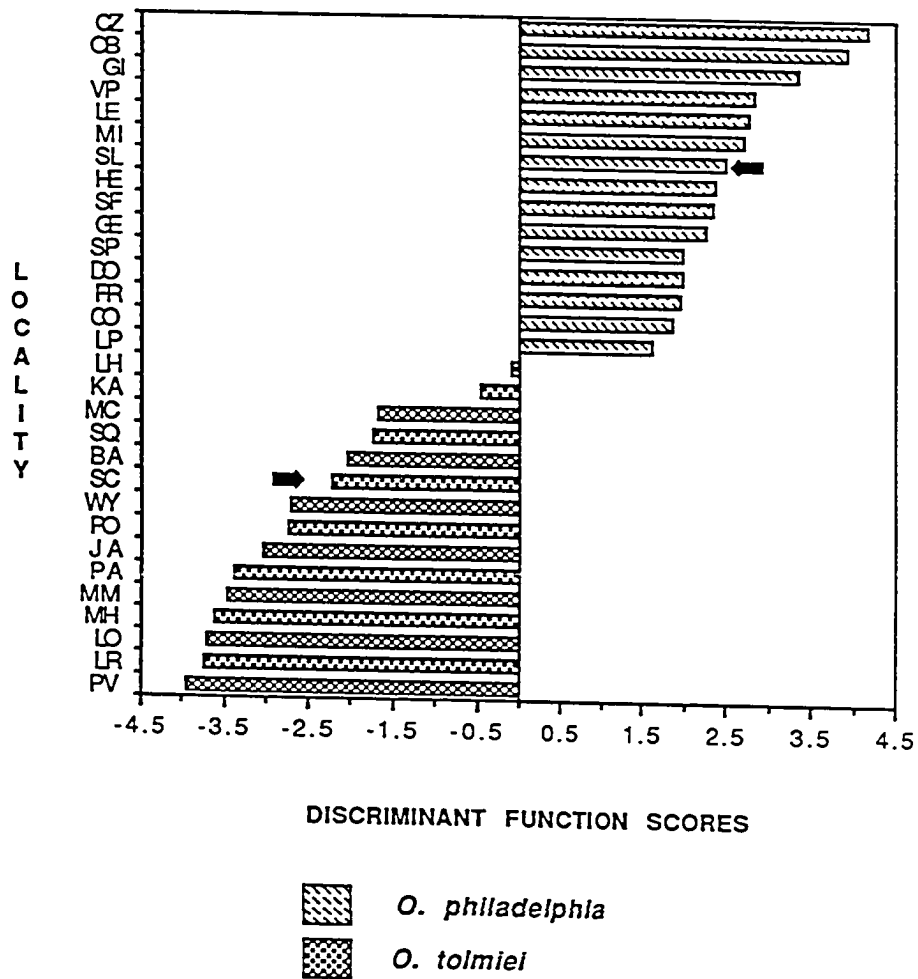


Figure 73. Plots of Discriminant Function scores for *O. philadelphia* and *O. tolmiei* OTU's for leg complex variables.

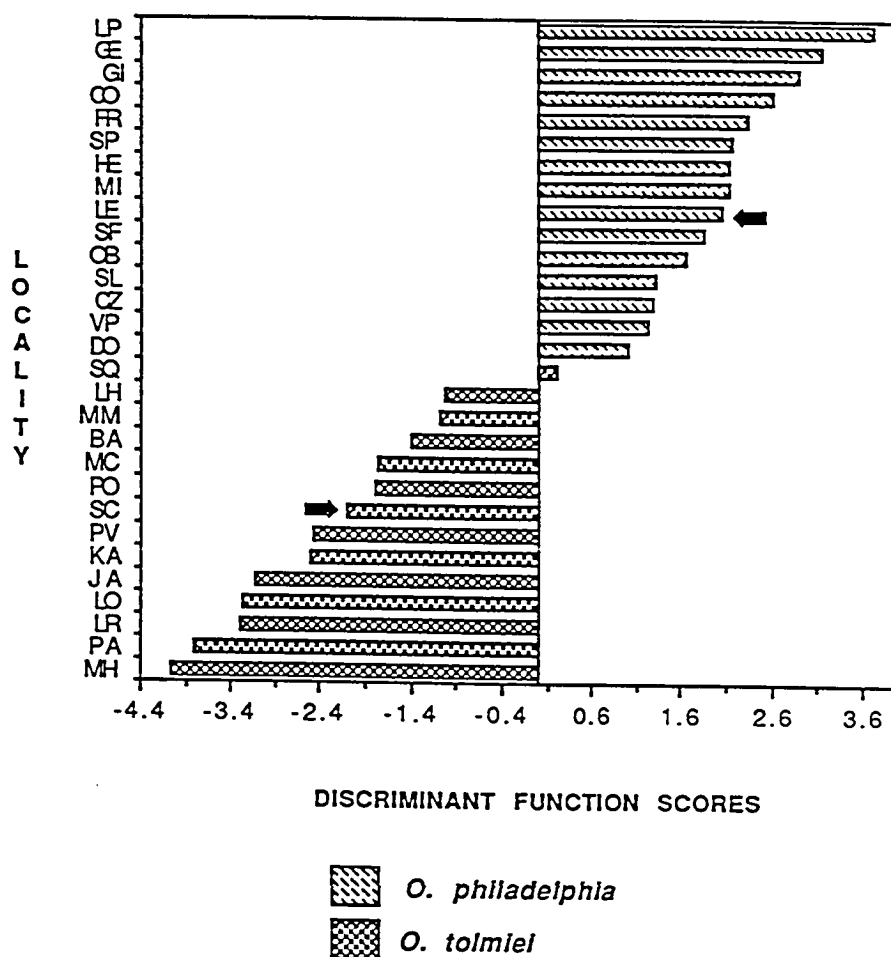


Figure 74. Plots of Discriminant Function scores for *O. philadelphia* and *O. tolmiei* OTU's for wing complex variables.

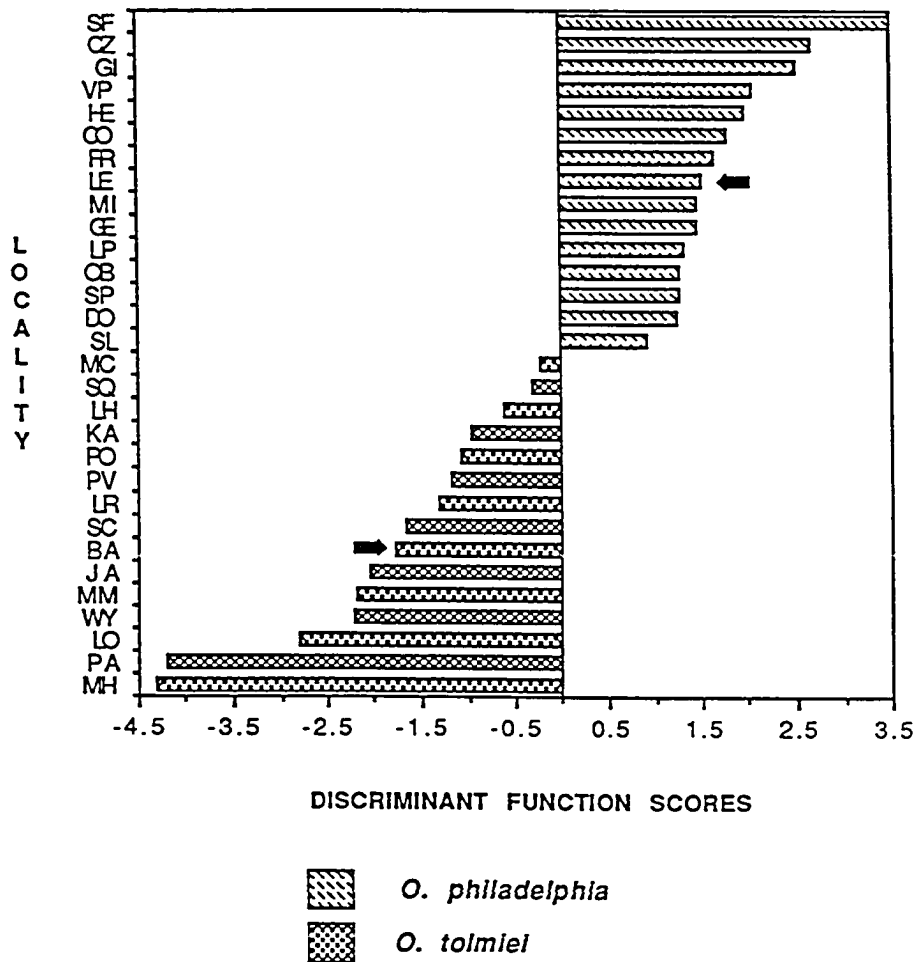


Figure 75. Plots of Discriminant Function scores for *O. philadelphia* and *O. tolmiei* OTU's for all skeletal complex variables.

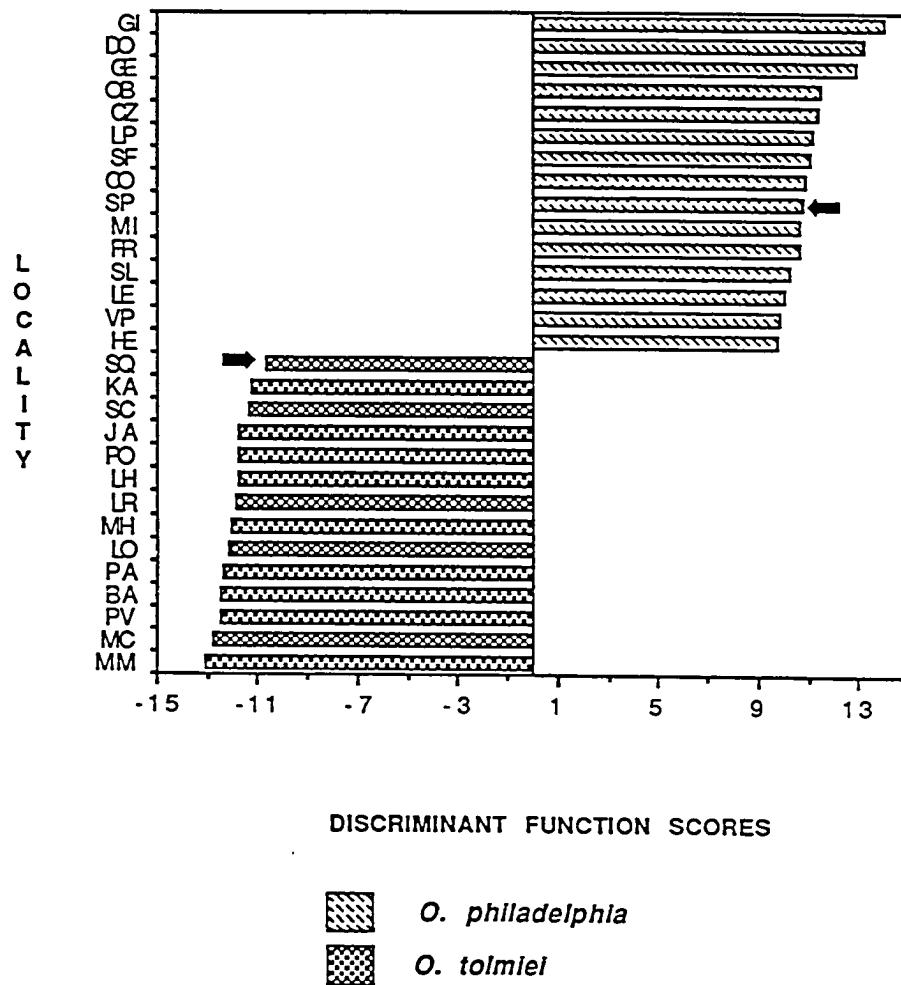
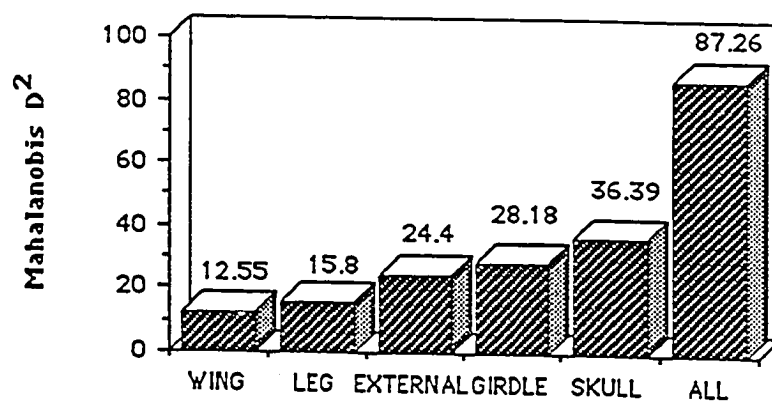


Figure 76. Mahalanobis' D^2 for each skeletal complex and for all skeletal complexes combined.



CHAPTER 6 - SONG

6.1 UNIVARIATE ANALYSIS OF PHYSICAL PARAMETERS OF SONG: DIFFERENCES BETWEEN LOCALITIES AND REGRESSION AND CORRELATION WITH ENVIRONMENTAL VARIABLES

This section of Chapter 6 describes the results of univariate analyses of the physical parameters of song. The reader should refer back to Figure 6 which illustrates these parameters.

NUMBER OF PARTS PER SONG (NPSO). *Oporornis tolmiei* averaged 15.6% more parts per song than *O. philadelphia* (Table 24) (APPENDIX G). At the population level however, not all *O. philadelphia* locality means were significantly different from all *O. tolmiei* locality means (Figure 77). All three subsets were composed of samples of *O. philadelphia* and *O. tolmiei*. Bivariate plots of NPSO and NSSO showed moderate separation of *O. philadelphia* and *O. tolmiei* populations (Figure 78). Regression analyses of NPSO on latitude and longitude yielded different results for these taxa. In *O. philadelphia* song became less complex from south to north ($p < .001$) (Table 25). Variation in latitude accounted for 22.3% of the variation in NPSO. Regression of NPSO on longitude was also highly significant for *O. philadelphia* ($p < .001$) but only accounted for 6.4% of the variation. No significant linear relationships with latitude or longitude existed for *O. tolmiei*. Results of Correlation analyses of NPSO with environmental variables were different for *O. philadelphia* and *O. tolmiei*. In *O. philadelphia* NPSO was positively correlated with all temperature variables ($p < .001$) (Table 26). No significant

correlations between NPSO and environmental variables were observed for *O. tolmiei*.

NUMBER OF SYLLABLES PER SONG (NSSO). Fewer syllables composed *O. philadelphia* song than *O. tolmiei* song (APPENDIX G). *Oporornis tolmiei* averaged 18.7% more syllables per song than *O. philadelphia* (Table 24). Not all *O. tolmiei* populations were significantly different from *O. philadelphia* populations (Figure 79). Two of four subsets were composed exclusively of *O. tolmiei* samples. The remaining two subsets contained a mixture of populations from both taxa. For results of Bivariate plots, see NPSO. Only *O. philadelphia* exhibited a significant regression on latitude ($p < .014$) (Table 25). The number of syllables decreased from south to north but only 3.3% of the variation in this character could be attributed to variation in latitude. Neither taxon showed a significant relationship with longitude. Correlations between NSSO and environmental variables were different in *O. philadelphia* and *O. tolmiei*. In *O. philadelphia* NSSO increased with corresponding increases in the following temperature variables: MEJUNT ($p < .01$), MAJUNT ($p < .006$), MEJULT ($p < .03$), MAJULT ($p < .03$) (Table 26). NSSO decreased with increasing RELH for *O. tolmiei* ($p < .02$) (Table 27).

NUMBER OF DIFFERENT SYLLABLES PER SONG (NDSO). *Oporornis tolmiei* males sang more different syllables per song on the average than did *O. philadelphia* males (APPENDIX G). *Oporornis tolmiei* averaged 14.09% more different syllables per song than *O. philadelphia* (Table 24). However, many populations of *O. philadelphia* were not significantly different

from *O. tolmiei* populations (Figure 80). Both subsets contained populations of *O. philadelphia* and *O. tolmiei*. Two syllable songs were characteristic of eastern populations of *O. philadelphia* while one syllable songs were dominant in western populations. Bivariate plots of NPSO and NDSO showed nearly complete overlap of *O. philadelphia* and *O. tolmiei* populations (Figure 78). Regressions of NDSO on latitude and longitude were different for these taxa. *O. philadelphia* exhibited significant regressions with latitude ($p < .001$) and longitude ($p < .002$). Variation in latitude (19.3%) accounted for more of the variation in this character than did longitudinal variation (5.1%). There were no significant linear relationships between NDSO and latitude or longitude for *O. tolmiei* ($p > .05$). NDSO was highly correlated with temperature variables in *O. philadelphia* but showed no significant correlation with any environmental variables in *O. tolmiei*. For *O. philadelphia* NDSO was positively correlated with MEJUNT ($p < .001$), MIJUNT ($p < .001$), MAJUNT ($p < .001$), MEJULT ($p < .001$), MIJULT ($p < .006$), MAJULT ($p < .001$) (Table 26).

SONG DURATION (DUR). *Oporornis tolmiei* averaged 13.9% longer songs than *O. philadelphia* (Table 24) (APPENDIX G). All *O. philadelphia* localities were not significantly different from *O. tolmiei* localities for DUR (Figure 81). All three subsets contained a mixture of populations from both taxa. Bivariate plots of NPSO and DUR showed less than moderate overlap between populations of *O. philadelphia* and *O. tolmiei* (Figure 78). Regression analyses of DUR on latitude and longitude were different for *O. philadelphia* and *O. tolmiei* (Table 25). Songs became shorter from north to south and from east to west in *O. philadelphia* but only 2.9% and 2.5% of the

variation was attributed to latitudinal and longitudinal variation respectively. For *O. tolmiei* DUR did not show a significant linear relationship with latitude or longitude. No significant correlations existed between DUR and environmental variables for either taxon.

MINIMUM FREQUENCY OF SONG (MINS). *Oporornis tolmiei* averaged 19.9% higher MINS than *O. philadelphia* (Table 24) (APPENDIX G). However, not all *O. philadelphia* locality means were significantly different from *O. tolmiei* locality means (Figure 82). Bivariate plots of NPSO and MINS showed moderate overlap between *O. philadelphia* and *O. tolmiei* populations (Figure 78). The patterns of variation in MINS with respect to latitude and longitude were very similar in *O. philadelphia* and *O. tolmiei* (Table 25). MINS increased with increasing latitude in both taxa. Variation in latitude accounted for 4.3% of the variation in MINS for *O. philadelphia* and 2.5% for *O. tolmiei*. Neither taxon showed a significant regression of MINS on longitude. Correlations with environmental variables yielded different results for each taxon. MINS decreased with increasing temperature in *O. philadelphia* (Table 26). No significant correlations with environmental variables were evident for *O. tolmiei*.

MAXIMUM FREQUENCY OF SONG (MAXS). *Oporornis tolmiei* averaged 8.3% higher MAXS than *O. philadelphia* (Table 24) (APPENDIX G). Many *O. philadelphia* and *O. tolmiei* locality means were not significantly different from each other (Figure 83). All four subsets contained populations from each taxon. Bivariate plots of NPSO and MAXS showed nearly complete

overlap of *O. philadelphia* and *O. tolmiei* populations (Figure 78). Regressions of MAXS on latitude and longitude were similar for these taxa. MAXS decreased significantly from south to north in both taxa ($p < .001$) (Table 25). Variation in latitude accounted for more of the variation in *O. philadelphia* (25.8%) than in *O. tolmiei* (11.2%). Only *O. philadelphia* exhibited a significant linear relationship between MAXS and longitude ($p < .001$). MAXS decreased from east to west. Longitudinal variation accounted for 31.6% of the variation in MAXS. Both taxa showed significant positive correlations between MAXS and temperature variables. For *O. philadelphia* MAXS increased with increasing MEJUNT ($p < .001$), MIJUNT ($p < .001$), MEJULT ($p < .001$) and MIJULT ($p < .001$) (Table 26). MAXS was also positively correlated with MEJUNT ($p < .04$), MAJUNT ($p < .001$), MIJULT ($p < .001$), MAJULT ($p < .001$) in *O. tolmiei* (Table 27). Also for *O. tolmiei* MAXS was negatively correlated with MEJUNP ($p < .001$), MEJULP ($p < .001$) and RELH ($p < .01$) (Table 27).

NUMBER OF NOTES PER MA SYLLABLE (NNA). *Oporornis philadelphia* averaged 4.3% more MA syllables per song than *O. tolmiei* (Table 24) (APPENDIX G). However, not all *O. philadelphia* locality means were significantly different from all *O. tolmiei* locality means (Figure 84). All four subsets were comprised of both *O. philadelphia* and *O. tolmiei* populations. There was a great deal of overlap between *O. philadelphia* and *O. tolmiei* populations as shown by Bivariate plots of NNA and IMC (Figure 85). Regressions analyses yielded different results for *O. philadelphia* and *O. tolmiei*. *O. philadelphia* exhibited a significant linear relationship between NNA and latitude ($p < .001$) (Table 25). Variation in latitude accounted for 19.2%

of the variation in NNA. No significant relationship with latitude or longitude was evident for *O. tolmiei*. For *O. philadelphia* NNA decreased from east to west ($p < .001$). Variation in longitude was attributed to 31.7% of the variation in NNA. Significant correlations with environmental variables were different in these taxa. NNA was positively correlated with MEJUNT ($p < .01$), MEJULT ($p < .001$), MIJULT ($p < .001$), and MEJULP ($p < .005$) in *O. philadelphia* (Table 26). For *O. tolmiei* there were no significant correlations with environmental variables.

NUMBER OF NOTES PER MB SYLLABLE (NNB). *Oporornis philadelphia* averaged 5.3% more MB syllables per song than *O. tolmiei* (Table 24) (APPENDIX G). Relatively few *O. philadelphia* and *O. tolmiei* locality means were significantly different from each other for NNB (Figure 86). Bivariate plots showed that there was complete overlap between populations of both taxa (Figure 85). Regressions of NNB on latitude and longitude were different for *O. philadelphia* and *O. tolmiei* (Table 25). NNB decreased from north to south ($p < .001$) and from east west ($p < .001$) in the range of *O. philadelphia*. Variation in latitude accounted for 25.2% of the variation in NNB while variation in longitude accounted for 37.6% of the variation. No significant linear relationships between NNB and latitude or longitude existed for *O. tolmiei*. Results of correlation analyses of NNB with environmental variables were also different between these taxa. For *O. philadelphia* NNB was positively correlated with the following temperature variables: MEJUNT ($p < .009$), MIJUNT ($p < .03$), MEJULT ($p < .001$), and MIJULT ($p < .001$). MEJULP was also positively correlated with NNB ($p < .001$) in this taxon (Table 26). In *O. tolmiei*

there were no significant correlations between NNB and environmental variables.

NUMBER OF NOTES PER MC SYLLABLE (NNC). *Oporornis philadelphia* averaged 4.9% more MC syllables per song than *O. tolmiei* (Table 24) (APPENDIX G). Significant differences existed between some but not all *O. philadelphia* and *O. tolmiei* populations (Figure 86). All five subsets contained mixtures of populations from both taxa. Bivariate plots of NNA and NNC showed near complete overlap of *O. philadelphia* and *O. tolmiei* populations (Figure 85). Regressions of NNC on latitude and longitude were different for *O. philadelphia* and *O. tolmiei*. NNC decreased significantly from south to north and east to west for *O. philadelphia* ($p < .001$) (Table 25). Regression on latitude explained 29.8% of the variation in NNC. Variation in longitude accounted for 37.6% of the variation in this character. No significant north-south or east-west patterns were observed for *O. tolmiei*. Results of correlations with environmental variables were similar to results obtained for NNB and NNA. *O. philadelphia* showed highly significant correlations with temperature variables while no significant correlations were observed for *O. tolmiei*. For *O. philadelphia* NNC increased with increases in MEJUNT ($p < .001$), MIJUNT ($p < .003$), MAJUNT ($p < .04$), MEJULT ($p < .001$), MIJULT ($p < .001$) and MEJULP ($p < .001$) (Table 26).

INTERVAL BETWEEN MA AND MB (IMA). *Oporornis philadelphia* averaged 14.2% longer IMA than *O. tolmiei* (Table 24) (APPENDIX G). Most populations of both taxa were not significantly different

from each other (Figure 88). Both subsets were comprised of *O. philadelphia* and *O. tolmiei* populations. Bivariate plots of NNA and IMA revealed almost complete overlap of *O. tolmiei* and *O. philadelphia* population means (Figure 85). Regressions of IMA on latitude and longitude were not significant for either taxon ($p > .05$). Significant correlations with environmental variables were present only in *O. tolmiei* (Table 27). IMA was negatively correlated with MEJUNT ($p < .03$) and EVAP ($p < .04$). Positive correlations were observed with MEJUNP ($p < .04$), MEJULP ($p < .009$), and RELH ($p < .01$).

INTERVAL BETWEEN MB AND MC (IMB). There were no differences between taxa for this character. Bivariate plots of NNA and IMB showed poor separation of *O. philadelphia* and *O. tolmiei* populations (Figure 85). IMB did not show any significant variation with latitude or longitude in *O. philadelphia* and *O. tolmiei*. Correlations between IMB and environmental variables were different for each taxon. For *O. philadelphia* IMB was negatively correlated with MIJULT ($p < .04$) (Table 26). IMB was positively correlated with MEJUNP ($p < .005$), MEJULP ($p < .005$) and RELH ($p < .004$) in *O. tolmiei* (Table 27). In *O. tolmiei* IMB decreased with increasing EVAP ($p < .01$) and JULWT ($p < .03$) (Table 27).

INTERVAL BETWEEN MC AND FA (IMC). There were no differences between *O. philadelphia* and *O. tolmiei* for IMC. Differences between populations of both taxa were minimal (Figure 89). One subset contained one *O. philadelphia* population. The rest of the populations from both taxa were significantly different from each other. For results of Bivariate

plots, see NNA. IMC showed similar variation with respect to latitude and longitude in each taxon (Table 25). IMC increased with increasing latitude in *O. philadelphia* ($p < .001$) and *O. tolmiei* ($p < .001$). Variation in latitude accounted for 19% of the variation in *O. philadelphia* and 19.5% of the variation in *O. tolmiei*. IMC also increased from east to west in *O. philadelphia* ($p < .001$). Longitudinal variation explained 21.7% of the variation in IMC. For *O. tolmiei* the relationship between IMC and longitude was also positive but less significant ($p < .02$) than *O. philadelphia*. Only 5.9% of the variation in this character was attributed to longitudinal variation. Correlations with environmental variables were negative for *O. philadelphia* and mostly positive for *O. tolmiei*. In *O. philadelphia* IMC decreased with increasing MEJUNT ($p < .01$), MAJUNT ($p < .04$), MEJULT ($p < .005$), MIJULT ($p < .04$) and MEJULP ($p < .04$) (Table 26). IMC was positively correlated with MEJUNP ($p < .001$), MEJULP ($p < .001$), RELH ($p < .005$) and negatively correlated with JULWT ($p < .01$) in *O. tolmiei* (Table 27).

MINIMUM FREQUENCY OF MA SYLLABLE (MIA). *Oporornis tolmiei* averaged 12.4% higher MIA than *O. philadelphia* (Table 24) (APPENDIX G). However, not all population means of *O. philadelphia* were significantly different from all *O. tolmiei* population means (Figure 90). All four subsets were composed of populations of both taxa. A great deal of overlap of *O. philadelphia* and *O. tolmiei* populations is shown by Bivariate plots of NNA and MIA (Figure 85). The pattern of variation with respect to latitude and longitude were different in each taxon (Table 25). MIA decreased from north to south in *O. philadelphia* ($p < .001$). Only 10.9% of the variation in this character

was attributed to latitudinal variation. In *O. tolmiei* variation with latitude was not significant ($p > .05$). There were no significant regressions on longitude for either taxon. Correlations with environmental variables were different in *O. philadelphia* and *O. tolmiei*. For *O. philadelphia* MIA was positively correlated with MEJUNT ($p < .008$), MIJUNT ($p < .001$), MAJUNT ($p < .03$), and MEJULT ($p < .005$) (Table 26). In *O. tolmiei* MIA was positively correlated with MIJULT ($p < .02$) and negatively correlated with EVAP ($p < .03$) (Table 27).

MINIMUM FREQUENCY OF MB SYLLABLE (MIB). *Oporornis tolmiei* averaged 13.8% higher MIB than *O. philadelphia* (Table 24) (APPENDIX G). Not all *O. tolmiei* populations were significantly different than *O. philadelphia* populations for this character (Figure 91). None of the five subsets were composed exclusively of one taxon or the other. Bivariate plots of NNA and MIB showed a great deal of overlap between populations of both taxa (Figure 85). Results of regression analyses of MIB on latitude and longitude were different for both taxa (Table 25). For *O. philadelphia* MIB decreased from north to south ($p < .001$) and east to west ($p < .04$). However only 10.1% of the variation in this character was attributed to latitudinal variation. Longitudinal variation explained only 2.3% of the variation in MIB. No significant east-west or north-south patterns were evident for *O. tolmiei*. Correlation results were similar to those obtained with MIB. In *O. philadelphia* MIB was positively correlated with MEJUNT ($p < .003$), MIJUNT ($p < .001$), MAJUNT ($p < .02$), MEJULT ($p < .001$) (Table 26). For *O. tolmiei* MIB increased with increasing MIJULT and decreased with increasing EVAP ($p < .03$) (Table 27).

MINIMUM FREQUENCY OF MC SYLLABLE (MIC). *Oporornis tolmiei* averaged 14.9% higher MIC than *O. philadelphia* (Table 24) (APPENDIX G). Many *O. philadelphia* and *O. tolmiei* populations means were not significantly different from each other (Figure 92). All four subsets were comprised of *O. philadelphia* and *O. tolmiei* populations. A large amount of overlap between *O. philadelphia* and *O. tolmiei* populations is evident from Bivariate plots of MIC and NNA (Figure 85). Regressions on latitude and longitude were similar to MIA and MIB (Table 25). In *O. philadelphia* MIC decreased from north to south ($p < .001$) and from east to west ($p < .02$). However, only 10.8% and 2.6% of the variation in this character was attributed to variation in latitude and longitude respectively. Results of correlation analyses of MIC and environmental variables followed the same trend as with MIA and MIB for both taxa. MIC was positively correlated with MEJUNT ($p < .001$), MIJUNT ($p < .001$), MAJUNT ($p < .01$), and MEJULT ($p < .001$) for *O. philadelphia* (Table 26). For *O. tolmiei* MIC was positively correlated with MIJULT ($p < .03$) and negatively correlated with EVAP ($p < .01$) (Table 27).

MAXIMUM FREQUENCY OF MA SYLLABLE. (MAA) *Oporornis tolmiei* averaged 6.2% higher MAA than *O. philadelphia* (Table 24) (APPENDIX G). Not all *O. philadelphia* locality means were significantly different from *O. tolmiei* locality means (Figure 93). Four subsets contained a mixture of populations of each taxon. Bivariate plots of NNA and MAA also revealed nearly complete overlap of *O. philadelphia* and *O. tolmiei* populations (Figure 85). Significant regressions on latitude and longitude were different for *O. philadelphia* and *O. tolmiei* (Table 25). MAA decreased significantly from

east to west ($p < .001$) and south to north ($p < .001$) in *O. philadelphia*. No significant linear relationships between MAA and latitude or longitude were observed for *O. tolmiei*. Results of correlation analyses between MAA and environmental variables were similar in *O. philadelphia* and *O. tolmiei*. For *O. philadelphia* MAA increased with increasing MEJUNT ($p < .001$), MIJUNT ($p < .04$), MEJULT ($p < .001$), and MIJULT ($p < .001$) (Table 26). In *O. tolmiei* MAA was positively correlated with MIJUNT ($p < .01$), MAJUNT ($p < .01$), MIJULT ($p < .006$), MAJULT ($p < .001$), and negatively correlated with MEJULP ($p < .006$) (Table 27).

MAXIMUM FREQUENCY OF MB SYLLABLE (MAB). *Oporornis tolmiei* averaged 6.0% higher MAB than *O. philadelphia* (Table 24) (APPENDIX G). All population means of *O. philadelphia* were not significantly different from all *O. tolmiei* population means (Figure 94). None of the five subsets were composed exclusively of one taxon. Bivariate plots revealed nearly complete overlap of populations of each taxon (Figure 85). Regressions on latitude and longitude were different for these taxa (Table 25). In *O. philadelphia* MAB decreased from south to north ($p < .001$) and from east to west ($p < .001$). Variation in longitude accounted for more variation in MAB than latitude for *O. philadelphia* (19.7% for latitude versus 22.3% for longitude). No significant regressions of MAB on latitude or longitude were evident for *O. tolmiei*. Correlations between MAB and environmental variables were similar for these taxa. In *O. philadelphia* MAB was positively correlated with MEJUNT ($p < .001$), MIJUNT ($p < .03$), MAJUNT ($p < .004$), MEJULT ($p < .001$), and MIJULT ($p < .001$) (Table 26). MAB was positively correlated with MEJUNT ($p < .01$),

MIJUNT ($p < .001$), MAJUNT ($p < .04$), MIJULT ($p < .01$), MAJULT ($p < .009$) and negatively correlated with MEJULP ($p < .004$) in *O. tolmiei* (Table 27).

MAXIMUM FREQUENCY OF MC SYLLABLE (MAC). *Oporornis tolmiei* averaged 6.7% higher MAC than *O. philadelphia* (Table 24) (APPENDIX G). Most localities of *O. philadelphia* and *O. tolmiei* were not significantly different from each other (Figure 95). All four subsets contained populations from each taxon. Bivariate plots of NNA and MAC showed poor separation of *O. philadelphia* and *O. tolmiei* populations (Figure 85). Regressions of MAC on latitude showed a decrease in *O. philadelphia* and *O. tolmiei*. This linear relationship was highly significant in *O. philadelphia* ($p < .001$) but less so in *O. tolmiei* ($p < .02$) (Table 25). In *O. philadelphia* 29.1% of the variation in MAC was attributed to latitudinal variation versus only 4.7% in *O. tolmiei*. Only *O. philadelphia* exhibited a significant linear relationship with longitude ($p < .001$). Variation in longitude explained 26.9% of the variation of MAC for *O. philadelphia*. MAC was correlated with similar environmental variables in *O. philadelphia* and *O. tolmiei*. For *O. philadelphia* MAC was positively correlated with MEJUNT ($p < .001$), MIJUNT ($p < .001$), MAJUNT ($p < .001$), MEJULT ($p < .001$), and MIJULT ($p < .001$) (Table 26). MAC was positively correlated with MIJUNT ($p < .01$), MAJUNT ($p < .02$), MIJULT ($p < .009$), MAJULT ($p < .006$) and negatively correlated with MEJUNP ($p < .006$) and MEJULP ($p < .003$) for *O. tolmiei* (Table 27).

NUMBER OF NOTES PER FA SYLLABLE (NFA). *Oporornis tolmiei* averaged 41.4% more FA syllables than *O. philadelphia* (Table 24)

(APPENDIX G). At the population level, all *O. tolmiei* populations means were not significantly different from each other (Figure 96). Paradise Valley songsters had a very high average NFA and formed its own subset. The other two subsets contained a mixture of *O. philadelphia* and *O. tolmiei* populations. Bivariate plots of NFA and MIFB showed the best separation of *O. philadelphia* and *O. tolmiei* populations (Figure 97). Both taxa had significant regressions of NFA on latitude (Table 25). NFA decreased from south to north. Variation in latitude explained 27.1% of the variation in NFA for *O. philadelphia* ($p < .001$) and 17.3% in *O. tolmiei* ($p < .001$). Only *O. philadelphia* exhibited a significant linear relationship between NFA and longitude. NFA decreased from east to west in *O. philadelphia* ($p < .001$). Results of correlation analyses between NFA and environmental variables were different in these taxa. In *O. philadelphia* NFA increased with increasing MEJULT ($p < .01$) and MIJULT ($p < .02$) (Table 26). NFA was negatively correlated with MEJUNT ($p < .004$), MIJUNT ($p < .02$), MEJUNP ($p < .001$), MEJULP ($p < .02$), RELH ($p < .04$) and positively correlated with MAJULT ($p < .03$) and JULWT ($p < .009$) for *O. tolmiei* (Table 27).

NUMBER OF NOTES PER FB SYLLABLE (NFB). *Oporornis tolmiei* averaged 45.2% more FB syllables than *O. philadelphia* (Table 24) (APPENDIX G). However, not all *O. philadelphia* populations were significantly different from all *O. tolmiei* populations for NFB. None of the five subsets contained exclusively *O. tolmiei* or *O. philadelphia* populations (Figure 98). Bivariate plots of NFA and NFB also showed poor separation of *O. philadelphia* and *O. tolmiei* populations (Figure 97). Results of regression analyses of NFB were similar for latitude but not longitude in these taxa (Table 25). NFB

decreased significantly from south to north in *O. philadelphia* ($p < .001$) and *O. tolmiei* ($p < .001$). However, only 11.3% and 13.2% of the variation in this character was attributed to latitudinal variation for *O. philadelphia* and *O. tolmiei* respectively. NFB showed a significant linear relationship with longitude only in *O. philadelphia* ($p < .001$). Longitudinal variation explained only 12.4% of the variation in NFB in *O. philadelphia*. Correlations between NFB and environmental variables were different in *O. philadelphia* and *O. tolmiei*. NFB was positively correlated with temperature in *O. philadelphia* but negatively correlated with temperature in *O. tolmiei*. Both taxa exhibited negative correlations with precipitation variables. NFB was positively correlated with MIJULT ($p < .007$) and negatively correlated with MEJULP ($p < .04$) in *O. philadelphia* (Table 26). In *O. tolmiei* NFB was negatively correlated with MEJUNT ($p < .004$) and MEJUNP ($p < .04$) (Table 27).

INTERVAL BETWEEN FA AND FB (IFA). *Oporornis tolmiei* averaged 40.0% longer IFA than *O. philadelphia* (Table 24) (APPENDIX G). Some *O. philadelphia* populations were not significantly different from some *O. tolmiei* populations (Figure 99). Two subsets contained mixtures of populations from each taxon. For results of Bivariate plots, see NFA. Regressions of IFA on latitude were similar for both taxa (Table 25). IFA increased from south to north in *O. philadelphia* ($p < .001$) and *O. tolmiei* ($p < .001$). Variation in latitude explained more of the variation in IFA for *O. philadelphia* (34.1%) than for *O. tolmiei* (18.8%). Regression on longitude was significant only for *O. philadelphia* ($p < .001$). Longitudinal variation explained 39.6% of the variation in this character. Correlation analyses yielded different results for *O.*

philadelphia and *O. tolmiei*. Precipitation variables were positively correlated with IFA in *O. tolmiei* and negatively correlated with IFA in *O. philadelphia*. In *O. philadelphia* IFA was negatively correlated with MEJUNT ($p < .01$), MAJUNT ($p < .02$) and MEJULP ($p < .03$) (Table 26). For *O. tolmiei* IFA was positively correlated with MEJUNP ($p < .001$), MEJULP ($p < .005$), and RELH ($p < .01$) (Table 27).

INTERVAL BETWEEN FB AND FC (IFB). *Oporornis tolmiei* averaged 40.0% longer IFB than *O. philadelphia* (Table 24). However, results of an ANOVA revealed that no significant differences existed between all *O. philadelphia* and *O. tolmiei* populations. Bivariate plots of NFA and IFB showed good separation of *O. philadelphia* and *O. tolmiei* populations (Figure 97). Regressions of IFB on latitude and longitude were not significant for either taxon ($p > .05$). Significant correlations with environmental variables were evident only for *O. tolmiei*. IFB was positively correlated with MEJUNP ($p < .001$), MEJULP ($p < .01$) and RELH ($p < .04$) (Table 27).

MINIMUM FREQUENCY OF FA (MIFA). *Oporornis tolmiei* averaged 26.5% higher MIFA than *O. philadelphia* (Table 24) (APPENDIX G). At the population level, most *O. philadelphia* localities were significantly different from most *O. tolmiei* localities (Figure 100). Bivariate plots of NFA and MIFA also showed good separation of *O. philadelphia* and *O. tolmiei* populations (Figure 97). All three subsets were composed of populations from each taxon. MIFA did not show a significant linear relationship with latitude or longitude for either taxon. Significant correlations between MIFA and

environmental variables were evident only for *O. tolmiei*. MIFA increased with increasing MEJULP ($p < .02$) (Table 27).

MINIMUM FREQUENCY OF FB (MIFB). *Oporornis tolmiei* averaged 26.7% higher MIFB than *O. philadelphia* (Table 24) (APPENDIX G). Not all *O. philadelphia* localities were significantly different from *O. tolmiei* localities (Figure 101). Three subsets contained populations from both taxa. However, populations of both taxa were separated on Bivariate plots of NFA and MIFB (Figure 97). Only *O. philadelphia* showed significant linear relationships with latitude ($p < .006$) and longitude ($p < .007$) for this character (Table 25). Variation in latitude and longitude explained 34.1% and 5.8% of the variation in MIFB respectively. MIFB was negatively correlated with temperature in *O. philadelphia* (Table 26) and positively correlated with precipitation variables in *O. tolmiei* (Table 27). MIFB decreased with increasing MIJULT ($p < .04$) in *O. philadelphia*. For *O. tolmiei* MIFB increased with MEJULP ($p < .02$) (Table 27).

MAXIMUM FREQUENCY OF FA (MAFA). *Oporornis tolmiei* averaged 26.8% higher MAFA than *O. philadelphia* (Table 24) (APPENDIX G). However, all *O. philadelphia* locality means were not significantly different from all *O. tolmiei* locality means (Figure 102). One of five subsets was composed exclusively of *O. tolmiei* localities. The remaining subsets were composed of localities from both taxa. Bivariate plots of MAFA and NFA showed little overlap between populations of *O. philadelphia* and *O. tolmiei* (Figure 97). Regressions of MAFA on latitude and longitude were different for *O.*

philadelphia and *O. tolmiei* (Table 25). In *O. philadelphia* MAFA decreased from north to south ($p < .004$). A similar pattern was found in *O. tolmiei* ($p < .006$). However variation in latitude explained only 6.0% and 7.5% of the variation in MAFA for *O. philadelphia* and *O. tolmiei* respectively. Correlations between MAFA and environmental variables were different for each taxon. In *O. philadelphia* MAFA was negatively correlated with MAJULT ($p < .04$) (Table 26). MAFA was positively correlated with MAJUNT ($p < .001$), MIJULT ($p < .009$), MAJULT ($p < .001$), EVAP ($p < .006$), JULWT ($p < .007$) and negatively correlated with MEJUNP ($p < .001$), MEJULP ($p < .01$) and RELH ($p < .002$) in *O. tolmiei* (Table 27).

MAXIMUM FREQUENCY OF FB (MAFB). *Oporornis tolmiei* averaged 30.4% higher MAFB than *O. philadelphia* (Table 24) (APPENDIX G). Most *O. philadelphia* and *O. tolmiei* population means were significantly different from each other (Figure 103). Only one of four subsets was comprised exclusively of *O. tolmiei* populations. Three subsets contained a mixture of populations of both taxa. *O. philadelphia* and *O. tolmiei* population means showed almost complete separation on bivariate plots of NFA and MAFB (Figure 97). Regression of MAFB on latitude was significant only for *O. tolmiei* ($p < .001$). However, only 11.1% of the variation could be explained by latitudinal variation. MAFB did not vary significantly with longitude for *O. philadelphia* or *O. tolmiei*. Correlations between MAFB and environmental variables were similar to results obtained for MAFA. For *O. philadelphia* MAFB was negatively correlated with MEJULP ($p < .007$) (Table 26). MAFB was negatively correlated with MEJUNP ($p < .001$) MEJULP ($p < .01$) and RELH

($p < .005$) in *O. tolmiei* (Table 27). Also in *O. tolmiei*, MAFB was positively correlated with MAJUNT ($p < .001$), MIJULT ($p < .005$), MAJULT ($p < .003$), RELH ($p < .006$), and JULWT ($p < .009$) (Table 27).

6.2 MULTIVARIATE ANALYSIS OF SONG PARAMETERS

CA's, PCA's, and DFA's have been widely used in the literature, either separately or in conjunction with one or both of the others to describe variation in different taxa. I used three multivariate analyses to determine the degree of distinctness of each taxon based on different song character complexes. I performed each of these analyses on different levels (complexes) of primary song parameters to assess the distinctness of each taxon for each song complex and all complexes combined. Finally the degree of concordance of each analysis is discussed.

In each of these analyses the OTU's were the populations and the data were the means per population for each character. Sample sizes for both taxa ranged from four to twenty-five individuals for the different populations.

6.2.1 CLUSTER ANALYSIS (CA)

I performed CA's on the song parameter data to assess the phenetic similarity of *O. philadelphia* and *O. tolmiei* populations. Populations were the OTU's and the population means for each parameter variable were the data used in these analyses. Separate analyses were conducted for each of the different song parameter complexes - frequency, duration/interval and syllable

complexes and. An analysis of all song variables combined was also performed on these data.

If these taxa are separate in multivariate space, than two large homogeneous clusters of populations should emerge from each of the CA's, one composed only of *O. philadelphia* populations and the other containing only *O. tolmiei* populations. This may also vary with the character complex used. These taxa may be more different for one complex of variables than another (also indicated by the univariate data). The degree of heterogeneity of composition of the larger clusters reflects the degree of separation of these taxa based on the complex used in the analysis.

6.2.1.1 CA - FREQUENCY COMPLEX

The frequency complex was the best discriminator of populations of these taxa. Three major clusters emerge at the 1.20 distance mark (Figure 104). Cluster 1 contains only *O. tolmiei* populations. Within cluster 1 there are two smaller clusters - 1A composed of southwestern *O. tolmiei* populations and 1B composed of some northern populations (LO, SC, MC and one southern population - CE). Cluster 2 is composed of *O. philadelphia* populations which are further subdivided into eastern, western and Newfoundland clusters (2A, 2B, 2C respectively). Cluster 2A is mixed, containing one western population - OB. The *O. philadelphia* Fort Nelson River population was the most divergent population, joining with the two majors clusters at the 1.50 distance mark.

Frequency variables are the best variables used for separating *O. philadelphia* and *O. tolmiei* primary song. Two distinct homogeneous

clusters emerged. The greatest differences in primary song between these taxa lie in this parameter complex. The results of clustering of OTU's based on variables from this complex best represented the actual geographic locations where songs were recorded.

6.2.1.2 CA - DURATION/INTERVAL COMPLEX

At the 1.05 distance mark three major clusters emerge (Figure 105). All three clusters are heterogeneous, composed of populations from both taxa. The smaller clusters were also heterogeneous, except for 2B.

No discernible pattern of separation was evident from the clusters based on variables in this complex. The duration of primary song and timing between syllables appears to be very similar in each taxon. This trend was also shown by the univariate data.

6.2.1.3 CA - SYLLABLE COMPLEX

The syllable complex also poorly discriminates populations of each taxon (Figure 106). At the 1.05 distance mark on the phenogram three major clusters (1, 2, 3) emerge. Clusters 1 and 2 are heterogeneous, composed of populations from both taxa. The first cluster contains *O. tolmiei* populations from the middle latitudes of its breeding range along with eastern populations of *O. philadelphia*. Within the first cluster at the 0.60 distance mark three smaller clusters are apparent (1A, 1B, 1C). A majority of the populations of 1A are *O. tolmiei* along with two eastern *O. philadelphia* populations (VP, DO). 1B

contains only *O. philadelphia* populations. One *O. tolmiei* population belonged to 1C (FK). Cluster 2 contains only two northern populations of *O. tolmiei* (LO, MC) but 5 northwestern populations (SL, WH, FR, LP) and one eastern population (MI) of *O. philadelphia*. The third cluster contains only Newfoundland *O. philadelphia* populations.

Except for the divergent Newfoundland populations, mainland populations of *O. philadelphia* and *O. tolmiei* show some overlap for the syllable complex. Major clusters are heterogeneous. However, the smaller clusters within them are relatively homogeneous with little mixing of populations from both taxa.

6.2.1.4 CA - ALL COMPLEXES

Two major clusters were evident at the 1.00 distance mark when all parameter variables were considered simultaneously (Figure 107). A third cluster contained one western *O. philadelphia* population from Alberta (SL). Clusters 1 and 2 were homogeneous containing only *O. philadelphia* (2) or *O. tolmiei* (1) populations. There were no geographic patterns within clusters 1 and 2. Eastern, western, northern and southern populations were mixed together in minor clusters.

When all variables are considered simultaneously separation of populations of each taxon is complete with one highly divergent *O. philadelphia* population from central Alberta. However, no spatial pattern within either taxon is apparent.

6.2.2 PRINCIPAL COMPONENTS ANALYSIS (PCA)

I used PCA's to study variation in song parameters of populations of *O. philadelphia* and *O. tolmiei* and to assess the degree of separation of these populations based on the first three Principal Components extracted from variance-covariance matrices. I performed separate PCA's on each of the song parameter complexes - frequency, duration/interval and syllable complexes. A separate PCA was also performed on all the parameter variables combined. The OTU's were populations from both taxa. Populations means for each song parameter were used in each analysis. For each complex I used MacSpin 1.1 to plot Principal Component scores for the first three components in three dimensions. Axes were rotated until the best separation of OTU's was achieved.

The distribution of the OTU's in 3D space reflects the degree of separation based on the first three Principal Components for each complex. The degree of separation depends on degree of distinctness between taxa for each song parameter complex.

6.2.2.1 PCA - FREQUENCY COMPLEX

O. philadelphia and *O. tolmiei* OTU's were completely separated along the first three component axes (Figure 108). Lower frequency populations were plotted on the lower left part of the graph and higher frequency populations on the upper right of the graph. There was no relationship between the proximity of OTU's on the plot and geographic proximity of samples for either taxon.

PRIN1 accounted for 65.6% of the total variation (Table 28). All frequency variables were positively correlated with PRIN1. MAFA and MIFA had the highest loading on PRIN1. PRIN1 is a "frequency factor" for PART II syllables of primary song. PRIN2 accounted for 17.2% of the total variation. Two minimum frequency variables were negatively weighted on PRIN2. PRIN3 accounted for only 9.8% of the total variation. Only MIA was positively correlated with PRIN3. It also had the highest loading on PRIN3.

6.2.2.2 PCA - DURATION/INTERVAL COMPLEX

Plots of the first three principal components scores for this complex separated most populations of *O. philadelphia* and *O. tolmiei* (Figure 109). Three *O. philadelphia* populations from Newfoundland (CB, RO AND SV) were widely separated from mainland populations of both taxa. One Newfoundland population (SA) and a Quebec population (SP) was mixed in with *O. tolmiei* OTU's. All other *O. philadelphia* OTU's clustered together with each other in the right part of the plot, separate from the remaining *O. tolmiei* populations which also clustered together with each other in the lower left. Ontario, Alberta and British Columbia OTU's of *O. philadelphia* were above the PRIN1 axis. Quebec, Maine and one Alberta population segregated below the PRIN1 axis. There was no geographic pattern to the clustering of *O. tolmiei* populations.

PRIN1 accounted for 84.4% of the total variation (Table 29). IMA and DUR had the highest loadings on PRIN1. PRIN2 accounted for 8.9% of the total variation. IMA and IMB had high loadings on this component. PRIN3 was the only component where all characters were positively correlated with it. It

accounted for 6.7% of the total variation. DUR had the highest loading on PRIN3.

6.2.2.3 PCA - SYLLABLE COMPLEX

There was some overlap between *O. philadelphia* and *O. tolmiei* OTU's along the first three principal component axes for syllable variables (Figure 110). *O. philadelphia* populations from Newfoundland (PS, CB, SV, RO) clustered together in the upper left of the plot. *O. philadelphia* OTU's from Alberta (WH, LP, SL, OB) and British Columbia (FR) clustered near the Newfoundland populations. *O. philadelphia* populations from Ontario and Quebec and Maine clustered along the PRIN2 axis. One *O. philadelphia* population from Ontario (MI) was mixed with *O. tolmiei* OTU's. There was no geographic pattern to the clustering of *O. tolmiei* OTU's. MC from British Columbia was separated from other *O. tolmiei* populations.

PRIN1 accounted for 50.1% of the total variation (Table 30). NPSO and NDSO had the highest loadings on PRIN1. This was a "song complexity" factor since both variables described the number of different syllables per song. Populations in the lower part of the plot had more complex songs than populations in the upper half of the plot. PRIN2 was the only component which was positively correlated with all syllable variables. PRIN2 accounted for 43.7% of the total variation. NNA, NNB and NNC had the highest loadings on PRIN2. PRIN3 accounted for only 2.6% of the total variation. NSSO had the highest loading on PRIN3.

6.2.2.4 PCA - ALL SONG COMPLEXES

When all song parameters were considered simultaneously separation between *O. philadelphia* and *O. tolmiei* OTU's was complete (Figure 111). OTU's within taxa that are in close geographic proximity of one another were not necessarily clustered together in the 3D plot. For example in *O. philadelphia* populations OTU's from Ontario, Quebec, Maine and Alberta were mixed.

PRIN1 accounted for 46.4% of the total variation (Table 31). NFA and NFB had the highest loadings on PRIN1. In contrast to PRIN1, PRIN2 had variables which were positively and negatively correlated with it. Interval and some frequency variables were negatively weighted on PRIN2. IFA, IMC and NFA had the highest loadings on PRIN2. PRIN3 accounted for only 7.9% of the total variation. Some characters from each of the song parameter complexes weighted positively and others were weighted negatively on PRIN3. IMA, IMB and NFB had the highest loadings on PRIN3.

6.2.3 DISCRIMINANT FUNCTION ANALYSIS (DFA)

In addition to CA's and PCA's used above I also used DFA's on song parameter characters to further test distinctness of primary song of each taxon. As in the analyses above, OTU's were populations from each taxon and the data were population means for each parameter character. Four separate DFA's were performed on the data; one for each of the different complexes - frequency, duration/interval, syllable and a separate analysis using characters

from all the complexes simultaneously. Populations were labeled prior to the analysis as *O. philadelphia* or *O. tolmiei*.

I present standardized coefficients and classification functions from canonical variates analysis for each complex. As in the morphological DFA's the standardized coefficients reveal the relative importance of each song parameter character in discriminating these taxa. Classification functions were also computed for OTU's. As in the morphological DFA's these were used to assign OTU's to *O. philadelphia* or *O. tolmiei*. The per cent of OTU's correctly classified to each taxon indicates the relative discriminatory power of the complex used. However, in order to include data from as many songsters as possible these functions were generated based on character means per locality and not raw scores for each songster. Therefore caution must be exercised when using these functions to classify unknown **songsters**. I also plotted DF scores for each song parameter analysis.

I was interested in the nature and extent of variation in song parameter complexes. Therefore I graphed Mahalanobis' D^2 between taxa for each of the different song parameter complexes - frequency, duration/interval and syllable complexes. These intertaxon phenetic distances serve the same function as those calculated for different morphological complexes - i.e., reveal the amount of differentiation between taxa for different song parameter complexes.

6.2.3.1 DFA - FREQUENCY COMPLEX

MIFA and MAFA had higher standardized coefficients and most effectively discriminated between *O. philadelphia* and *O. tolmiei* while MIA was

least effective (Table 32). Projections of *O. philadelphia* and *O. tolmiei* OTU's scores on the discriminant function axis showed that one *O. philadelphia* from central Alberta (LP) was classified as *O. tolmiei* (Figure 112).

6.2.3.2 DFA - DURATION/INTERVAL COMPLEX

DUR and IFA were the best discriminators of *O. philadelphia* and *O. tolmiei* while IMA was the worst (Table 33). Plots of DF scores did not completely separate *O. philadelphia* and *O. tolmiei* OTU's. Two OTU's (from central Alberta and the Gaspé Peninsula in Quebec) were misclassified as *O. tolmiei* OTU's (Figure 113).

6.2.3.3 DFA - SYLLABLE COMPLEX

According to the standardized coefficients NSSO and NFA were the most effective discriminators of *O. philadelphia* and *O. tolmiei* OTU's (Table 34). Projections of canonical variate scores on the discriminant function axis did not separate all OTU's. SP from the Gaspé Peninsula and VP in central Quebec were misclassified as *O. tolmiei* (Figure 114).

6.2.3.4 DFA - ALL SONG CHARACTERS

Plots of DF scores on the discriminant function axis did not separate all OTU's. One *O. philadelphia* population from Newfoundland was misclassified as *O. tolmiei* (Figure 115). Two syllable parameters (NPSO, NDSO) and

several frequency parameters (MAXS, MIA, MIB, MIC, MAC) most effectively discriminated between *O. philadelphia* and *O. tolmiei* OTU's. Characters which least effectively discriminated between taxa included NNA, IMA, IMC, and MAFA (Table 35).

6.2.3.5 Mahalanobis' D^2 BETWEEN TAXA FOR THE SONG PARAMETER COMPLEXES

Mahalanobis' D^2 between group centroids was greatest when all characters were used for the discriminant function and least for SYLLABLE complex characters (Figure 116). Distance between taxa was also small for DURATION/INTERVAL complex characters. Mahalanobis' D^2 ranged from 3.94 for the SYLLABLE complex to 488.38 when all parameter characters were analyzed simultaneously. Among the three different complexes the greatest differentiation between taxa exists for FREQUENCY complex characters.

6.2.3.6 STEPWISE DFA FOR ALL SONG PARAMETERS

I performed a STEPWISE DFA using all the song parameter characters to determine which combination of these characters provided the best separation of *O. philadelphia* and *O. tolmiei* OTU's. As in the STEPWISE DFA for morphological characters the song parameters were entered one at a time (forward selection) based on the level of a F test from analysis of covariance. The overall significance level for entry or removal of variables was 0.15.

The STEPWISE DFA proceeded for five steps in the song parameter analysis. In order of entry, the combination of MIFA, NFA, NNC, NNB and IMA provided the best separation of *O. philadelphia* and *O. tolmiei* OTU's (Table 36). In each step of the DFA Wilk's Lambda approached 0.00 and was highly significant based on the F approximation from Wilk's Lambda (Table 36). The results indicate that variables from each of the different song parameter complexes - FREQUENCY, DURATION/INTERVAL and SYLLABLE are necessary to provide the best separation of *O. philadelphia* and *O. tolmiei* OTU's.

6.3 ANALYSIS OF GEOGRAPHIC DISTRIBUTION OF SONG SYLLABLES

SYLLABLE SHARING BETWEEN *O. philadelphia* AND *O. tolmiei*. From the sonographs of *O. philadelphia* and *O. tolmiei* males' song I constructed separate syllable catalogues for each taxon and compared the syllable repertoires of each taxon. There was little overlap or syllable sharing between taxa. From the combined total of 173 syllables and variants (*O. tolmiei* - 125 and *O. philadelphia* - 48), only six (3.46%) were shared between taxa. These syllables were: MA88 = MO1B, MA85 = MO99F, MA74 = MO99I, MA73 = MO6, MA23 = MO16C, MA12 = MO9 (Figure 117). These syllables were not perfect matches. There are frequency differences as well as some subtle differences between the notes which make up each syllable. Therefore syllable sharing between these taxa is minimal (however, I have not sampled all the syllables throughout each taxon's range). It is important to note that **syllables were shared by individuals, not populations.**

A major difference between the two taxa was the greater diversity of syllables and syllable variants in the repertoire of *O. tolmiei* compared to *O. philadelphia*. I compared the number of new syllables and variants encountered with each new males' song for *O. philadelphia* and *O. tolmiei* separately which indicates the different patterns of syllable diversity in these taxa. Figure 118 shows that more new syllables and variants are encountered per new *O. tolmiei* male than per new *O. philadelphia* male. From the 107 *O. tolmiei* males' songs there were 125 different syllables and variants while there were only 48 syllables and variants from 185 *O. philadelphia* males sampled. From these data I calculated a simple diversity index for each taxon: $D = (\text{Total number of syllables and variants}) / (\text{Number of songsters})$, $D_{O. tolmiei} = 125/107 = 1.168$ $D_{O. philadelphia} = 48/185 = 0.259$. $D_{O. philadelphia}$ is much greater than $D_{Oporornis tolmiei}$.

***Oporornis philadelphia*: ISOGLOSS RESULTS.** For each syllable I enclosed localities which shared the given syllable type (see APPENDIX J for geographic distribution of syllables and variants) with isoglosses. These isoglosses represent boundaries which contain the syllables. Only those syllables which were found in two or more localities were plotted on the map.

In the range of *O. philadelphia* isogloss analysis uncovered three regional dialect systems (Figure 119). A regional dialect is a large community of songsters which share the same song type over distances of 1000km - 1500km. The Newfoundland populations compose the easternmost system. This is adjacent to an eastern continental system which stretches from the Gaspé Peninsula to western Ontario. The third regional dialect begins in

western Ontario reaching the western boundary of the breeding range in Alberta and British Columbia. There is no syllable sharing between the Newfoundland system and either continental system. However, some birds in the two continental systems do share some syllables.

MO18 and MO19 syllables are the dominant syllables in the Newfoundland regional dialect (Figure 120). None of the mainland birds sang these syllables. Sampling along the eastern coast of Quebec and southern Labrador is needed to confirm the absence of these syllables from the mainland.

MO1 and MO99 syllables are the most common syllables in the eastern continental system (Figure 121). Three males in central Alberta also sang the MO1 syllables. Within this continental eastern system is a smaller regional dialect system in central Quebec and Maine, spilling over into eastern Ontario. This represents a concentration of different MO1 and MO99 variants.

The western regional dialect is dominated by songs with MO6 syllables (Figure 122). Most MO6 songs were monosyllabic which easily separated them from the two syllable *O. tolmiei* song types near the contact points in Alberta and British Columbia. Eight birds from western Ontario also sang the MO6 syllable. In addition to the MO6 syllables there were some males with MO8, MO9, MO10, MO14, MO16, MO17 or MO84 syllables in the western system. Another minor regional dialect in central Alberta is evident in the larger western system. This represents a concentration of the MO8 - MO84 syllables. The western birds were more variable than the eastern continental and Newfoundland songsters.

***Oporornis philadelphia*: CA RESULTS.** The results of the CA for *O. philadelphia* were similar to the isogloss results. The dendrogram of *O. philadelphia* songsters also shows three major regional dialects - Newfoundland, eastern continental and western continental systems (Figure 123). This is a condensed version of the original dendrogram output from NTSYS in order to fit on to the page, individuals songsters are not shown). The Newfoundland cluster is composed only of Newfoundland songsters while the other two clusters are mixed. The eastern continental cluster contained nine songsters from Alberta. These western birds possessed some eastern syllables in their songs. For instance, three Alberta males sang a MO1 syllable in combination with MO16 or MO86 or MO89 syllables. The other Alberta birds which clustered with the eastern regional dialect sang the MO16 syllable with either MO8 or MO9 syllables. The western birds made up less than 10% of the entire eastern continental system. Seventeen males from Ontario clustered together with the western regional dialect. MO6 is the dominant syllable of Alberta and British Columbia males but was also found in Ontario. Ontario males which clustered with the western birds possessed MO6 or MO90 syllables. These birds made up 50% of the western continental cluster.

Western Ontario appears to be an area of mixing of the two major continental regional dialects. Songsters from this area sang MO6 or MO1 syllables. This was the only area in eastern Canada where MO1 was not the sole syllable type of Part I of the song. Birds to the east (except in Newfoundland) sang only MO1 syllables and birds to the west sang MO6 or other syllables and an rarely an MO1 syllable.

Males within a cluster sang the same syllables or variants as the other members within the cluster. Most *O. philadelphia* males joined together to form clusters between the 0.95 - 1.00 similarity levels. This indicates a strong resemblance among songsters within a given cluster. There was little individual variation in syllables among individuals within clusters. Individual variation in song was manifested in the number of syllables, interval between syllables and frequency parameters.

***Oporornis tolmiei*: ISOGLOSS RESULTS.** I used the same isogloss procedure outlined above for mapping *O. tolmiei* syllables (see APPENDIX K for geographic distribution of syllables).

Figure 124 shows a haphazard distribution of MA syllables in the breeding range of *O. tolmiei*. Sonograph tracings in Figure 125 illustrate the diversity of song types within a *O. tolmiei* locality (Jarbidge, Nevada). None of the song syllables from three males from Jarbidge, Nevada are shared across individuals. This type of syllable differentiation within a locality is common to all *O. tolmiei* localities except in Washington and Oregon. There was some segregation of songsters in central and northern Oregon and Washington (Figure 126). However, most syllables were shared by songsters from breeding localities scattered throughout the range of *O. tolmiei*.

***Oporornis tolmiei*: CA RESULTS.** Because most males sang a unique song type which did not bare a strong resemblance to its nearest neighbor, the results of the CA of *O. tolmiei* males songsters did not reveal any major regional or local dialect systems similar to those found in *O. philadelphia*. There were six major clusters around the 0.05 similarity mark (Figure 127). However each of these major clusters was composed of males scattered

throughout the breeding range of *O. tolmiei* (except for a minor group in cluster 5). The minor cluster in cluster 5 contained males from central and northern Oregon along with some males from Washington. This was the only cluster where all the songsters were within 600km of each other. These results are consistent with the isogloss results. In the breeding range of *O. tolmiei* there appears to be a segregation of songsters with similar song types in Washington and Oregon but the remainder of songsters from the breeding range *O. tolmiei* do not show any spatial pattern of syllable distribution. More sampling is needed in the breeding range of *O. tolmiei*.

In contrast to *O. philadelphia* males which clustered together below the 0.50 similarity mark, most *O. tolmiei* males joined together at the 0.50 similarity mark or higher. This indicates that within any given cluster *O. philadelphia* males were more similar to each other than *O. tolmiei* males were with each other. Individual variation among *O. tolmiei* males was manifested in both the syllable and song parameters.

6.4 RESULTS OF SONG PLAYBACK EXPERIMENTS

Twenty-two males from both taxa were subjected to song playback experiments (Table 37). Songsters which continued to attack the same speaker after song types had been switched or spent the entire duration of the playback experiment in the midway between the two speakers were scored as unable to discriminate song types.

Only one *O. tolmiei* male from Liard River from northeastern British Columbia was unable to discriminate between *O. philadelphia* and *O. tolmiei*

song types. Five *O. tolmiei* males from the potential contact areas and two allopatric *O. tolmiei* (McBride, British Columbia) males discriminated between *O. tolmiei* and *O. philadelphia* song types. Four *O. philadelphia* males from the allopatric portion of the species range and 10 males from the potential contact zones were able to discriminate *O. philadelphia* from *O. tolmiei* songs. This evidence indicates that *O. philadelphia* and *O. tolmiei* males are able to discriminate species identity by recognizing conspecific song versus other. Dilger (1956) assumed that females also discriminate between taxa based on song. Although no tests for this were carried out in this study I assume that *O. philadelphia* and *O. tolmiei* females are also discriminating similarly to males.

6.5 SUMMARY

UNIVARIATE ANALYSES - SPECIES DIFFERENCES. Species differences exist for all but two song parameters (Table 24). Per cent differences between species for song parameters ranged from 0.0% (IMB, IMC) - 45.2% (NFB) (Table 24). The average per cent difference between taxa for the syllable complex of variables was 18.7% (Table 24). Species differences in the number of notes per syllable were greatest for Part II syllables. Part I differences between taxa were slight. Differences between taxa ranged from 4.3% (NNA) to 45.2% (NFB) (Table 24) for the syllable complex. *Oporornis philadelphia* averaged more notes per Part I syllables (MA, MB and MC) while *O. tolmiei* had more notes per Part II syllables (FA, FB) and greater NSSO, NDSO, NPSO. *Oporornis tolmiei* averaged more NDSO, NSSO and NPSO (Table 24). The average per cent difference between taxa for duration and

interval variables was 18.0%. *Oporornis tolmiei* averaged 13.9% longer songs than *O. philadelphia* and longer intervals between Part II syllables.

Differences ranged from 0.0% (IMB, IMC) to 40.0% (IFA, IFB) (Table 24).

Species differences were greatest for intervals between Part II syllables and smallest (or non-existent) for intervals between Part I syllables. The average per cent difference for frequency variables was 16.5% higher frequencies in *O. tolmiei* song. Larger differences existed between taxa for Part II syllable frequencies. Differences were slight (% difference < 7.0%) between maximum frequencies of Part I syllables.

SPECIES DIFFERENCES - BIVARIATE PLOTS. Different bivariate plots of song variables revealed different degrees of separation of *O. philadelphia* and *O. tolmiei* populations. ENTIRE SONG CHARACTERS. Separation of *O. philadelphia* and *O. tolmiei* populations was poor for characters from this complex (Figure 78). NPSO x MINS was better than other combinations but still showed some overlap between populations from these taxa. PART I CHARACTERS. Bivariate plots of PART I elements also revealed poor separation of these taxa (Figure 85). Overlap was nearly complete for all PART I characters plotted against NNA. PART II CHARACTERS. There was little or no overlap between these taxa when PART II elements were plotted against NFA (Figure 97).

According to bivariate plots the greatest differentiation between these taxa occurred in the PART II CHARACTER complex. Differentiation in ENTIRE SONG and PART I complexes was absent. Differences between these taxa have evolved in the second half of the song. Some *O. philadelphia* songsters (e.g., MO6) had songs with only PART I while all *O. tolmiei* songsters had at

least two parts per song (and in some cases three parts). The absence of PART II in some *O. philadelphia* songs and strong differentiation between *O. philadelphia* and *O. tolmiei* songsters for PART II elements could serve as species markers in primary song of each taxon.

GEOGRAPHIC VARIATION - UNIVARIATE ANALYSES. Many *O. philadelphia* and *O. tolmiei* population means for song characters were not significantly different from each other. Subsets of population means from SNK analyses often contained combinations of *O. philadelphia* and *O. tolmiei* populations.

GEOGRAPHIC VARIATION - REGRESSION ANALYSES. Results of regressions analyses of song characters on latitude and longitude were similar to morphological findings. Characters exhibiting significant linear regressions with latitude and longitude differed between taxa. In *O. philadelphia* there were 18 negative and three positive significant regressions of song characters on latitude while in *O. tolmiei* only five significant negative and three positive relationships between song characters and latitude were found (Table 25). Some frequencies, song duration and some syllable numbers decreased from south to north and intervals between MC-FA and FA-FB syllables increased in the range of *O. philadelphia* (Table 25). All frequency characters which varied significantly with latitude (except MIFB) covaried in the same direction (negative versus positive variation in MIFB) in *O. philadelphia's* range. Frequency variables also decreased together with increasing latitude in *O. tolmiei's* range except for MAFB which increased. Syllable characters covaried in the same direction (decreasing from south to north) in each taxon's range. Interval characters (MC-FA and FA-FB) and MIFB

increased with latitude in the range of *O. philadelphia*. In *O. tolmiei* intervals between MC-FA and FA-FB syllables also increased along with MAFB from south to north. In both taxa frequency variables for some PART I song frequencies decreased from south to north while some PART II frequencies increased. Intervals between song PARTS I and II (IMC) and between FA-FB (IFA) syllables increased in each taxon.

Sixteen negative and three positive significant regressions of song characters on longitude were found in *O. philadelphia*. Only one character was significantly related to longitude in *O. tolmiei*. In *O. philadelphia* all syllable variables covaried in the same direction (decreasing from east to west). All frequency variables with significant regressions (except MIFB which increased) also decreased from east to west in *O. philadelphia's* range. Although song duration decreased from east to west, intervals between PARTS I and II and between FA-FB syllables increased in the same direction. In *O. philadelphia* most characters which varied significantly with latitude also varied significantly with longitude. The interval between PART I and PART II of *O. philadelphia* and *O. tolmiei* song increased from east to west. For a majority of characters analyzed there was little reverse character variation between characters from the same complex (frequency, duration/interval, syllable).

Song characters for *O. philadelphia* were more often significantly related to latitude and longitude than characters for *O. tolmiei*. Most of the significant regressions on latitude and longitude in *O. philadelphia* and *O. tolmiei* were negative.

GEOGRAPHIC VARIATION - CORRELATION ANALYSES.

Significant correlations between song characters and environmental variables

were different for both taxa. The trend in correlations with Temperature and Precipitation variables was similar to the morphological correlation results. In *O. philadelphia* song characters were more often correlated with temperature variables while *O. tolmiei* characters were more often correlated with precipitation variables (Table 27). Seventy positive and eight negative correlations with Temperature variables were found for *O. philadelphia*. Only 27 positive and three negative correlations with Temperature variables were found for *O. tolmiei*. In *O. tolmiei* 25 positive and 24 negative correlations with Precipitation variables were significant. However, in *O. philadelphia*, only three positive and four negative correlations with Precipitation variables were significant.

A majority of the correlations between Temperature variables and different song parameters were positive for *O. philadelphia*. Songs from warmer regions contained more syllables and higher frequencies than songs from cooler parts of the breeding range. Intervals between some Part I and II syllables and MINS decreased in warmer climates. The number of notes per Part I syllables increased in areas where the Mean July precipitation increased in the range of *O. philadelphia* while syllables, intervals between syllables and maximum frequency of some Part II syllables decreased.

Except for Part I syllable frequencies, correlations between song elements and environmental data were different in *O. tolmiei*. Songs with higher Part I frequencies were found in warmer climates. Intervals between Part I syllables were shorter in climates with higher Wet Bulb temperatures and higher Relative Humidity. The minimum frequency also was lower in areas with high humidity. In areas with higher Mean July Precipitation the maximum

frequencies of Part II syllables was lower than in areas with lower July rainfall. These same frequencies were also lower in areas of high humidity. Although significant relationships between song parameters and July environmental variables exist I am not sure as to the biological significance of these results since singing activity deteriorates rapidly after the middle of July.

These correlations suggest *Oporornis philadelphia* song is more sensitive to temperature while *O. tolmiei* is affected more by precipitation variables.

MULTIVARIATE ANALYSIS. In each of the multivariate analyses the best separation of *O. philadelphia* and *O. tolmiei* OTU's was achieved using FREQUENCY COMPLEX parameters. Complete separation was also achieved when variables from each of the complexes were analyzed simultaneously. SYLLABLE and DURATION/INTERVAL COMPLEXES were poor discriminators of OTU's from these taxa.

CA's of FREQUENCY COMPLEX variables showed the best separation of *O. philadelphia* and *O. tolmiei* OTU's while DURATION/INTERVAL and SYLLABLE COMPLEXES showed poor separation of OTU's. Allopatric populations as well as those from the potential contact areas were mixed together in the latter two CA's. When characters from each of the complexes were considered simultaneously there was complete separation of *O. philadelphia* and *O. tolmiei* OTU's.

Plots of PCA scores also showed different degrees of separation of OTU's based on the different complexes. The best separation of *O. philadelphia* and *O. tolmiei* OTU's was achieved when PCA scores from the FREQUENCY COMPLEX were plotted together. Plots of PCA scores of

DURATION/INTERVAL COMPLEX variables revealed a mix of *O. philadelphia* OTU's from Quebec (SP) and Newfoundland (SA) with *O. tolmiei* OTU's and a separation of the remaining Newfoundland OTU's from all other *O. philadelphia* and *O. tolmiei* OTU's. A similar pattern occurred in the PCA of the SYLLABLE COMPLEX with the Newfoundland populations clustering by themselves. A single *O. philadelphia* OTU from Ontario was mixed with the *O. tolmiei* OTU's. Complete separation of *O. philadelphia* and *O. tolmiei* OTU's was achieved when PCA scores were derived from all characters using all the complexes simultaneously.

DFA of FREQUENCY COMPLEX variables and projections of OTU's on the DF axis using CVA revealed 100% discrimination of *O. philadelphia* and *O. tolmiei* OTU's. In contrast to the CA's and PCA's DFA of DURATION/INTERVAL variables showed good separation of OTU's of each taxon. The classification functions only misclassified one *O. philadelphia* OTU from Ontario and one *O. tolmiei* OTU from Washington. Plots of DF scores on the DF axis did not separate two *O. philadelphia* OTU's from Alberta and Quebec. DFA' and CVA's of SYLLABLE COMPLEX variables also provided good separation of OTU's. Only one *O. philadelphia* OTU from Alberta and one *O. tolmiei* OTU from central Washington were misclassified. The CVA of this complex only misclassified two *O. philadelphia* OTU's from Quebec. When characters from each of the complexes were considered simultaneously only one *O. philadelphia* from Newfoundland was misclassified. In contrast to the morphological analyses the problem OTU's from the DFA's of song complexes were from the allopatric portions of the range of *O. philadelphia* as opposed to the potential contact areas in Alberta and British Columbia.

The degree of differentiation between taxa for different song parameter complexes was evaluated using Mahalanobis D^2 . Like the results of the morphological analysis of different body regions, different song parameter complexes also exhibited inconsistencies in the amounts of differentiation between taxa. Mahalanobis D^2 between taxa was greatest when characters from each of the parameter complexes were considered simultaneously (Figure 116). Mahalanobis D^2 was next greatest for the FREQUENCY COMPLEX followed by DURATION/INTERVAL and SYLLABLE COMPLEXES (Figure 116). Frequency parameters are the best discriminators of *O. philadelphia* and *O. tolmiei* song types.

In the STEPWISE DFA the best combination of song parameter variables included characters from the FREQUENCY (MIFA), DURATION?INTERVAL (IMA), and SYLLABLE (NFA, NNB, NNC) Complexes. As in the morphological STEPWISE DFA, the best separation of *O. philadelphia* and *O. tolmiei* OTU's is achieved using a combination of characters from different complexes.

GEOGRAPHIC VARIATION IN SYLLABLES. The pattern of geographic variation in syllables types is strikingly different in *O. philadelphia* and *O. tolmiei*. In *O. philadelphia* the pattern is comparatively conservative with three major regional dialects - western continental, eastern continental and Newfoundland systems. In each of these systems there is a syllable or syllable combination which dominates the system. There is little individual variation even over distances of 1500km. In western Ontario there is a mixing of the two continental song patterns but neither shares syllables with the Newfoundland system.

In *O. tolmiei* the pattern of variation was different than in *O. philadelphia*. Almost every *O. tolmiei* songster sang a unique song type. Except for some homogeneity in northern Oregon and Washington there was no discernible regional or local dialects system in the breeding range of *O. tolmiei*. This is similar to song variation described for two closely related species of *Zonotrichia* - the White-crowned (*Z. leucophrys*) and White-throated Sparrows (*Z. albicollis*). Male White-throated Sparrows sing unique songs (Borror and Gunn 1965). "This *Zonotrichia* species reveals an enigmatic pattern of individualistic song and syllable structure at both the local and regional levels" (Mundinger 1982, p. 192). In contrast major dialects systems covering hundreds of kilometers have been described in the breeding range of the White-crowned Sparrow (Baptista and King 1980).

PLAYBACK EXPERIMENTS. In all but one case *O. philadelphia* and *O. tolmiei* songsters recognized their own song type and directed aggression towards it versus the alien song type. An *O. tolmiei* male from Liard River, British Columbia was the only male which did appear to differentiate *O. tolmiei* song from *O. philadelphia* song.

Table 24. Comparison of taxon Means (mm) per song character for each taxon and per cent difference between taxa.

SONG CHARACTERS	<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	Per Cent Difference	Taxon Difference
MINS**	1933.24	2416.05	19.9%	<i>tolmiei>philadelphia</i>
MAXS**	5458.81	5953.18	8.3%	<i>tolmiei>philadelphia</i>
MIA**	2721.63	3108.23	12.4%	<i>tolmiei>philadelphia</i>
MIB**	2662.69	3093.15	13.8%	<i>tolmiei>philadelphia</i>
MIC**	2635.59	3097.47	14.9%	<i>tolmiei>philadelphia</i>
MAA**	5248.91	5601.56	6.2%	<i>tolmiei>philadelphia</i>
MAB**	5332.68	5674.61	6.0%	<i>tolmiei>philadelphia</i>
MAC**	5347.24	5734.00	6.7%	<i>tolmiei>philadelphia</i>
MIFA**	1942.13	2643.87	26.5%	<i>tolmiei>philadelphia</i>
MIFB**	1895.29	2618.59	26.7%	<i>tolmiei>philadelphia</i>
MAFA**	3975.13	5437.49	26.8%	<i>tolmiei>philadelphia</i>
MAFB**	3744.93	5388.10	30.4%	<i>tolmiei>philadelphia</i>
FREQUENCY COMPLEX AVERAGE			16.5%	<i>tolmiei>philadelphia</i>
DUR*	1.11	1.29	13.9%	<i>tolmiei>philadelphia</i>
IMA*	0.07	0.06	14.2%	<i>philadelphia>tolmiei</i>
IMB*	0.06	0.06	0.0%	<i>no difference</i>
IMC*	0.05	0.05	0.0%	<i>no difference</i>
IFA*	0.03	0.05	40.0%	<i>tolmiei>philadelphia</i>
IFB*	0.03	0.05	40.0%	<i>tolmiei>philadelphia</i>
DURATION/INTERVAL COMPLEX AVERAGE			18.0%	<i>tolmiei>philadelphia</i>
NPSO	1.72	2.04	15.6%	<i>tolmiei>philadelphia</i>
NSSO	5.68	6.99	18.7%	<i>tolmiei>philadelphia</i>
NDSO	1.71	2.01	14.9%	<i>tolmiei>philadelphia</i>
NNA	4.58	4.38	4.3%	<i>philadelphia>tolmiei</i>
NNB	4.84	4.58	5.3%	<i>philadelphia>tolmiei</i>
NNC	4.86	4.62	4.9%	<i>philadelphia>tolmiei</i>
NFA	2.54	4.34	41.4%	<i>tolmiei>philadelphia</i>
NFB	2.18	3.98	45.2%	<i>tolmiei>philadelphia</i>
SYLLABLE COMPLEX AVERAGE			18.7%	<i>tolmiei>philadelphia</i>

* - seconds.

** - Hz.

Bold face type - indicates that *O. philadelphia* is greater than *O. tolmiei* for that character.

Table 25. Results of Regression Analyses of physical parameters of primary song on latitude and longitude.

SONG CHAR.	LATITUDE				LONGITUDE			
	<i>O. philadelphia</i>		<i>O. tolmiei</i>		<i>O. philadelphia</i>		<i>O. tolmiei</i>	
	Signif. Level	R2	Signif. Level	R2	Signif. Level	R2	Signif. Level	R2
NPSO	.001(-)	22.3			.001(-)	6.4		
NSSO	.014(-)	3.3						
NDSO	.001(-)	19.3			.002(-)	5.1		
DUR	.022(-)	2.9			.02(-)	2.9		
MINS	.005(+)	4.3			.03(+)	2.5		
MAXS	.001(-)	25.8	.001(-)	11.2	.001(-)	31.6		
NNA	.001(-)	19.2			.001(-)	31.7		
NNB	.001(-)	25.2			.001(-)	36.7		
NNC	.001(-)	19.2			.001(-)	37.6		
IMA								
IMB								
IMC	.001(+)	19.0	.001(+)	19.5	.001(+)	21.7	.02(+)	5.9
MIA	.001(-)	10.6						
MIB	.001(-)	10.1			.04(-)	2.3		
MIC	.001(-)	10.8			.02(-)	2.6		
MAA	.001(-)	20.2			.001(-)	23.5		
MAB	.001(-)	19.7			.001(-)	22.3		
MAC	.001(-)	29.1	.02(-)	4.7	.001(-)	26.9		
NFA	.001(-)	27.1	.001(-)	17.3	.001(-)	34.7		
NFB	.001(-)	11.3	.001(-)	13.2	.001(-)	12.4		
IFA	.001(+)	34.1	.001(+)	18.8	.001(+)	39.6		
IFB								
MIFA								
MIFB	.006(+)	6.0			.007(+)	5.8		
MAFA	.004(-)	6.0	.006(-)	7.5	.001(-)	8.8		
MAFB			.001(-)	11.1				

Table 26. Results of Spearman Rank Order Correlation Analyses between morphological characters and environmental variables for *O. philadelphia*.

SONG CHAR.	MEJUNT	MUJUNT	MAJUNT	MEULT	MULT	MAULT	MEJUNP	MEJUP	REH	EVAP	JULWT
NPSO	.001(+)		.001(+)	.001(+)	.001(+)	.001(+)		.001(+)			
NSSO	.01(+)		.006(+)	.03(+)	.03(+)	.001(+)		.001(+)			
NDSO	.001(+)	.001(+)		.001(+)		.006(+)					
DUR											
MINS	.04(-)		.01(-)	.001(+)	.01(-)						
MAXS	.001(+)	.001(+)									
NNA	.01(+)		.001(+)	.001(+)	.001(+)		.005(+)				
NNB	.003(+)	.03(+)	.001(+)	.001(+)	.001(+)		.001(+)				
NNC	.001(+)	.003(+)	.04(+)	.001(+)		.001(+)			.001(+)		
IWA											
IWB											
MC	.01(-)		.04(-)	.005(-)	.04(-)		.04(-)				
MIA	.008(+)	.001(+)		.03(+)	.005(+)						
MB	.003(+)	.001(+)		.02(+)	.001(+)						
MIC	.001(+)	.001(+)		.01(+)	.001(+)						
MAA	.001(+)	.04(+)		.001(+)	.001(+)						
MAB	.001(+)	.03(+)		.004(+)	.001(+)		.001(+)				
MAC	.001(+)	.001(+)		.001(+)		.001(+)					
NFA											
NFB			.01(+)								
F/A	.01(-)		.02(-)								
IFB											
MI/FA											
MI/FB				.04(-)							
MA/FA					.03(-)						
MA/FB											
MA/FB											

.007(-)

Table 27. Results of Spearman Rank Order Correlation Analyses between physical parameters of primary song and environmental variables for *O. tolmiei*.

SONG CHAR.	MEUNT	MUUNT	MAUNT	MEULT	MULT	MAULT	MEUNP	MEUP	REH	EVAP	JULWT
NPSO								.02(-)			
NDSO											
DUR											
MIN5											
MAX5	.04(+)		.001(+)	.001(+)	.001(-)	.001(-)	.01(-)				
NVA											
NNB											
NMC											
MMA	.03(-)				.04(+)	.009(+)	.01(+)	.04(-)		.004(+)	.01(-)
MIB					.005(+)	.005(+)	.005(+)				
MIC					.001(+)	.001(+)	.005(+)				
MMA				.02(+)			.03(-)				
MIB				.03(+)			.02(-)				
MIC				.006(+)			.006(-)				
MMA	.01(+)	.01(+)	.04(+)	.01(+)	.003(+)	.004(-)	.006(-)			.003(-)	
MIB	.001(+)	.02(+)		.009(+)	.006(+)	.006(-)	.006(-)			.009(+)	
MIC	.004(-)	.04(-)		.001(+)	.001(+)	.001(+)	.001(+)			.01(+)	
MMA	.004(-)			.04(-)			.05(+)				
MIB				.001(+)			.01(+)				
MIC				.02(+)			.02(+)				
MMA				.001(+)			.01(-)				
MIB				.001(+)			.001(-)				
MIC				.001(+)			.001(-)				
MMA				.001(+)			.001(-)				
MIB				.001(+)			.001(-)				
MIC				.001(+)			.001(-)				
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MMA				.001(+)			.001(-)				
MIB				.00							

Table 28. Loadings of Frequency Complex Variables on Principal Components.

Frequency Character	PC1	PC2	PC3
MINS	0.355	-0.373	-0.119
MAXS	0.212	0.536	-0.131
MIA	0.288	0.076	0.952
MAA	0.163	0.460	-0.060
MIFA	0.564	-0.500	-0.101
MAFA	0.632	0.322	-0.217
% Variance ¹	65.6%	17.2%	9.8%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 29. Loadings of Duration/Interval Complex Variables on Principal Components.

Duration/Interval Character	PC1	PC2	PC3
DUR	-0.733	-0.020	0.997
IMA	0.834	-0.548	0.050
IMB	0.545	0.835	0.056
% Variance ¹	84.4%	8.9%	6.7%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 30. Loadings of Syllable Complex Variables on Principal Components.

Syllable Character	PC1	PC2	PC3
NPSO	0.607	0.272	-0.106
NSSO	0.294	0.092	0.837
NDSO	0.612	0.262	-0.256
NNA	-0.309	0.485	-0.105
NNB	-0.232	0.531	0.390
NNC	-0.137	0.574	-0.239
% Variance ¹	50.1%	43.7%	2.6%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 31. Loadings of Song Complex Variables on Principal Components.

Song Character	PC1	PC2	PC3
NPSO	0.090	0.085	0.004
NSSO	0.128	0.047	-0.153
NDSO	0.092	0.090	-0.016
DUR	0.090	0.069	-0.089
MINS	0.187	-0.0568	-0.032
MAXS	0.063	0.073	-0.047
NNA	-0.033	0.196	-0.013
NNB	-0.077	0.269	0.141
NNC	-0.078	0.271	0.142
IMA	-0.169	-0.031	0.627
IMB	-0.082	-0.131	0.498
IMC	0.041	-0.387	-0.080
MIA	0.083	0.046	0.141
MIB	0.091	0.039	0.118
MIC	0.105	0.058	0.120
MAA	0.064	0.055	-0.110
MAB	0.053	0.075	-0.081
MAC	0.053	0.089	-0.042
NFA	0.484	0.334	0.015
NFB	0.491	0.218	0.383
IFA	0.322	-0.595	0.187
IFB	0.178	-0.254	-0.008
MIFA	0.223	-0.074	-0.110
MIFB	0.216	-0.085	-0.073
MAFA	0.228	0.0271	-0.018
MAFB	0.264	-0.010	-0.078
% Variance ¹	46.4%	29.8%	7.9%

1 - % of the variance explained by these principal components, may not always equal 100% because of the existence of more than three PC's for that complex.

Table 32. Discriminant Function Coefficients for
Frequency Complex Variables.

		CLASSIFICATION FUNCTIONS	STANDARDIZED COEFFICIENTS
Frequency Parameter			
Complex	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
CONSTANT	-10806.40	-11551.88	
MINS	369.14	393.74	0.6316
MAXS	1231.41	1273.14	-0.6690
MIA	-190.74	-204.91	0.0347
MAA	364.36	344.67	0.5265
MIFA	-240.30	-248.83	0.8989
MAFA	1063.59	1129.31	0.9728

Table 33. Discriminant Function Coefficients for
Duration/Interval Complex Variables.

Duration/Interval Parameter Complex	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
CONSTANT	-136.50	-169.25	
DUR	44.31	55.82	1.5855
IMA	-17.29	-27.66	-0.1341
IMC	-97.77	-109.68	-0.6801
IFA	4.31	11.19	1.2129

Table 34. Discriminant Function Coefficients for Syllable Complex Variables.

Syllable Parameter Complex	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
CONSTANT	-49.53	-55.94	
NPSO	-2.09	2.88	-1.0474
NSSO	32.00	38.26	1.5372
NNA	44.85	71.11	-0.6102
NFA	-34.04	-62.74	1.3460

Table 35. Discriminant Function Coefficients for all Song Parameter Variables.

	CLASSIFICATION FUNCTIONS		STANDARDIZED COEFFICIENTS
Song Parameter Complex	<i>O. philadelphia</i>	<i>O. tolmiei</i>	
CONSTANT	-586093.95	-605900.15	
MINS	8277.33	9461.20	34.921
MAXS	27282.41	27958.20	-133.080
MIA	5079.24	4898.33	164.548
MIB	-257453.41	-262287.08	-111.570
MIC	217606.33	222252.23	-125.680
MAA	0.00	0.00	64.869
MAB	0.00	0.00	-49.633
MAC	0.00	0.00	116.749
MIFA	0.00	0.00	-38.847
MIFB	0.00	0.00	5.418
MAFA	0.00	0.00	0.9728
DUR	13688.09	12235.57	-21.799
IMA	-197933.41	-199275.54	-0.1341
IMB	36519.54	36962.94	20.570
IMC	-22444.03	-22578.74	-0.6801
IFA	0.00	0.00	1.2129
NPSO	40213.85	41608.96	187.621
NDSO	-36447.26	-37013.93	-218.750
NSSO	-12344.66	-10425.87	90.379
NNA	141500.35	142688.64	-0.6102
NFA	0.00	0.00	65.2276

Table 36. Results of STEPWISE DFA for Song Parameters.

VARIABLE	STEP	F STATISTIC	PROB > F *	WILKS' LAMBDA**	PROB > LAMBDA***
MIFA	1	54.564	0.0001	0.296	0.0001
NFA	2	9.313	0.0059	0.208	0.0001
NNC	3	6.511	0.0186	0.159	0.0001
NNB	4	4.999	0.0369	0.127	0.0001
IMA	5	2.770	0.1125	0.111	0.0001

* - probability level after the variable has been entered.

** - likelihood ratio statistic for testing whether the taxon means are significantly different.

*** - probability level based on the F approximation to Wilk's Lambda.

Table 37. Results of Song Playback Experiments.

PB #	Species*	Locality	Type**	Aggression***	Switched****
1	<i>O. philadelphia</i>	ST. PAULE	MO1	<i>O. philadelphia</i>	yes
2	<i>O. philadelphia</i>	ST. PAULE	MO1	<i>O. philadelphia</i>	yes
3	<i>O. philadelphia</i>	LEBEL-SUR.	MO1	<i>O. philadelphia</i>	yes
4	<i>O. philadelphia</i>	LEBEL-SUR.	MO4	<i>O. philadelphia</i>	yes
5	<i>O. tolmiei</i>	MCBRIDE	?	<i>O. tolmiei</i>	yes
6	<i>O. tolmiei</i>	MCBRIDE	?	<i>O. tolmiei</i>	yes
7	<i>O. tolmiei</i>	LIARD RIVER	MA73	NEUTRAL	NO
8	<i>O. tolmiei</i>	LIARD RIVER	MA32	<i>O. tolmiei</i>	yes
9	<i>O. tolmiei</i>	LIARD RIVER	MA33	<i>O. tolmiei</i>	yes
10	<i>O. philadelphia</i>	STEAMBOAT	MO6	<i>O. philadelphia</i>	yes
11	<i>O. philadelphia</i>	FT. NELSON	MO6	<i>O. philadelphia</i>	yes
12	<i>O. philadelphia</i>	FT. NELSON	MO12	<i>O. philadelphia</i>	yes
13	<i>O. philadelphia</i>	WHITECOURT	MO6	<i>O. philadelphia</i>	yes
14	<i>O. philadelphia</i>	WHITECOURT	?	<i>O. philadelphia</i>	yes
15	<i>O. philadelphia</i>	OBED	MO12	<i>O. philadelphia</i>	yes
16	<i>O. philadelphia</i>	BATTLE LK.	?	<i>O. philadelphia</i>	yes
17	<i>O. tolmiei</i>	KANANASKIS	MA24	<i>O. tolmiei</i>	yes
18	<i>O. tolmiei</i>	KANANASKIS	?	<i>O. tolmiei</i>	yes
19	<i>O. tolmiei</i>	KANANASKIS	MA8	<i>O. tolmiei</i>	yes
20	<i>O. philadelphia</i>	LODGEPOLE	MO12	<i>O. philadelphia</i>	yes
21	<i>O. philadelphia</i>	LODGEPOLE	MO14	<i>O. philadelphia</i>	yes
22	<i>O. philadelphia</i>	LODGEPOLE	MO9	<i>O. philadelphia</i>	yes

* - species identification of male subjects.

** - song type is identified by the syllable which occurs most often in the song.

*** - song type which the subject first directed aggression towards during the playback experiment.

**** - indicates whether or not the male subject switched speakers when the song types were switched in each speaker.

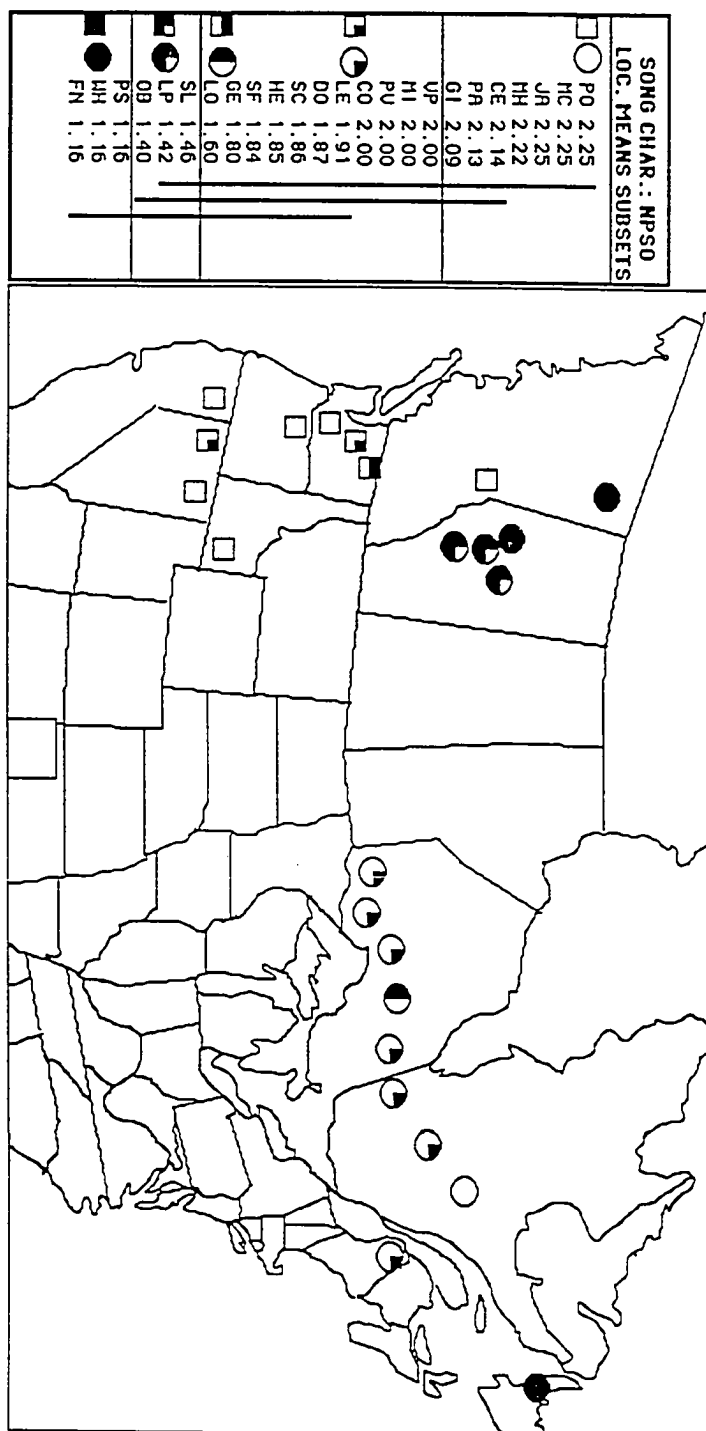


Figure 77. Geographic distribution of NPSO means for populations of *D. philadelphia* and *D. tolmiei*.

Figure 78. Bivariate plots of population means:
NPSO, NSSO, NDSO, DUR, MINS, MAXS.

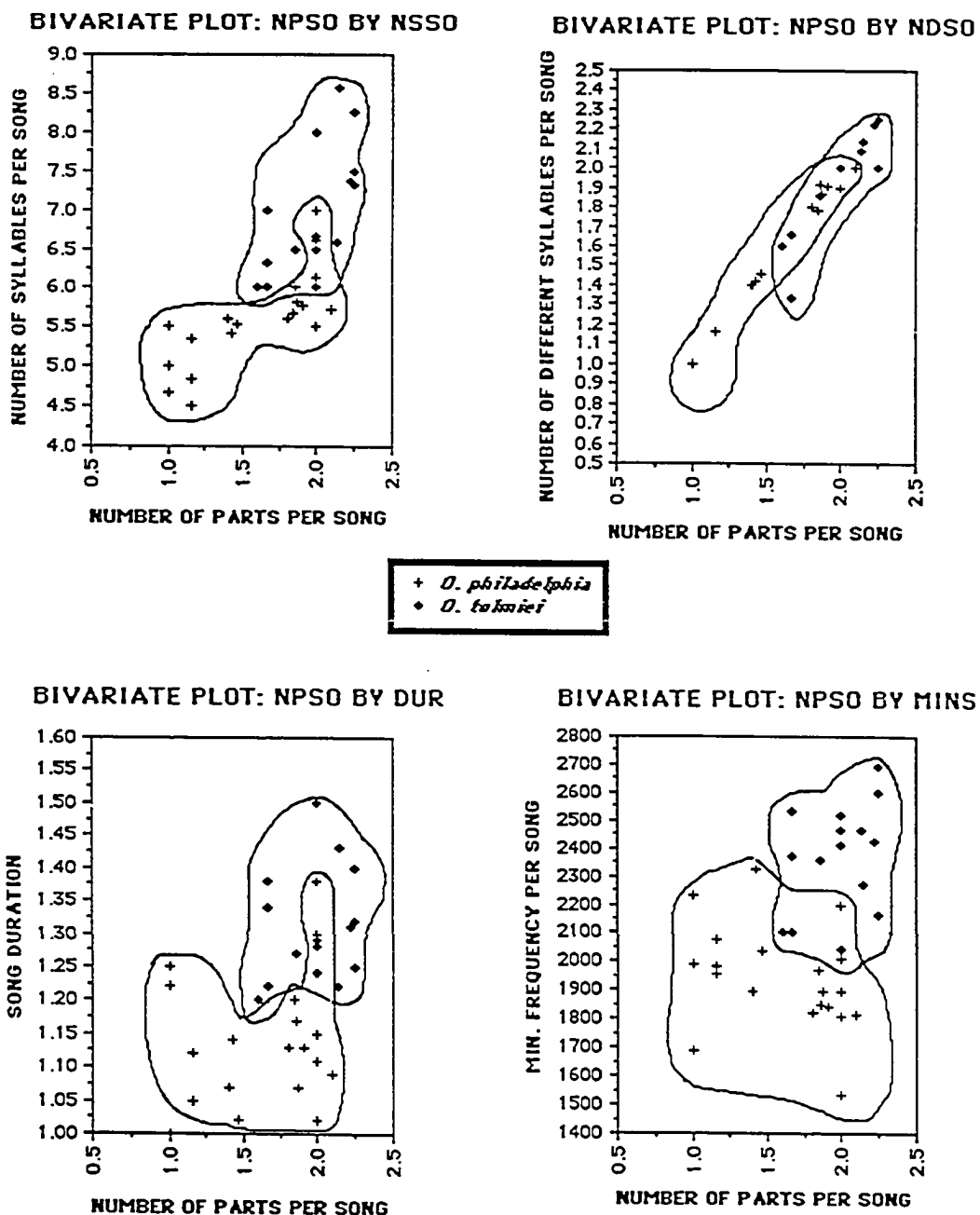
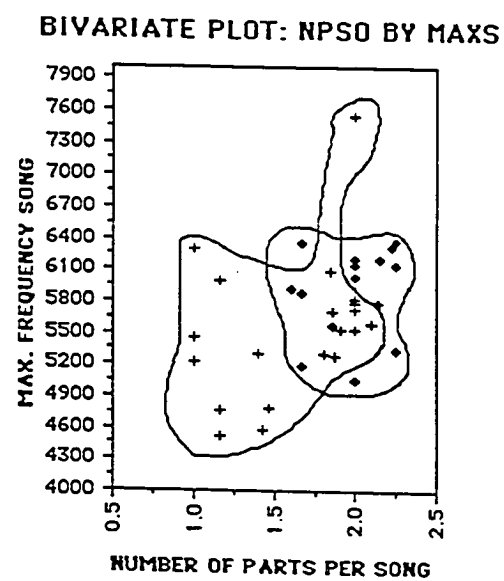
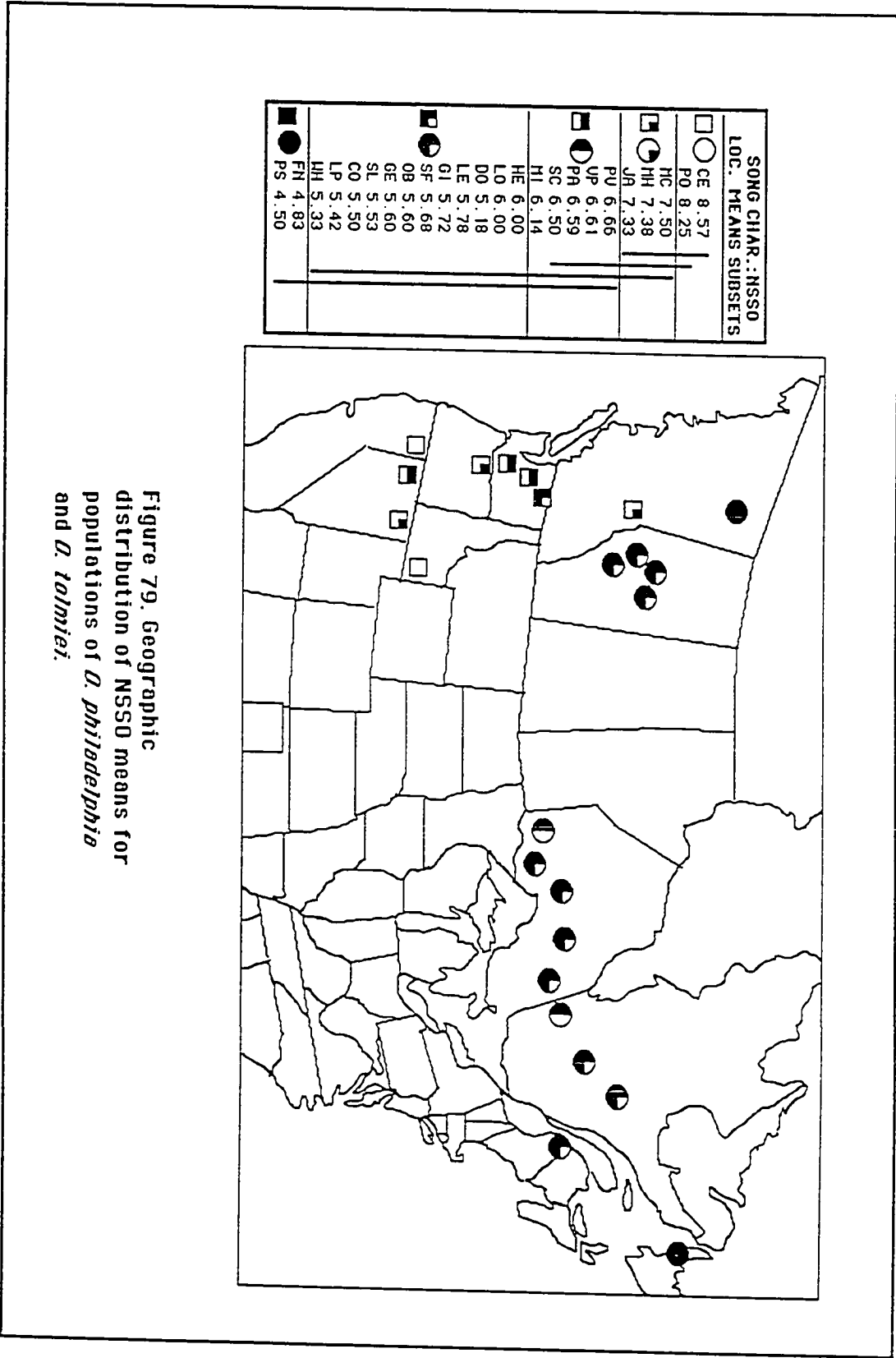


Figure 78. Bivariate plots of population means:
NPSO, NSSO, NDSO, DUR, MINS, MAXS (cont'd).





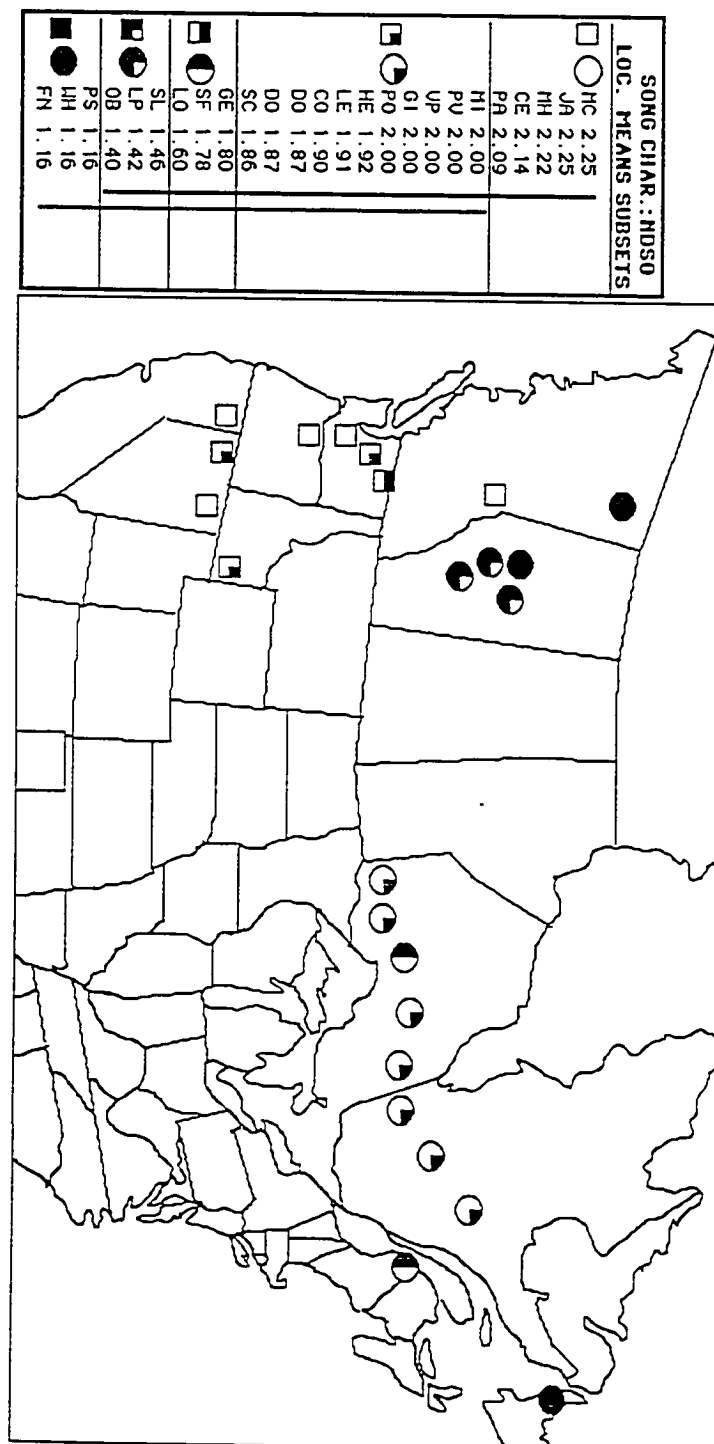
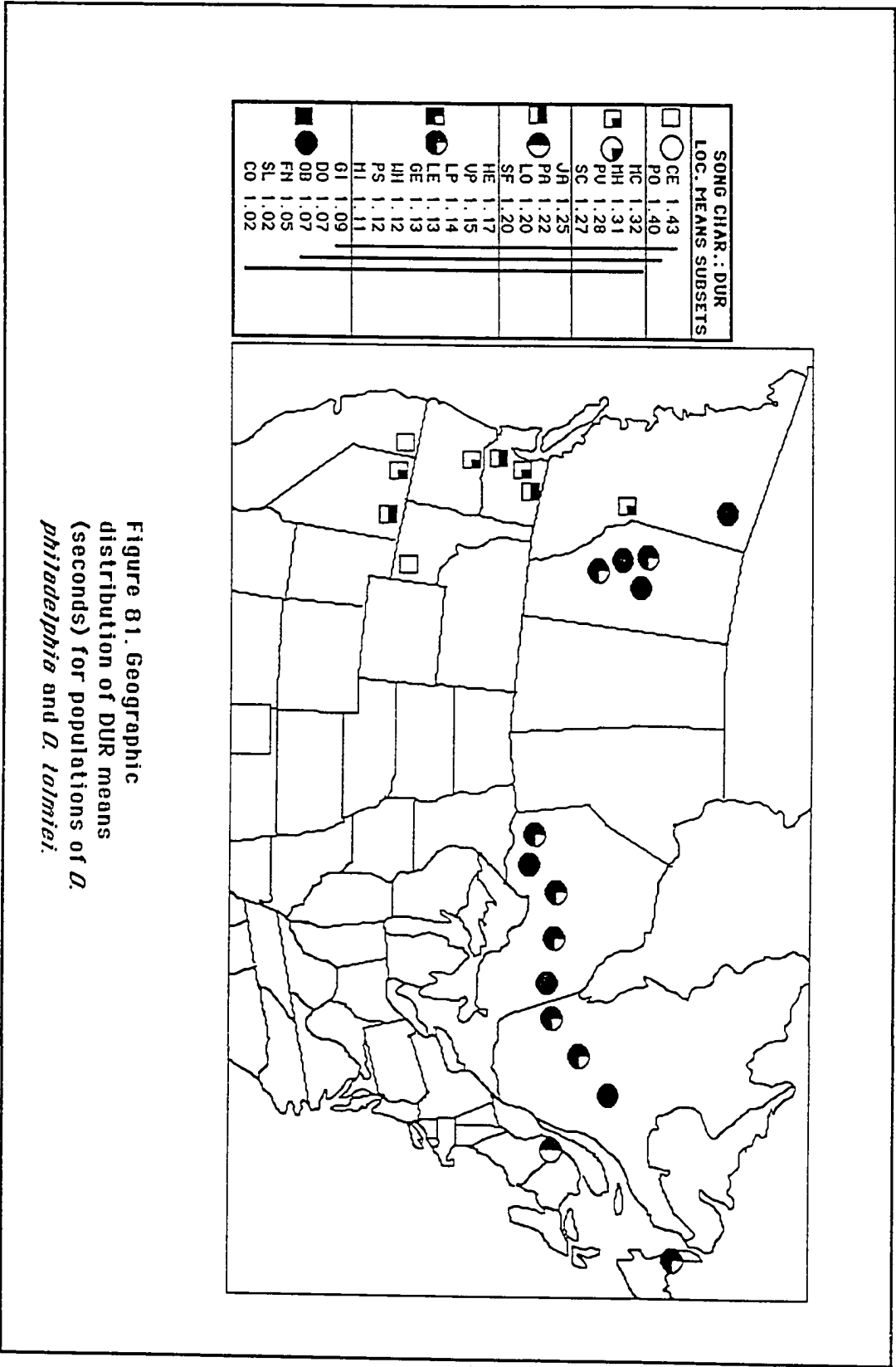


Figure 80. Geographic distribution of NDSO means for populations of *O. philadelphia* and *O. talmiei*.



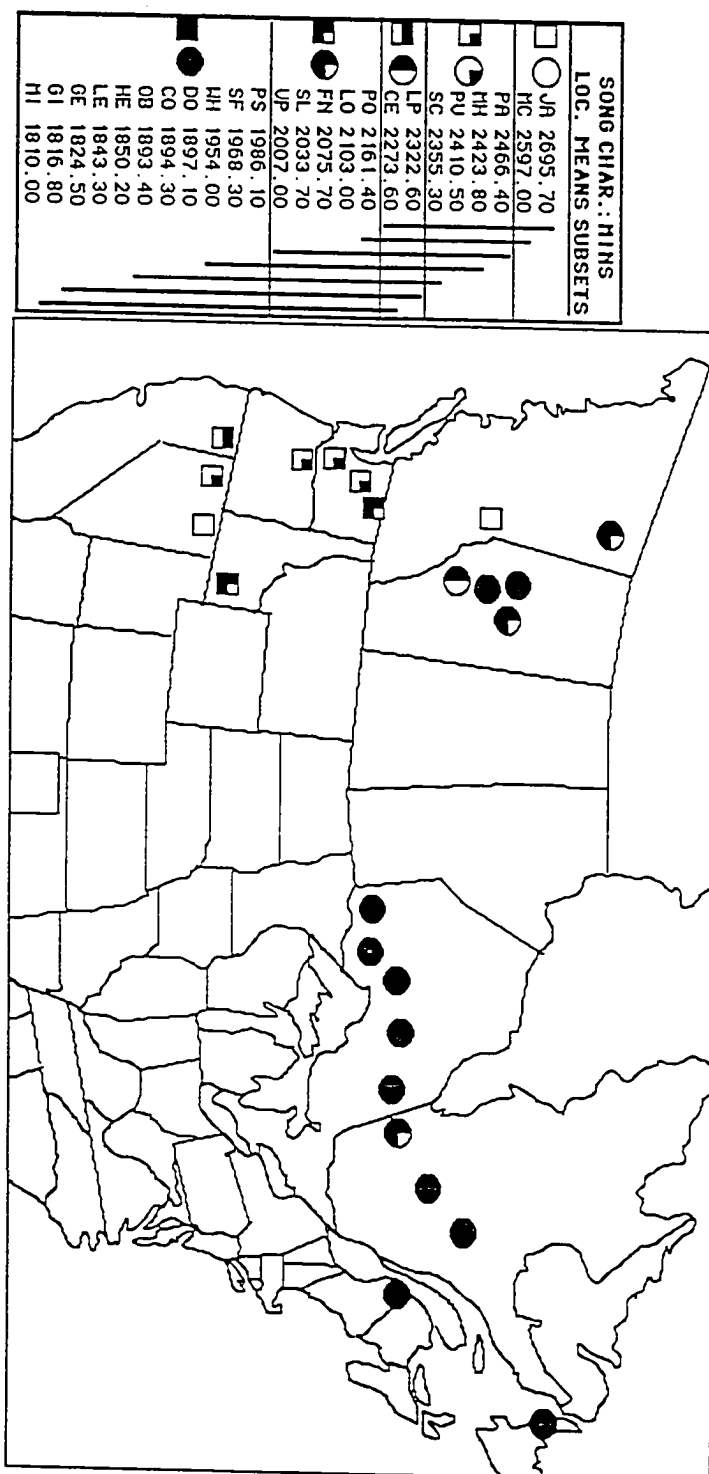


Figure 82. Geographic
distribution of MINS means (Hz)
for populations of *Q. philadelphia*
and *Q. tolmiei*.

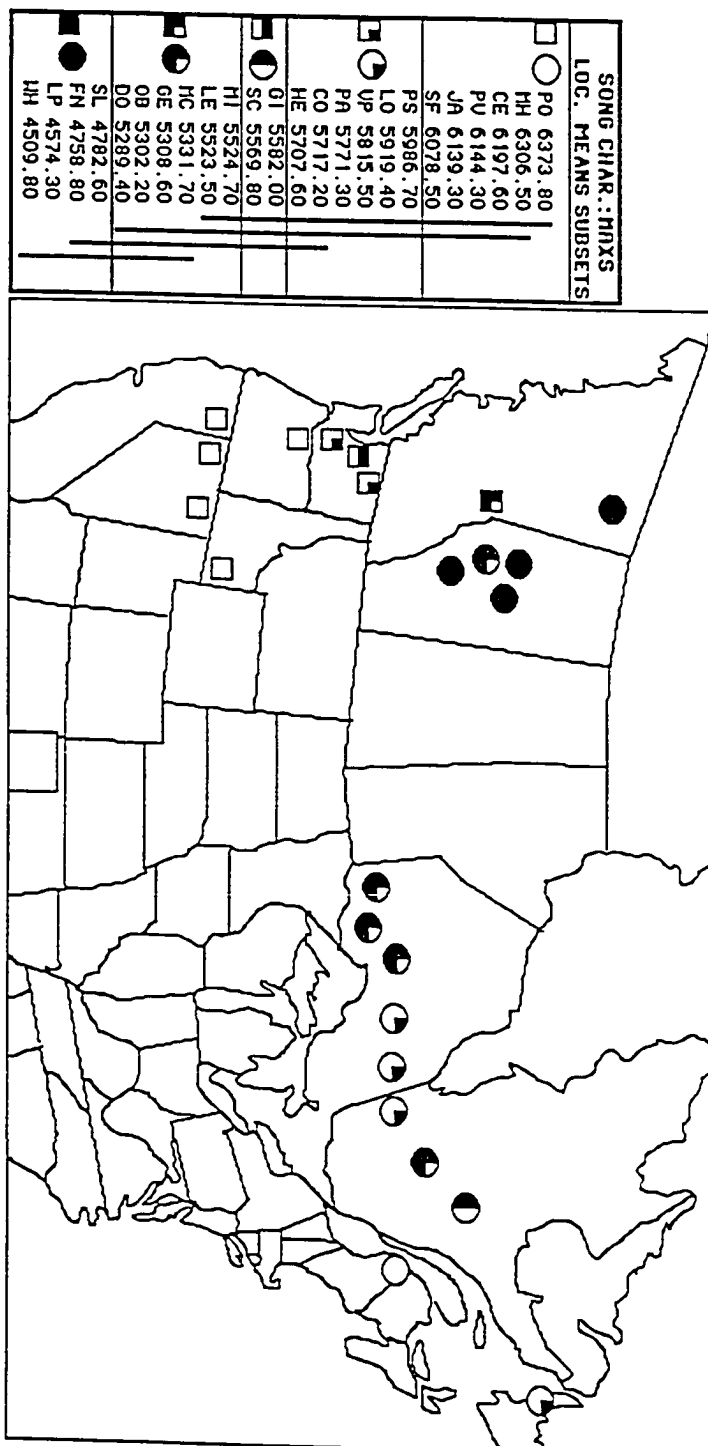


Figure 83. Geographic
distribution of MAXS means (Hz)
for populations of *D.*
philadelphia and *D. tolmiei*.

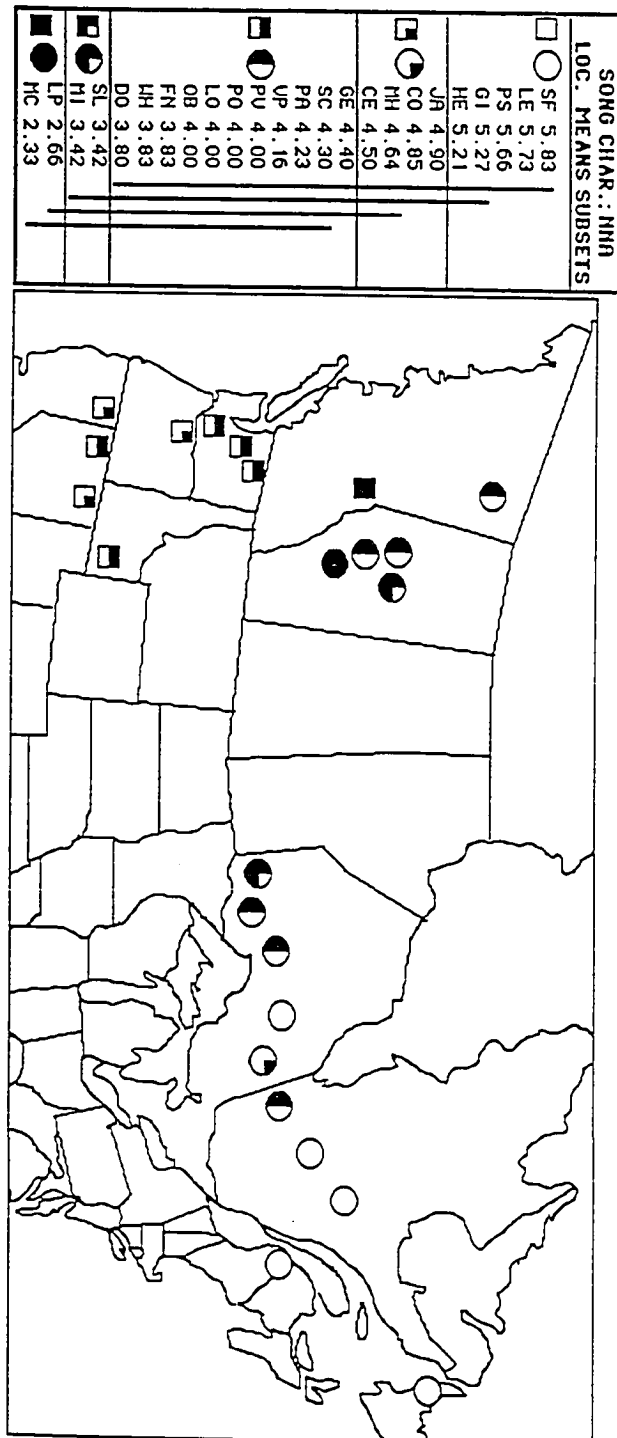


Figure 84. Geographic distribution of NNA means for populations of *Q. philadelphica* and *Q. tolmiei*.

Figure 85. Bivariate plots of population means: NNA, NNB, NNC, IMA, IMB, IMA, IMB, IMC, MIC, MAA, MAB, MAC (cont'd).

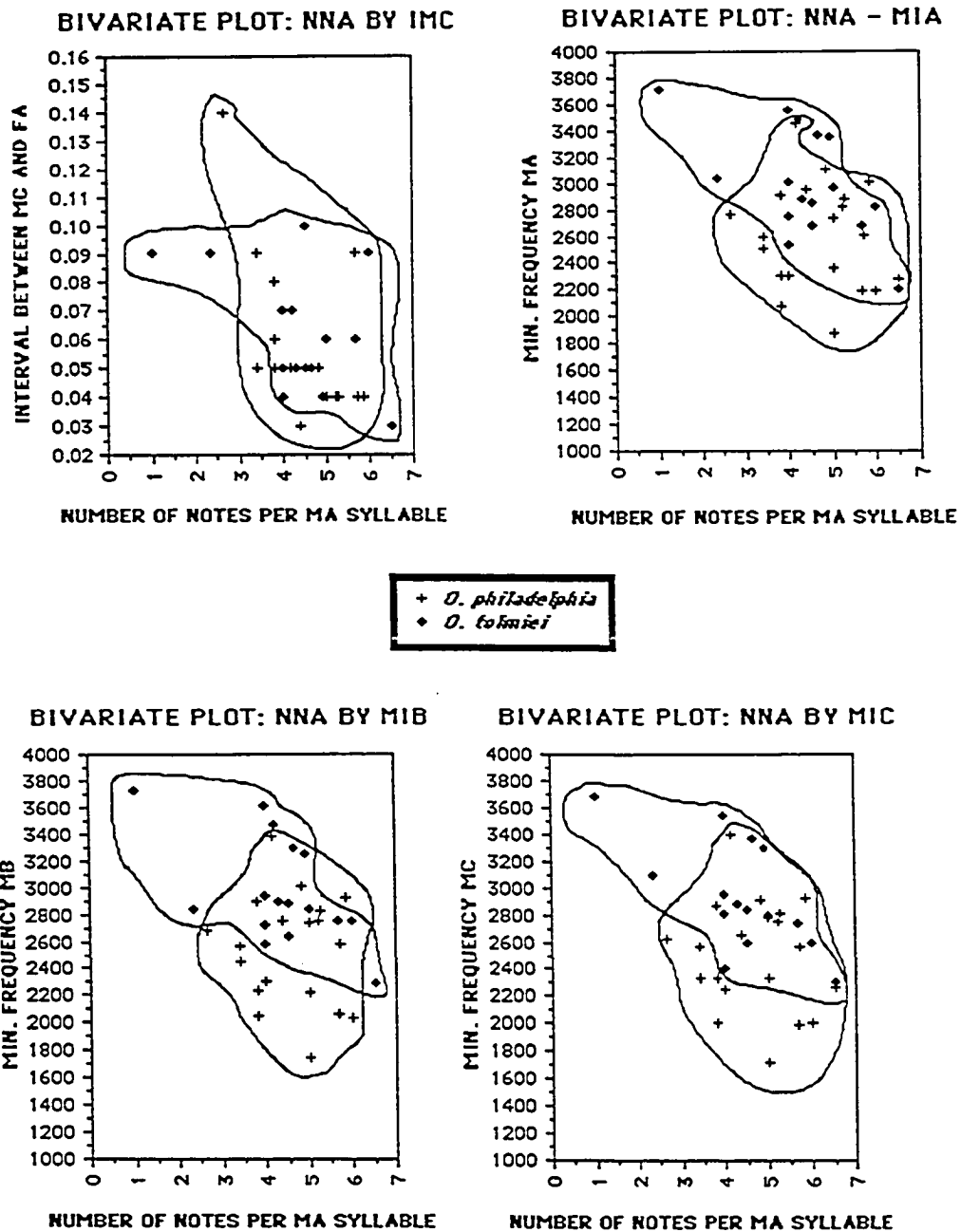


Figure 85. Bivariate plots of population means: NNA, NNB, NNC, IMA, IMB, IMA, IMB, IMC, MIC, MAA, MAB, MAC.

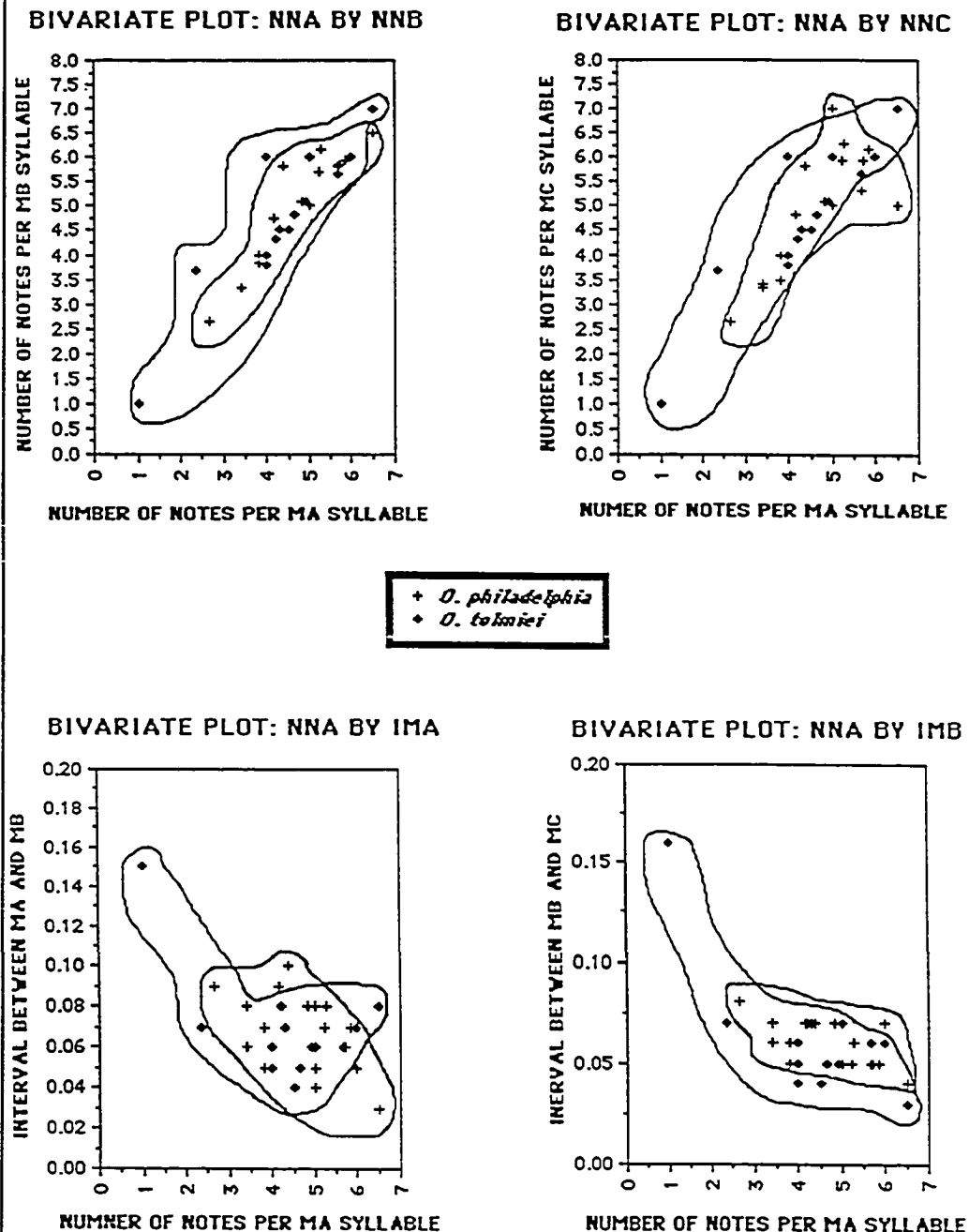
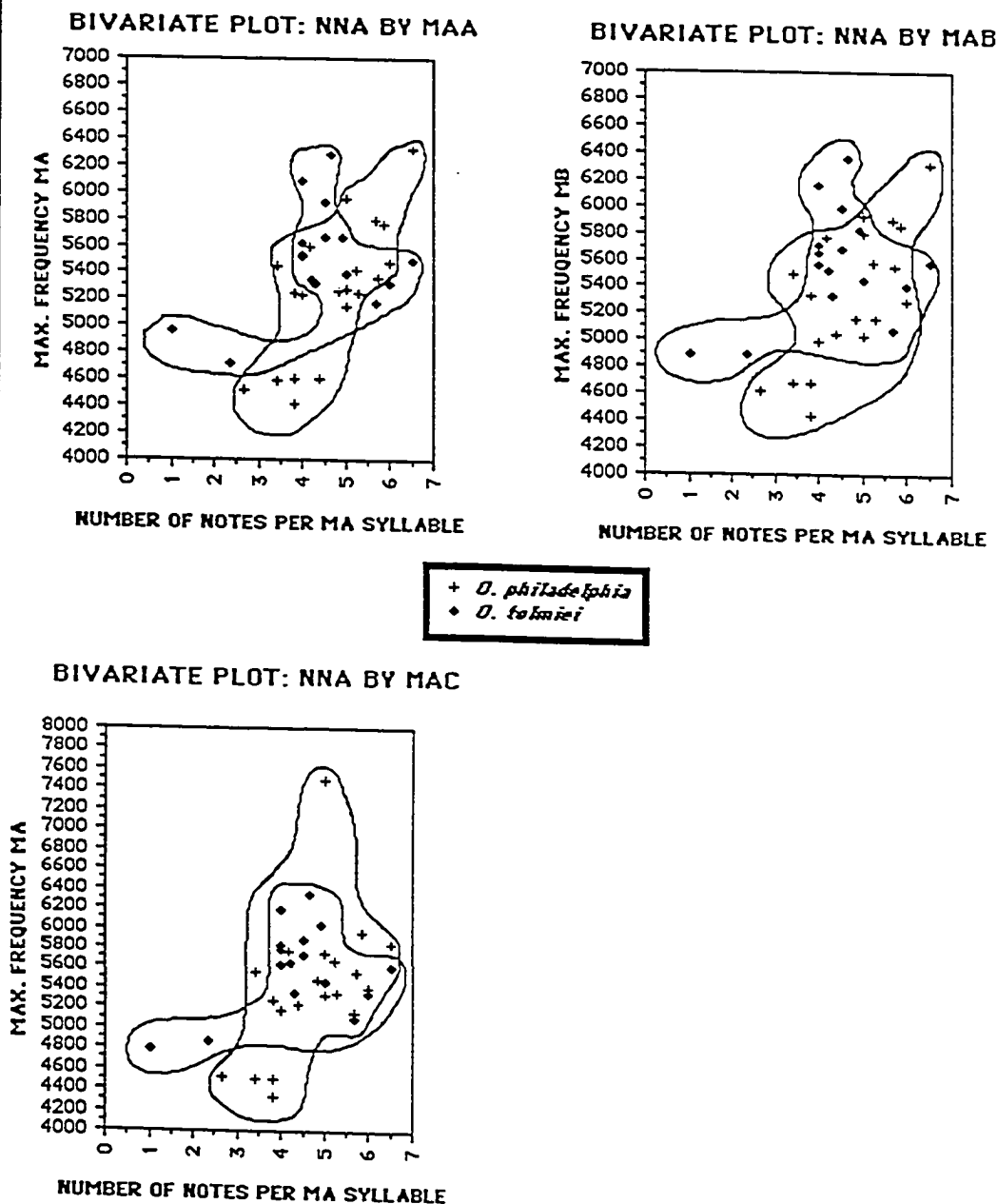


Figure 85. Bivariate plots of population means: NNA, NNB, NNC, IMA, IMB, IMA, IMB, IMC, MIC, MAA, MAB, MAC (cont'd).



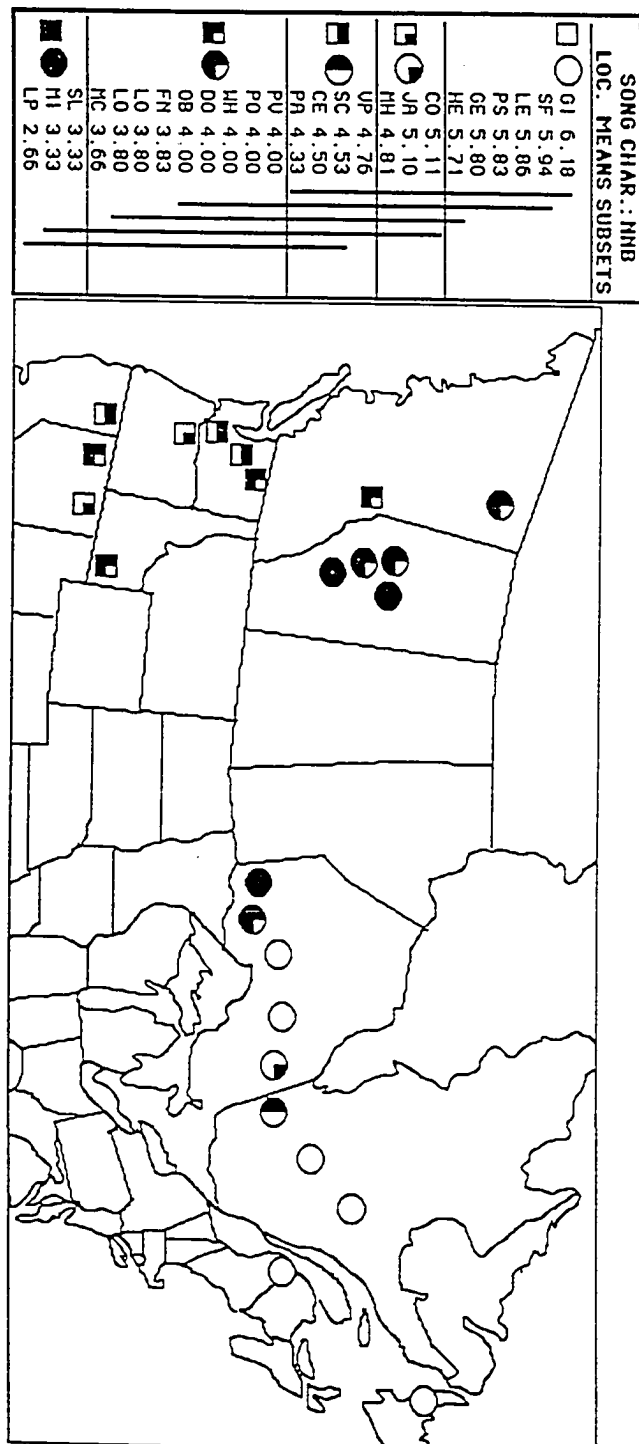
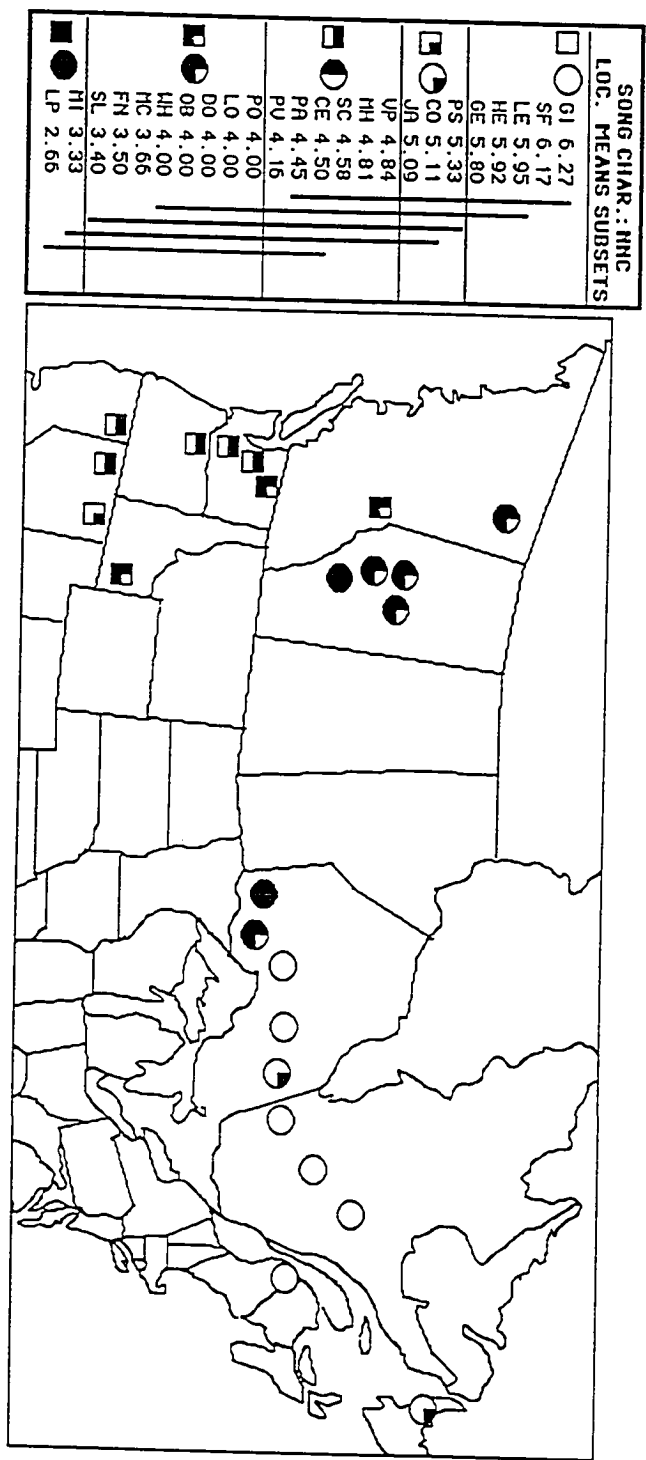


Figure 86. Geographic distribution of NNB means for populations of *O. philadelphia* and *O. tolmiei*.



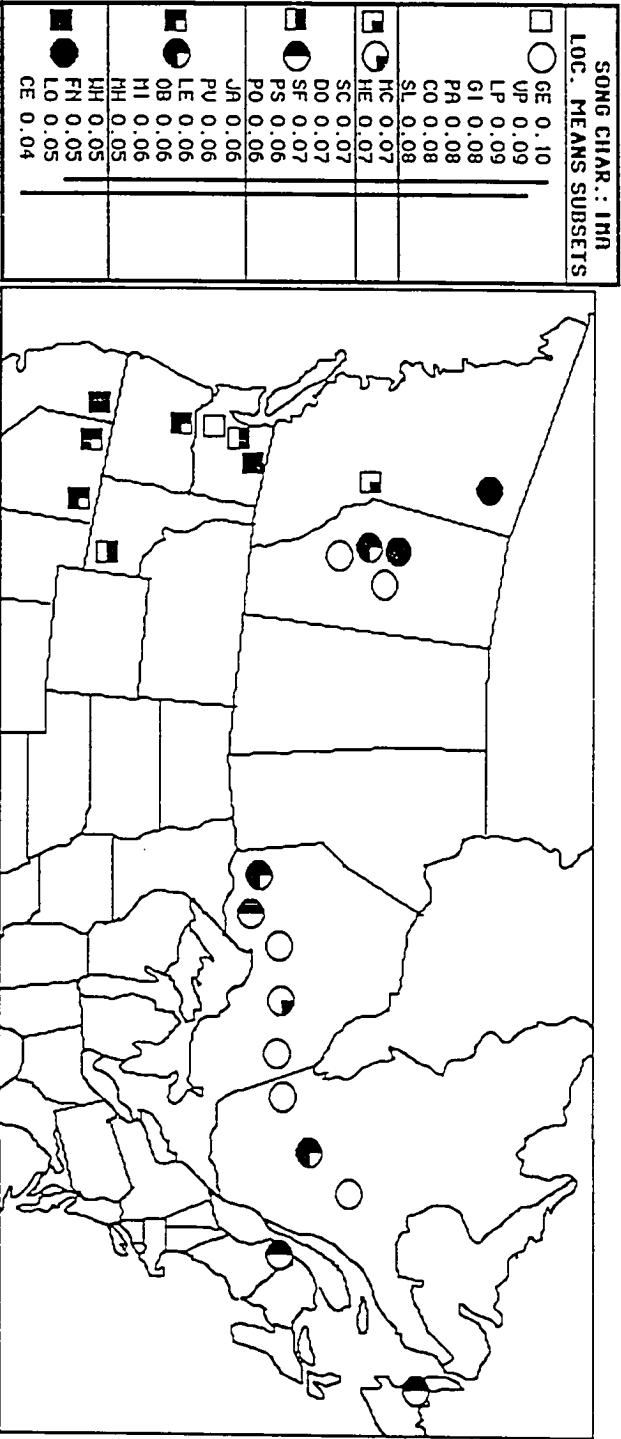


Figure 88. Geographic
distribution of IMA means
(seconds) for populations of *Q.
philadelphica* and *Q. tolmiei*.

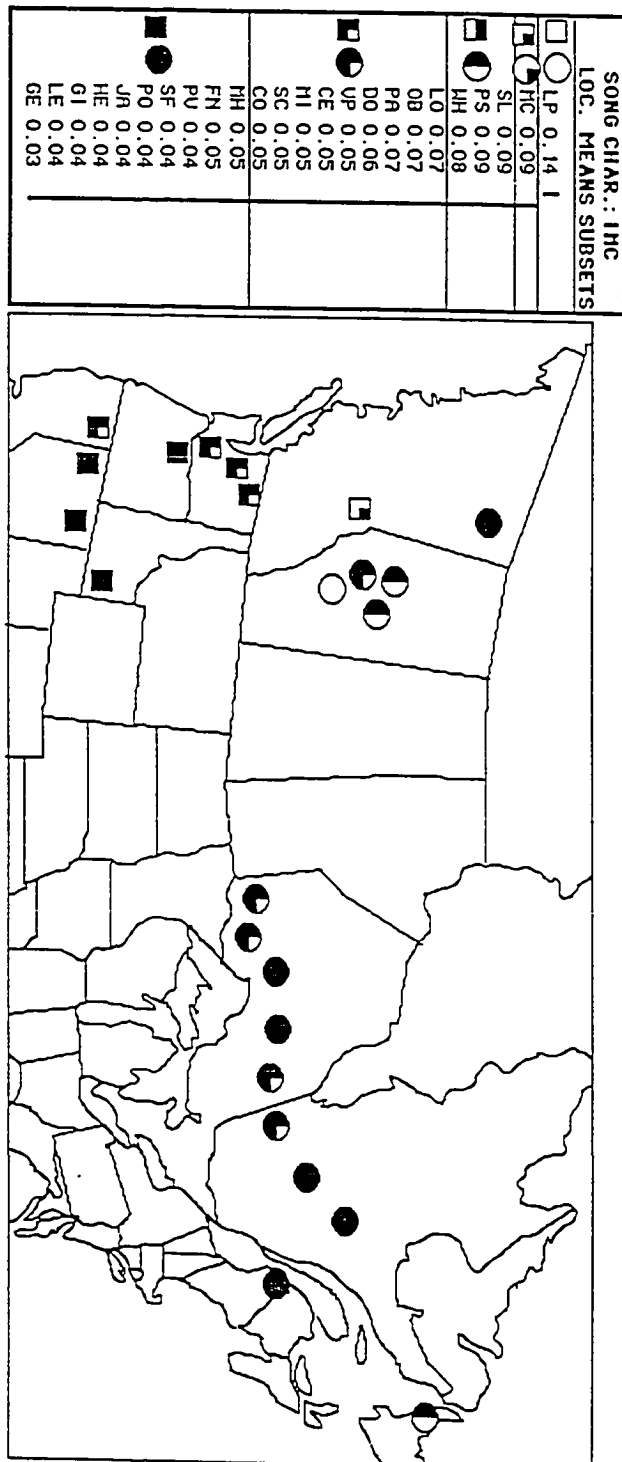


Figure 89. Geographic
distribution of IMC means
(seconds) for populations of *D.*
philadelphia and *D. tolmiei*.

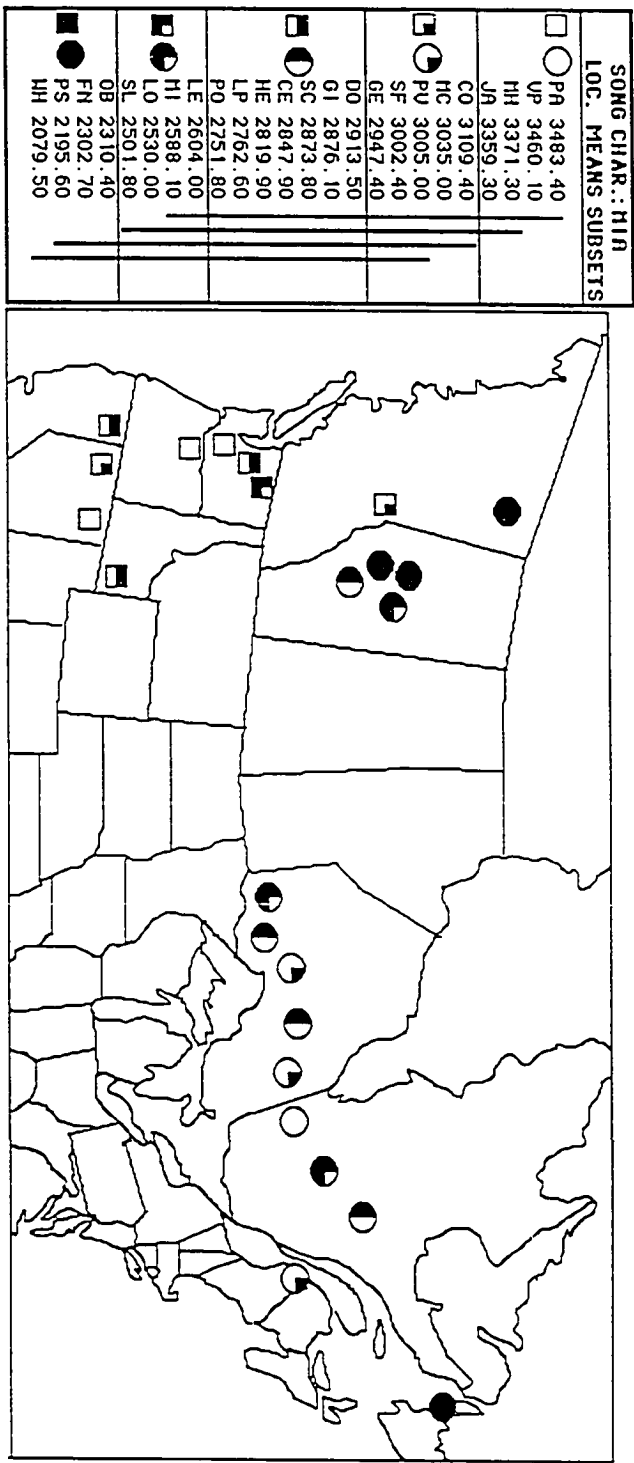


Figure 90. Geographic distribution of MIA means (Hz) for populations of *D. philadelphia* and *D. tolmiei*.

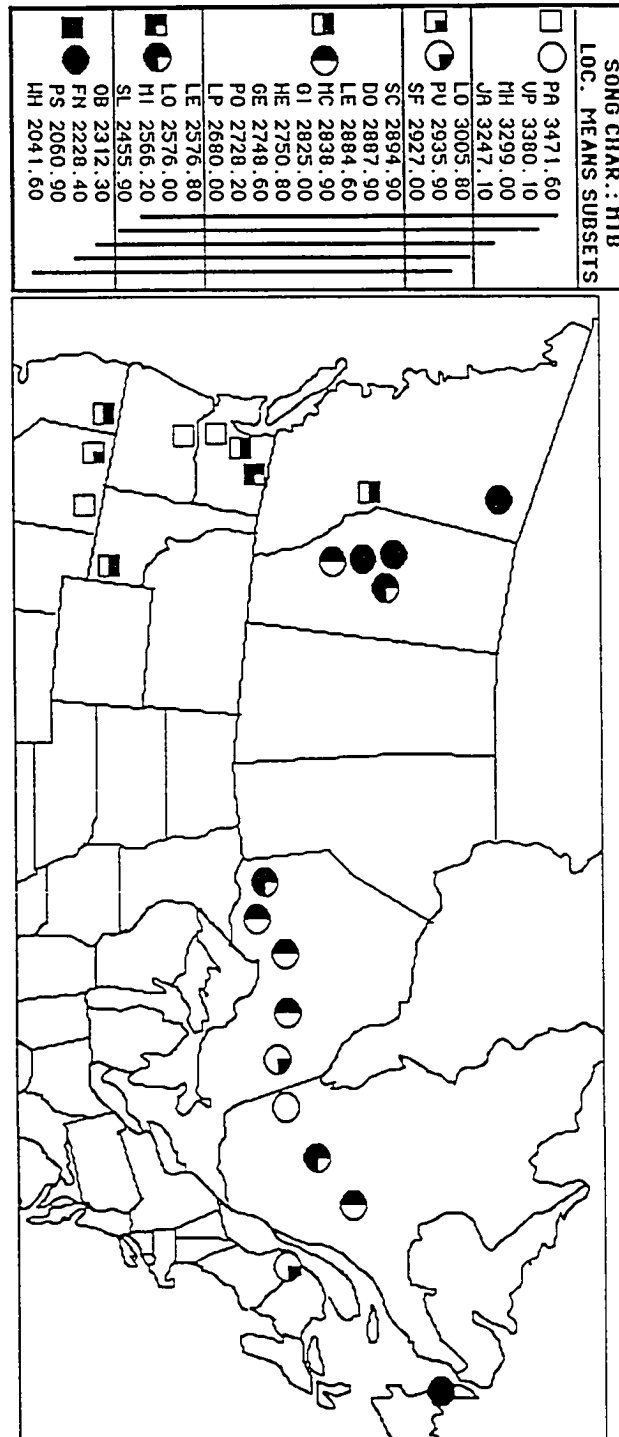


Figure 91. Geographic
distribution of MIB means (Hz)
for populations of *Q.*
philadelphica and *Q. tolmiei*.

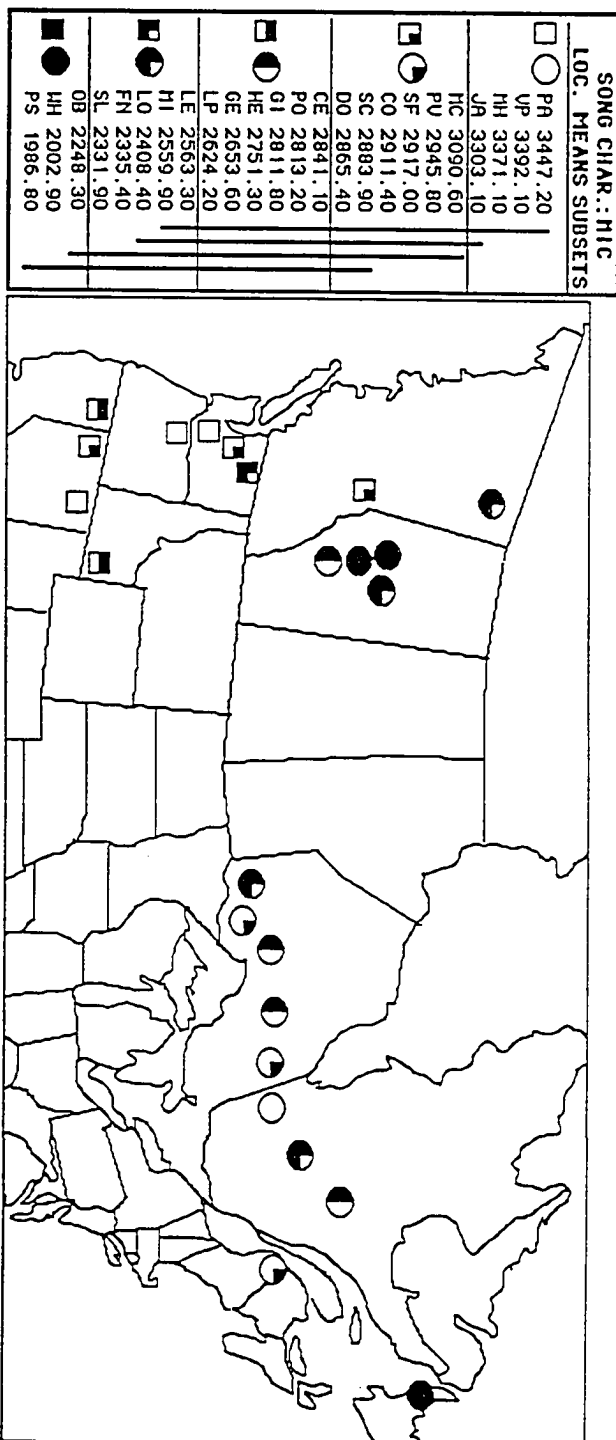


Figure 92. Geographic
distribution of HIC means (Hz)
for populations of *Q.*
philadelphica and *Q. tolmiei*.

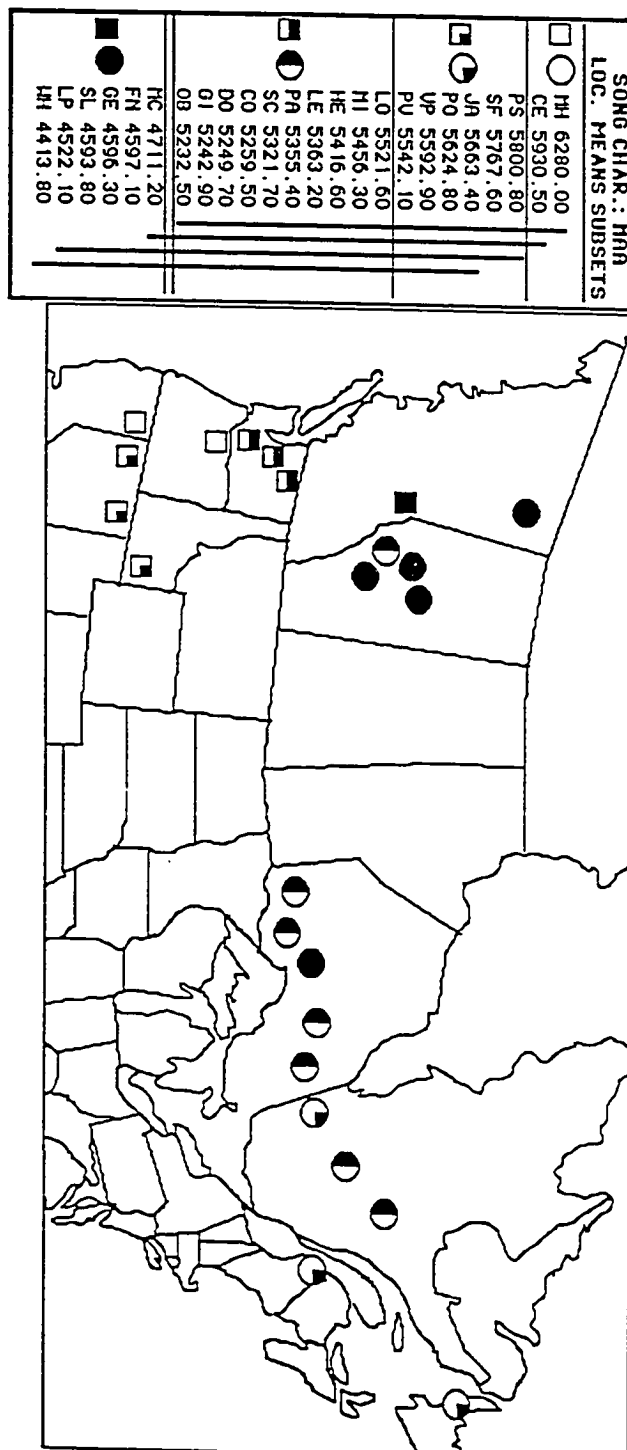


Figure 93. Geographic distribution of MAA means (Hz) for populations of *D. philadelphia* and *D. tolmiel*.

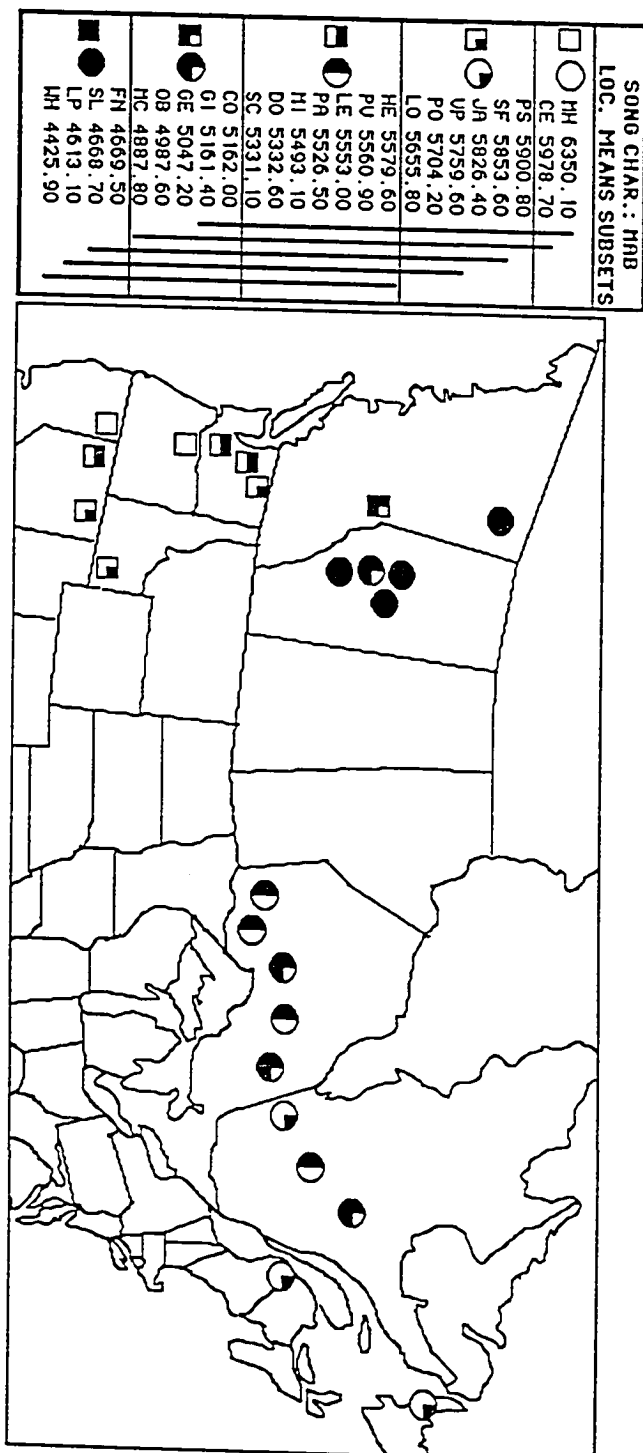


Figure 94. Geographic
distribution of MAB means (Hz)
for populations of *D. philadelphia*
and *D. tolmiei*.

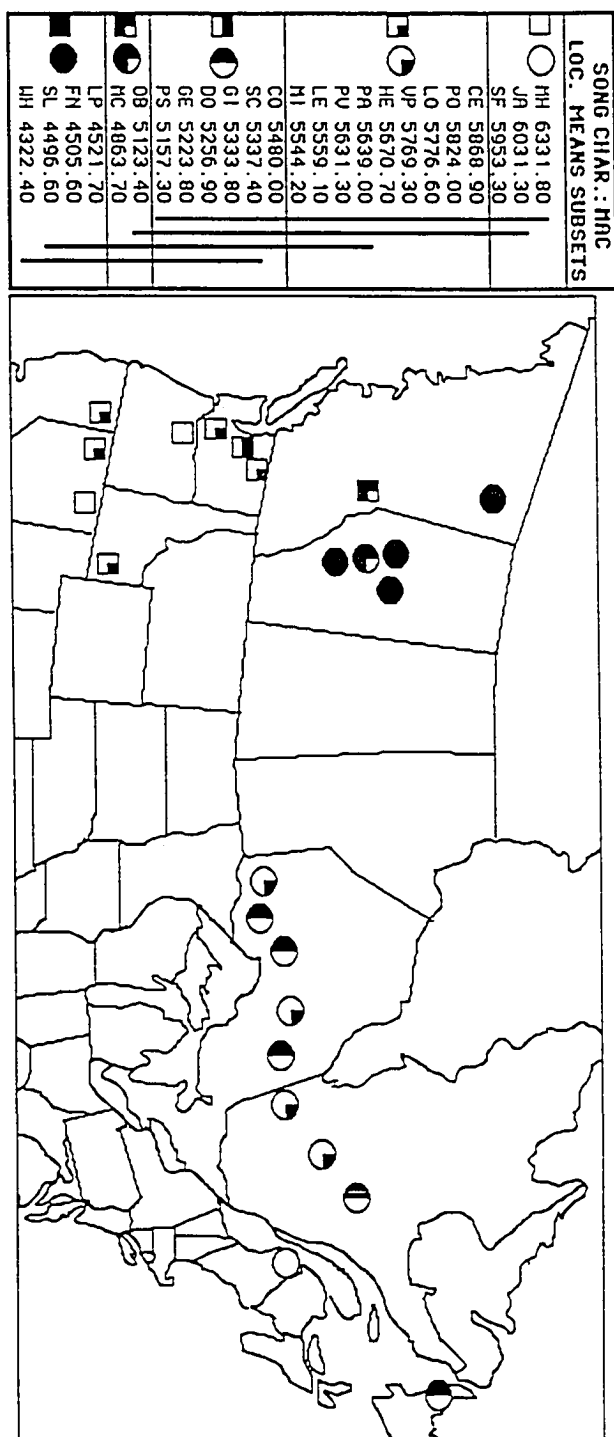


Figure 95. Geographic
distribution of MAC means (Hz)
for populations of *D.*
philadelphia and *D. tolmei*.

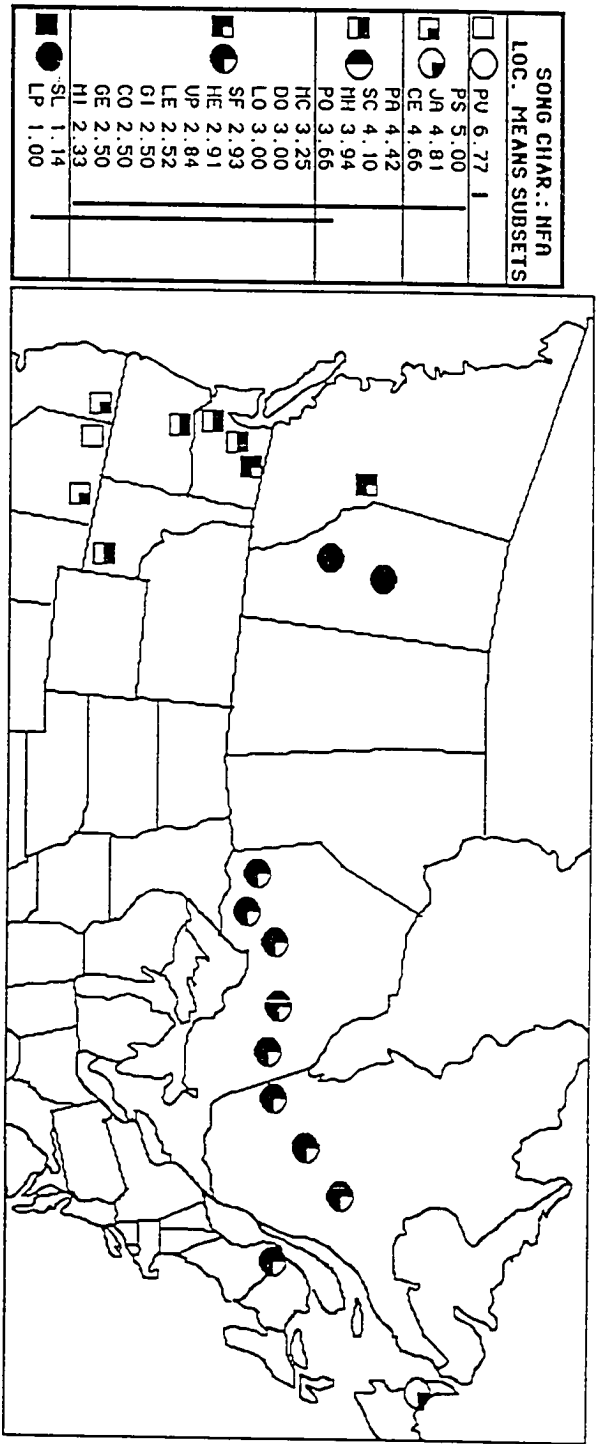


Figure 96. Geographic distribution of NFA means for populations of *D. philadelphie* and *D. tolmiei*.

Figure 97. Bivariate plots of population means:
NFA, NFB, IFA, IFB, MIFA, MIFB, MAFA, MAFB.

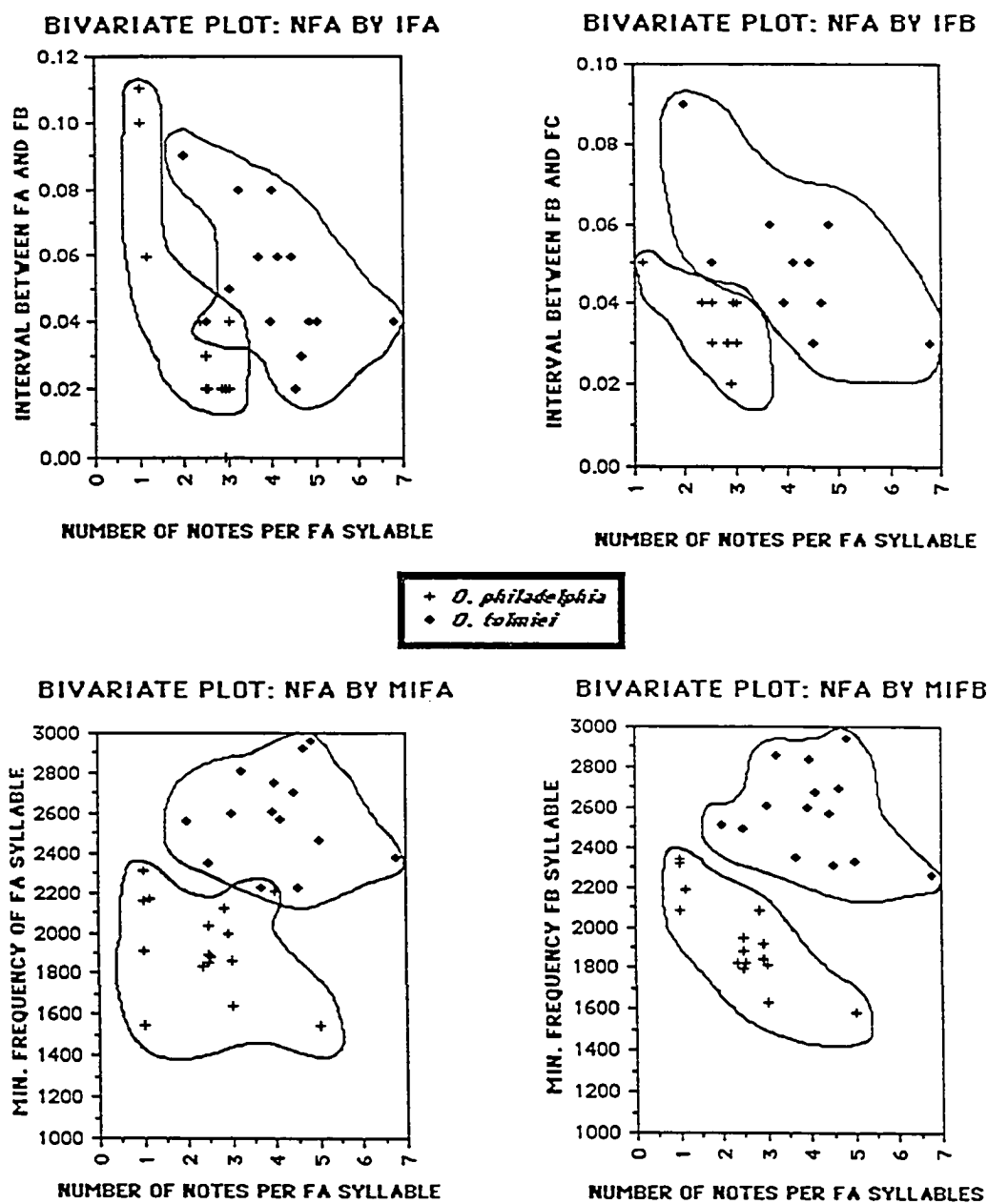
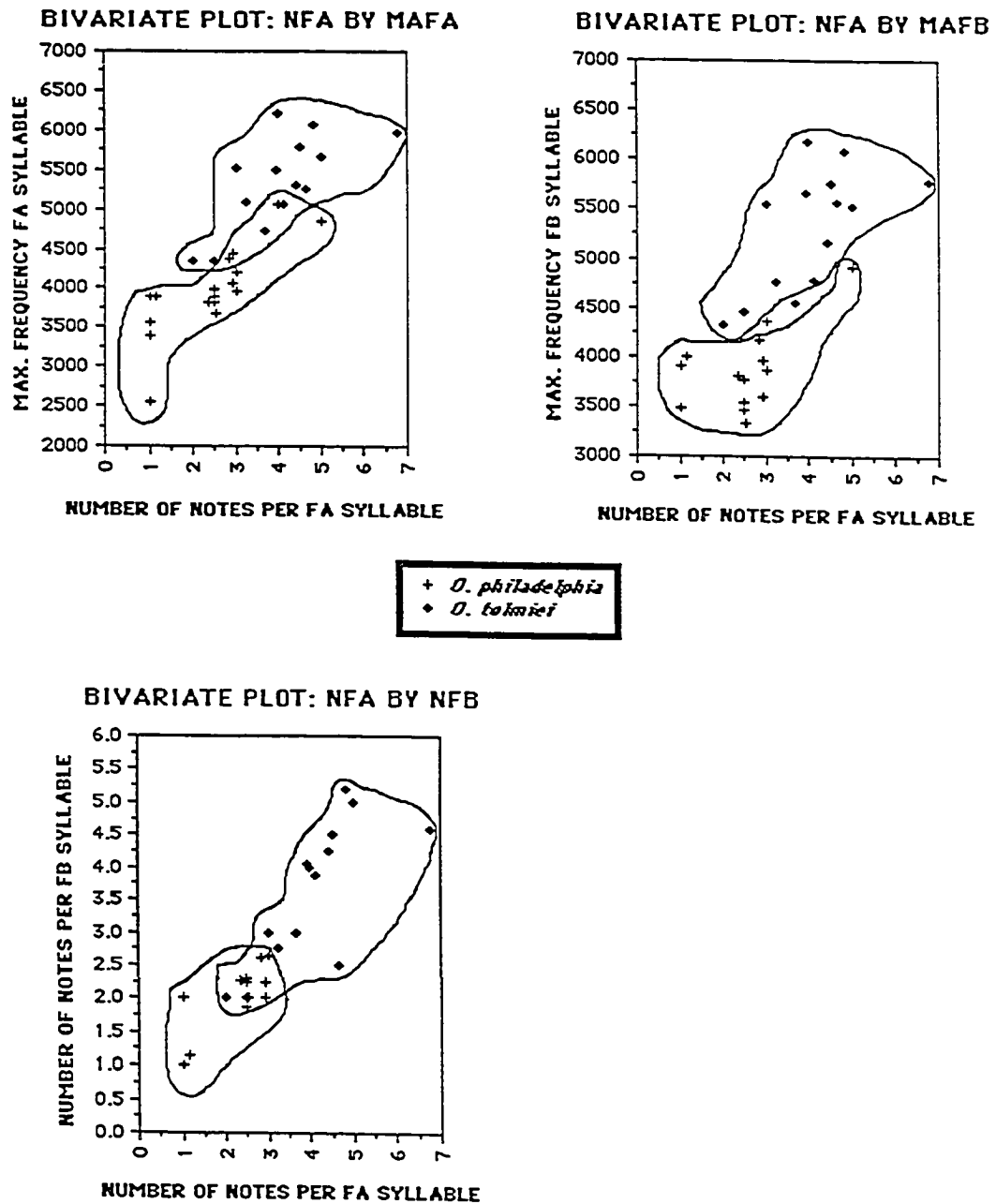


Figure 97. Bivariate plots of population means:
NFA, NFB, IFA, IFB, MIFA, MIFB, MAFA, MAFB (cont'd).



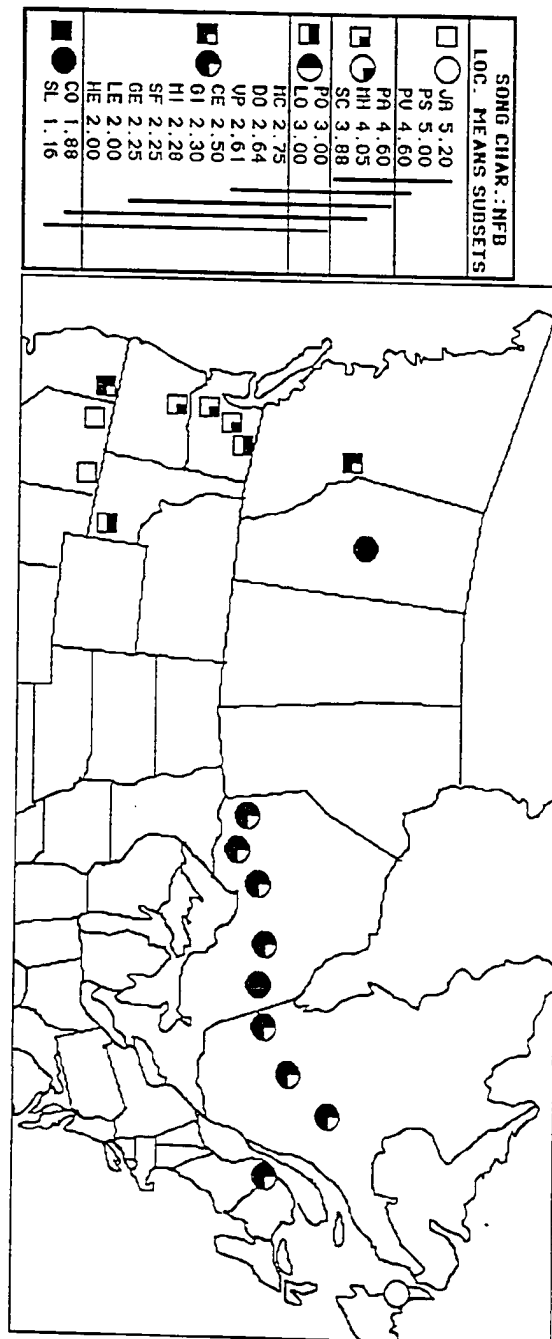


Figure 90. Geographic distribution of NFB means for populations of *Q. philadelphica* and *Q. tolmiei*.

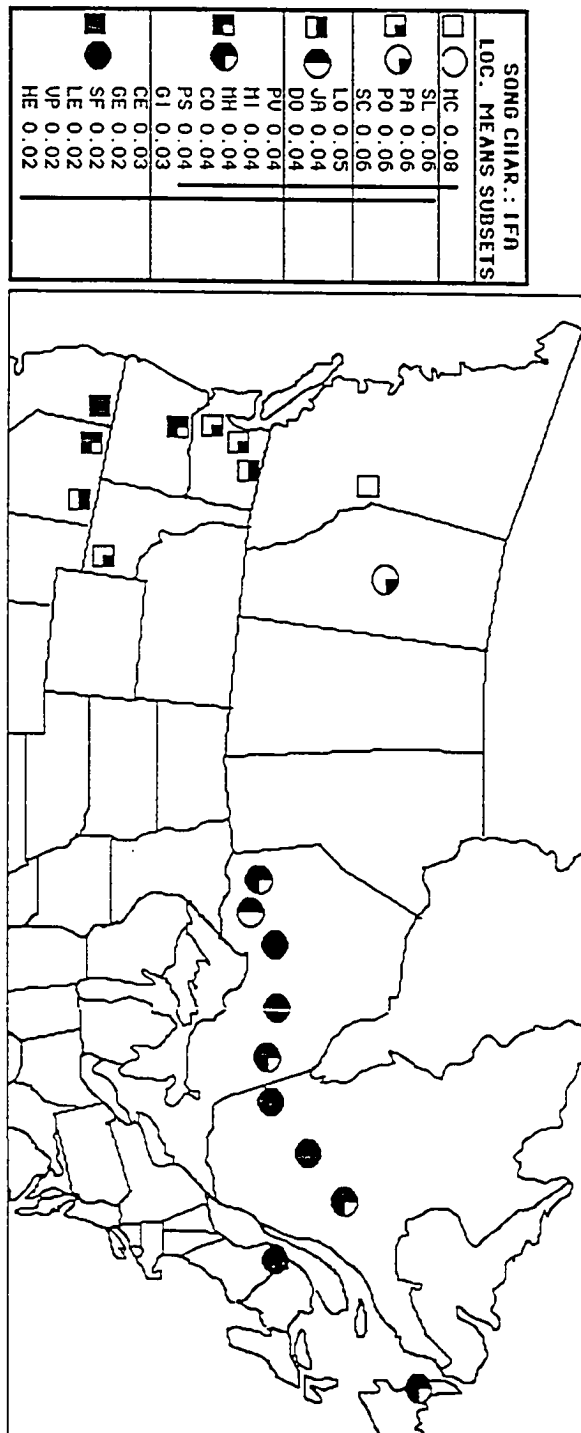


Figure 99. Geographic distribution of IFA means (seconds) for populations of *D. philadelphia* and *D. tolmiei*.

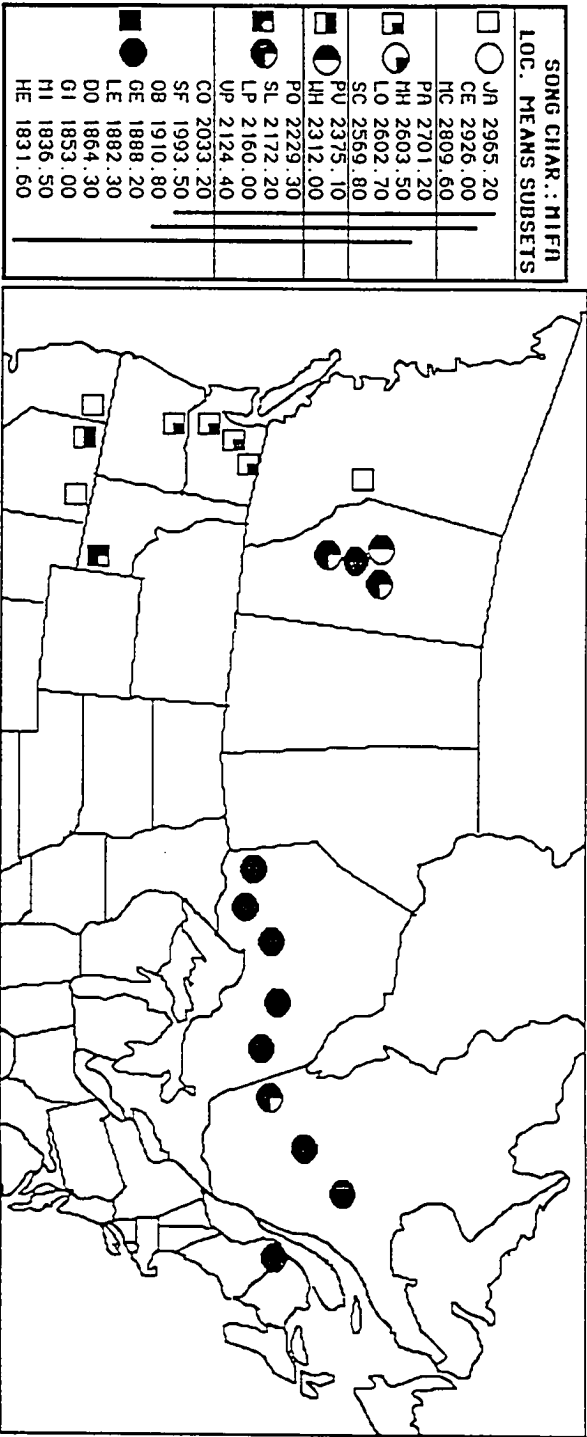


Figure 100. Geographic distribution
of MIFA means (Hz) for
populations of *D. philadelphia*
and *D. tolmiei*.

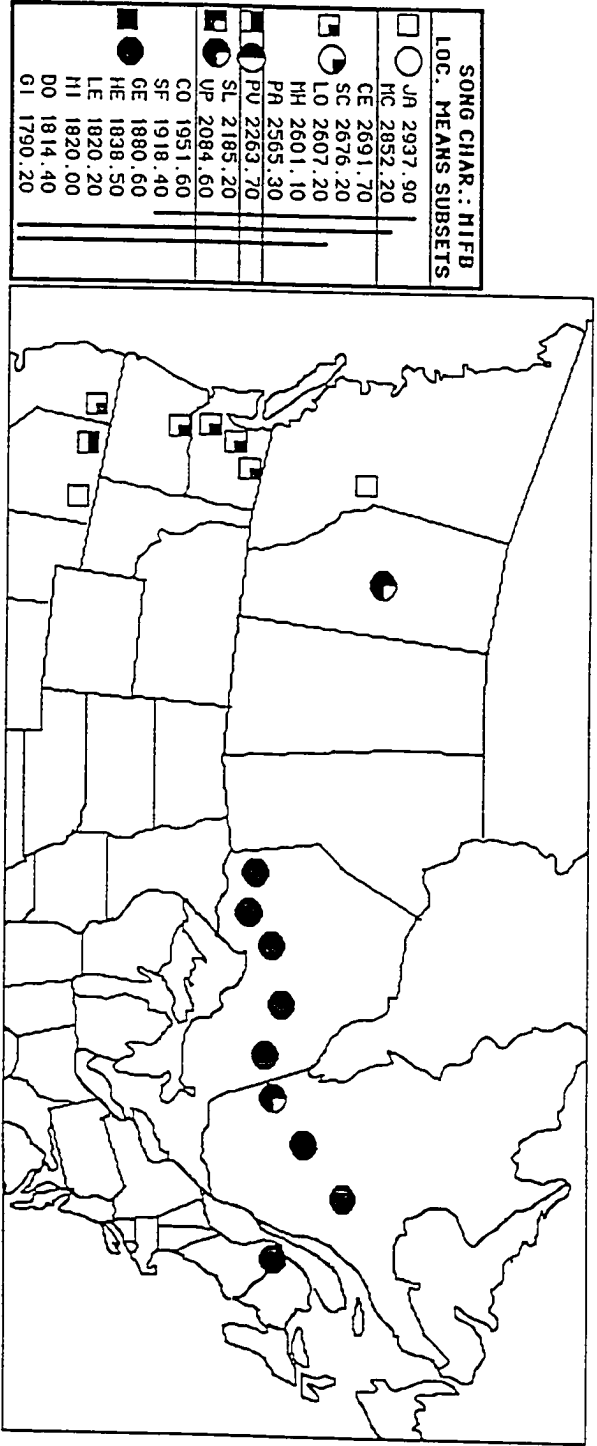


Figure 101. Geographic
distribution of MIFB means (Hz)
for populations of *Q. philadelphica*
and *Q. tolmiei*.

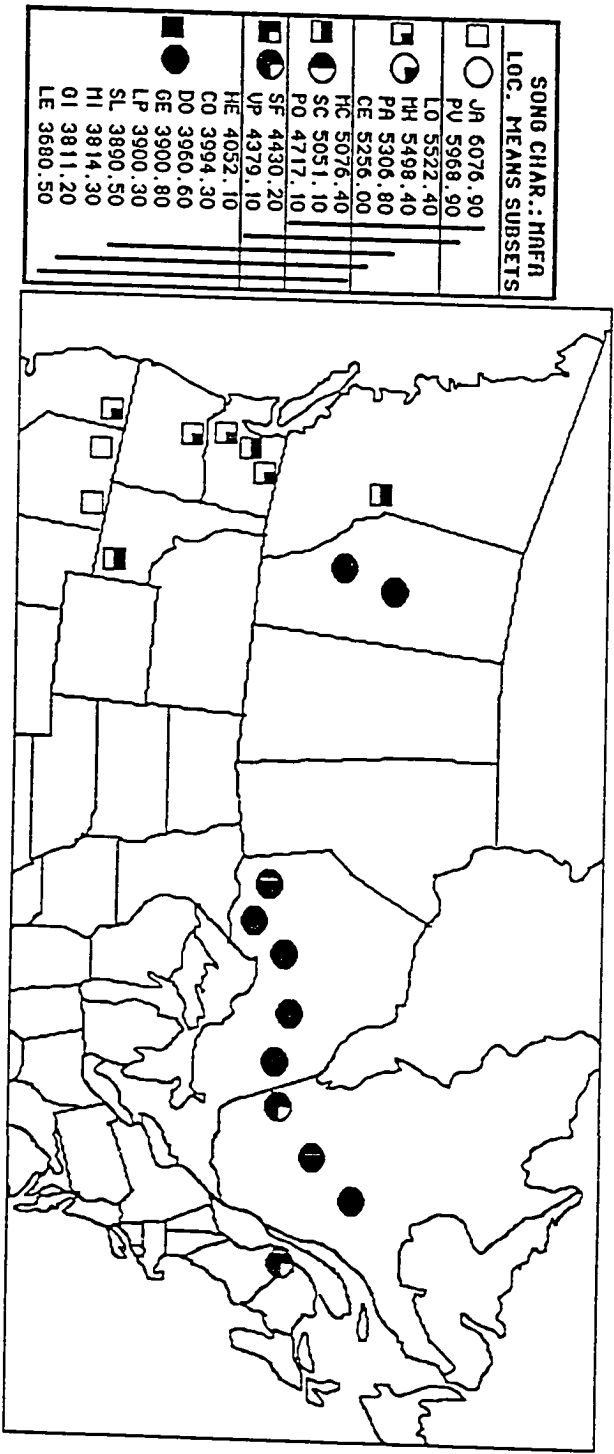


Figure 102. Geographic
distribution of MFA means (Hz)
for populations of *Q.*
philadelphica and *Q. tolmiei*.

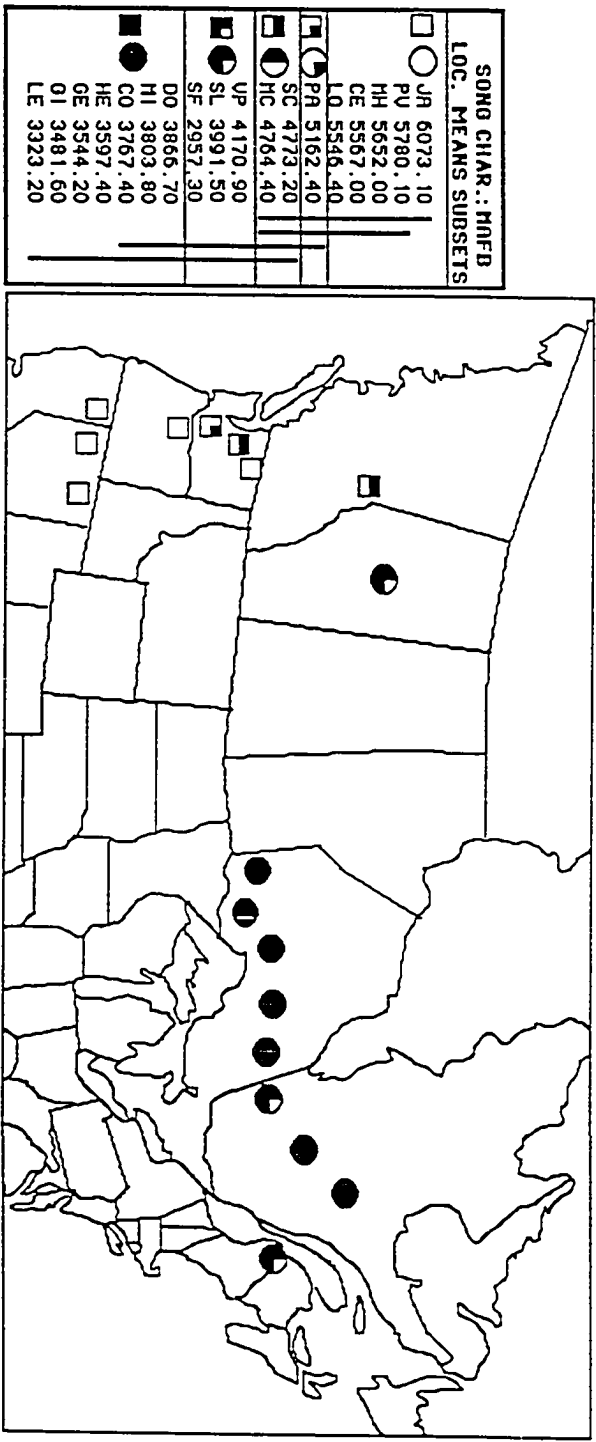
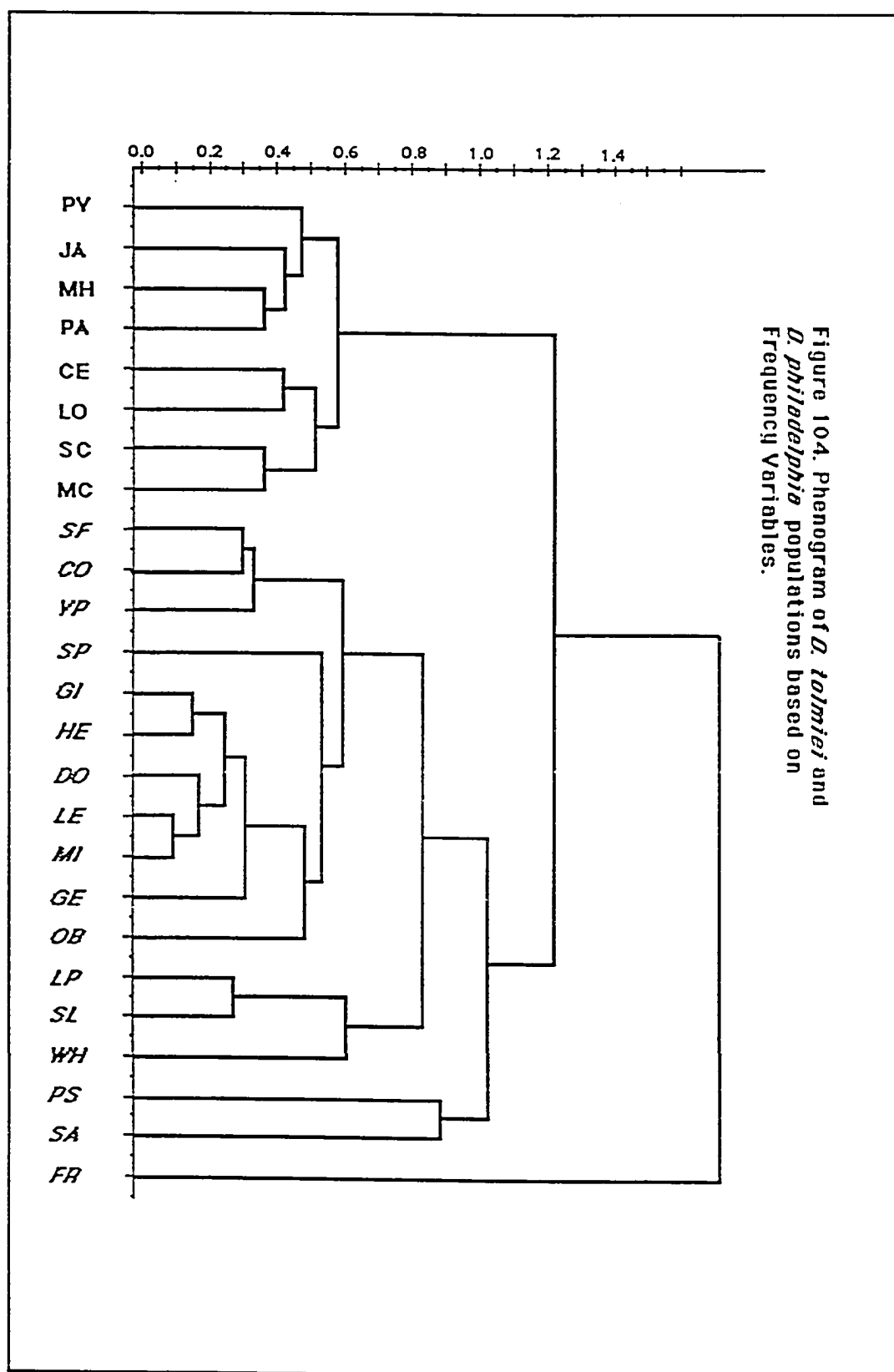
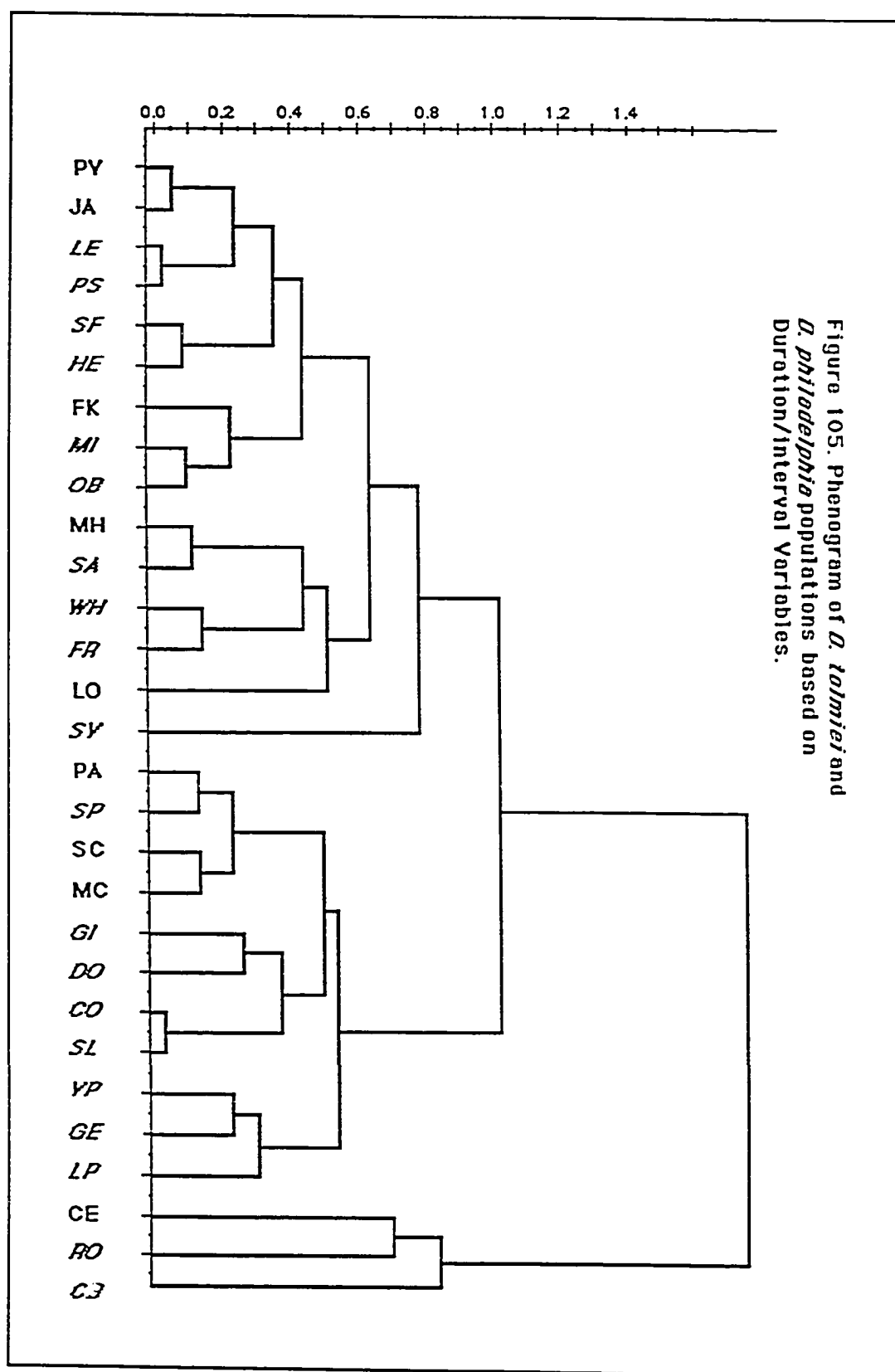


Figure 103. Geographic distribution of MAFB means (Hz) for populations of *D. philadelphia* and *D. talpiae*.





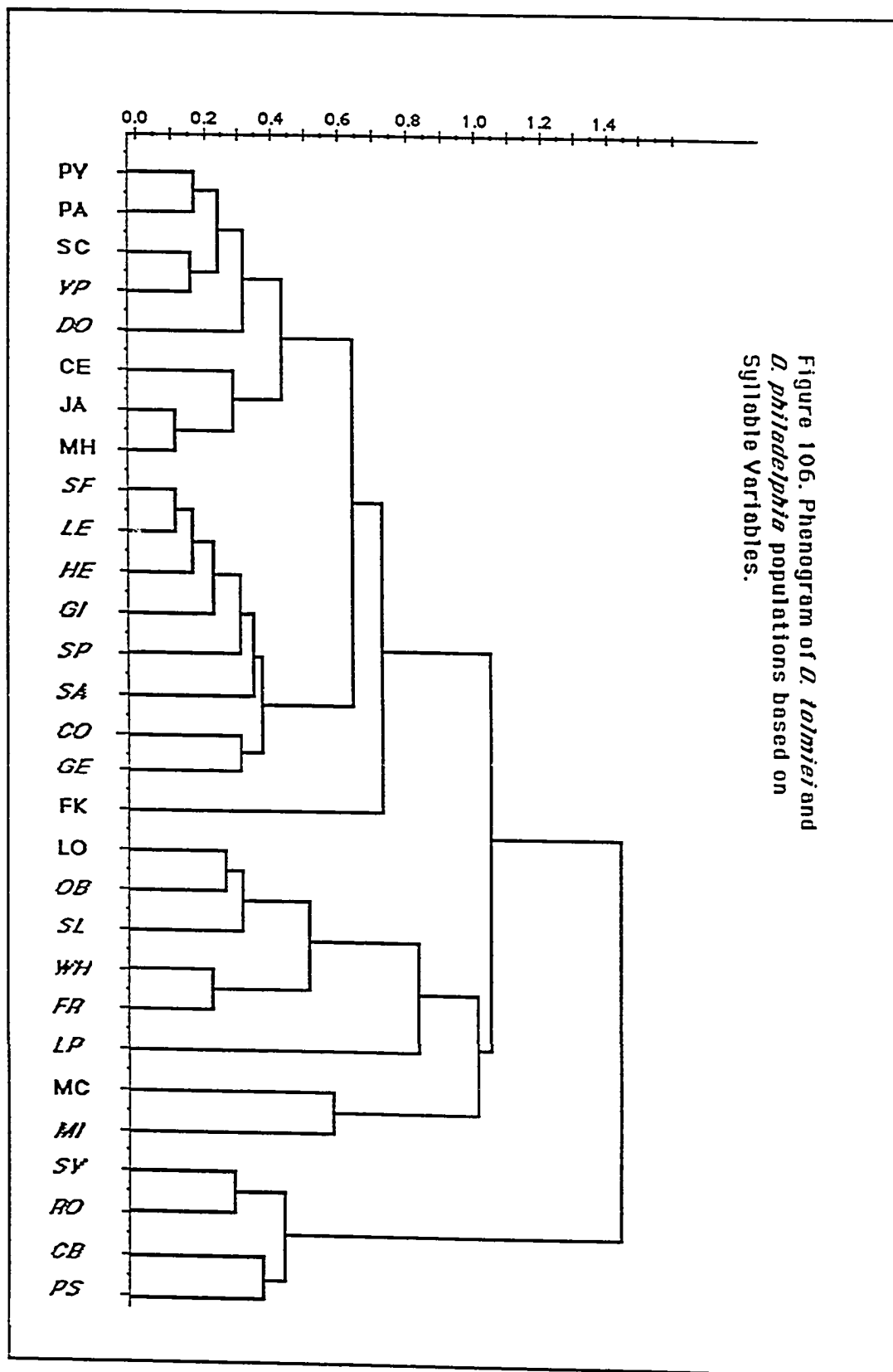


Figure 106. Phenogram of *Q. tolmiei* and *Q. philadelphia* populations based on Syllable Variables.

Figure 107. Phenogram of *O. tolmiei* and *O. philadelphia* populations based on all song Variables.

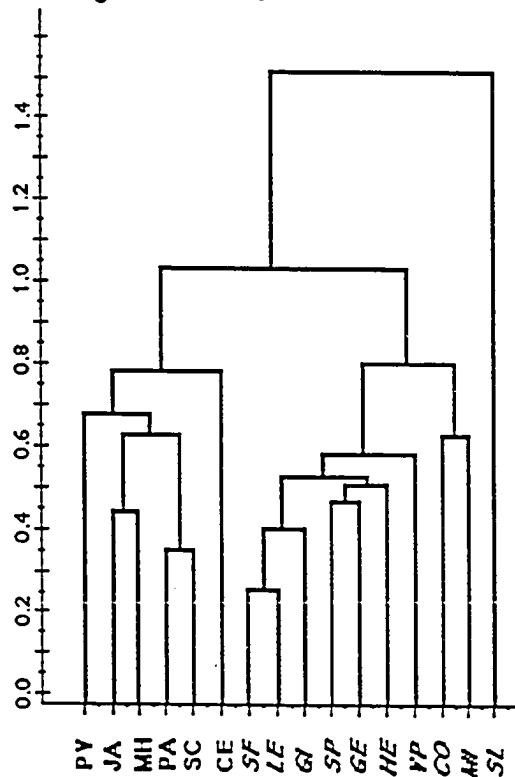


Figure 108. 3D plots of Principal Components 1, 2, 3 based on Frequency variables.

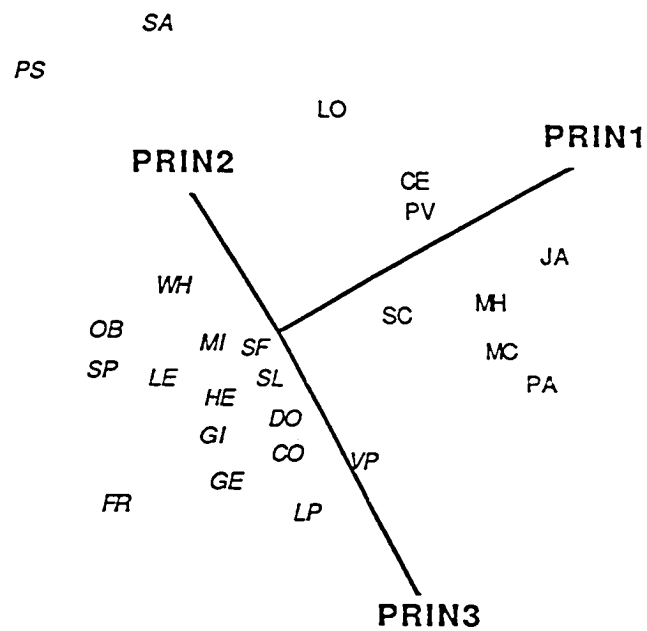


Figure 109. 3D plots of Principal Components 1, 2, 3 based on Duration/Interval variables.

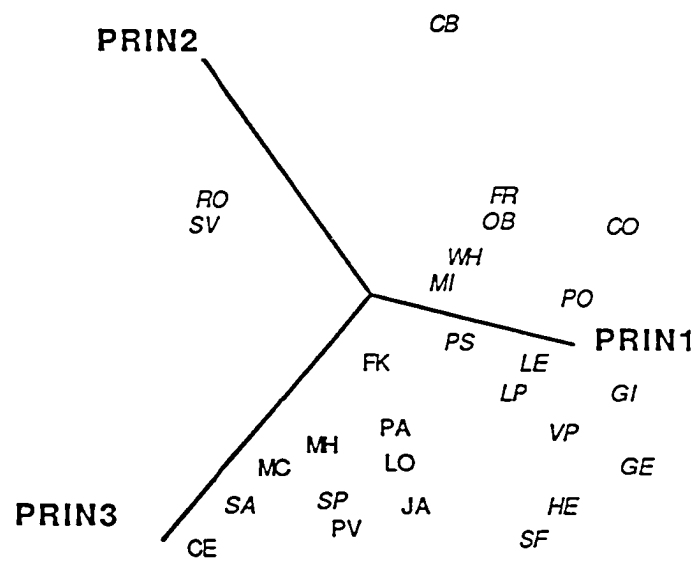


Figure 110. 3D plots of Principal Components 1, 2, 3 based on Syllable variables.

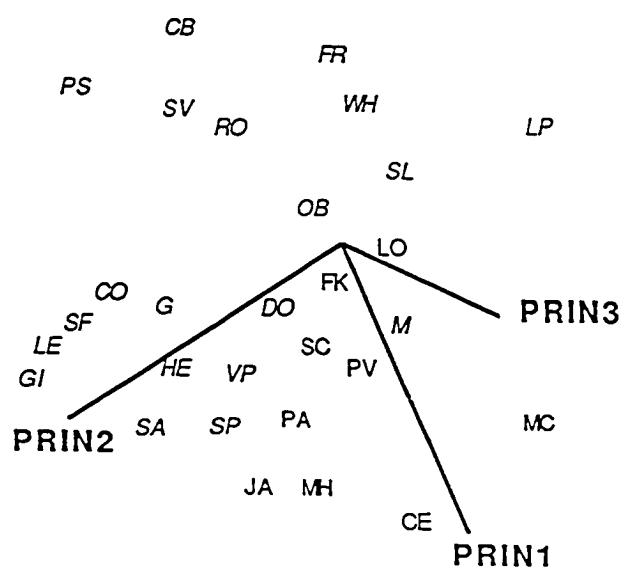


Figure 111. 3D plots of Principal Components 1, 2, 3 based on all song variables.

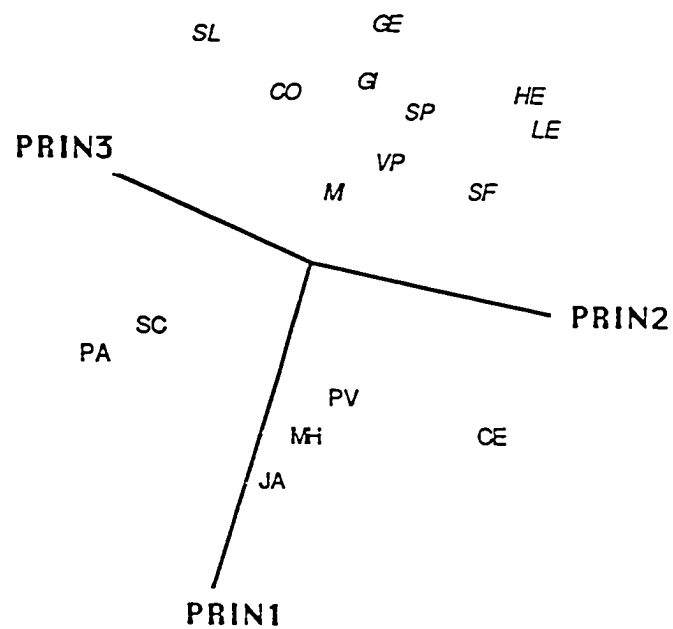


Figure 112. Plots of Discriminant Function Scores for *O. philadelphia* and *O. tolmiei* OTU's for frequency complex variables.

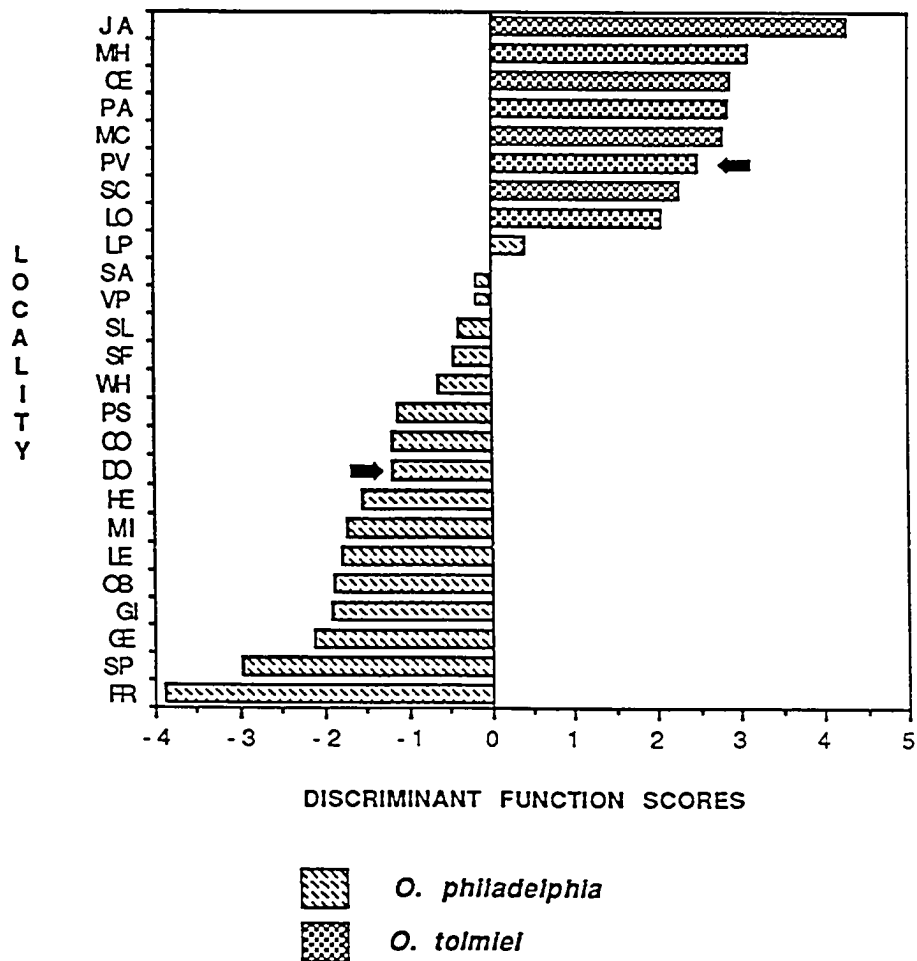


Figure 113. Plots of Discriminant Function Scores for *O. philadelphia* and *O. tolmiel* OTU's for duration/interval complex variables.

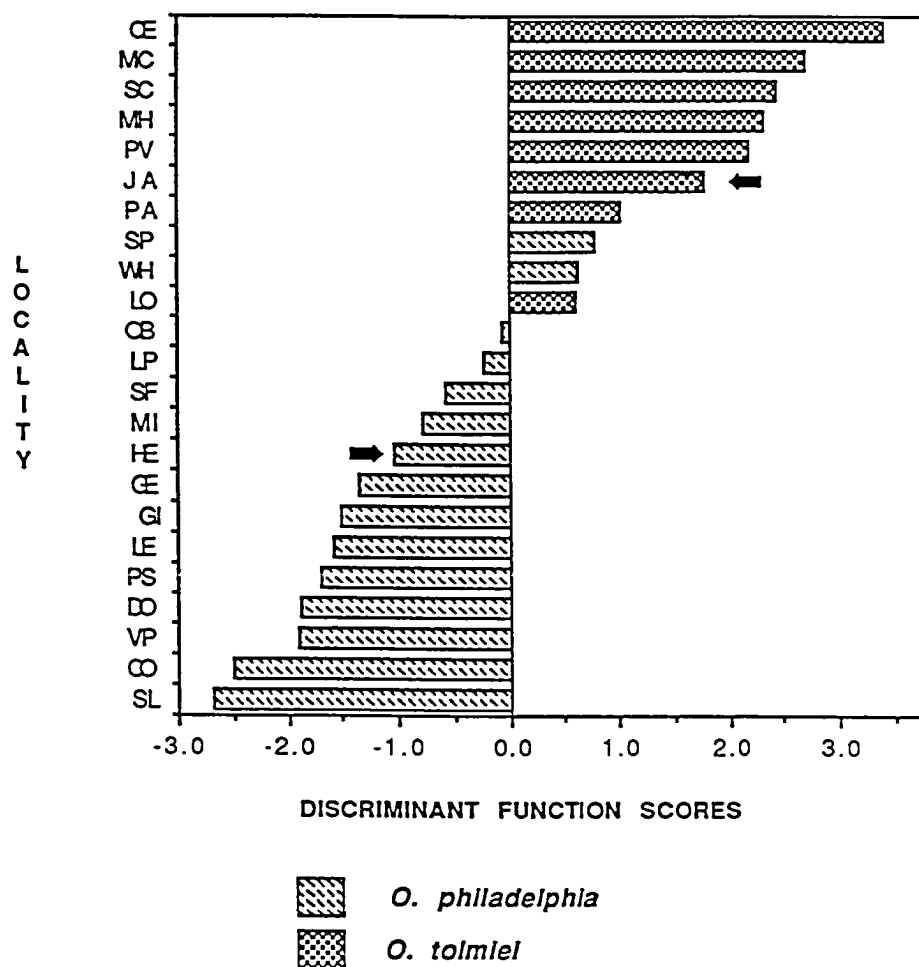


Figure 114. Plots of Discriminant Function Scores for *O. philadelphia* and *O. tolmiei* OTU's for syllable complex variables.

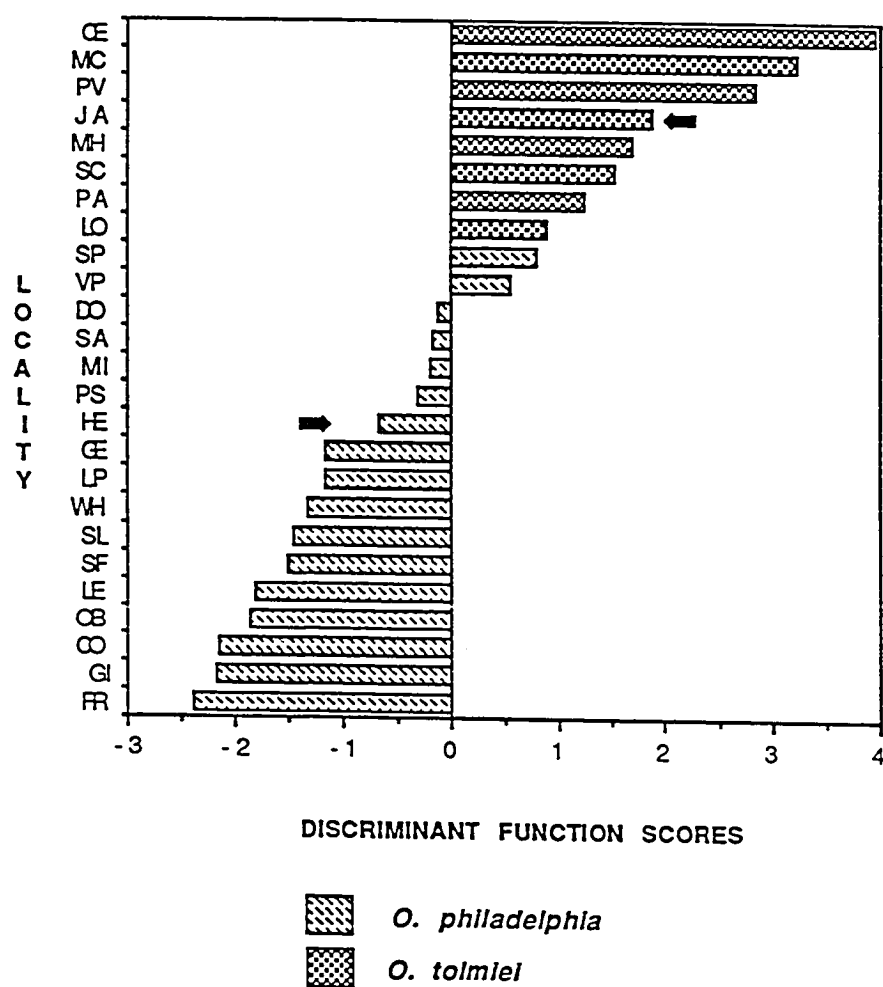


Figure 115. Plots of Discriminant Function Scores for *O. philadelphia* and *O. tolmiei* OTU's for all song parameter complex variables.

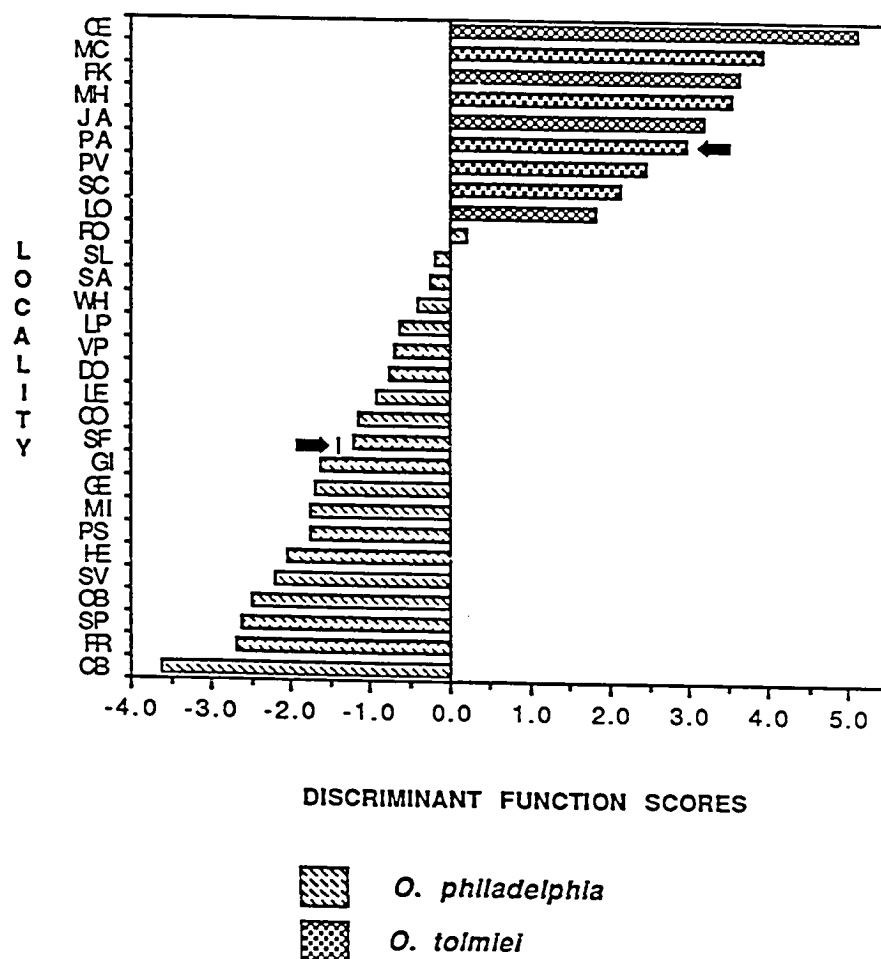


Figure 116. Mahalanobis' D^2 for each song parameter complex and for all parameter complexes combined.

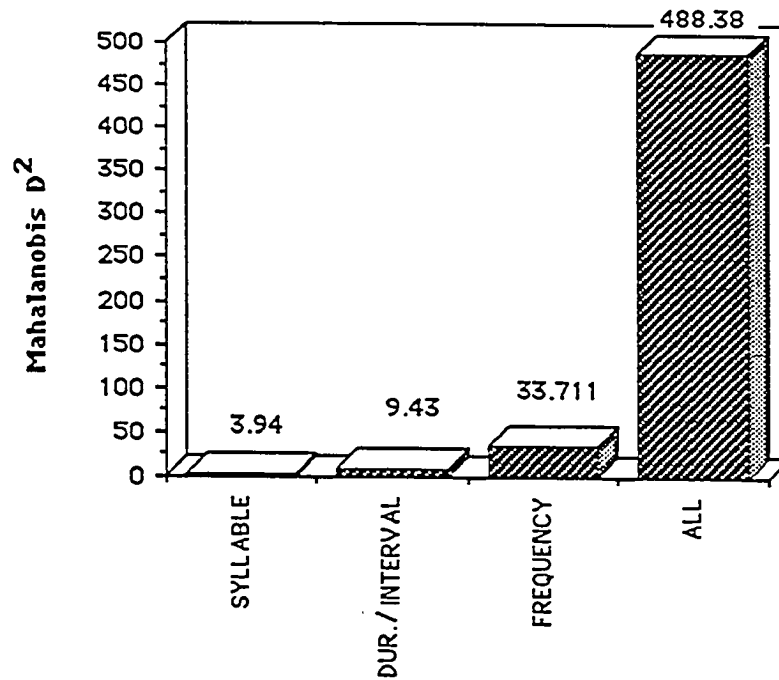


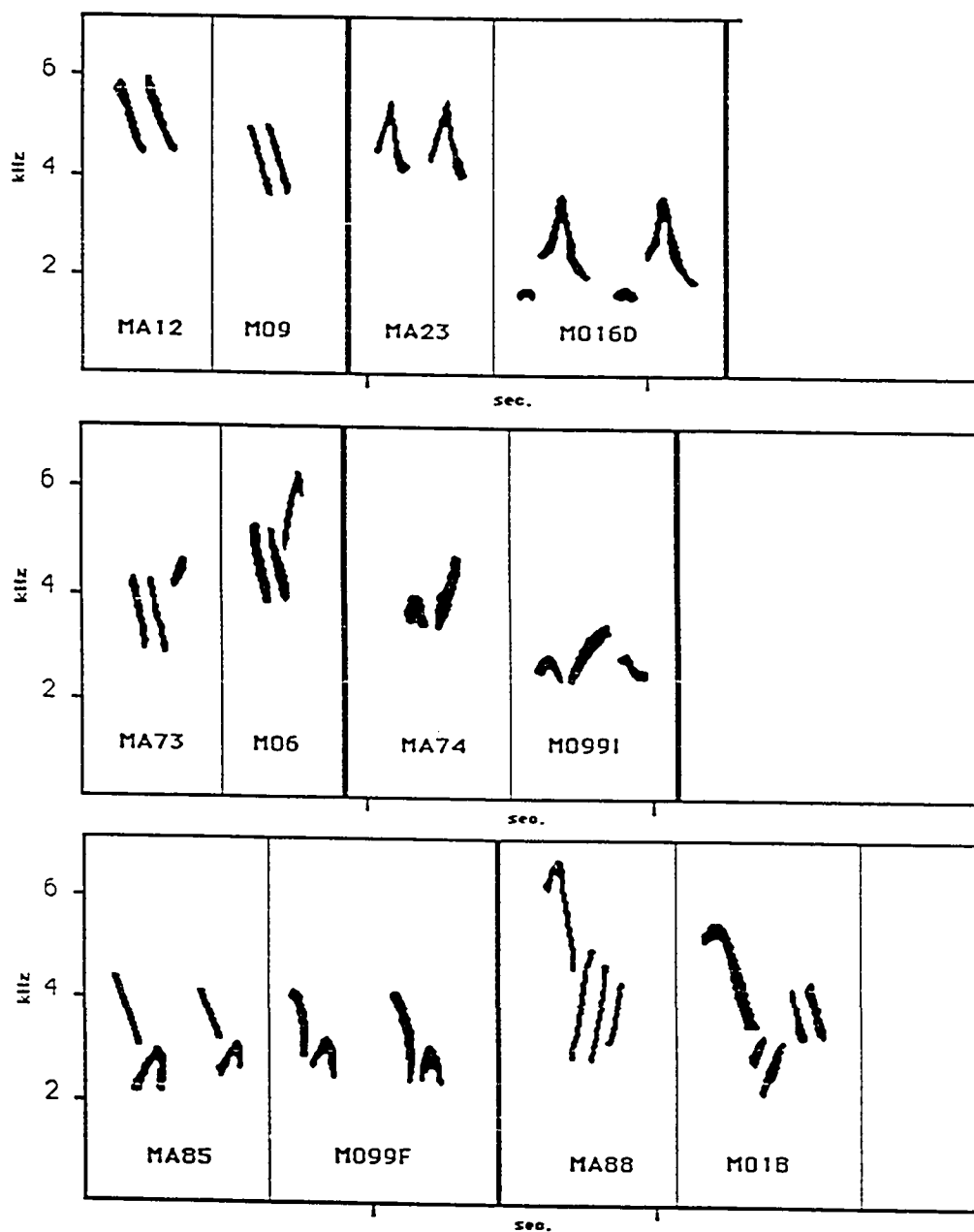
Figure 117. Syllables shared by *O. philadelphia* and *O. tolmiei*

Figure 118. Graph of the number of new syllables encountered with each new individual sampled.

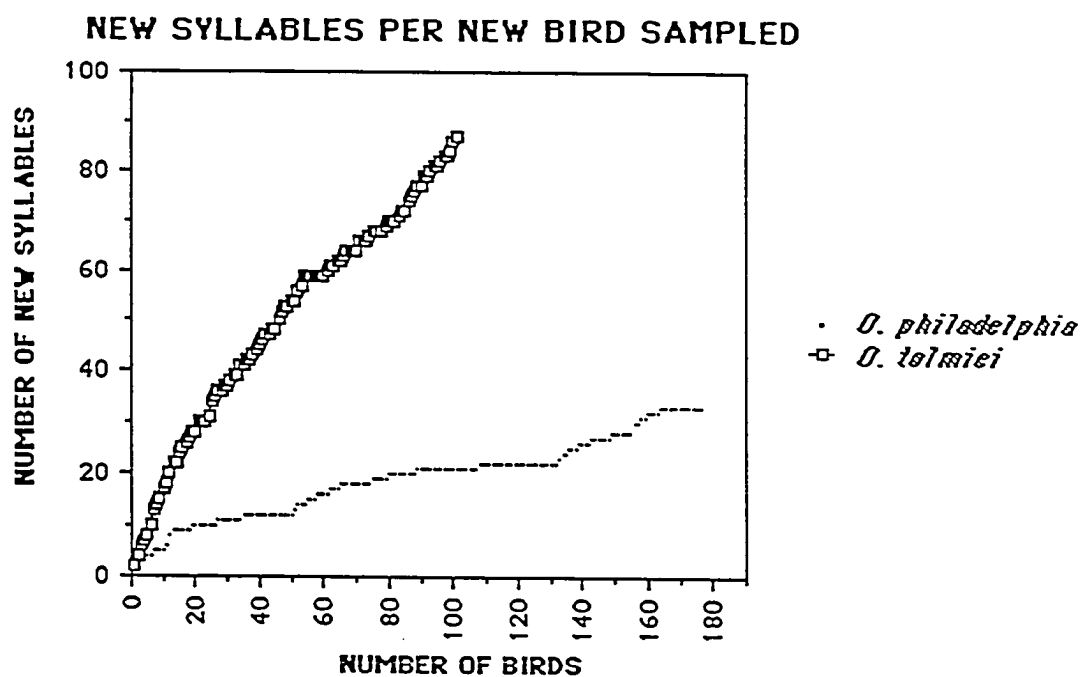


Figure 119. Distribution of M0
Syllables and Variants in the
of *A. philadelphia*

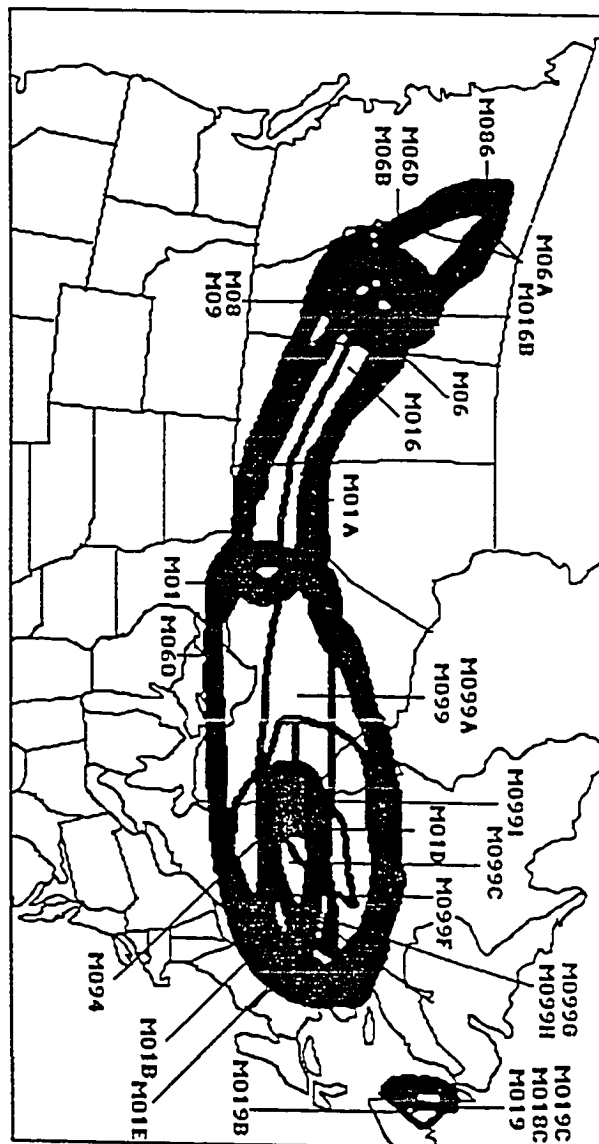


Figure 120. Sonographs of Newfoundland songsters.

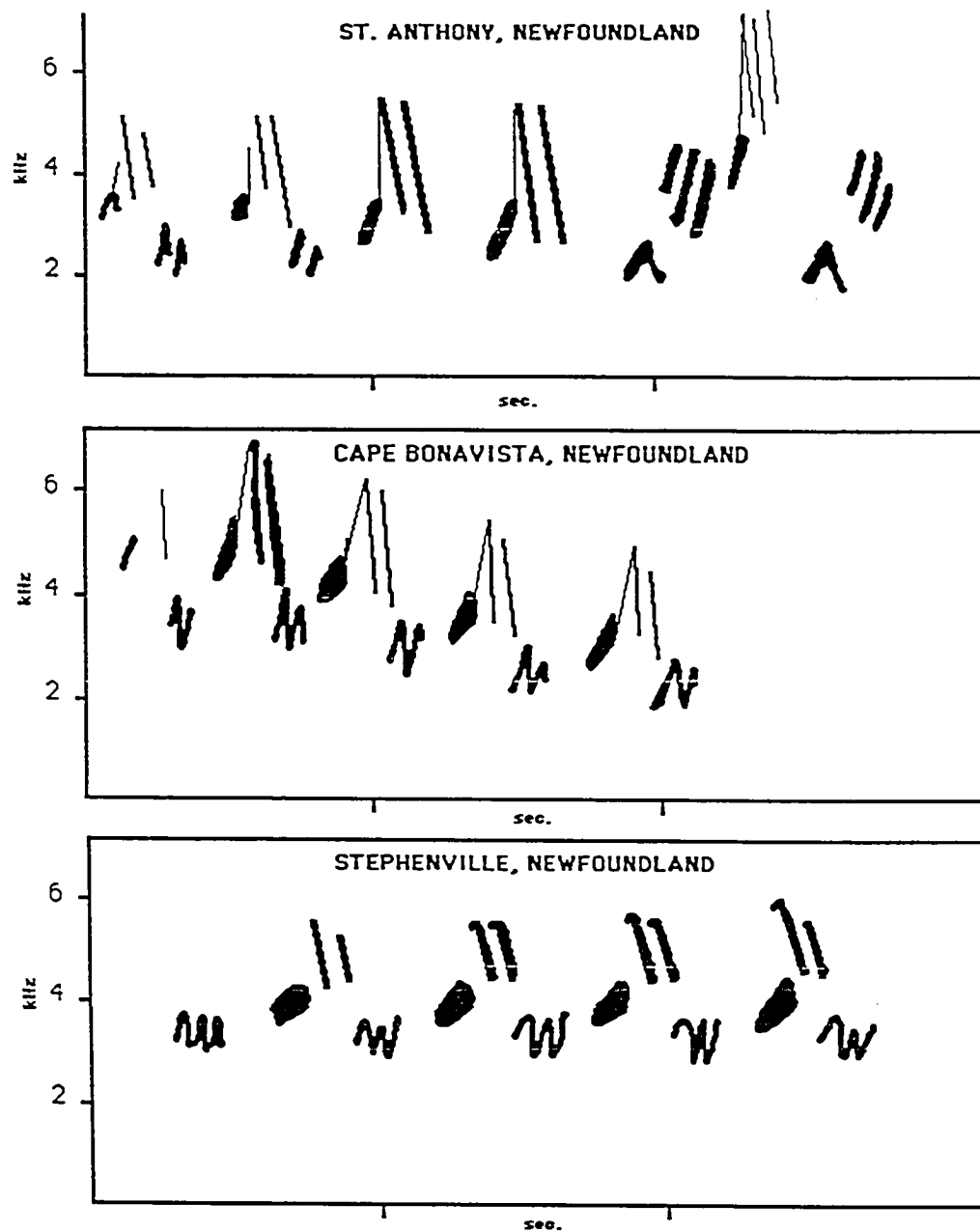


Figure 121. Sonographs of eastern continental songsters.

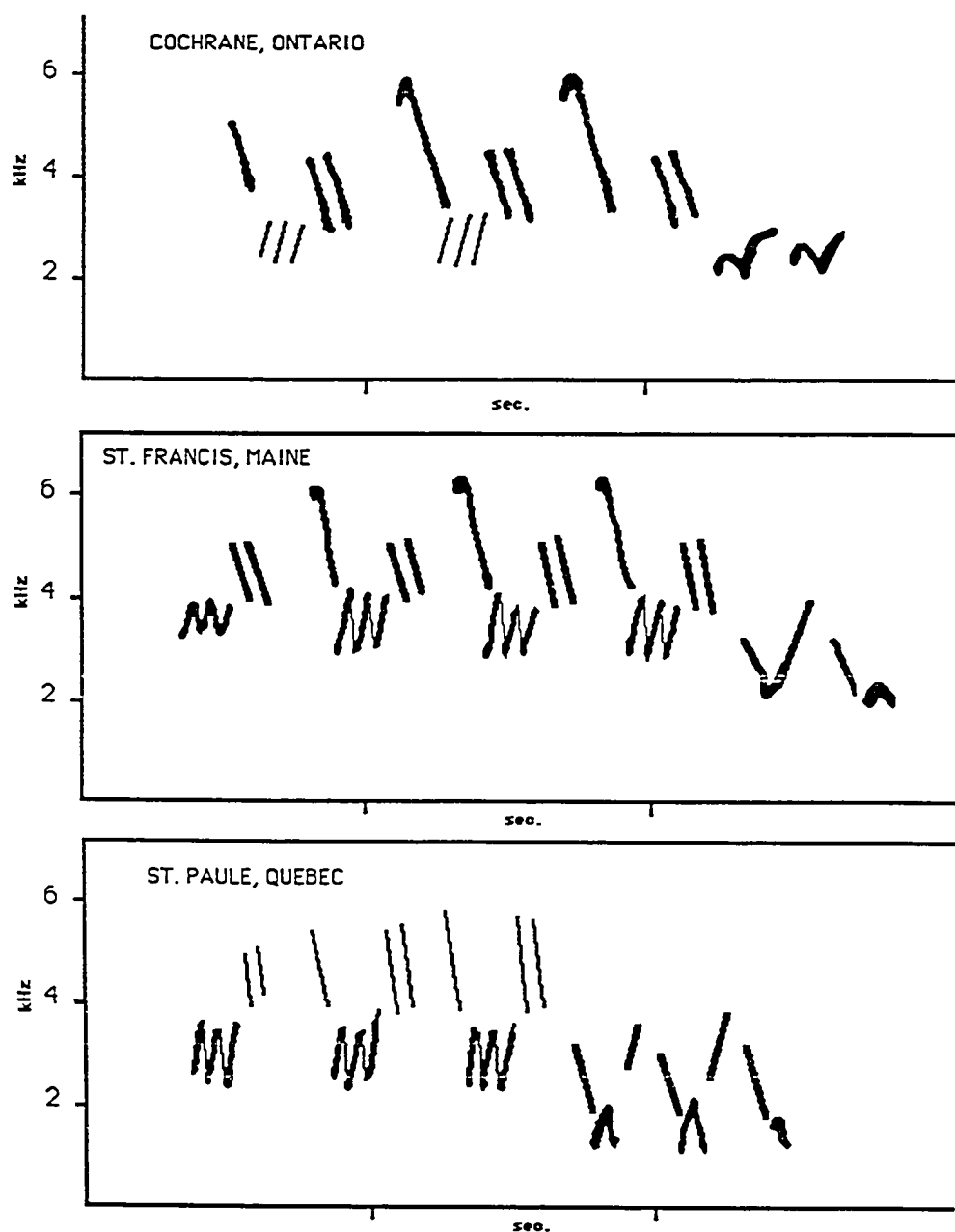


Figure 122. Sonographs of western continental songsters.

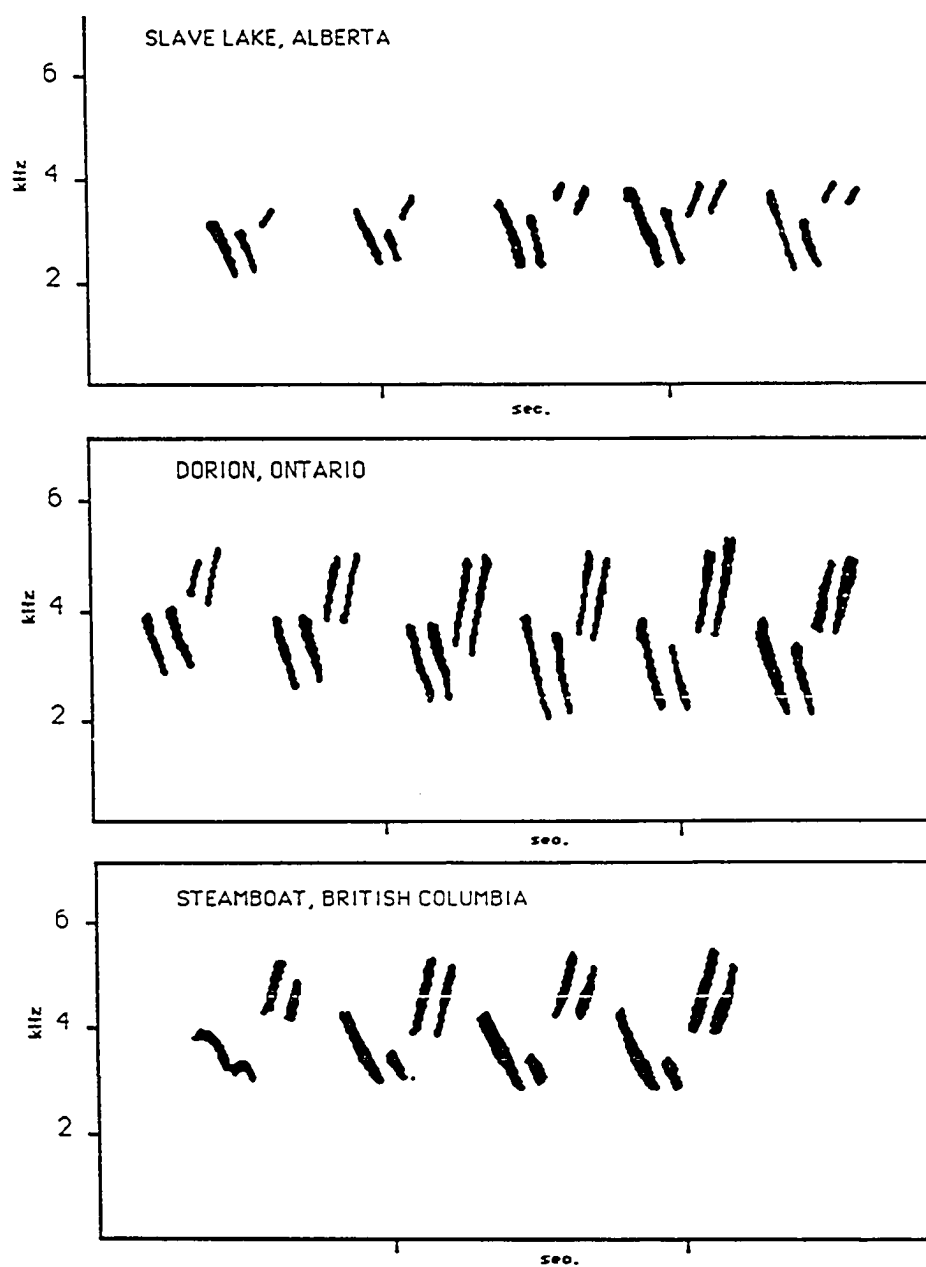


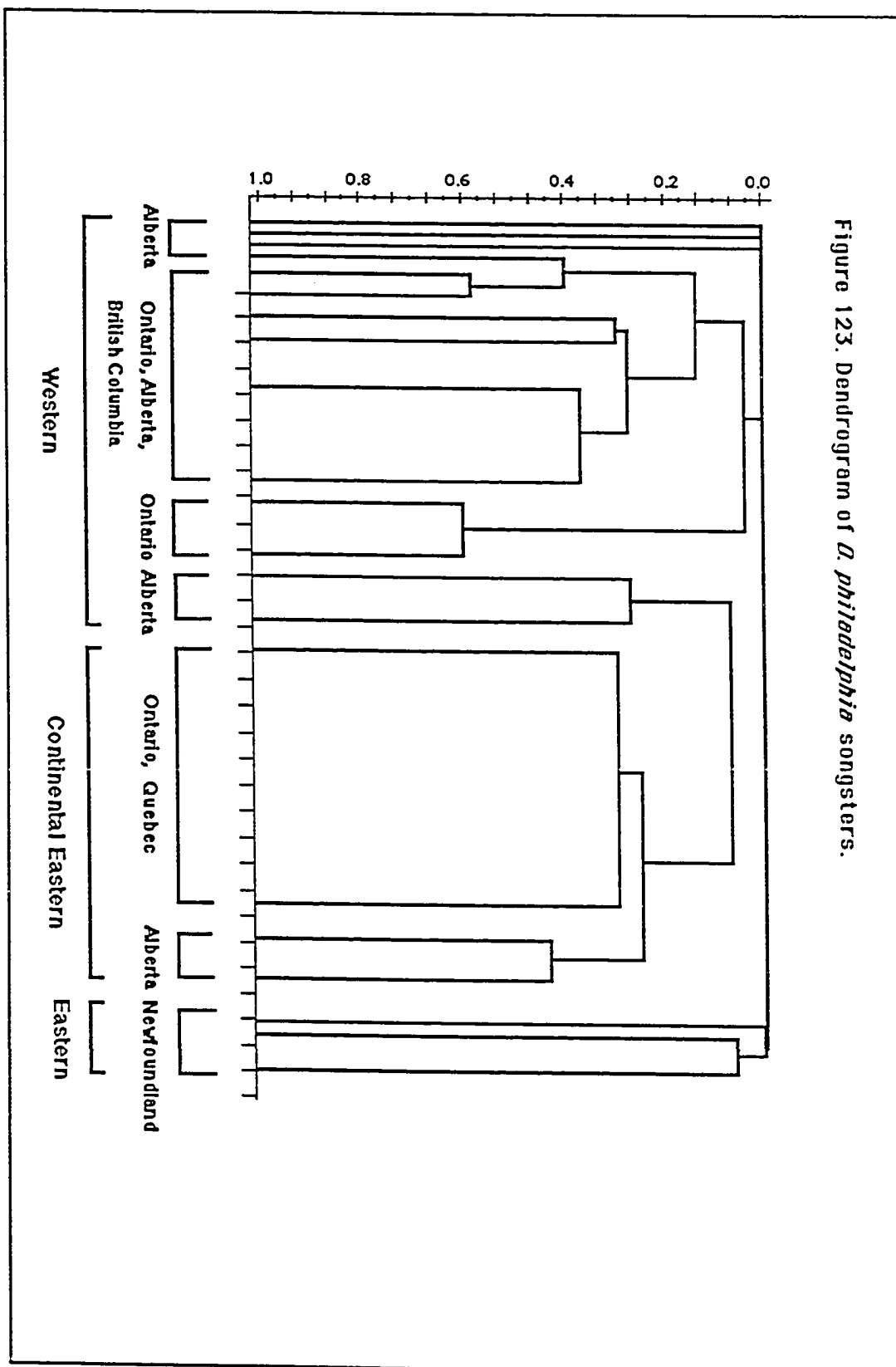
Figure 123. Dendrogram of *A. philadelphica* songsters.

Figure 124. Distribution of MA Syllables and Variants in the range of *O. tolmiei*.

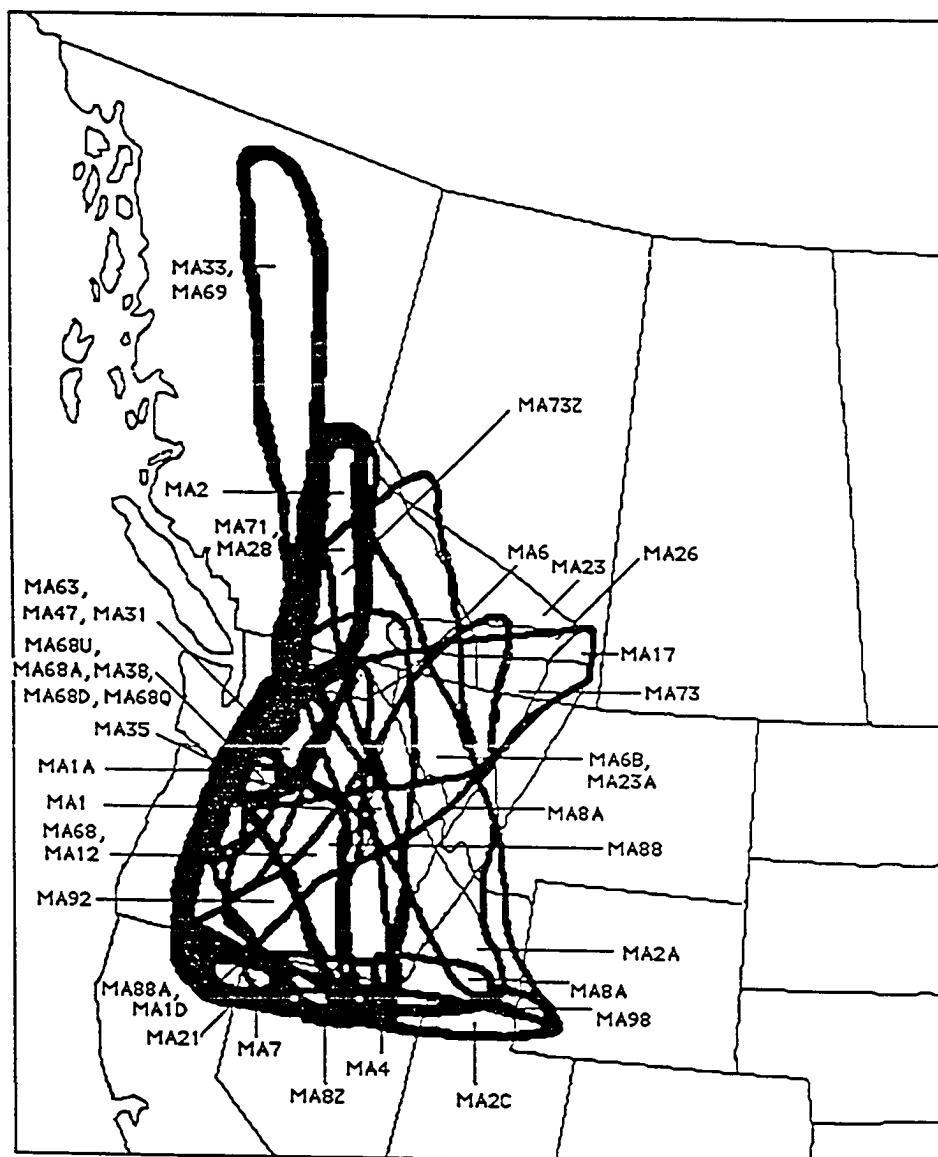


Figure 125. Sonographs of Jarbidge, Nevada songsters.

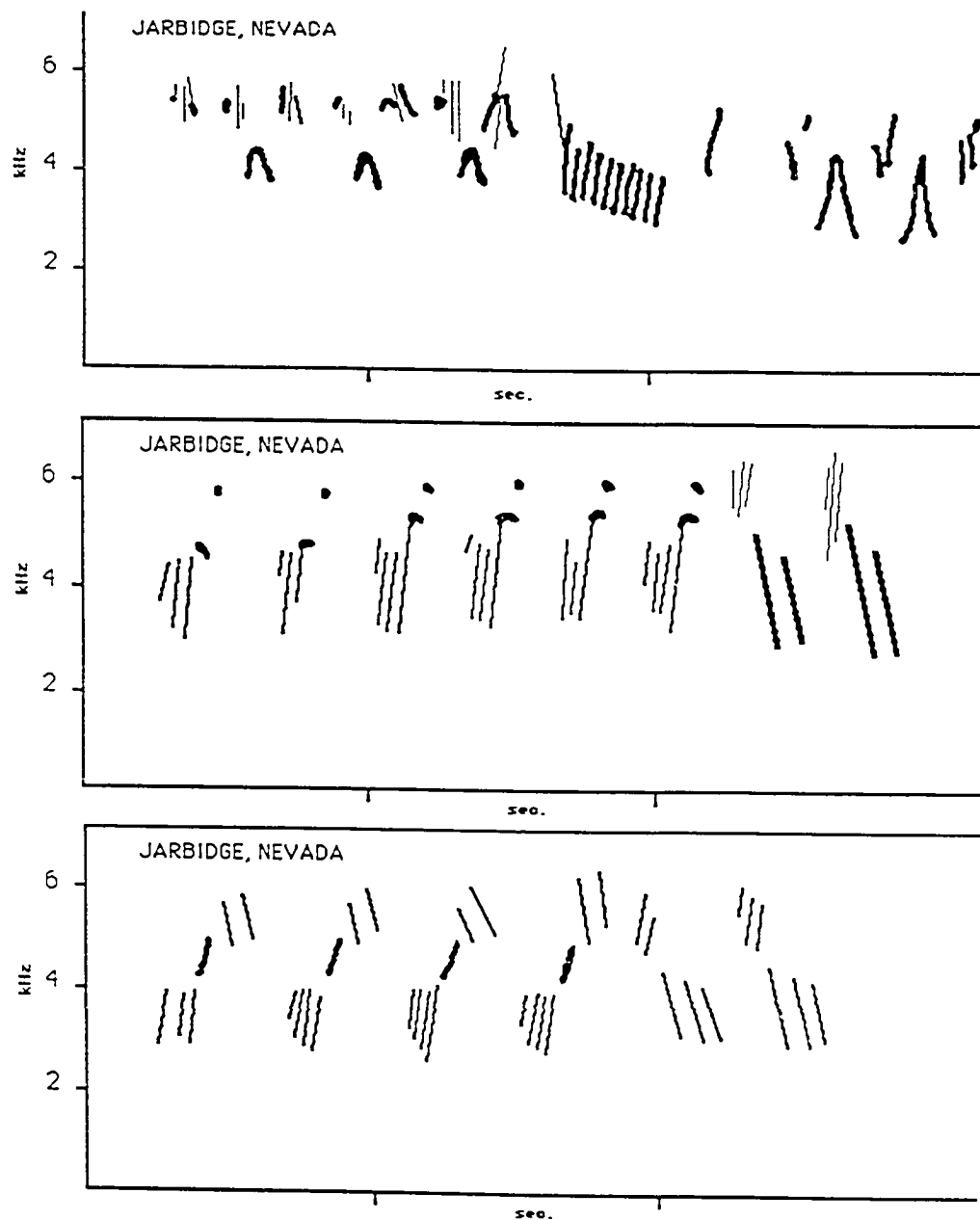
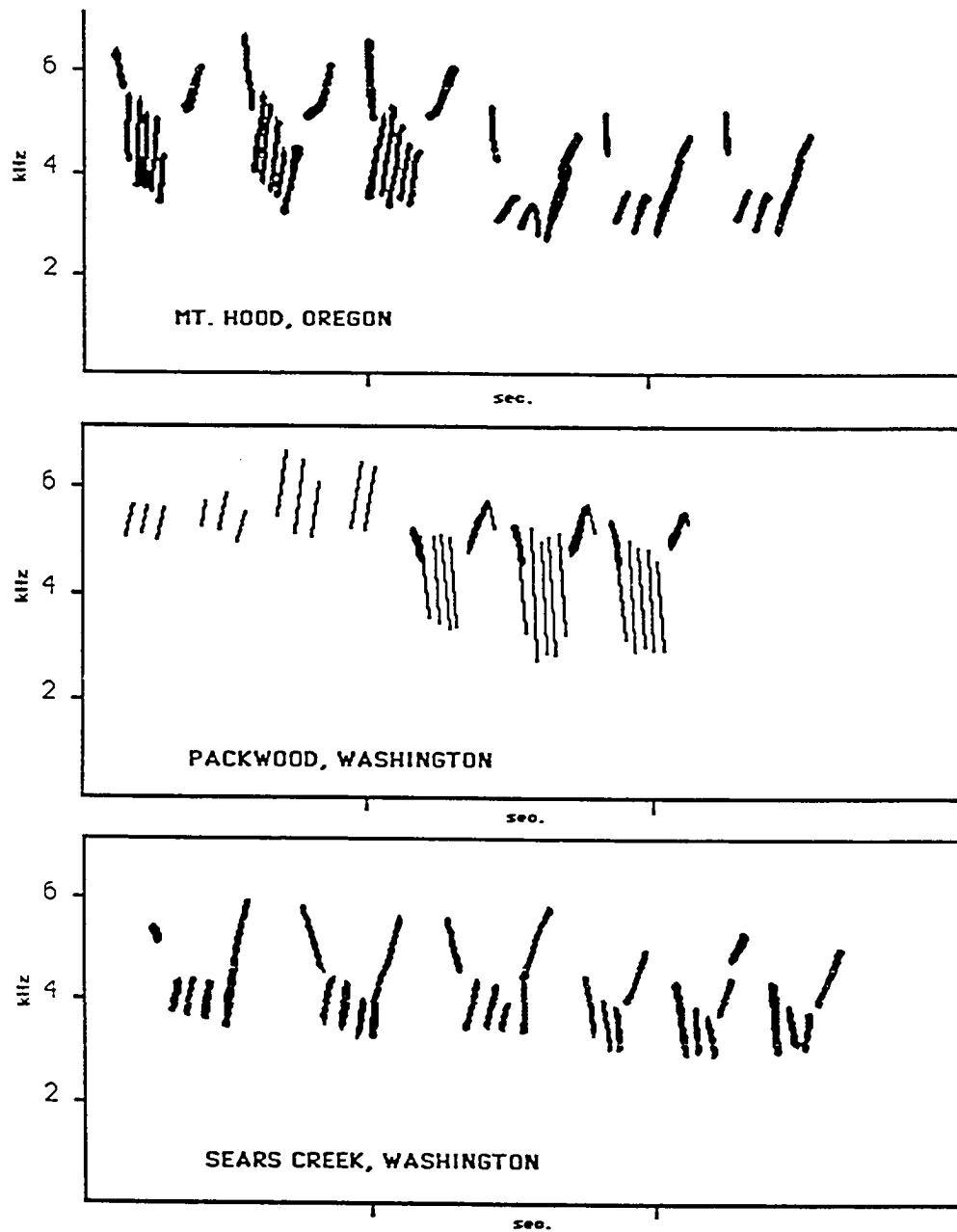
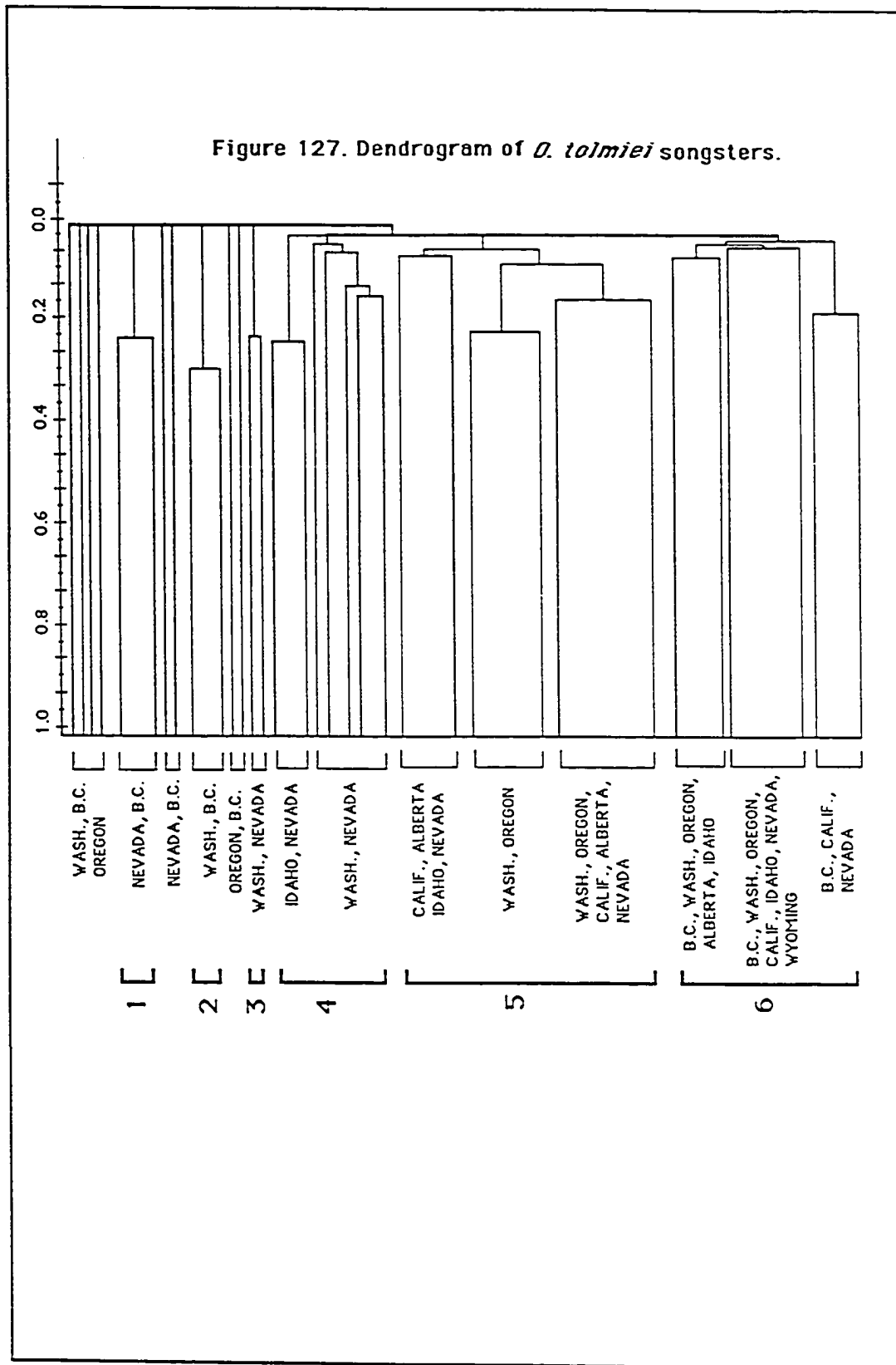


Figure 126. Sonographs of Oregon and Washington songsters.





CHAPTER 7 -- DISCUSSION

7.1 MORPHOLOGY

7.1.1 SPECIES DIFFERENCES: MORPHOLOGY-UNIVARIATE ANALYSIS

PLUMAGE AND EXTERNAL CHARACTERS. Traditional plumage and mensural characters are sufficient for separating all but extreme specimens of *O. philadelphia* from specimens of *O. tolmiei*. The combination of dark lores, eye-arcs, amount of black on the bib and W-T will distinguish most male *O. philadelphia* specimens. Of all the specimens collected in this study or any previous studies (Phillips 1947, Lanyon and Bull 1967, Hall 1979) there were no *O. tolmiei* specimens with *O. philadelphia* - like plumage characters. However, I found *O. philadelphia* males with *tolmiei* - like plumage characters scattered throughout the breeding range of *O. philadelphia*. A majority of *O. philadelphia* males lacked dark lores but *O. philadelphia* males with dark lores were not uncommon throughout the breeding range of *O. philadelphia* (APPENDIX I) (Figure 28). More importantly dark lores of *O. tolmiei* were uniform throughout the breeding range where in *O. philadelphia*'s breeding range there was some variation in the intensity of the lores. The non-significant regression of specimens with dark lores on longitude indicates that there is no segregation of or increase in *O. philadelphia* males with dark lores in the western part of its breeding range near the contact areas and hybridization is an unlikely explanation for their occurrence. *O. philadelphia* males with white eye-arcs were found in lesser numbers than birds with dark lores but in some cases composed over 16% of the sample (Cochrane, Ontario). In each case the

O. philadelphia specimens' eye-arcs were not as thick and did not cover the top of the eye as much as in *O. tolmiei* specimens. Extreme specimens which possessed both eye-arcs and dark lores were extremely rare (APPENDIX I). The distribution of birds with eye-arcs was scattered throughout the breeding range of *O. philadelphia*. The number of birds with eye-arcs did not increase westward towards the potential contact points.

W-T is sufficient for separating most specimens. But there are occasional specimens from the allopatric portions of each taxon's range and from the potential contact areas which can not be separated by W-T. I found that like the plumage characters above, the majority of extreme specimens for W-T were *O. philadelphia* (APPENDIX I). Even though extreme *O. philadelphia* males did possess at least one *tolmiei* - like plumage or external measurement no individuals collected in this study possessed them all. This is perhaps the best means of identifying extreme *O. philadelphia* study skin specimens from the allopatric portions of each taxon's range because they are always incomplete in their possession of *tolmiei* - like characters. Identification of hybrids based on these characters is not possible because of the sporadic distribution of these characters throughout the allopatric portions of *O. philadelphia's* breeding range.

SKELETAL CHARACTERS. At the univariate level the greatest intertaxon differences (per cent differences) were for external characters, followed by GIRDLE, SKULL, LEG and WING complexes of the skeleton (Table 5). Per cent differences in skeletal measurements were less than external measurement differences. The largest difference between taxa for each complex was for W-T, SCAPW, INORW, TARD and HTRL (Table 5). *O.*

philadelphia averaged larger than *O. tolmiei* for all morphological characters except for SKW, KEED, TARL and TAIL.

Bivariate plots of population means for each character showed complete separation of *O. philadelphia* and *O. tolmiei* for most skeletal and external characters. For skull variables PRL x INORW showed the best separation of taxa. The plots of CORL x KEEL, STERL, and KEED girdle characters revealed the best separation for this complex. All leg character plots showed good separation. HTRL x HUML provided the best separation of WING complex variables. Bivariate plots from each of the body regions successfully discriminated OTU's of these taxa indicating size differences exist between *O. philadelphia* and *O. tolmiei* and pervades all skeletal elements.

I used an ANOVA to evaluate differences among *O. philadelphia* and *O. tolmiei* population means separately for each morphological character. Although there were significant differences between populations for most mensural characters, many *O. philadelphia* and *O. tolmiei* population means were not significantly different from each other. There was a great deal of overlap between *O. philadelphia* and *O. tolmiei* population means for most morphological characters when they were analyzed individually. ANOVA of W-T was best at separating *O. philadelphia* and *O. tolmiei* populations. ANOVA's of all other character means of populations did not produce homogeneous subsets of pure *O. philadelphia* or *O. tolmiei* populations.

Patterns of geographic variation in different morphological character means were not concordant with other characters within *O. philadelphia* or *O. tolmiei*. Some characters exhibited the same or reversed clines as other characters while others varied in a haphazard way. This trend was evident from

the ANOVA's above and regressions on latitude and longitude. I used regression analyses to determine whether 1) *O. philadelphia* specimens exhibited longitudinal clines in morphological characters which showed the birds were becoming smaller from east to west (inverse relationship between size and longitude) as they approached the breeding range of *O. tolmiei* ; 2) *O. tolmiei* specimens exhibited latitudinal clines which showed that specimens were becoming larger from south to north (positive relationship between size and latitude) as they approached the range of *O. philadelphia* . For *O. philadelphia* , 12 characters exhibited negative relationships with longitude but less than 21% ($R^2=.21$) of the variation in any characters was attributed to variation in longitude (Table 6). Ten characters exhibited some clinal trend with latitude in *O. tolmiei* . Significant trends in *O. tolmiei* were equally mixed between positive and negative relationships with latitude. Little of the variation in these morphological characters could be attributed to variation in latitude. There is no regression evidence that variation is continuous between *O. philadelphia* and *O. tolmiei* .

7.1.2 SPECIES DIFFERENCES: MORPHOLOGY-MULTIVARIATE ANALYSIS

Morphological characters were analyzed simultaneously for species differences for each of the body regions and with all regions combined. I used multivariate analyses as an alternative to the univariate approach of previous authors. I also added another suite of characters for multivariate analysis- skeletal measurements which might provide better characters for separating *O. philadelphia* and *O. tolmiei* . CA's, PCA's and DFA's produced concordant

results - near or complete separation of *O. philadelphia* and *O. tolmiei* OTU's for each body region and for all regions combined. In the CA's complete separation of *O. philadelphia* and *O. tolmiei* OTU's was achieved using EXTERNAL, GIRDLE and WING complexes. Separate plots of PCA scores for each complex and all complexes combined also showed good separation of all *O. philadelphia* and *O. tolmiei* OTU's. Characters from each complex with the highest loadings of the PRIN1 axis when skeletal complexes were analyzed individually were INORW, KEED, FEDW, HTRL and W-T (Tables 12, 13, 14, 15 respectively). When all regions were considered simultaneously characters with the highest loadings were TARD and INORW (Table 16). DFA's of each body region except the LEG complex also yielded 100% separation of *O. philadelphia* and *O. tolmiei* OTU's. Only one *O. tolmiei* OTU from Montana was misclassified by the DFA using the LEG complex. *O. philadelphia* and *O. tolmiei* OTU's were easily identified using SKULL, GIRDLE, WING and EXTERNAL characters separately or when using characters from all the complexes combined. Characters which contributed the most to the discrimination of OTU's when each complex was analyzed separately were as follows: EXTERNAL - TAIL ; SKULL - INORW; GIRDLE - SCAPW; LEG - FEDW; WING - HTRL. Considered simultaneously the best discriminators are KEEL, STERL and HUML. The multivariate results provides evidence that these taxa are separate in multivariate space.

Mahalanobis D^2 between taxa was greatest when characters from all body regions are considered simultaneously. For individual regions SKULL elements showed the greatest amount of differentiation between taxa with the

highest Mahalanobis D^2 followed successively by GIRDLE, EXTERNAL, LEG, and WING.

7.2 SONG

7.2.1 SPECIES DIFFERENCES: SONG-UNIVARIATE ANALYSIS

Although most *O. philadelphia* and *O. tolmiei* specimens can be identified by a combination of study skin characters and or skeletal measurements some problem specimens remain. Extreme *O. philadelphia* male specimens still present a classification problem to the taxonomist. I tried to record as many specimens as possible in the field before collecting in order to compare specimens of known voice recordings. In all cases of extreme *O. philadelphia* males for which I had recordings the song type of these specimens was the same as *O. philadelphia* specimens with normal *O. philadelphia* plumage (APPENDIX I). *O. philadelphia* males with eye-arcs, dark lores, $W-T < 11\text{mm}$ or various combinations thereof all sang *O. philadelphia* song (same song types of specimens which lacked these characters). There were no cases where males with normal *O. philadelphia* plumage sang an *O. tolmiei* song type. Song type of each specimen is the best character for identifying *O. philadelphia* and *O. tolmiei* males. It is the only character which can be used with 100% accuracy for males.

The song types are different but where do the differences lie? One major difference discussed below lies in the differences between syllables. Another set of differences lies in the parameters measured for each song. *O.*

philadelphia had songs with just one Part or with two Parts. *O. tolmiei* sang either a two Part song or a three Part song but never a one Part song. On this basis alone all males with one part songs were *O. philadelphia* and all males with three part songs were *O. tolmiei*. Males with two part songs underwent further analyses for specific distinctness.

On the average *O. tolmiei* song has more parts per song, more syllables per song, more notes per Part II syllables (FA, FB) higher maximum frequencies, higher minimum frequencies, longer songs, and longer intervals between Part II syllables (Table 24). The largest per cent differences between taxa was for the SYLLABLE complex followed by DURATION/INTERVAL and FREQUENCY complexes (Table 24). The characters with the largest per cent differences within each complex were NFB, IFA or IFB and MAFB. All of these characters are from Part II of the song which is where the greatest species differences lie. *O. philadelphia* and *O. tolmiei* two Part song types were more different for Part II elements than for other song elements.

Bivariate plots of song parameters differed in their ability to discriminate *O. philadelphia* and *O. tolmiei* OTU's. Characters measured for the entire song (as opposed to just Part I or Part II parameters) were poor discriminators of *O. philadelphia* and *O. tolmiei* OTU's. Similar results were observed for bivariate plots of Part I characters. However, plots of Part II elements showed complete or near complete separation of *O. philadelphia* and *O. tolmiei* OTU's. NFA x IFB and MIFB were the best combinations for separating *O. philadelphia* and *O. tolmiei* populations. These results suggest that Part II contains species markers used by males (and probably females??) to discriminate alien song types.

The results of ANOVA's of *O. philadelphia* and *O. tolmiei* sample means were similar to the morphological results. When characters were analyzed individually there was a great deal of overlap in (character) means between the two taxa. ANOVA's did not produce pure homogeneous subsets of either *O. philadelphia* or *O. tolmiei* population means. Subsets were mixed and spatial patterns of variation in these characters were not concordant within taxa. Some song parameters characters varied clinally while others varied in a haphazard manner.

Regression analyses addressed the question of whether *O. philadelphia* and *O. tolmiei* song became more similar near the boundaries of each other's breeding ranges. Did *O. tolmiei* song become more like *O. philadelphia* song from south to north as *O. tolmiei* approached the breeding range of *O. philadelphia*? If *O. tolmiei* song became more like *O. philadelphia* song then one would expect negative relationships between characters and latitude (decreases in the song elements northwards). Eight characters exhibited negative relationships but latitudinal variation accounted for less than 20% of the variation in these characters (range 4.7% - 19.5%, Table 25). Did *O. philadelphia* song become more like *O. tolmiei* song from east to west as *O. philadelphia* approached the breeding range of *O. tolmiei*? If so then there should be a positive relationship between song parameters and longitude. Most observed regressions on longitude were negative in the breeding range of *O. philadelphia* and longitudinal variation accounted for less than 40% of the variation in any one character (range 2.3% - 39.6%, Table 25). Therefore, song types of these taxa do not become more similar as the breeding ranges approach one another. Spatial trends in song parameter characters are

independent of one another in the breeding ranges of these taxa. A majority of song parameter characters exhibited haphazard distributions.

7.2.2 SPECIES DIFFERENCES: SONG-MULTIVARIATE ANALYSIS

Results of the three multivariate analyses of different song parameter complexes were concordant. The degree of separation of OTU's of these taxa in multivariate space differed between song parameter complexes. The same complexes showed poor or complete separation in the CA's, PCA's and DFA's. In the CA's the FREQUENCY complex was the best discriminating complex while DURATION/INTERVAL and SYLLABLE complexes were unable to separate *O. philadelphia* and *O. tolmiei* OTU's. When characters from all the complexes were considered simultaneously all *O. philadelphia* and *O. tolmiei* OTU's were separated.

Plots of PCA scores of the FREQUENCY complex variables showed complete separation of *O. philadelphia* and *O. tolmiei*. MAFA and MIFA from Part II song syllables had the highest loadings of PRIN1. Plots of PCA scores of the DURATION/INTERVAL and SYLLABLE complexes showed overlap between *O. philadelphia* and *O. tolmiei* OTU's. Complete separation of *O. philadelphia* and *O. tolmiei* OTU's was attained when PCA scores, based on characters from all the complexes were used simultaneously and plotted in 3D space. NFA and NFB from Part II syllables had the highest loadings on PRIN1 in this PCA.

DFA's were more successful at discriminating taxa for each parameter complex than CA's and PCA's. A DFA of FREQUENCY complex variables

separated 100% of *O. philadelphia* and *O. tolmiei* OTU's. MIFA and MAFA from Part II syllables contributed the most to the discrimination. The CVA of FREQUENCY complex variables misclassified one *O. philadelphia* OTU from central Alberta. Ninety per cent of all OTU's were assigned correctly by the DFA of DURATION/INTERVAL COMPLEX variables. One *O. philadelphia* OTU and one *O. tolmiei* OTU which were misclassified by the DFA were not from the potential contact areas. DUR and IFA were the best discriminators for this complex. CVA misclassified two *O. philadelphia* OTU's from the eastern part of the breeding range. DFA's of the SYLLABLE COMPLEX also correctly classified over 90% of the OTU's. One *O. philadelphia* OTU from central Alberta (300 km from potential contact with *O. tolmiei*) and one OTU from Washington were misclassified. NSSO and NFA most effectively discriminated these taxa. In the CVA two *O. philadelphia* OTU's from Quebec were misclassified as *O. tolmiei* .

Song parameter characters from Part II contributed the most to discrimination of OTU's of these taxa in the multivariate analyses. The greatest differences between song types of these taxa appears in the second half of primary song. Classification functions have been provided for assignment of unknowns.

The FREQUENCY COMPLEX was the most effective complex at discriminating between taxa. This may be due to the fact that there was also little or no overlap in the 95% confidence intervals between taxa for frequency variables from Parts I and II. *O. tolmiei* sang higher frequency songs than *O. philadelphia*. *Oporornis tolmiei* is also the smaller of the two species based on most mensural characters. This size/frequency relationship has been

observed in other avian taxa. Lanyon (1978) found smaller *Myiarchus* species had higher frequency songs compared to larger taxa.

7.2.3 SYLLABLE ANALYSIS AND SPECIES DIFFERENCES

Spatial patterns of variation in *O. philadelphia* and *O. tolmiei* song are different. In *O. tolmiei* almost every male sang a unique song type. Neighboring *O. tolmiei* males sang songs which were as different as *O. tolmiei* males from 2000km away. There was some syllable sharing in northern Oregon and Washington but this was the only exception in the range of *O. tolmiei*. In contrast *O. philadelphia* males as far as 1500km apart sang nearly identical songs. In the range of *O. philadelphia* there were three major regional dialects - two continental systems and one in Newfoundland. Within each of these systems a majority of the birds sang the same song type as others within the system.

Males from both taxa have univalent repertoires. There is little syllable sharing between *O. philadelphia* and *O. tolmiei* (Figure 117). For each syllable common to both taxa the sharing only involved one male from each species. **There was no evidence that syllables were shared at the population level.** There was also no evidence that entire songs were shared by individuals or populations from these taxa. I have not sampled the entire range of each taxon and more variation will probably be found upon doing so.

Differences between cultural units (songs, syllables, notes) and frequency parameters in these taxa suggest that there are two different communication systems involved. The different patterns of geographic variation

in cultural units provides additional evidence that the communication systems are unique.

The following is a key which utilizes syllable and parameter differences in primary song of *O. philadelphia* and *O. tolmiei*. The numbers listed below for frequency and notes per syllable are based on the lower limits of 98% confidence intervals (Mean - [2 x SE]) for *O. tolmiei*. Scores for *O. philadelphia* songsters fall below these confidence limits.

1. Univalent repertoire, 8 - 14 syllables per song, songs contain 1 - 3 parts (mono -, di -, and tri-syllabic songs, each part containing a different syllable), in two and three part songs the first part of the song is always longer than the second or third parts, usually 2 - 6 notes per syllable.
2. Two part songs.....3
 - 2A. One part songs.....*O. philadelphia*
 - 2B. Three part songs.....*O. tolmiei*
3. Two part songs contain MO syllables (see *O. philadelphia* syllable catalogue), less than three notes per FA and FB syllables, maximum frequency of FA and FB syllables less than 5000Hz, minimum frequency of FA and FB syllables less than 2200Hz.....*O. philadelphia*
 - 3A. Two part songs contain MA syllables (see *O. tolmiei* syllable catalogue), three or more notes per FA and FB syllables, maximum frequency of FA and FB syllables - 5000Hz or greater, minimum frequency of FA syllables - 2200Hz or greater.....*O. tolmiei*

7.3 NATURE AND STABILITY OF HYBRID CONTACT BETWEEN *O. philadelphia* AND *O. tolmiei*

There are two areas in North America where the breeding ranges of *O. philadelphia* and *O. tolmiei* approach each other - 1) central Alberta and 2) northern British Columbia. However, the extent and stability of hybrid contact

between these taxa was unknown. 1) When Cox (1973) studied these birds in the 1960's there was little agriculture between Edmonton and Red Deer, Alberta and along the Red Deer River. The boreal forest extended up against the foothills of the Rocky Mountains between Jasper and Banff along the border with British Columbia. The stronghold of *O. tolmiei* in central Alberta was along the southern part of the Red Deer River, the Sheep River in Kananaskis, Alberta and in the Rocky Mountains along the British Columbia - Alberta border with an occasional "spillover" of males into the eastern foothills in Alberta. Several Hybrid specimens from central Alberta have been described by Cox (1973). Salt (1973) also made tape recordings of an *O. tolmiei* male in amongst several territorial *O. philadelphia* males near Edmonton. Although the hybrids probably fall into the range of normal plumage variation in *O. philadelphia* (Hall 1979), the recordings by Salt (1973) offer firm evidence that there is occasional contact in this area. 2) In the northeastern part of British Columbia, east of Fort Nelson to Liard River the boreal forest approaches the eastern foothills of the Rocky Mountains and offers potential contact. Both species were sighted near Liard River in British Columbia by Erskine and Davidson (1976).

During my own field work in these two areas in 1985 I did not observe contact between these taxa. In central Alberta I found only two *O. tolmiei* males in the foothills from Hinton to the Sheep River in Kananaskis. The two males were approximately 50km west of *O. philadelphia* males in Obed. These *O. tolmiei* males came closest to *O. philadelphia* breeders. My survey of the rest of central Alberta and along the Red Deer River produced only *O. philadelphia* in appropriate habitat. There were also no *O. tolmiei* east of Kananaskis until

the Cypress Hills along the Saskatchewan border. In British Columbia I also did not find *O. philadelphia* and *O. tolmiei* in contact. I collected *O. philadelphia* 20km east of Fort Nelson, British Columbia. There were no *O. philadelphia* or *O. tolmiei* from that point to Liard River where I collected and recorded only *O. tolmiei*. In the early 1970's Erskine and Davidson (1976) had reported only *O. philadelphia* in Liard River based on song (no specimens were collected). The local checklist for Liard River Provincial Park compiled by the Canadian Wildlife Service also lists *O. philadelphia* as the breeding warbler and *O. tolmiei* as uncommon. If these sight and sound records are accurate then there has been a complete turnover of *Oporornis* species breeding at this locality over a ten year period from *O. philadelphia* to *O. tolmiei*. Thus, the amount of contact between these taxa is between very few individuals and is not stable on an annual basis. However, results of univariate and multivariate analyses of morphological differences in external measurements between these taxa suggests that morphometric differences in external characters between *O. philadelphia* and *O. tolmiei* in the potential contact areas are relatively stable over a 23 year interval.

The fact that some OTU's from the potential contact zones were misclassified by some of the multivariate analyses of morphological data might indicate that these intermediate populations might be the result of hybrid events. However study of the potential contact areas showed that contact is rare on a spatial and temporal basis and could not explain the intermediacy of these populations.

The dry Lodgepole Pine forests which dominate the vegetation along the eastern foothills of the Rocky Mountains do not contain suitable breeding

habitat and act as a major habitat barrier to *O. philadelphia* and *O. tolmiei* . Pine and other more xeric plant species compose the vegetation along the rain shadow which extends over the drier eastern foothills of the Rocky Mountains. The preferred habitat of *O. philadelphia* and *O. tolmiei* - chokecherry, wild strawberry, wild raspberry, combined with poplars and birches - rarely occurs in this pine forest. Recent agricultural practices have also narrowed the zone of potential contact between these taxa. Areas in central Alberta which were originally boreal forest are now barren cattle pastures (along the Red Deer River) or used to grow a variety of crops. This has further fragmented the breeding range of *O. philadelphia* in central Alberta and pushed it back to the north. The breeding range of *O. tolmiei* in Alberta has also been pushed back to the south and west in Alberta by cattle ranching. The opportunity for contact has been reduced by agricultural practices which have widened the gap between areas with suitable habitat for these taxa. Contact between these taxa will become even rarer than before as these species are pushed farther apart by habitat loss.

7.4 TAXONOMIC RECOMMENDATIONS

The presence of some *tolmiei* - like birds in the range of *O. philadelphia* prompted some investigators to suggest that hybridization might be responsible and that *O. philadelphia* and *O. tolmiei* may be allopatric subspecies interbreeding in Alberta and British Columbia. A current review of the evidence above from my recent field work points out that there are *tolmiei* - like individuals scattered throughout the range of *O. philadelphia* but these extreme

individuals are not segregated near the potential hybrid contact areas. There are size differences at the multivariate level of analysis which separate almost all *O. philadelphia* and *O. tolmiei* OTU's, except some populations from or near the potential contact points. Based on morphological evidence alone there still is some doubt as to the specific status of each taxon. However, I never found contact between these taxa during my field work and other investigators (Cox 1973, Salt 1976) also found little or no contact. The hybrid zone would have to be very large to produce results consistent with a hybridization explanation of the scattered occurrence of *O. philadelphia* individuals with *tolmiei* - like plumage and mensural characters. Contact between very few individuals and on an irregular basis could not account for the consistent presence of *tolmiei* - like individuals scattered throughout the range of *O. philadelphia*. Another argument against hybridization is the fact that there were no *O. tolmiei* individuals with *philadelphia* - like plumage characters in my study or the work of Cox (1973) or Hall (1979). Every case of avian hybridization studied thus far has shown a two-way exchange between the hybridizing taxa.

Behavioral evidence strongly suggests that *O. philadelphia* and *O. tolmiei* are separate species. Extreme *O. philadelphia* specimens with *tolmiei* - like plumage and or mensural characters sang *O. philadelphia* song types in all cases where the specimens were recorded (APPENDIX I). Syllable and song parameter differences between taxa and song discrimination by both taxa exist in the allopatric and potential hybrid areas. The behavioral evidence supports the contention that there is a lack of interbreeding between taxa and the different song types are considered apomorphies for each species. I

recommend that *O. philadelphia* and *O. tolmiei* be considered separate species which probably fall into the realm of sibling or allospecies of a superspecies complex.

There was no evidence of subspecific variation in either taxon. Variation in most morphological characters was either clinal or mosaic and not concordant for both taxa. Similar patterns were evident for song characters. This agrees with Phillips' (1947) discussion for *O. philadelphia* but not for *O. tolmiei* which he broke down into four subspecies based on an examination of less than fifty specimens from a limited area of the breeding range (United States Rocky Mountains). His subspecies were based primarily on external measurement differences and secondarily on color variation. Phillips (1947) also noted that **the mensural and color variation was clinal** yet he described subspecies anyway in *O. tolmiei*. After more thorough sampling, I suggest that Phillips' subspecies should not be accorded formal subspecies recognition due to the clinal nature of the mensural variation in external and skeletal measurements.

7.5 IDENTIFICATION OF PROBLEM SPECIMENS

Field Identification. The traditional plumage characters mentioned earlier in the Introduction can be used to identify a majority of birds in the field. Only some extreme *O. philadelphia* specimens will be difficult. Use of binoculars alone will not help with identification because of the subtle plumage differences between these birds and true *O. tolmiei* (see below). The best character for identification in the field is voice for males. The songs are similar but distinct to the well-trained ear. *O. tolmiei* song has a higher frequency on

the average and it sounds slightly more buzzy than *O. philadelphia* song. However, this does not help for females and immatures. They can best be identified by breeding locality since these taxa are allopatric with irregular co-occurrences in central Alberta and possibly British Columbia. **All problem specimens should be collected.**

Study Skins. The traditional plumage characters are reliable for identifying most specimens. However some intermediate *O. philadelphia* specimens present problems. When confronted with these birds the next step is to assess combinations of these plumage characters on problem specimens. Where all good *O. tolmiei* male specimens possess dark lores, eye-arcs and lack the black bib, most problem *O. philadelphia* specimens will not possess all these characters simultaneously. Below I have constructed a key which emphasizes identification of *O. philadelphia* males.

Key to problem specimens of *O. philadelphia*¹

Olive back, yellow underparts, gray hood.

1. Eye-ring, larger size.....*O. agilis*.
2. Eye-arcs present in immatures, smaller size.
 - 2A. Eye-arcs, gray hood with black feathers on the throat and chest.
 - 2A1. Full eye-arc.....3
 - 2A2. Weak eye-arc.....*O. philadelphia* male.
 - 2B. Eye-arcs, gray hood lacking black feathers on the throat and chest.
 - 2B1. Full eye-arc.....4
 - 2B2. Weak eye-arc.....*O. philadelphia*.
 - 2C. Lacks eye-arcs.....*O. philadelphia* adults.
3. Full eye-arc², absence of black bib, dark lores,
 - W-T<11mm.....*O. tolmiei* male.
 - 3B. Full eye-arc, absence of black bib, dark lores,
 - W-T>11mm.....*O. tolmiei* male.

3C. Full eye-arc, W-T<11mm, no lores, black bib...*O. philadelphia* male.

4. Full eye-arc⁴, W-T<11mm.....*O. tolmiei* female.

4A. Full eye-arc, W-T>10mm.....*O. philadelphia* female.

1 - Results from this study and Kowalski's (1983) have shown that the W-T character used by Lanyon and Bull (1969) and plumage characters are equivocal for separating extreme specimens. Therefore this key **emphasizes combinations** of these characters for identifying extreme specimens. It is also important to keep in mind that all problem birds are *O. philadelphia* specimens which resemble *O. tolmiei*. No cases of the reverse have been found thus far.

2 - Full eye-arcs contain thick layers of white feathers above and below the eye. Typical full eye-arcs are comparable to those found in the allopatric portions of *O. tolmiei*'s breeding range.

3 - Eye-arcs in *O. philadelphia* specimens range from full to weak. Full eye-arcs are comparable to *O. tolmiei* specimens from the allopatric portions of the breeding range where weak eye-arcs are incomplete and often required examination with a magnifying glass. Specimens whose eye-arcs were about 50% as complete or less than typical *O. tolmiei* eye-arcs are considered weak.

4 - Since this study was concerned primarily with males the reader is referred to Lanyon and Bull's (1969) key for identifying females. Geographic variation in females of these taxa has not been performed.

Skeletons. Use of the classification functions generated by the DFA's provide the best means of identifying unknown skeletons. Measurements from skeletons with unknown status are multiplied by the coefficients of the two classification functions (*O. philadelphia* and *O. tolmiei*) and added to their respective constants which places the unknown onto the discriminant axis. I have given several classification functions, each based on different skeletal complexes. Therefore partial skeletons missing the skull or limb can still be assigned to either taxon by using a classification function for the leg or girdle complex.

However, caution is suggested when using these functions since they are based on means from populations and not individual specimens.

APPENDIX A SAMPLE LOCALITIES

Sample localities are listed by taxon and from north to south - east to west by province/state (e.g., British Columbia, Washington, Oregon, Alberta, Idaho, Nevada, etc...). The two letter code is an abbreviation identifying these localities on the map (Figure 1). Latitude and longitude (in degrees) are enclosed in parentheses.

Oporornis tolmiei Localities. British Columbia: **LR** - LIARD RIVER (59.47 126.30) (CRT), **MC** - MCBRIDE (53.35 120.32) (CRT), **BA** - BALFOUR (49.91 116.98) (CR); Washington: **LO** - LOOMIS (48.82 119.64) (CR), **SC** - SEARS CREEK (47.83 121.78) (CR), **PA** - PACKWOOD (46.61 121.52) (CR); Oregon: **MH** - MT. HOOD (45.71 121.52) (CR), **LB*** - LAVA BUTTE (44.06 121.30) (CR), **FK** - FT. KLAMATH (42.07 121.99) (CR); California: **CE** - CEDARVILLE (41.53 120.17) (CR); Nevada: , **JA** - JARBIDGE (41.88 115.43) (CR), **PV** - PARADISE VALLEY (41.49, 117.53) (CR); Alberta: **HI** - HINTON (53.40 117.58) (CRT), **KA** - KANANASKIS (50.63 115.05) (CRT), **CH** - CYPRESS HILLS (49.47 109.50) (R); Idaho: **PO** - POCA TELLO (42.87 112.45) (CR), **MM** - MAGIC MOUNTAIN (42.56 114.47) (CR); Montana: **LH** - LOLO HOT SPRINGS (46.73 114.53) (C), **SQ** - SQUAW CREEK (45.68 111.04) (C); Wyoming: **WY** - ALLRED FLATS (42.73 110.93) (CR).

Oporornis philadelphia Localities. British Columbia: **FN** - FORT NELSON (58.82 122.53) (CRT); Alberta: **SL** - SLAVE LAKE (55.28 114.72) (CRT), **WH** - WHITECOURT (54.17 115.63) (CRT), **OB*** - OBED (53.55 117.22)

(CRT), **LP*** - LODGEPOLE (53.17 115.17) (CRT), Ontario: **DO** - DORION (49.82 88.55) (CR), **MI** - MINITAKI (49.80 92.80) (CR), **GE** - GERALDTON (49.73 86.98) (CR), **HE** - HEARST (49.7 83.67) (CR), **CO** - COCHRANE (49.07 81.03) (CR); Quebec: **LE** - LEBEL-SUR-QUEVILLION (48.92 77.17) (CR), **VP** - VAL PARADIS (48.80 78.48) (CR), **GI** - GIRARDVILLE (48.05 72.27) (CR), **SP** - ST. PAULE (47.97 69.17) (CR),; Newfoundland: **SA** - ST. ANTHONY (51.37 55.28) (R), **PS*** - PORT SAUNDERS (50.65 57.3) (R), **RO** - RODDICKTON (50.37 56.13) (R), **SV** - STEPHENVILLE (48.55 58.58) (R), **CB*** - CAPE BONAVISTA (48.62 53.12) (R); Maine: **SF** - ST. FRANCIS (47.26 68.56) (CR); New York: **CZ** - CHAZY (44.88 73.48) (CT).

C - specimens only (no tissues).

CR - specimens and recordings.

CT - specimens and tissues only (results of electrophoretic analyses will be published

separately).

CRT - specimens, tissues and recordings.

R - recordings only.

* - not on map.

APPENDIX B MORPHOLOGICAL VARIABLES

EXTERNAL CHARACTERS

External characters follow descriptions from Phillips (1947) and Lanyon and Bull (1967).

WING (W). Flattened wing was straightened and measured with a wing ruler.

TAIL (T). Measured from insertion of two central tail feathers to the tip of the longest tail feather.

W-T. Wing measurement minus tail measurement.

WEIGHT. Weight measured immediately upon collection to nearest 0.5 grams with Pesola scales.

SKELETAL CHARACTERS

The descriptions of skeletal measurements follow Schnell (1970). Some of Schnell's (1970) measurements have been modified to account for skeletal differences between Larids and warblers.

SKULL COMPLEX

PREMAXILLARY LENGTH (PRL). Medially, just before the Nasal bone to the tip of the premaxilla.

BILL DEPTH (BDEP). Medially, depth at the anterior edge of the narial openings.

NASAL BONE WIDTH. Transversely, width of Nasal bone.

INTERORBITAL WIDTH (INORW). Transversely, least width of the frontal bone.

SKULL WIDTH (SKW). Transversely, the maximum skull width between parietals.

SKULL LENGTH (SKL). Medially, from tip of Premaxilla to farthest posterior part of supraoccipital.

MANDIBLE LENGTH (MANL). Lateromedially, from postarticular process to dentary symphysis.

MANDIBLE DEPTH (MAND). Depth at foramen.

GIRDLE COMPLEX

CORACOID LENGTH (CORL). From distal to proximal edge of Coracoid.

SCAPULA WIDTH (SCAPW). Width from glenoid facet to acromion.

STERNUM LENGTH (STERL). Medially, from posterior edge of sternum to anterior edge of manubrial spine.

KEEL LENGTH (KEEL). Medially, from anterior edge of Keel to posterior edge of sternum.

KEEL DEPTH (KEED). Medially, from dorsal edge of manubrial spine to ventral surface of Keel.

SYNSACRUM WIDTH (SYNW). Transversely, from right acetabulum to left acetabulum.

MINIMUM SYNSACRUM WIDTH (SYNMW). Transversely, width between lateral edges of ilia.

LEG COMPLEX

FEMUR DISTAL END WIDTH (FEDW). Transversely, from flattened surface of distal end to lateral edge of condyle.

FEMUR LENGTH (FEL). From trochanter to condyle.

TIBIOTARSUS LENGTH (TIBL). From articular surfaces to condyle.

TARSOMETATARSUS LENGTH (TARL). From proximal to distal end.

TARSOMETATARSUS DISTAL END WIDTH (TARD). Transversely, from trochlea of digit 2 to digit 4.

WING COMPLEX

HUMERUS TROCHANTER LENGTH (HTRL). From head of proximal end to deltoid crest.

HUMERUS DISTAL END WIDTH (HDEW). From entepicondylar to ectepicondylar prominence.

HUMERUS LENGTH (HURL). From head to internal condyle.

ULNA LENGTH (ULNL). From base of olecranon to external condyle.

CARPOMETARCARPUS LENGTH (CARPL). From facet of digit 3 to carpal trochlea.

APPENDIX C
PER CENT DIFFERENCES BETWEEN TAXA
FOR MORPHOLOGICAL VARIABLES

Elementary Statistics and Per Cent Differences for External Characters

EXTERNAL CHARACTERS*	<i>Oporornis</i> <i>philadelphia</i>	<i>Oporornis</i> <i>tolmiei</i>	PER CENT DIFFERENCE
WEIGHT	14.24	13.17	7.5%
SE	0.04	0.06	
CV	0.04	0.05	
N	239	139	
WING	61.56	60.15	2.2%
SE	0.11	0.14	
CV	0.03	0.03	
N	270	211	
TAIL	49.32	54.78	9.9%
SE	0.12	0.21	
CV	0.04	0.05	
N	263	202	
W-T	12.21	5.37	56.0%
SE	0.12	0.19	
CV	0.16	0.50	
N	261	202	

* - all measurements in millimeters.

Elementary Statistics and Per Cent Differences for Skull Characters

SKELETAL CHARACTERS*	<i>Oporornis</i> <i>philadelphia</i>	<i>Oporornis</i> <i>tolmiei</i>	PER CENT DIFFERENCE
PRL	13.72	13.43	7.4%
SE	0.04	0.04	
CV	0.04	0.04	
N	230	176	
BDEP	1.12	1.06	5.3%
SE	0.00	0.00	
CV	0.10	0.11	
N	245	180	

NASW	5.95	5.62	5.5%
SE	0.02	0.02	
CV	0.05	0.04	
N	249	170	
INORW	3.03	2.66	12.2%
SE	0.01	0.01	
CV	0.08	0.07	
N	240	165	
SKW	13.35	13.38	0.2%
SE	0.02	0.02	
CV	0.02	0.01	
N	221	121	
SKL	30.74	30.42	1.0%
SE	0.05	0.05	
CV	0.02	0.02	
N	194	122	
MANL	22.32	21.89	1.9%
SE	0.04	0.04	
CV	0.02	0.02	
N	235	167	
MAND	1.51	1.39	7.9%
SE	0.00	0.00	
CV	0.50	0.05	
N	252	187	

* - all measurements in millimeters.

Elementary Statistics and Per Cent Differences for Girdle Characters

SKELETAL CHARACTERS*	<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	PER CENT DIFFERENCE
CORL	14.59	13.81	5.3%
SE	0.02	0.02	
CV	0.02	0.02	
N	238	184	
SCAPW	1.94	1.78	8.2%
SE	0.01	0.01	
CV	0.09	0.08	
N	251	191	
STERL	16.44	15.37	6.5%
SE	0.03	0.04	
CV	0.03	0.03	
N	222	165	

KEEL	14.71	13.58	7.6%
SE	0.05	0.05	
CV	0.05	0.04	
N	223	171	
KEED	6.32	5.84	7.2%
SE	0.02	0.02	
CV	0.05	0.05	
N	225	172	
SYNW	8.90	8.79	1.2%
SE	0.01	0.02	
CV	0.03	0.03	
N	220	152	
SYNMW	5.04	4.99	0.9%
SE	0.01	0.01	
CV	0.05	0.04	
N	235	168	

* - all measurements in millimeters.

Elementary Statistics and Per Cent Differences for Leg Characters

SKELETAL CHARACTERS*	<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	PER CENT DIFFERENCE
FEDW	2.61	2.53	3.0%
SE	0.00	0.00	
CV	0.03	0.03	
N	242	188	
FEL	15.48	14.76	4.6%
SE	0.02	0.02	
CV	0.02	0.02	
N	232	171	
TIBL	28.14	27.51	2.2%
SE	0.05	0.09	
CV	0.02	0.02	
N	156	44	
TARL	20.57	20.60	0.1%
SE	0.04	0.05	
CV	0.03	0.02	
N	189	146	
TARD	2.21	2.07	6.3%
SE	0.01	0.01	
CV	0.10	0.08	

N 229 174

* - all measurements in millimeters.

Elementary Statistics and Per Cent Differences for Wing Characters

SKELETAL CHARACTERS*	<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	PER CENT DIFFERENCE
HTRL	3.64	3.48	4.3%
SE	0.00	0.00	
CV	0.04	0.03	
N	249	164	
HDEW	3.30	3.24	1.8%
SE	0.00	0.00	
CV	0.04	0.03	
N	244	151	
HUML	14.50	13.93	3.9%
SE	0.01	0.03	
CV	0.02	0.02	
N	236	136	
ULNL	16.53	16.03	3.0%
SE	0.03	0.03	
CV	0.03	0.02	
N	187	129	
CARPL	9.46	9.20	2.7%
SE	0.02	0.02	
CV	0.03	0.03	
N	159	135	

* - all measurements in millimeters.

APPENDIX D
ELEMENTARY STATISTICS OF MORPHOLOGICAL VARIABLES
FOR *O. philadelphia* AND *O. tolmiei* LOCALITIES

Elementary Statistics for External Characters: *O. philadelphia* Localities

LOCALITY	WEIGHT	WING	TAIL	W-T
CHAZY	12.77	60.58	50.06	10.51
SE	0.25	0.69	0.68	0.39
CV	0.06	0.03	0.04	0.12
N	12	12	12	12
ST. FRANCIS	13.92	60.56	48.70	11.91
SE	0.12	0.33	0.33	0.34
CV	0.04	0.02	0.03	0.14
N	23	25	24	24
ST. PAULE	14.03	62.28	49.66	12.83
SE	0.14	0.52	0.60	0.42
CV	0.03	0.03	0.04	0.11
N	14	14	12	12
GIPARDVILLE	14.26	61.95	49.35	12.60
SE	0.09	0.38	0.37	0.41
CV	0.03	0.02	0.03	0.14
N	20	20	20	20
VAL PARADIS	14.40	62.00	48.71	13.15
SE	0.12	0.40	0.50	0.40
CV	0.03	0.02	0.03	0.11
N	15	14	14	13
LEBEL-SUR-QUEV.	13.94	62.22	48.95	13.14
SE	0.11	0.46	0.36	0.47
CV	0.03	0.03	0.03	0.16
N	24	22	21	21
COCHRANE	14.50	61.80	48.80	13.00
SE	0.07	0.57	0.47	0.54
CV	0.02	0.04	0.04	0.18
N	20	20	20	20
HEARST	14.59	61.50	48.05	13.31
SE	0.09	0.48	0.52	0.37
CV	0.02	0.03	0.04	0.12
N	19	20	19	19
GERALDTON	14.87	62.69	49.53	13.15
SE	0.07	0.66	0.41	0.57
CV	0.01	0.03	0.03	0.15
N	14	13	13	13
MINITAKI	14.69	61.81	49.64	12.07
SE	0.12	0.31	0.38	0.38

CV	0.03	0.02	0.02	0.11
N	19	16	14	14
DORION	14.37	61.17	0.52	12.56
SE	0.10	0.29	0.52	0.45
CV	0.03	0.02	0.05	0.17
N	21	23	24	23
LODGEPOLE	14.48	61.50	50.00	11.28
SE	0.21	0.82	0.74	0.59
CV	0.04	0.03	0.03	0.13
N	9	8	7	7
OBED + WHITEC.	14.46	61.50	51.40	10.09
SE	0.24	0.37	0.49	0.61
CV	0.04	0.01	0.02	0.17
N	6	8	8	8
SLAVE LAKE	14.44	60.90	50.47	10.42
SE	0.16	0.33	0.37	0.35
CV	0.04	0.02	0.03	0.15
N	16	20	20	20
FORT NELSON	14.28	61.14	50.79	10.34
SE	0.15	0.45	0.30	0.37
CV	0.02	0.01	0.01	0.09
N	7	7	7	7

* - all measurements in millimeters.

Elementary Statistics for Skull Complex: *O. philadelphia* Localities

LOCALITY	PRL	BDEP	NASW	INORW	SKW	SKL	MANL	MAND
CHAZY	13.99	1.10	6.20	3.07	13.60	31.29	22.59	1.56
SE	0.13	0.02	0.07	0.07	0.05	0.14	0.15	0.02
CV	0.03	0.08	0.04	0.08	0.01	0.01	0.02	0.06
N	12	12	13	12	11	11	13	13
ST. FRANCIS	13.72	1.11	5.84	3.05	13.28	30.37	22.13	1.51
SE	0.12	0.02	0.08	0.05	0.07	0.19	0.12	0.01
CV	0.04	0.10	0.07	0.08	0.02	0.02	0.02	0.05
N	21	24	25	25	21	18	21	24
ST. PAULE	13.80	1.11	6.03	3.07	13.38	30.63	22.44	1.54
SE	0.10	0.01	0.09	0.07	0.12	0.20	0.12	0.01
CV	0.02	0.05	0.05	0.08	0.03	0.01	0.02	0.03
N	14	15	15	13	11	9	14	15
GIRARDVILLE	13.80	1.18	5.96	3.09	13.38	31.01	22.42	1.52
SE	0.09	0.02	0.08	0.06	0.06	0.14	0.12	0.01
CV	0.02	0.07	0.06	0.08	0.02	0.02	0.02	0.05

N	19	20	20	19	20	18	20	20
VAL PARADIS	14.02	1.17	6.07	3.12	13.39	31.13	22.34	1.53
SE	0.12	0.03	0.10	0.05	0.07	0.13	0.13	0.02
CV	0.03	0.10	0.06	0.06	0.02	0.01	0.02	0.05
N	15	15	16	15	13	13	16	16
LEBEL	13.82	1.18	6.01	3.08	13.15	30.87	22.24	1.50
SE	0.09	0.02	0.05	0.06	0.08	0.10	0.11	0.00
CV	0.03	0.08	0.04	0.09	0.03	0.01	0.02	0.03
N	23	24	23	23	22	19	22	23
COCHRANE	13.81	1.12	5.87	3.04	13.53	30.77	22.15	1.48
SE	0.13	0.02	0.09	0.04	0.07	0.20	0.21	0.02
CV	0.03	0.10	0.06	0.07	0.02	0.02	0.03	0.06
N	16	17	18	19	14	14	14	19
HEARST	14.18	1.09	6.00	3.00	13.41	31.06	22.42	1.48
SE	0.11	0.02	0.06	0.04	0.06	0.12	0.13	0.01
CV	0.03	0.09	0.04	0.07	0.02	0.01	0.02	0.04
N	19	18	20	20	19	18	20	19
GERALDTON	13.84	1.15	6.06	3.15	13.42	30.81	22.31	1.51
SE	0.12	0.04	0.04	0.04	0.04	0.24	0.19	0.01
CV	0.03	0.12	0.03	0.05	0.01	0.02	0.03	0.04
N	14	14	14	14	12	10	13	14
MINITAKI	13.74	1.14	5.87	2.93	13.39	31.08	22.28	1.57
SE	0.13	0.02	0.07	0.07	0.09	0.15	0.21	0.01
CV	0.04	0.10	0.05	0.09	0.02	0.01	0.04	0.04
N	18	18	19	14	16	13	18	19
DORION	13.85	1.14	5.90	3.00	13.27	30.64	22.30	1.51
SE	0.09	0.01	0.07	0.05	0.05	0.13	0.10	0.01
CV	0.03	0.08	0.05	0.09	0.01	0.01	0.02	0.05
N	25	25	23	22	20	20	23	25
LODGEPOLE	12.80	1.04	5.96	2.88	13.35	29.86	22.34	1.43
SE	0.15	0.04	0.05	0.03	0.07	0.17	0.23	0.02
CV	0.03	0.12	0.02	0.04	0.01	0.01	0.02	0.05
N	7	8	9	9	8	6	6	9
OBED + WHITEC.	12.56	1.06	5.86	2.91	13.17	29.40	22.19	1.43
SE	0.25	0.02	0.13	0.05	0.13	0.19	0.35	0.03
CV	0.05	0.06	0.06	0.05	0.02	0.01	0.04	0.06
N	7	8	8	8	7	6	8	8
SLAVE LAKE	13.21	1.06	5.86	2.93	13.37	30.53	22.43	1.49
SE	0.21	0.02	0.05	0.05	0.04	0.28	0.08	0.01
CV	0.05	0.09	0.03	0.08	0.01	0.03	0.01	0.05
N	13	18	16	18	16	11	18	19
FORT NELSON	12.74	1.07	5.84	2.93	13.34	29.96	22.28	1.49
SE	0.23	0.06	0.13	0.05	0.11	0.28	0.28	0.03
CV	0.04	0.16	0.06	0.04	0.02	0.02	0.03	0.06
N	5	7	7	7	7	6	7	7

* - all measurements in millimeters.

Elementary Statistics for Girdle Complex: *O. philadelphia* Localities

LOCALITY	CORL	SCAPW	STERL	KEEL	KEED	SYNW	SYNMW
CHAZY	14.91	1.89	16.85	15.08	6.45	9.04	5.06
SE	0.08	0.03	0.09	0.15	0.04	0.05	0.08
CV	0.02	0.06	0.01	0.03	0.02	0.02	0.05
N	13	12	11	10	11	12	12
ST. FRANCIS	14.50	2.14	16.23	14.51	6.27	8.73	5.03
SE	0.06	0.06	0.11	0.12	0.08	0.04	0.06
CV	0.02	0.15	0.03	0.04	0.06	0.02	0.06
N	25	24	22	23	23	24	25
ST. PAULE	14.56	1.96	16.46	14.92	6.40	9.04	5.03
SE	0.09	0.04	0.17	0.22	0.08	0.08	0.06
CV	0.02	0.08	0.03	0.05	0.04	0.02	0.04
N	12	15	12	11	11	10	12
GIRARDVILLE	14.72	1.95	16.52	14.73	6.50	8.95	4.96
SE	0.07	0.02	0.13	0.13	0.08	0.06	0.05
CV	0.02	0.05	0.03	0.03	0.05	0.03	0.04
N	19	20	15	16	17	17	17
VAL PARADIS	14.51	1.99	16.46	14.71	6.42	8.92	5.16
SE	0.09	0.02	0.13	0.17	0.08	0.07	0.06
CV	0.02	0.05	0.03	0.04	0.05	0.02	0.04
N	15	15	14	15	15	13	15
LEBEL-SUR-QUEV.	14.56	1.98	16.43	14.70	6.35	8.85	4.97
SE	0.07	0.03	0.10	0.14	0.07	0.06	0.04
CV	0.02	0.08	0.03	0.04	0.05	0.03	0.04
N	23	24	21	22	22	21	22
COCHRANE	14.51	1.91	16.48	14.75	6.13	8.96	4.97
SE	0.09	0.04	0.13	0.13	0.09	0.06	0.04
CV	0.02	0.10	0.03	0.03	0.06	0.03	0.03
N	16	20	17	17	18	19	18
HEARST	14.62	1.87	16.46	14.88	6.28	8.90	5.09
SE	0.05	0.02	0.09	0.13	0.08	0.05	0.06
CV	0.01	0.06	0.02	0.03	0.05	0.02	0.05
N	19	20	20	18	17	18	19
GERALDTON	14.62	1.89	16.59	14.98	6.22	9.01	5.08
SE	0.08	0.04	0.18	0.21	0.13	0.04	0.11
CV	0.02	0.07	0.03	0.04	0.07	0.01	0.07
N	13	12	11	11	12	12	13
MINITAKI	14.42	1.88	16.39	14.60	6.39	8.85	5.11
SE	0.10	0.03	0.13	0.13	0.09	0.07	0.04
CV	0.02	0.08	0.03	0.03	0.05	0.03	0.04

N	15	19	17	17	17	18	18
DORION	14.42	1.95	16.27	14.49	6.31	8.89	5.11
SE	0.08	0.03	0.12	0.15	0.06	0.06	0.04
CV	0.02	0.09	0.03	0.04	0.04	0.03	0.04
N	24	24	23	20	20	22	22
LODGEPOLE	14.57	1.83	16.38	14.81	6.32	9.01	4.90
SE	0.06	0.04	0.14	0.12	0.03	0.12	0.07
CV	0.01	0.06	0.02	0.02	0.01	0.03	0.04
N	9	9	8	8	8	7	8
OBED + WHITEC.	14.65	1.90	16.63	14.91	6.37	8.74	4.96
SE	0.14	0.03	0.17	0.22	0.10	0.12	0.12
CV	0.02	0.04	0.02	0.03	0.04	0.03	0.06
N	8	8	7	7	7	5	8
SLAVE LAKE	14.65	1.89	16.38	14.65	6.26	8.87	5.08
SE	0.10	0.02	0.11	0.13	0.06	0.07	0.05
CV	0.02	0.05	0.02	0.03	0.04	0.03	0.05
N	18	20	17	19	19	14	17
FORT NELSON	14.77	1.83	16.28	14.45	6.32	9.05	5.00
SE	0.15	0.07	0.20	0.17	0.09	0.13	0.09
CV	0.02	0.10	0.02	0.02	0.03	0.03	0.05
N	7	7	5	6	6	6	7

* - all measurements in millimeters.

Elementary Statistics for Leg Complex: *O. philadelphia* Localities

LOCALITY	FEDW	FEL	TIBL	TARL	TARD
CHAZY	2.66	15.31	28.03	20.67	2.30
SE	0.01	0.11	0.22	0.23	0.05
CV	0.02	0.02	0.02	0.03	0.08
N	13	11	12	12	13
ST. FRANCIS	2.59	15.42	27.99	20.35	2.16
SE	0.01	0.08	0.23	0.16	0.03
CV	0.03	0.02	0.03	0.03	0.06
N	25	24	16	16	15
ST. PAULE	2.59	15.59	28.23	20.68	2.30
SE	0.01	0.12	0.32	0.20	0.05
CV	0.02	0.02	0.03	0.02	0.09
N	13	10	8	8	15
GIRARDVILLE	2.61	15.78	28.36	20.83	2.29
SE	0.01	0.08	0.17	0.15	0.05
CV	0.02	0.02	0.02	0.03	0.10
N	20	20	15	17	20

VAL PARADIS	2.62	15.39	28.06	20.73	2.30
SE	0.01	0.09	0.18	0.17	0.05
CV	0.02	0.02	0.02	0.03	0.08
N	15	14	12	13	14
LEBEL-SUR-QUEV.	2.62	15.58	28.20	20.79	2.42
SE	0.01	0.08	0.20	0.14	0.03
CV	0.03	0.02	0.02	0.03	0.07
N	24	24	15	19	23
COCHRANE	2.61	15.66	27.76	20.25	2.22
SE	0.02	0.10	0.16	0.14	0.03
CV	0.03	0.02	0.02	0.02	0.07
N	16	15	13	15	20
HEARST	2.60	15.56	28.29	20.73	2.16
SE	0.01	0.07	0.15	0.08	0.04
CV	0.03	0.01	0.01	0.01	0.09
N	17	17	8	15	19
GERALDTON	2.65	15.59	28.46	20.60	2.13
SE	0.01	0.13	0.19	0.20	0.08
CV	0.02	0.03	0.02	0.03	0.12
N	13	13	10	9	11
MINITAKI	2.62	15.66	28.25	20.92	2.30
SE	0.01	0.10	0.17	0.16	0.06
CV	0.02	0.02	0.02	0.02	0.11
N	19	19	14	12	15
DORION	2.59	15.31	27.71	20.32	2.10
SE	0.02	0.10	0.22	0.13	0.05
CV	0.04	0.03	0.02	0.02	0.11
N	23	22	9	16	23
LODGEPOLE	2.56	15.91	28.18	20.35	2.15
SE	0.02	0.09	0.20	0.27	0.05
CV	0.02	0.01	0.01	0.03	0.06
N	8	8	4	7	7
OBED + WHITEC.	2.61	15.24	27.95	20.18	1.92
SE	0.03	0.21	0.49	0.44	0.08
CV	0.03	0.04	0.03	0.04	0.11
N	8	8	4	5	6
SLAVE LAKE	2.59	15.13	28.36	20.43	2.06
SE	0.02	0.09	0.14	0.11	0.03
CV	0.03	0.02	0.01	0.02	0.07
N	19	18	10	17	19
FORT NELSON	2.60	15.40	28.46	20.53	2.01
SE	0.04	0.19	0.43	0.27	0.11
CV	0.04	0.03	0.03	0.03	0.15
N	7	7	5	6	7

* - all measurements in millimeters.

Elementary Statistics for Wing Complex: *O. philadelphia* Localities

LOCALITY	HTRL	HDEW	HUML	ULNL	CARPL
CHAZY	3.75	3.36	14.54	16.61	9.51
SE	0.03	0.02	0.10	0.10	0.10
CV	0.03	0.02	0.02	0.01	0.01
N	12	12	11	9	9
ST. FRANCIS	3.75	3.27	14.36	16.64	9.20
SE	0.06	0.03	0.05	0.11	0.10
CV	0.08	0.05	0.01	0.03	0.04
N	26	26	26	19	17
ST. PAULE	3.56	3.29	14.47	16.39	8.99
SE	0.03	0.02	0.08	0.14	0.30
CV	0.03	0.03	0.02	0.02	0.06
N	15	15	15	7	4
GIRARDVILLE	3.67	3.34	14.69	16.81	9.66
SE	0.03	0.02	0.05	0.07	0.11
CV	0.03	0.03	0.01	0.01	0.03
N	20	19	19	15	11
VAL PARADIS	3.64	3.32	14.52	16.82	9.49
SE	0.03	0.04	0.08	0.05	0.05
CV	0.03	0.05	0.02	0.01	0.01
N	15	16	15	12	10
LEBEL-SUR-QUEV.	3.61	3.26	14.50	16.42	9.45
SE	0.02	0.02	0.06	0.09	0.19
CV	0.02	0.03	0.02	0.02	0.05
N	22	23	22	18	8
COCHRANE	3.64	3.29	14.59	16.40	9.56
SE	0.03	0.03	0.05	0.06	0.05
CV	0.03	0.04	0.01	0.01	0.02
N	20	20	20	16	15
HEARST	3.64	3.32	14.56	16.75	9.55
SE	0.02	0.02	0.05	0.12	0.06
CV	0.03	0.03	0.01	0.02	0.02
N	20	20	20	14	11
GERALDTON	3.59	3.28	14.52	16.60	9.51
SE	0.04	0.03	0.07	0.19	0.13
CV	0.04	0.04	0.01	0.03	0.04
N	13	13	13	9	8
MINITAKI	3.63	3.31	14.56	16.48	9.58
SE	0.02	0.04	0.07	0.18	0.13
CV	0.02	0.05	0.02	0.04	0.04
N	18	18	18	15	12

DORION	3.62	3.26	14.36	16.23	9.26
SE	0.02	0.03	0.06	0.18	0.08
CV	0.03	0.04	0.02	0.04	0.03
N	24	23	22	17	16
LODGEPOLE	3.63	3.27	14.38	16.35	9.41
SE	0.01	0.01	0.13	0.12	0.10
CV	0.01	0.01	0.02	0.02	0.03
N	9	8	6	9	8
OBED + WHITEC.	3.66	3.34	14.50	16.36	9.48
SE	0.03	0.05	0.18	0.20	0.12
CV	0.02	0.04	0.03	0.03	0.03
N	7	8	7	6	6
SLAVE LAKE	3.62	3.29	14.42	16.39	9.59
SE	0.01	0.02	0.07	0.09	0.06
CV	0.02	0.03	0.01	0.02	0.02
N	20	16	15	16	18
FORT NELSON	3.60	3.26	14.46	16.65	9.52
SE	0.04	0.09	0.16	0.34	0.10
CV	0.02	0.06	0.02	0.03	0.02
N	6	5	5	3	5

* - all measurements in millimeters.

Elementary Statistics for External Characters: *O. tolmiei* Localities

LOCALITY	WEIGHT	WING	TAIL	W-T
PARADISE VALLEY	13.35	60.50	57.21	3.28
SE	0.14	0.35	0.53	0.51
CV	0.04	0.02	0.03	0.59
N	13	16	14	14
CEDARVILLE		60.00	56.60	3.50
SE		1.15	1.50	0.50
CV		0.03	0.03	0.20
N		3	2	2
JARBIDGE	60.31	56.47	3.88	
SE		0.27	0.54	0.49
CV		0.01	0.04	0.53
N		19	17	17
FORT KLAMATH		60.50	57.50	3.00
SE		1.50	0.50	1.00
CV		0.03	0.01	0.47
N		2	2	2

MAGIC MTN.	13.55	61.00	57.84	3.15
SE	0.13	0.42	0.76	0.60
CV	0.03	0.02	0.04	0.69
N	13	13	13	13
ALLRED FLATS		60.53	57.58	3.08
SE		0.29	0.48	0.45
CV		0.01	0.02	0.50
N		13	12	12
POCATELLO		61.30	56.20	5.10
SE		0.63	0.92	0.87
CV		0.03	0.05	0.54
N		10	10	10
LAVA BUTTE		55.00	55.00	0
SE				
CV				
N		1	1	1
SQUAW CREEK	13.54	61.30	55.45	5.81
SE	0.17	0.26	0.47	0.29
CV	0.04	0.01	0.02	0.16
N	13	13	11	11
MT. HOOD	12.61	58.72	52.88	5.83
SE	0.14	0.57	0.59	0.69
CV	0.05	0.04	0.04	0.50
N	19	18	18	18
PACKWOOD	13.13	58.30	52.76	5.53
SE	0.15	0.44	0.60	0.51
CV	0.04	0.02	0.04	0.33
N	13	13	13	13
LOLO HOT SPRINGS	13.48	59.57	55.14	4.42
SE	0.32	0.42	1.80	1.68
CV	0.06	0.01	0.08	1.00
N	7	7	7	7
SEARS CREEK	13.01	58.28	53.71	4.57
SE	0.23	1.12	0.56	0.67
CV	0.06	0.07	0.03	0.55
N	14	14	14	14
LOOMIS	13.04	59.90	52.36	7.54
SE	0.25	0.49	0.69	0.62
CV	0.06	0.02	0.04	0.27
N	10	11	11	11
CYPRESS HILLS		60.68	53.25	7.43
SE		0.37	0.46	0.33
CV		0.02	0.03	0.18
N		16	16	16
BALFOUR	12.58	60.20	53.00	7.44
SE	0.21	0.55	0.37	0.62
CV	0.05	0.02	0.02	0.25

N	11	10	9	9
KANANASKIS	13.78	61.42	54.21	7.21
SE	0.32	0.75	1.93	1.45
CV	0.06	0.03	0.09	0.54
N	7	7	7	7
MCBRIDE	13.48	60.76	54.41	6.35
SE	0.12	0.50	0.58	0.39
CV	0.03	0.03	0.03	0.22
N	13	13	13	13
HINTON	13.20	61.00	52.00	8.91
SE				
CV				
N	1	1	1	1
LIARD RIVER	13.00	60.50	52.11	8.38
SE	0.16	0.22	0.97	0.78
CV	0.02	0.01	0.04	0.22
N	5	6	6	6

* - all measurements in millimeters.

Elementary Statistics for Skull Complex: *O. tolmiei* Localities

LOCALITY	PRL	BDEP	NASW	INORW	SKW	SKL	MANL	MAND
PARADISE VALLEY	13.52	1.16	5.56	2.63	13.47	30.38	21.89	1.38
SE	0.15	0.04	0.06	0.04	0.08	0.13	0.11	0.02
CV	0.04	0.12	0.04	0.05	0.02	0.01	0.01	0.05
N	13	14	13	13	11	13	13	14
CEDARVILLE	12.90	1.05	5.56	2.54	13.50	29.60	21.25	1.39
SE	0.12	0.06	0.10	0.06	0.09		0.03	0.08
CV	0.01	0.10	0.03	0.04	0.01		0.01	0.10
N	2	3	3	3	2	1	2	3
JARBIDGE	13.68	1.06	5.54	2.52	13.31	30.54	21.86	1.36
SE	0.12	0.02	0.08	0.04	0.05	0.15	0.14	0.01
CV	0.03	0.10	0.05	0.07	0.01	0.01	0.02	0.04
N	18	18	14	16	12	13	14	16
FORT KLAMATH	13.88	1.05	5.77	2.87	13.38	31.28	21.98	1.40
SE	0.16	0.00	0.34				0.33	0.02
CV	0.01	0.00	0.08				0.02	0.02
N	2	2	2	1	1	1	2	2
MAGIC MTN.	13.67	1.04	5.48	2.61	13.47	30.49	21.86	1.38
SE	0.11	0.03	0.07	0.05	0.11	0.18	0.16	0.02
CV	0.03	0.10	0.04	0.07	0.02	0.02	0.02	0.07
N	13	13	12	13	11	11	12	13

ALLRED FLATS	13.63	1.03	5.60	2.64	13.42	30.82	21.70	1.42
SE	0.10	0.02	0.07	0.03		0.23	0.29	0.01
CV	0.02	0.07	0.04	0.04		0.01	0.04	0.04
N	11	11	12	11	1	3	9	12
POCATELLO	13.77	1.27	5.61	2.69	13.38	30.47	22.16	1.42
SE	0.10	0.03	0.13	0.05	0.10	0.12	0.16	0.02
CV	2.34	0.10	0.06	0.05	0.01	0.10	0.02	0.06
N	10	10	7	7	6	6	10	10
LAVA BUTTE	12.85	1.10		2.88		30.10	21.00	1.33
SE								
CV								
N	1	1	1		1	1	1	
SQUAW CREEK	13.64	1.13	5.64	2.62	13.39	30.98	21.90	1.44
SE	0.14	0.03	0.06	0.03	0.11	0.10	0.15	0.01
CV	0.03	0.11	0.04	0.04	0.02	0.01	0.02	0.04
N	11	12	12	12	10	7	10	13
MT. HOOD	13.39	1.04	6.65	2.71	13.26	30.18	21.89	1.38
SE	0.10	0.03	0.06	0.03	0.08	0.17	0.13	0.01
CV	0.03	0.14	0.04	0.05	0.02	0.01	0.02	0.03
N	18	18	16	15	13	12	15	19
PACKWOOD	13.38	1.02	5.72	2.78	13.49	30.54	21.70	1.40
SE	0.09	0.03	0.07	0.06	0.04	0.19	0.15	0.02
CV	0.02	0.11	0.04	0.07	0.01	0.01	0.02	0.05
N	15	15	14	12	4	6	14	14
LOLO HOT SPR.	13.37	1.07	5.54	2.65	13.44	30.51	21.77	1.40
SE	0.20	0.05	0.12	0.08	0.09	0.32	0.24	0.04
CV	0.04	0.13	0.05	0.06	0.01	0.02	0.02	0.08
N	7	7	6	4	6	5	7	7
SEARS CREEK	13.62	1.02	5.64	2.69	13.33	30.70	21.93	1.39
SE	0.09	0.02	0.06	0.06	0.06	0.13	0.11	0.01
CV	0.02	0.09	0.04	0.08	0.01	0.01	0.01	0.05
N	13	13	14	14	10	11	12	14
LOOMIS	13.49	1.02	5.55	2.75	13.38	30.50	21.79	1.33
SE	0.12	0.02	0.11	0.06	0.11	0.17	0.16	0.03
CV	0.02	0.05	0.06	0.06	0.02	0.01	0.02	0.07
N	10	8	10	8	9	8	11	11
BALFOUR	13.34	1.18	5.69	2.64	13.36	30.60	22.11	1.39
SE	0.08	0.03	0.06	0.06	0.06	0.12	0.16	0.01
CV	0.01	0.09	0.03	0.08	0.01	0.01	0.02	0.03
N	9	9	9	11	9	7	10	11
KANANASKIS	12.57	1.00	5.85	2.79	13.61	29.61	22.39	1.43
SE	0.29	0.01	0.06	0.07	0.09	0.30	0.20	0.02
CV	0.05	0.04	0.02	0.06	0.01	0.02	0.02	0.04
N	6	7	7	7	6	5	7	7
MCBRIDE	12.79	1.04	5.63	2.63	13.46	29.96	22.02	1.43
SE	0.21	0.02	0.09	0.07	0.08	0.30	0.14	0.02
CV	0.05	0.08	0.06	0.09	0.01	0.03	0.02	0.06

N	12	12	12	11	8	9	11	13
HINTON	12.46	1.13	4.98				21.11	1.33
SE								
CV								
N	1	1	1			1	1	
LIARD RIVER	12.87	0.99	5.73	2.68	13.35	29.86	21.73	1.39
SE	0.30	0.02	0.06	0.03	0.05	0.20	0.10	0.02
CV	0.04	0.05	0.02	0.02	0.01	0.01	0.01	0.04
N	4	6	6	6	4	3	6	6

* - all measurements in millimeters.

Elementary Statistics for Girdle Complex: *O. tolmiei* Localities

LOCALITY	CORL	SCAPW	STERL	KEEL	KEED	SYNW	SYNMW
PARADISE VALLEY	13.82	1.71	15.05	13.26	5.56	8.61	4.78
SE	0.07	0.04	0.16	0.21	0.06	0.06	0.06
CV	0.01	0.09	0.03	0.05	0.04	0.02	0.04
N	13	14	12	13	14	10	12
CEDARVILLE	13.63	1.76	15.44	13.49	5.89	8.97	4.92
SE	0.17	0.12	0.24	0.41	0.10	0.13	0.12
CV	0.02	0.12	0.02	0.05	0.03	0.02	0.04
N	3	3	3	3	3	3	3
JARBIDGE	13.78	1.74	15.31	13.51	5.83	8.81	5.00
SE	0.06	0.02	0.13	0.16	0.06	0.11	0.04
CV	0.01	0.07	0.03	0.04	0.04	0.03	0.03
N	19	19	14	14	14	9	18
FORT KLAMATH	13.72	1.84	15.16	13.41	5.54	8.44	
SE	0.04	0.08		0.08	0.09		
CV	0.01	0.06		0.01	0.02		
N	2	2	1	2	2	1	
MAGIC MTN.	13.72	1.75	15.47	13.51	5.74	9.05	5.00
SE	0.07	0.03	0.07	0.08	0.08	0.09	0.06
CV	0.02	0.08	0.01	0.02	0.05	0.03	0.04
N	13	14	13	13	13	12	13
ALLRED FLATS	13.77	1.77	15.28	13.46	5.94	8.79	5.08
SE	0.07	0.03	0.14	0.14	0.08	0.08	0.05
CV	0.01	0.06	0.03	0.03	0.05	0.02	0.03
N	11	11	11	12	12	9	10
POCATELLO	13.88	1.82	15.30	13.65	5.89	8.75	5.09
SE	0.08	0.04	0.20	0.20	0.11	0.07	0.10
CV	0.02	0.08	0.04	0.04	0.06	0.02	0.06
N	11	11	10	9	9	7	11

LAVA BUTTE	13.61	1.74	14.63	13.04	5.97	8.55	5.19
SE							
CV							
N	1	1	1	1	1	1	1
SQUAW CREEK	13.99	1.86	15.80	14.02	5.74	8.91	5.12
SE	0.09	0.03	0.09	0.11	0.15	0.07	0.07
CV	0.02	0.07	0.02	0.20	0.08	0.02	0.05
N	13	13	12	11	11	13	13
MT. HOOD	13.40	1.77	15.17	13.15	5.67	8.67	4.93
SE	0.07	0.03	0.13	0.15	0.07	0.04	0.05
CV	0.02	0.08	0.03	0.04	0.05	0.02	0.04
N	17	19	13	15	15	17	15
PACKWOOD	13.57	1.69	15.02	13.06	5.84	8.63	4.93
SE	0.09	0.03	0.12	0.14	0.09	0.12	0.07
CV	0.02	0.07	0.02	0.03	0.05	0.04	0.05
N	15	15	13	12	12	11	12
LOLO HOT SPRINGS	14.13	1.83	15.72	13.81	6.09	8.74	4.89
SE	0.07	0.02	0.19	0.13	0.06	0.15	0.05
CV	0.01	0.03	0.02	0.02	0.02	0.04	0.02
N	5	6	5	6	6	6	5
SEARS CREEK	13.80	1.73	15.38	13.67	5.99	8.73	5.00
SE	0.06	0.03	0.14	0.19	0.11	0.07	0.07
CV	0.01	0.07	0.03	0.04	0.06	0.02	0.05
N	13	14	12	12	12	8	12
LOOMIS	13.61	1.73	15.07	13.17	5.79	8.72	4.93
SE	0.10	0.04	0.15	0.16	0.09	0.07	0.07
CV	0.02	0.08	0.03	0.04	0.05	0.02	0.04
N	10	11	10	11	11	10	9
BALFOUR	13.91	1.94	15.54	14.05	6.05	8.82	5.09
SE	0.11	0.02	0.12	0.22	0.14	0.07	0.08
CV	0.02	0.05	0.02	0.05	0.07	0.02	0.05
N	11	11	9	10	10	10	9
KANANASKIS	14.37	1.82	15.94	14.35	6.05	8.95	4.97
SE	0.17	0.03	0.31	0.35	0.06	0.08	0.06
CV	0.03	0.04	0.05	0.06	0.03	0.02	0.03
N	7	7	7	7	7	7	7
MCBRIDE	14.18	1.85	15.74	14.12	5.94	8.97	5.00
SE	0.10	0.01	0.14	0.15	0.06	0.08	0.07
CV	0.02	0.03	0.03	0.04	0.04	0.03	0.05
N	13	13	13	13	13	12	12
HINTON	13.85	1.85	15.62	14.06	6.18	9.13	5.13
SE							
CV							
N	1	1	1	1	1	1	1
LIARD RIVER	13.99	1.80	15.02	13.72	5.88	8.64	5.11
SE	0.16	0.06	0.27	0.19	0.09	0.09	0.06
CV	0.02	0.09	0.04	0.03	0.04	0.02	0.02

CV	0.02	0.02	0.01	0.02	0.08
N	13	13	3	11	12
MT. HOOD	2.47	14.61	26.86	20.33	2.11
SE	0.01	0.10		0.15	0.02
CV	0.03	0.02		0.02	0.05
N	19	14	1	14	17
PACKWOOD	2.46	14.51	27.13	20.25	2.06
SE	0.01	0.07	0.28	0.27	0.05
CV	0.02	0.01	0.02	0.03	0.80
N	14	14	4	8	12
LOLO HOT SPRINGS	2.55	15.15	26.87	20.12	2.07
SE	0.02	0.07		0.29	0.06
CV	0.02	0.01		0.02	0.06
N	6	5	1	4	4
SEARS CREEK	2.52	14.84	27.09	20.20	2.14
SE	0.02	0.12	0.51	0.20	0.04
CV	0.03	0.03	0.03	0.03	0.07
N	14	13	3	11	13
LOOMIS	2.51	14.57	27.22	20.35	2.00
SE	0.02	0.09	0.30	0.09	0.09
CV	0.03	0.02	0.02	0.01	0.14
N	10	10	5	9	10
BALFOUR	2.53	14.98	27.68	20.65	2.09
SE	0.01	0.20	0.20	0.17	0.02
CV	0.01	0.01	0.01	0.02	0.04
N	10	10	2	9	11
KANANASKIS	2.56	14.64	27.80	20.77	2.25
SE	0.02	0.10	0.25	0.33	0.04
CV	0.02	0.01	0.01	0.03	0.04
N	7	7	3	6	6
MCBRIDE	2.58	14.74	27.79	20.66	2.05
SE	0.01	0.11	0.47	0.12	0.06
CV	0.02	0.02	0.03	0.01	0.10
N	13	13	4	10	2
HINTON	2.40	14.41	26.61	20.07	2.31
SE					
CV					
N	1	1	1	1	1
LIARD RIVER	2.45	14.64	27.52	20.54	1.91
SE	0.04	0.23	0.21	0.11	0.09
CV	0.04	0.03	0.01	0.01	0.10
N	6	6	3	5	5

* - all measurements in millimeters.

Elementary Statistics for Wing Complex: *O. tolmiel* Localities

LOCALITY	HTRL	HDEW	HUML	ULNL	CARPL
PARADISE VALLEY	3.45	3.22	14.19	16.13	9.21
SE	0.01	0.02	0.04	0.07	0.09
CV	0.01	0.01	0.01	0.01	0.03
N	9	7	6	9	8
CEDARVILLE	3.58	3.38	14.08	15.80	9.24
SE	0.04	0.09	0.17	0.39	0.13
CV	0.02	0.04	0.02	0.04	0.02
N	3	3	3	3	3
JARBIDGE	3.44	3.22	13.95	16.04	9.04
SE	0.02	0.02	0.05	0.10	0.09
CV	0.02	0.03	0.01	0.02	0.03
N	17	16	15	10	12
FORT KLAMATH	3.44	3.33	13.88		9.47
SE					
CV					
N	1	1	1		1
MAGIC MTN.	3.50	3.30	13.98	16.05	9.17
SE	0.02	0.03	0.10	0.13	0.07
CV	0.02	0.03	0.02	0.02	0.02
N	14	12	11	10	12
ALLRED FLATS	3.44	3.27	14.06	16.08	9.10
SE	0.03	0.02	0.14	0.03	0.05
CV	0.03	0.01	0.02	0.01	0.01
N	9	8	5	7	7
POCATELLO	3.46	3.23	14.08	16.38	9.18
SE	0.03	0.03	0.09	0.13	0.07
CV	0.02	0.02	0.01	0.02	0.01
N	8	8	8	7	6
LAVA BUTTE	3.35				
SE					
CV					
N	1				
SQUAW CREEK	3.59	3.28	14.13	16.25	9.40
SE	0.04	0.05	0.14	0.13	0.09
CV	0.03	0.03	0.03	0.02	0.03
N	9	9	9	7	9
MT. HOOD	3.41	3.21	13.58	15.64	9.03
SE	0.02	0.02	0.07	0.11	0.03
CV	0.02	0.03	0.02	0.02	0.01
N	18	18	16	11	15
PACKWOOD	3.42	3.20	13.49	15.77	9.06
SE	0.02	0.03	0.12	0.13	0.13

CV	0.02	0.04	0.02	0.02	0.04
N	14	11	10	9	8
LOLO HOT SPRINGS	3.56	3.32	14.34	16.16	9.45
SE	0.01	0.04	0.05	0.43	0.13
CV	0.01	0.02	0.01	0.03	0.02
N	6	3	2	2	2
SEARS CREEK	3.48	3.21	13.88	16.10	9.12
SE	0.02	0.03	0.13	0.15	0.08
CV	0.03	0.03	0.03	0.03	0.06
N	13	12	12	14	13
LOOMIS	3.43	3.20	13.74	16.10	9.18
SE	0.02	0.04	0.07	0.07	0.09
CV	0.02	0.01	0.01	0.01	0.02
N	10	10	10	8	8
BALFOUR	3.56	3.30	14.14	15.89	9.60
SE	0.04	0.02	0.05	0.10	0.07
CV	0.03	0.02	0.01	0.01	0.02
N	9	8	7	8	8
KANANASKIS	3.52	3.29	14.23	16.25	9.41
SE	0.04	0.05	0.16	0.18	0.15
CV	0.03	0.04	0.02	0.02	0.04
N	7	7	6	6	6
MCBRIDE	3.58	3.23	14.11	16.06	9.34
SE	0.03	0.03	0.07	0.10	0.04
CV	0.02	0.03	0.01	0.02	0.01
N	9	11	8	11	13
HINTON	3.45	3.17	13.70	15.81	8.97
SE					
CV					
N	1	1	1	1	1
LIARD RIVER	3.46	3.20	14.06	16.01	9.09
SE	0.02	0.04	0.10	0.15	0.18
CV	0.01	0.03	0.01	0.02	0.03
N	6	6	6	6	3

* - all measurements in millimeters.

APPENDIX E ENVIRONMENTAL VARIABLES

Environmental variables were taken from data issued by Environment Canada (Atmospheric and Environmental Services 1982a, 1982b, 1984a, 1984b) and the National Weather Service (ESSA 1968 and Vischer 1954). Weather data from the United States were converted to metric values (i.e., degrees F to degrees C and inches to millimeters) for statistical analyses.

TEMPERATURE VARIABLES

MEJUNT. Mean dry bulb temperature for June based on weather data collected from 1951-1980.

MIJUNT. Mean minimum dry bulb temperature for June based on weather data collected from 1951-1980.

MAJUNT. Mean maximum dry bulb temperature for June based on weather data collected from 1951-1980.

MEJULT. Mean dry bulb temperature for July based on weather data collected from 1951-1980.

MIJULT. Mean minimum dry bulb temperature for July based on weather data collected from 1951-1980.

MAJULT. Mean maximum dry bulb temperature for July based on weather data collected from 1951-1980.

PRECIPITATION VARIABLES

MEJUNP. Mean precipitation for June based on weather data collected from 1951-1980.

MEJULP. Mean precipitation for July based on weather data collected from 1951-1980.

RELH. Mean relative humidity for July based on weather data collected from 1951-1980.

EVAP. Pan lake evapotranspiration for July based on weather data collected from 1951-1980.

JULWT. Mean wet bulb temperature for July based on weather data collected from 1951-1980.

APPENDIX F SONG VARIABLES

Terminology of cultural units of primary song and physical parameters have been modified following Shiovitz (1975) and Baptista (1977). Parameters such as frequency, duration and interval were measured in millimeters to the nearest 0.05mm and then converted into Hz or seconds for statistical analysis. A pitch pipe (A-tone) was used in the field to calibrate the Uher for laboratory analysis. All sonograph measurements were based on these calibrations scattered throughout the tapes.

SYLLABLE COMPLEX

NUMBER OF PARTS PER SONG (NPSO). *O. philadelphia* and *O. tolmiei* song could easily be divided into Parts. A song part or song division was composed of the same syllable type, no matter how many syllables comprised that part. In some cases two different syllables were repeated one after the other and composed a song part. Other parts or divisions were composed of a different syllable type(s) (or combinations thereof).

NUMBER OF SYLLABLES PER SONG (NSSO). A syllable was composed of one to 10 notes. These song units may or may not have been the same note type but they were always sung together in the same order in each song. All such collections of notes described singularly as syllables were totalled for each song.

NUMBER OF DIFFERENT SYLLABLES PER SONG (NDSO). This was the total of different types of syllables per song.

NUMBER OF NOTES PER M-A SYLLABLE (NNA). The sum of all notes comprising the M-A syllable.

NUMBER OF NOTES PER M-B SYLLABLE (NNB). The sum of all notes comprising the M-B syllable.

NUMBER OF NOTES PER M-C SYLLABLE (NNC). The sum of all notes comprising the M-C syllable.

NUMBER OF NOTES PER F-A SYLLABLE (NFA). The sum of all notes comprising the F-A syllable.

NUMBER OF NOTES PER F-B SYLLABLE (NFB). The sum of all notes comprising the F- B syllable.

DURATION/INTERVAL COMPLEX

SONG DURATION (DUR). The length of a song from the leading edge of the first note to the trailing edge of the last note.

INTERVAL BETWEEN M-A AND M-B SYLLABLES (IMA). Distance between trailing edge of last note in syllable M-A to leading edge of syllable M-B.

INTERVAL BETWEEN M-B AND M-C SYLLABLES (IMB). Distance between trailing edge of last note in syllable M-B to leading edge of syllable M-C.

INTERVAL BETWEEN M-C AND F-A SYLLABLES (IMC). Distance between trailing edge of last note in syllable M-C to leading edge of syllable F-A.

INTERVAL BETWEEN F-A AND M-B SYLLABLES (IFA). Distance between trailing edge of last note in syllable F-A to leading edge of syllable F-B.

INTERVAL BETWEEN F-B AND F-C SYLLABLES (IFB). Distance between trailing edge of last note in syllable F-B to leading edge of syllable F-C.

FREQUENCY COMPLEX

MINIMUM FREQUENCY OF SONG (MINS). Measured from the bottom most etching of the lowest frequency song note to the x-axis of the sonograph.

MAXIMUM FREQUENCY OF SONG (MAXS). Measured from the top most etching of the highest frequency song note to the x-axis of the sonograph.

MINIMUM FREQUENCY OF M-A SYLLABLE (MIA). Measured from the bottom most etching of M-A to the x-axis of the sonograph.

MINIMUM FREQUENCY OF M-B SYLLABLE (MIB). Measured from the bottom most etching of M-B to the x-axis of the sonograph.

MINIMUM FREQUENCY OF M-C SYLLABLE (MIC). Measured from the bottom most etching of M-C to the x-axis of the sonograph.

MAXIMUM FREQUENCY OF M-A SYLLABLE (MAA). Measured from the top most etching of M-A to the x-axis of the sonograph.

MAXIMUM FREQUENCY OF M-B SYLLABLE (MAB). Measured from the top most etching of M-B to the x-axis of the sonograph.

MAXIMUM FREQUENCY OF M-C SYLLABLE (MAC). Measured from the top most etching of M-C to the x-axis of the sonograph.

MINIMUM FREQUENCY OF F-A SYLLABLE (MIFA). Measured from the bottom most etching of F-A to the x-axis of the sonograph.

MINIMUM FREQUENCY OF F-B SYLLABLE (MIFB). Measured from the bottom most etching of F-B to the x-axis of the sonograph.

MAXIMUM FREQUENCY OF F-A SYLLABLE (MAFA). Measured from the top most etching of F-A to the x-axis of the sonograph.

MAXIMUM FREQUENCY OF F-B SYLLABLE (MAFB). Measured from the top most etching of F-B to the x-axis of the sonograph.

APPENDIX G
PER CENT DIFFERENCES BETWEEN TAXA FOR SONG
PARAMETER VARIABLES

Elementary Statistics and Per Cent Difference for Entire Song

SONG CHARACTERS	<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	PER CENT DIFFERENCE
NPSO	1.72	2.04	15.6%
SE	0.03	0.05	
CV	0.26	0.30	
N	188	116	
NSSO	5.68	6.99	18.7%
SE	0.07	0.14	
CV	0.18	0.22	
N	186	115	
NDSO	1.71	2.01	14.9%
SE	0.03	0.06	
CV	0.26	0.32	
N	188	116	
DUR*	1.11	1.29	13.9%
SE	0.01	0.02	
CV	0.15	0.17	
N	182	112	
MINS**	1933.24	2416.05	19.9%
SE	22.01	31.74	
CV	0.15	0.13	
N	187	111	
MAXS**	5458.81	5953.18	8.3%
SE	52.13	63.69	
CV	0.12	0.10	
N	180	107	

* - seconds.

** - Hz.

Elementary Statistics and Per Cent Difference for Part I Song Variables

SONG CHARACTERS	<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	PER CENT DIFFERENCE

NNA	4.58	4.38	4.3%
SE	0.10	0.14	
CV	0.29	0.32	
N	174	100	
NNB	4.84	4.58	5.3%
SE	0.10	0.13	
CV	0.29	0.30	
N	183	105	
NNC	4.86	4.62	4.9%
SE	0.10	0.14	
CV	0.29	0.32	
N	183	103	
IMA*	0.07	0.06	14.2%
SE	0.00	0.00	
CV	0.43	0.48	
N	166	105	
IMB*	0.06	0.06	0.0%
SE	0.00	0.00	
CV	0.39	0.45	
N	173	102	
IMC*	0.05	0.05	0.0%
SE	0.00	0.00	
CV	0.48	0.46	
N	127	88	
MIA**	2721.63	3108.23	12.4%
SE	43.23	60.97	
CV	0.21	0.20	
N	180	107	
MIB**	2662.69	3093.15	13.8%
SE	41.85	59.00	
CV	0.21	0.19	
N	187	109	
MIC**	2635.59	3097.47	14.9%
SE	42.51	59.16	
CV	0.21	0.20	
N	186	112	
MAA**	5248.91	5601.56	6.2%
SE	55.08	84.74	
CV	0.13	0.14	
N	168	95	
MAB**	5332.68	5674.61	6.0%
SE	56.05	71.32	
CV	0.13	0.12	
N	176	105	
MAC**	5347.24	5734.00	6.7%
SE	56.80	72.89	
CV	0.14	0.12	

N 175 104

* - seconds.
** - Hz.

Elementary Statistics and Per Cent Difference for Part II Song Variables

SONG CHARACTERS	<i>Oporornis philadelphia</i>	<i>Oporornis tolmiei</i>	PER CENT DIFFERENCE
NFA	2.54	4.34	41.4%
SE	0.07	0.18	
CV	0.33	0.41	
N	133	95	
NFB	2.18	3.98	45.2%
SE	0.06	0.15	
CV	0.34	0.34	
N	125	85	
IFA*	0.03	0.05	40.0%
SE	0.00	0.00	
CV	0.60	0.47	
N	123	83	
IFB*	0.03	0.05	40.0%
SE	0.00	0.00	
CV	0.36	0.71	
N	30	44	
MIFA**	1942.13	2643.87	26.5%
SE	28.22	55.04	
CV	0.16	0.20	
N	134	93	
MIFB**	1895.29	2618.59	26.7%
SE	25.27	56.38	
CV	0.14	0.19	
N	124	85	
MAFA**	3975.13	5437.49	26.8%
SE	48.61	82.24	
CV	0.14	0.14	
N	132	95	
MAFB**	3744.93	5388.10	30.4%
SE	55.71	85.53	
CV	0.16	0.14	
N	122	85	

* - seconds.

** - Hz.

APPENDIX H
ELEMENTARY STATISTICS OF SONG VARIABLES
FOR *O. philadelphia* AND *O. tolmiei* LOCALITIES

Elementary Statistics for Entire Song Variables: *O. philadelphia* Localities

LOCALITY	NPSO	SSO	NDSO	DUR*	MINS**	MAXS**
ST. FRANCIS	1.84	5.68	1.78	1.20	1968.30	6078.52
SE	0.08	0.17	0.09	0.03	61.70	125.85
CV	0.20	0.13	0.23	0.11	0.13	0.09
N	19	19	19	19	19	19
ST. PAULE	2.00	7.00	2.00	1.30	1533.60	5780.00
SE						
CV						
N	1	1	1	1	1	1
GIRARDVILLE	2.09	5.72	2.00	1.09	1816.80	5582.00
SE	0.09	0.19	0.00	0.04	59.43	143.41
CV	0.14	0.11	0.00	0.12	0.10	0.08
N	11	11	11	11	11	11
STEPHEN.	1.00	5.00	1.00	1.25	1991.20	5452.80
SE						
CV						
N	1	1	1	1	1	1
CAPE BON.	1.00	4.66	1.00	1.00	1690.4	5222.40
SE	0.00	0.33	0.00	0.12	250.56	262.51
CV	0.00	0.12	0.00	0.21	0.25	0.08
N	3	3	3	3	3	3
VAL PAR.	2.00	6.61	2.00	1.15	2007.00	5815.50
SE	0.00	0.26	0.00	0.03	58.91	213.42
CV	0.00	0.14	0.00	0.11	0.10	0.12
N	13	13	13	12	13	12
LEBEL-SUR.	1.91	5.78	1.91	1.13	1843.30	5523.50
SE	0.06	0.25	0.06	0.03	71.70	122.00
CV	0.15	0.20	0.15	0.12	0.18	0.10
N	23	23	23	23	23	23
COCHRANE	2.00	5.50	1.90	1.02	1894.30	5717.20
SE	0.00	0.37	0.09	0.05	71.06	150.91
CV	0.00	0.21	0.15	0.17	0.11	0.07
N	11	10	11	9	10	8
HEARST	1.85	6.00	1.92	1.17	1850.17	5707.56
SE	0.09	0.29	0.12	0.04	80.57	132.03
CV	0.19	0.18	0.24	0.13	0.16	0.16
N	14	14	14	14	14	13
GERALDTON	1.80	5.60	1.80	1.13	1824.48	5308.64

SE	0.20	0.24	0.20	0.09	65.25	279.01
CV	0.24	0.09	0.24	0.19	0.07	0.11
N	5	5	5	5	5	5
MINITAKI	2.00	6.14	2.00	1.11	1810.00	5524.70
SE	0.00	0.27	0.00	0.05	34.13	141.96
CV	0.00	0.16	0.00	0.17	0.07	0.09
N	15	14	15	14	15	14
DORION	1.87	5.81	1.87	1.07	1897.1	5289.40
SE	0.08	0.22	0.08	0.05	80.02	189.08
CV	0.18	0.15	0.18	0.19	0.16	0.14
N	16	16	16	16	16	16
RODDICK.	1.00	5.50	1.00	1.22	2231.60	6295.20
SE	0.00	0.50	0.00	0.02	262.80	440.00
CV	0.00	0.12	0.00	0.02	0.16	0.09
N	2	2	2	2	2	2
PORT SA.	1.16	4.50	1.16	1.12	1986.10	5986.70
SE	0.16	0.22	0.16	0.09	104.96	120.35
CV	0.34	0.12	0.34	0.21	0.12	0.04
N	6	6	6	6	6	5
ST. ANT.	2.00	6.00	2.00	1.38	2194.40	7541.60
SE						
CV						
N	1	1	1	1	1	1
LODGE.	1.42	5.42	1.42	1.14	2322.60	4574.30
SE	0.20	0.36	0.20	0.06	119.56	123.33
CV	0.37	0.17	0.37	0.15	0.13	0.07
N	7	7	7	7	7	7
OBED	1.40	5.60	1.40	1.07	1893.40	5302.20
SE	0.24	0.50	0.24	0.07	110.99	199.72
CV	0.39	0.20	0.39	0.14	0.13	0.08
N	5	5	5	5	5	5
WHITEC.	1.16	5.33	1.16	1.12	1954.00	4509.80
SE	0.16	0.61	0.16	0.10	92.50	195.57
CV	0.34	0.28	0.34	0.20	0.11	0.09
N	6	6	6	5	6	5
SLAVE L.	1.46	5.53	1.46	1.02	2033.70	4782.60
SE	0.13	0.29	0.13	0.05	72.96	140.06
CV	0.35	0.20	0.35	0.20	0.13	0.01
N	15	15	15	15	15	15
FORT NEL.	1.16	4.83	1.16	1.05	2075.70	4758.80
SE	0.16	0.47	0.16	0.06	177.08	117.22
CV	0.34	0.24	0.34	0.14	0.20	0.06
N	6	6	6	6	6	6

* - seconds.
 ** - Hz.

Elementary Statistics for Part I Song Variables: *O. philadelphia* Localities

LOCALITY	NNA	NNB	NNC	IMA*	IMB*	IMC*
ST. FRANCIS	5.83	5.94	6.17	0.07	0.05	0.04
SE	0.25	0.28	0.17	0.00	0.00	0.00
CV	0.18	0.20	0.11	0.53	0.35	0.31
N	18	18	17	19	19	16
ST. PAULE	5.00	6.00	6.00	0.08	0.07	0.04
SE						
CV						
N	1	1	1	1	1	1
GIRARDVILLE	5.27	6.18	6.27	0.08	0.06	0.04
SE	0.42	0.44	0.42	0.00	0.00	0.00
CV	0.26	0.23	0.22	0.20	0.30	0.42
N	11	11	11	9	10	10
STEPHENVILLE	6.00	6.00	6.00	0.05	0.07	
SE						
CV						
N	1	1	1	1	1	
CAPE BON.	5.00	5.00	5.00	0.04	0.05	
SE	0.00	0.00	0.00	0.00	0.00	
CV	0.00	0.00	0.00	0.00	0.00	
N	3	3	3	2	2	
VAL PAR.	4.16	4.76	4.84	0.09	0.07	0.05
SE	0.34	0.34	0.29	0.01	0.01	0.00
CV	0.28	0.25	0.22	0.22	0.41	0.41
N	12	13	13	13	13	13
LEBEL-SUR.	5.73	5.86	5.95	0.06	0.05	0.04
SE	0.14	0.14	0.14	0.00	0.00	0.00
CV	0.11	0.11	0.11	0.29	0.39	0.29
N	19	23	23	19	22	21
COCHRANE	4.85	5.11	5.11	0.08	0.07	0.05
SE	0.55	0.45	0.42	0.00	0.00	0.00
CV	0.30	0.26	0.24	0.27	0.36	0.41
N	7	9	9	7	9	8
HEARST	5.21	5.71	5.92	0.07	0.05	0.04
SE	0.26	0.16	0.12	0.01	0.00	0.00
CV	0.18	0.10	0.08	0.51	0.33	0.20
N	14	14	14	14	14	11
GERALDTON	4.40	5.80	5.80	0.10	0.07	0.03
SE	0.81	0.20	0.20	0.01	0.00	0.00
CV	0.41	0.07	0.07	0.21	0.18	0.13

N	5	5	5	5	5	4
MINITAKI	3.42	3.33	3.33	0.06	0.06	0.05
SE	0.20	0.21	0.21	0.00	0.00	0.00
CV	0.22	0.24	0.24	0.40	0.47	0.36
N	14	15	15	13	14	14
DORION	3.80	4.00	4.00	0.07	0.06	0.06
SE	0.36	0.36	0.36	0.00	0.00	0.00
CV	0.37	0.36	0.36	0.41	0.44	0.47
N	15	16	16	15	15	13
RODDICK.	6.50	6.50	5.00	0.03	0.04	
SE	0.50	0.50	1.00	0.00	0.01	
CV	0.10	0.10	0.28	0.00	0.35	
N	2	2	2	2	2	
PORT SA.	5.66	5.83	5.33	0.06	0.05	0.09
SE	0.21	0.16	0.49	0.01	0.01	
CV	0.09	0.06	0.22	0.55	0.53	
N	6	6	6	5	5	1
ST. AN.	5.00	5.00	7.00	0.05	0.05	0.04
SE						
CV						
N	1	1	1	1	1	1
LODGE P.	2.66	2.66	2.66	0.09	0.08	0.14
SE	0.33	0.33	0.33	0.01	0.01	0.02
CV	0.30	0.30	0.30	0.49	0.54	0.25
N	6	6	6	6	5	3
OBED	4.00	4.00	4.00	0.06	0.06	0.07
SE	0.00	0.00	0.00	0.00	0.01	0.04
CV	0.00	0.00	0.00	0.26	0.42	0.08
N	5	4	5	5	5	2
WHITEC.	3.83	4.00	4.00	0.05	0.05	0.08
SE	0.40	0.25	0.25	0.00	0.00	
CV	0.25	0.15	0.15	0.18	0.23	
N	6	6	6	4	5	1
SLAVE L.	3.42	3.33	3.40	0.08	0.07	0.09
SE	0.22	0.25	0.25	0.00	0.00	0.01
CV	0.24	0.29	0.28	0.41	0.43	0.36
N	14	15	15	13	13	6
FORT NE.	3.83	3.83	3.50	0.05	0.05	0.05
SE	0.16	0.16	0.22	0.00	0.00	
CV	0.10	0.10	0.15	0.31	0.33	
N	6	6	6	6	6	1

* - seconds.

Elementary Statistics for Part I Song Variables (Cont'd.): *O. philadelphia*
Localities

LOCALITY	MIA**	MIB**	MIC**	MAA**	MAB**	MAC**
ST. FRANCIS	3002.40	2927.00	2917.00	5767.60	5853.60	5953.30
SE	137.87	129.36	130.59	130.59	131.90	142.68
CV	0.20	0.19	0.19	0.19	0.09	0.10
N	19	19	19	19	19	19
ST. PAULE	2740.80	2738.40	2781.60	5284.00	5788.80	5747.20
SE						
CV						
N	1	1	1	1	1	1
GIRAR.	2876.10	2825.00	2811.80	5242.900	5161.40	5333.80
SE	143.94	134.29	157.79	178.17	286.75	281.55
CV	0.16	0.15	0.18	0.10	0.18	0.17
N	11	11	11	10	11	11
STEPH.	2185.60	2036.80	2010.40	5472.80	5286.40	5392.80
SE						
CV						
N	1	1	1	1	1	1
CAPE BON.	1872.50	1744.00	1720.26	5153.90	5035.70	313.60
SE	229.29	271.83	214.27	327.74	186.89	313.60
CV	0.21	0.26	0.21	0.11	0.06	0.08
N	3	3	3	3	3	2
VAL P.	3460.10	3380.10	3392.10	5592.90	5759.60	5769.30
SE	146.74	145.24	139.07	223.66	198.51	193.45
CV	0.15	0.15	0.14	0.13	0.12	0.12
N	13	13	13	11	13	13
LEBEL-S.	2604.00	2576.80	2563.30	5363.20	5553.00	5559.10
SE	99.67	96.25	90.49	116.03	97.32	99.06
CV	0.17	0.17	0.16	0.09	0.08	0.08
N	21	23	23	19	21	22
COCHRANE	3109.40	3005.80	2911.40	5259.50	5162.00	5480.00
SE	222.01	216.74	224.78	332.95	382.54	227.10
CV	0.21	0.22	0.24	0.16	0.22	0.12
N	9	10	10	7	9	9
HEARST	2819.94	2750.80	2751.25	5416.57	5579.63	5670.73
SE	110.33	110.01	113.25	193.62	134.54	142.59
CV	0.14	0.14	0.15	0.13	0.08	0.08
N	14	14	14	14	13	12
GERALDTON	2947.36	2748.64	2653.60	4596.32	5047.20	5223.84
SE	331.59	347.88	378.99	434.42	432.05	358.30
CV	0.25	0.28	0.31	0.21	0.19	0.15
N	5	5	5	5	5	5
MINITAKI	2588.10	2566.20	2559.90	5456.30	5493.10	5544.20

SE	125.90	119.89	120.89	155.04	144.95	151.30
CV	0.18	0.18	0.18	0.10	0.09	0.10
N	14	15	15	13	14	14
DORION	2913.50	2887.90	2865.40	5249.70	5332.60	5256.90
SE	113.12	127.61	114.67	189.90	184.08	175.41
CV	0.15	0.17	0.16	0.13	0.13	0.12
N	15	16	16	14	15	15
RODDICKTON	2282.80	2307.20	2264.40	6325.60	6307.20	5846.80
SE	324.40	187.20	202.00	433.60	452.00	58.80
CV	0.20	0.11	0.12	0.09	0.10	0.10
N	2	2	2	2	2	2
PORT SA.	2195.60	2060.90	1986.80	5800.80	5900.80	5157.30
SE	110.27	125.11	106.94	214.49	106.21	305.16
CV	0.12	0.14	0.13	0.08	0.04	0.13
N	6	6	6	5	5	5
ST. ANT.	2360.00	2216.80	2330.40	5957.60	5919.20	7485.60
SE						
CV						
N	1	1	1	1	1	1
LODGE.	2762.60	2680.00	2624.20	4522.10	4613.10	4521.70
SE	124.31	109.49	119.58	101.87	157.29	100.58
CV	0.11	0.10	0.12	0.05	0.08	0.05
N	7	7	7	7	6	7
OBED	2310.40	2312.30	2248.30	5232.50	4987.60	168.13
SE	267.71	269.45	252.49	195.19	353.43	168.13
CV	0.25	0.26	0.25	0.08	0.14	0.07
N	5	5	5	5	4	5
WHITE.	2079.50	2041.60	2002.90	4413.80	4425.90	4322.40
SE	153.00	166.43	154.66	238.40	197.18	238.13
CV	0.18	0.19	0.18	0.12	0.09	0.11
N	6	6	6	5	5	4
SLAVE L.	2501.80	2455.90	2331.90	4593.80	4668.70	4496.60
SE	130.19	110.91	118.91	113.64	144.91	149.03
CV	0.19	0.17	0.19	0.09	0.12	0.12
N	14	15	15	14	15	14
FORT NEL	2302.70	2228.40	2335.40	4597.10	4669.50	4505.60
SE	174.54	138.04	153.79	106.78	121.55	78.61
CV	0.18	0.15	0.14	0.05	0.06	0.04
N	6	6	5	6	6	6

** - Hz.

Elementary Statistics for Part II Song Variables: *O. philadelphia* Localities

LOCALITY	NFA	NFB	IFA*	IFB*	MIFA**	MIFB**	MAFA**	MAFB**

ST. FRANCIS	2.93	2.25	0.02	0.04	1993.50	1918.40	4430.20	3957.30
SE	0.19	0.19	0.00		61.28	59.85	112.08	166.40
CV	0.26	0.34	0.33		0.12	0.12	0.10	0.16
N	16	16	16	1	16	16	16	16
ST. PAULE	3.00	3.00	0.02	0.03	1638.40	1634.40	4208.00	4359.20
SE								
CV								
N	1	1	1	1	1	1	1	1
GIRARDV.	2.50	2.30	0.03	0.04	1853.00	1790.20	3811.20	3459.80
SE	0.16	0.15	0.00	0.00	53.96	66.74	143.35	209.12
CV	0.21	0.21	0.40	0.35	0.09	0.11	0.12	0.19
N	10	10	10	4	11	10	11	10
VAL PAR.	2.84	2.61	0.02	0.03	2124.40	2084.60	4379.10	4170.90
SE	0.10	0.14	0.00	0.00	64.39	68.74	129.87	160.85
CV	0.13	0.19	0.43	0.41	0.10	0.11	0.10	0.13
N	13	13	13	10	13	13	13	13
LEBEL-S.	2.52	2.00	0.02	0.04	1882.30	1820.20	3680.50	3323.20
SE	0.11	0.07	0.00	0.02	96.07	63.11	93.57	89.88
CV	0.20	0.16	0.41	0.70	0.23	0.15	0.11	0.12
N	21	20	20	2	21	20	21	20
COCHRANE	2.50	1.88	0.04	0.03	2033.20	1951.60	3994.30	3767.40
SE	0.16	0.20	0.00	0.00	103.42	106.09	172.69	241.07
CV	0.21	0.31	0.37	0.41	0.15	0.15	0.12	0.18
N	10	9	8	3	9	8	9	8
HEARST	2.91	2.00	0.00	0.02	86.11	1838.46	4052.07	3597.40
SE	0.08	0.12	0.00		86.11	70.57	145.66	166.95
CV	0.09	0.21	0.40		0.16	0.13	0.11	0.16
N	12	12	11	1	12	12	11	12
GERALD.	2.50	2.25	0.02	0.03	1888.20	1880.60	3900.00	3544.20
SE	0.28	0.47	0.00		93.57	86.63	332.49	446.56
CV	0.23	0.42	0.34		0.09	0.09	0.17	0.25
N	4	4	4	1	4	4	4	
MINITAKI	2.33	2.28	0.04	0.04	1836.50	1820.00	3814.30	3803.80
SE	0.18	0.19	0.00	0.00	35.12	38.14	127.33	136.44
CV	0.31	0.31	0.29	0.00	0.07	0.07	0.12	0.13
N	15	14	14	2	15	13	15	14
DORION	3.00	2.64	0.04	0.04	1864.30	1814.40	3960.60	3866.70
SE	0.27	0.22	0.00	0.00	33.13	29.97	133.46	118.96
CV	0.34	0.31	0.36	0.28	0.06	0.06	0.12	0.11
N	14	14	14	4	14	14	14	14
PORT SA.	5.00	5.00	0.04		1546.40	1580.80	4852.00	4916.00
SE								
CV								
N	1	1	1	1	1	1	1	
ST. ANT.	4.00		2208.80		5070.40			
SE								
CV								
N	1		1		1			
LODGE.	1.00	2.00	0.11		2160.00	2338.40	3900.30	3898.80
SE	0.00	0.01		198.69	260.00	125.20	122.80	
CV	0.00	0.12		0.15	0.15	0.05	0.04	
N	3	1	2	3	1	3	2	
OBED	1.00	1.00	0.10		1910.80	2084.80	3397.20	
SE	0.00				287.60		537.20	
CV	0.00				0.21		0.22	
N	2	1	1		2	1	2	
WHITE	1.00	1.00	0.10		2312.00	2323.20	3544.80	3481.60
SE								

CV								
N	1	1	1	1	1	1	1	
SLAVE L.	1.14	1.16	0.06	0.05	2172.20	2185.20	3890.50	3991.50
SE	0.14	0.16	0.00		211.91	248.82	223.51	299.83
CV	0.33	0.34	0.38		0.25	0.27	0.15	0.16
N	7	6	6	1	7	6	7	5
FORT N.	1.00				1548.00	2556.00		
SE								
CV								
N	1				1	1		

* - seconds.

** - Hz

Elementary Statistics for Entire Song Variables: *O. tolmiei* Localities

LOCALITY	NPSO	NSSO	NDSO	DUR*	MINS**	MAXS**
PARADISE V.	2.00	6.66	2.00	1.28	2410.53	6144.33
SE	0.21	0.39	0.21	0.07	92.25	143.25
CV	0.36	0.20	0.36	0.19	0.13	0.08
N	12	12	12	12	12	12
CEDARVILLE	2.14	8.57	2.14	1.43	2273.60	6197.60
SE	0.26	0.86	0.26	0.05	165.77	223.03
CV	0.32	0.26	0.32	0.10	0.19	0.09
N	7	7	7	7	7	7
JARBIDGE	2.25	7.33	2.25	1.25	2695.70	6139.33
SE	0.21	0.56	0.21	0.08	68.21	139.09
CV	0.33	0.26	0.33	0.23	0.08	0.07
N	12	12	12	12	11	12
MAGIC MTN.	1.66	6.00	1.66	1.34	2368.80	5884.53
SE	0.33	0.00	0.33	0.07	173.49	432.08
CV	0.34	0.00	0.34	0.10	0.12	0.12
N	3	3	3	3	3	3
ALLRED FLATS	2.00	6.50	2.00	1.29	2044.00	6032.00
SE	0.00	0.50	0.00	0.12	207.20	261.60
CV	0.00	0.10	0.00	0.13	0.14	0.06
N	2	2	2	2	2	2
POCATELLO	2.25	8.25	2.00	1.40	2161.40	6373.80
SE	0.25	0.47	0.40	0.14	230.94	234.84
CV	0.22	0.11	0.40	0.20	0.21	0.07
N	4	4	4	4	4	4
MT. HOOD	2.22	7.38	2.22	1.31	2423.76	6306.50
SE	0.12	0.30	0.15	0.05	103.29	136.98
CV	0.24	0.17	0.29	0.17	0.17	0.08

N	18	18-	18	17	17	16
PACKWOOD	2.13	6.59	2.09	1.22	2466.36	5771.32
SE	0.13	0.33	0.14	0.04	62.17	173.93
CV	0.29	0.24	0.32	0.16	0.11	0.13
N	22	22	22	21	21	20
FORT KLAMATH	1.66	6.33	1.33	1.22	2529.33	6344.53
SE	0.33	0.66	0.33	0.13	94.23	192.57
CV	0.34	0.18	0.43	0.18	0.06	0.05
N	3	3	3	3	3	3
SEARS CREEK	1.86	6.50	1.86	1.27	2355.31	5569.80
SE	0.16	0.44	0.16	0.05	62.43	161.53
CV	0.34	0.25	0.34	0.15	0.09	0.10
N	15	14	15	13	14	12
LOOMIS	1.60	6.00	1.60	1.20	2103.00	5919.40
SE	0.24	0.63	0.24	0.13	118.47	430.35
CV	0.34	0.23	0.34	0.25	0.11	0.14
N	5	5	5	5	4	4
BALFOUR	2.00	6.00	2.00	1.24	2518.40	6201.60
SE						
CV						
N	1	1	1	1	1	1
KANANASKIS	1.66	7.00	1.66	1.38	2101.06	5193.06
SE	0.33	0.57	0.33	0.09	243.66	135.64
CV	0.34	0.14	0.34	0.12	0.20	0.04
N	3	3	3	3	3	3
MCBRIDE	2.25	7.50	2.25	1.32	2597.00	5331.73
SE	0.25	0.28	0.25	0.03	99.20	348.20
CV	0.22	0.07	0.22	0.04	0.07	0.11
N	4	4	4	4	4	3
HINTON	2.00	8.00	2.00	1.50	2467.20	5044.80
SE						
CV						
N	1	1	1	1	1	1
LIARD RIVER	1.67	7.00	1.66	1.31	2542.93	5758.40
SE	0.33	0.00	0.33	0.07	119.02	390.14
CV	0.34	0.00	0.34	0.01	0.08	0.11
N	3	3	3	3	3	3

* - seconds.

** - Hz.

Elementary Statistics for Part I Song Variables: *O. tolmiei* Localities

LOCALITY	NNA	NNB	NNC	IMA*	IMB*	IMC*

PARADISE VALLEY	4.00	4.00	4.16	0.06	0.05	0.04
SE	0.24	0.24	0.29	0.01	0.00	0.00
CV	0.21	0.21	0.24	0.59	0.57	0.29
N	12	12	12	12	12	9
CEDARVILLE	4.50	4.50	4.50	0.04	0.04	0.05
SE	0.84	0.84	0.84	0.00	0.00	0.02
CV	0.46	0.46	0.46	0.24	0.27	0.87
N	6	6	6	7	7	6
JARBIDGE	4.90	5.10	5.09	0.06	0.05	0.04
SE	0.31	0.34	0.28	0.00	0.00	0.00
CV	0.20	0.21	0.18	0.39	0.32	0.51
N	10	10	11	12	12	11
MAGIC MTN.	5.00	6.00	6.00	0.06	0.07	0.06
SE	1.00	0.00	0.00	0.01	0.00	0.12
CV	0.34	0.00	0.00	0.34	0.14	0.23
N	3	2	2	3	3	2
ALLRED FLATS	6.50	7.00	10.0	0.08	0.03	0.03
SE	0.50	2.00		0.05	0.02	0.01
CV	0.10	0.40		0.91	100.00	0.60
N	2	2	1	2	2	2
POCATELLO	4.00	4.00	4.00	0.06	0.06	0.04
SE	0.70	0.70	0.70	0.00	0.01	0.00
CV	0.35	0.35	0.35	0.29	0.42	0.24
N	4	4	4	4	4	4
MT. HOOD	4.64	4.81	4.81	0.05	0.05	0.05
SE	0.38	0.33	0.36	0.00	0.00	0.00
CV	0.31	0.27	0.30	0.31	0.38	0.29
N	14	16	16	14	16	15
PACKWOOD	4.23	4.33	4.45	0.08	0.07	0.07
SE	0.25	0.24	0.26	0.00	0.00	0.00
CV	0.24	0.25	0.26	0.47	0.37	0.43
N	17	21	20	19	17	17
FORT KLAMATH	4.00	6.00	4.66	0.06	0.06	0.05
SE	1.00	0.57	1.45	0.00	0.00	0.00
CV	0.43	0.16	0.53	0.16	0.08	0.00
N	3	3	3	3	3	2
SEARS CREEK	4.30	4.53	4.58	0.07	0.07	0.05
SE	0.45	0.46	0.51	0.01	0.01	0.00
CV	0.38	0.36	0.38	0.47	0.48	0.31
N	13	13	12	12	10	8
LOOMIS	4.00	3.80	4.00	0.05	0.04	0.07
SE	0.44	0.37	0.44	0.00	0.00	0.00
CV	0.25	0.22	0.25	0.28	0.32	0.20
N	5	5	5	5	5	3
BALFOUR	6.00	6.00	6.00	0.07	0.06	0.09

SE						
CV						
N	1	1	1	1	1	1
KANANASKIS	5.66	5.66	5.66	0.06	0.06	0.06
SE	0.66	0.66	0.66	0.01	0.01	0.01
CV	0.20	0.20	0.20	0.31	0.43	0.32
N	3	3	3	3	3	2
MCBRIDE	2.33	3.66	3.66	0.07	0.07	0.09
SE	1.33	0.66	0.66	0.02	0.03	0.02
CV	0.98	0.31	0.31	0.52	0.60	0.48
N	3	3	3	3	2	3
HINTON	1.00	1.00	1.00	0.15	0.16	0.09
SE						
CV						
N	1	1	1	1	1	1
LIARD RIVER	4.50	4.50	4.50	0.04	0.04	0.10
SE	0.50	0.50	0.50	0.01	0.00	0.00
CV	0.15	0.15	0.15	0.49	0.32	0.06
N	2	2	2	3	3	2

* - seconds.

Elementary Statistics for Part I Song Variables (Cont'd.): *O. tolmiei* Localities

LOCALITY	MIA**	MIB**	MIC**	MAA**	MAB**	MAC**
PARADISE V.	3005.00	2936.86	2945.80	5542.13	5560.86	5631.33
SE	153.44	139.32	146.55	76.70	80.76	107.48
CV	0.17	0.16	0.17	0.04	0.05	0.06
N	12	12	12	12	12	12
CEDARVILLE	2847.88	2884.57	2841.14	5930.53	5978.66	5868.93
SE	164.83	188.97	179.27	226.50	346.63	290.52
CV	0.15	0.17	0.16	0.09	0.14	0.12
N	7	7	7	6	6	6
JARBIDGE	3359.33	3247.05	3303.13	5663.40	5826.42	6031.34
SE	175.13	164.03	159.41	176.56	176.53	187.61
CV	0.18	0.16	0.16	0.09	0.10	0.10
N	7	11	12	10	11	11
MAGIC MTN.	2963.20	2833.60	2795.73	5386.13	5444.53	5448.53
SE	216.28	232.92	133.10	19.13	154.51	139.10
CV	0.12	0.14	0.08	0.00	0.04	0.04
N	3	3	3	3	3	3
ALLRED FLA.	2208.00	2292.00	2304.00	5498.80	5585.60	5614.80

SE	242.40	452.80	459.20	384.40	209.60	197.20
CV	0.15	0.27	0.28	0.09	0.05	0.04
N	2	2	2	2	2	2
POCATELLO	2751.80	2728.20	2813.20	5624.80	5704.20	5824.00
SE	325.66	288.76	252.24	461.66	514.7	514.55
CV	0.23	0.21	0.17	0.16	0.18	0.17
N	4	4	4	4	4	4
MT. HOOD	3371.25	3298.96	3371.05	6280.00	6350.05	6331.75
SE	155.53	133.46	123.38	110.16	107.29	106.58
CV	0.17	0.16	0.15	0.06	0.06	0.06
N	15	17	17	14	16	16
PACKWOOD	3483.37	3471.58	3447.16	5355.42	5526.52	5638.98
SE	162.48	155.58	159.24	407.75	191.60	201.77
CV	0.19	0.20	0.21	0.28	0.15	0.15
N	18	21	21	14	19	19
FORT KLAM.	3555.46	3615.46	3534.13	6087.20	6155.73	6184.00
SE	433.81	405.55	444.77	376.90	193.10	172.41
CV	0.21	0.19	0.21	0.10	0.05	0.04
N	3	3	3	3	3	3
SEARS CREEK	2873.77	2894.85	2883.94	5321.67	5331.13	5337.40
SE	127.71	123.77	129.79	220.43	267.38	282.46
CV	0.16	0.15	0.16	0.13	0.17	0.18
N	14	14	14	11	12	12
LOOMIS	2530.00	2576.00	2408.40	5521.60	5655.00	5776.60
SE	317.26	466.83	364.72	438.61	405.98	389.04
CV	0.25	0.31	0.30	0.15	0.14	0.13
N	4	3	4	4	4	4
BALFOUR	2821.00	2752.00	2593.60	5323.20	5412.00	5348.00
SE						
CV						
N	1	1	1	1	1	1
KANANAS.	2676.26	2752.80	2737.33	5182.66	5081.60	5087.73
SE	502.05	439.62	444.94	203.62	195.44	198.51
CV	0.32	0.27	0.28	0.06	0.06	0.06
N	3	3	3	3	3	3
MCBRIDE	3035.00	2838.93	3090.60	4711.20	4887.80	4863.73
SE	233.40	227.11	270.12	358.00	241.01	153.42
CV	0.15	0.13	0.17	0.13	0.09	0.05
N	4	3	4	3	4	3
HINTON	3712.00	3725.60	3684.80	4964.80	4884.80	4780.00
SE						
CV						
N	1	1	1	1	1	1
LIARD R.	2673.60	2637.33	2590.66	5664.26	5681.33	5718.66
SE	137.20	125.23	144.03	329.19	352.75	438.92
CV	0.08	0.08	0.09	0.10	0.10	0.13
N	3	3	3	3	3	3

 ** - Hz.

 Elementary Statistics for Part II Song Variables: *O. tolmiei* Localities

LOCALITY	NFA	NFB	IFA*	IFB*	MIFA**	MIFB**	MAFA**	MAFB**
PARADISE VALLEY	6.77	4.60	0.04	0.03	2375.11	2263.73	5968.88	5780.13
SE	0.89	0.67	0.00	0.00	84.96	97.80	212.48	262.69
CV	0.39	0.32	0.23	0.20	0.10	0.10	0.10	0.11
N	9	5	6	2	9	6	9	6
CEDARVILLE	4.66	2.50	0.03	0.04	2926.00	2691.73	5256.00	5567.00
SE	1.17	0.64	0.00	0.01	406.86	441.40	464.76	591.03
CV	0.61	0.52	0.47	0.44	0.34	0.40	0.21	0.21
N	6	4	4	3	6	6	6	4
JARBIDGE	4.81	5.20	0.04	0.06	2965.16	2937.86	6076.87	6073.12
SE	0.35	0.24	0.00	0.03	150.59	121.43	115.82	136.05
CV	0.24	0.15	0.52	1.00	0.16	0.12	0.06	0.07
N	11	10	10	7	11	9	11	10
MAGIC MTN.	5.00	5.00	0.04	2466.00	2331.60	5666.80	5534.80	
SE	2.00	2.00	0.00	114.00	250.00	998.00	1102.00	
CV	0.56	0.56	0.00		0.06	0.15	0.24	0.28
N	2	2	2		2	2	2	2
ALLRED FLATS	4.50	4.50	0.02	0.03	2225.20	2313.60	5776.80	5750.40
SE	1.50	1.50	0.01	51.60	54.40	425.60	600.00	
CV	0.47	0.47	0.84	0.03	0.03	0.10	0.14	
N	2	2	2	1	2	2	2	2
POCATELLO	3.66	3.00	0.06	0.06	2229.33	2352.00	4717.06	4554.00
SE	0.88	1.00	0.00		274.99	363.20	463.62	611.60
CV	0.41	0.47	0.00	0.21	0.21	0.17	0.18	
N	3	2	2	1	3	2	3	2
MT. HOOD	3.94	4.05	0.04	0.04	2603.51	2601.12	5498.35	5652.00
SE	0.34	0.30	0.00	0.00	149.42	141.85	213.05	145.03
CV	0.36	0.30	0.35	0.35	0.24	0.22	0.16	0.10
N	17	17	14	8	18	17	18	17
PACKWOOD	4.42	4.26	0.06	0.05	2701.24	2565.28	5306.75	5162.44
SE	0.22	0.25	0.00	0.00	100.85	98.03	157.63	169.03
CV	0.21	0.25	0.37	0.39	0.15	0.16	0.12	0.13
N	19	19	19	11	18	18	18	18
FORT KLAMATH	4.50	4.50	0.04	0.04	2394.40	2496.40	5432.00	5409.60
SE	0.50	0.50	0.00		0.00	121.20	161.60	184.00
CV	0.15	0.15	0.15		0.15	0.06	0.04	0.04
N	2	2	2	1	2	2	2	2
SEARS CREEK	4.10	3.88	0.06	0.05	2569.77	2676.20	5051.12	4773.24
SE	0.34	0.35	0.01	0.00	215.58	243.61	131.26	140.05
CV	0.26	0.27	0.56	0.35	0.25	0.25	0.08	0.08
N	10	9	10	6	9	8	10	9
LOOMIS	3.00	3.00		0.05	2602.66	2607.20	5522.40	5546.40
SE	0.57	0.57		0.00	198.82	186.26	380.61	378.70
CV	0.33	0.33		0.28	0.13	0.12	0.11	0.11
N	3	3		3	3	3	3	3
BALFOUR	4.00	4.00		0.08	2755.20	2838.40	6214.40	6177.60
SE								
CV								

N	1	1	1	1	1	1	1	
KANANASKIS	2.50	2.00	0.04	0.05	2348.80	2496.80	4340.80	4459.20
SE	0.50			206.40		25.60		
CV	0.28			0.12	0.00			
N	2	1	1	1	2	1	2	1
MCBRIDE	3.25	2.75	0.08		2809.60	2852.20	5076.40	4764.40
SE	0.94	0.75	0.02		89.45	153.81	341.15	459.48
CV	0.58	0.54	0.54	0.06	0.10	0.13	0.19	
N	4	4	3	4	4	4	4	
HINTON	2.00	2.00	0.09	0.09	2559.20	2514.40	4348.80	4321.60
SE								
CV								
N	1	1	1	1	1	1	1	1
LIARD RIVER	2.50	2.50	0.08		2797.60	2967.60	5478.40	5374.00
SE	1.50	1.50	0.00		23.20	28.40	1329.60	1221.20
CV	0.84	0.84	0.00		0.01	0.01	0.34	0.34

* - seconds.

** - Hz

APPENDIX I
EXTREME *Oporornis philadelphia* SPECIMENS WITH
O. tolmiei* - like CHARACTERS and EXTREME *O. tolmiei
SPECIMENS WITH *O. philadelphia* CHARACTERS.

***Oporornis philadelphia* SPECIMENS WITH EYE-ARCS**

JP777, New York: CHAZY (Sex - female), W-T = 11.4mm
 JP797, New York: CHAZY (Sex - female), W-T = no data
 JP799, New York: CHAZY (Sex - female), W-T = no data
 JP76, Quebec: LEBEL-SUR-QUEVILLION (Sex - male), W-T = 11.0mm
 JP109, Ontario: COCHRANE (Sex - male), W-T = 12.0mm
 JP110, Ontario: COCHRANE (Sex - male), W-T = 11.0mm
 JP112, Ontario: COCHRANE (Sex - male), W-T = 14.0mm, Song type - MO1
 JP146, Ontario: GERALDTON (Sex - male), W-T = 13.0mm
 JP157, Ontario: GERALDTON (Sex - male), W-T = 13.0mm
 JP165, Ontario: MINITAKI (Sex - male), W-T = 12.0mm
 JP170, Ontario: MINITAKI (Sex - male), W-T = 13.0mm, Song type - MO6
 JP188, Ontario: DORION (Sex - male), W-T = 15.0mm
 JP189, Ontario: DORION (Sex - male), W-T = 14.0mm, Song type - MO5
 JP196, Ontario: DORION (Sex - male), W-T = 14.0mm, Song type - MO6
 JP634, Alberta: SLAVE LAKE (Sex - male), W-T = 10.44mm
 JP689, Alberta: WHITECOURT (Sex - male), W-T = 12.76mm
 JP709, Alberta: LODGEPOLE (Sex - female), W-T = 12.63mm
 JP677, British Columbia: KLEDO CREEK (Sex - female), W-T = 12.82mm

***Oporornis philadelphia* MALE SPECIMENS WITH DARK LORES**

JP714, Alberta: BATTLE LAKE, Lores-weak, W-T = 8.60mm

JP708, Alberta: LODGEPOLE, Lores-strong, W-T = 13.67mm
 JP695, Alberta: OBED, Lores-strong, W-T = 7.52mm, Song type - MO6
 JP693, Alberta: OBED, Lores-weak, W-T = 11.57mm
 JP643, Alberta: SLAVE LAKE, Lores-strong, W-T = 10.13mm
 JP650, Alberta: SLAVE LAKE, Lores-strong, W-T = 13.58mm
 JP641, Alberta: SLAVE LAKE, Lores-strong, W-T = 12.98mm
 JP638, Alberta: SLAVE LAKE, Lores-strong, W-T = 10.68mm
 JP649, Alberta: SLAVE LAKE, Lores-strong, W-T = 9.54mm
 JP648, Alberta: SLAVE LAKE, Lores-strong, W-T = 9.59mm
 JP639, Alberta: SLAVE LAKE, Lores-weak, W-T = 13.36mm, Song type - MO6
 JP642, Alberta: SLAVE LAKE, Lores-weak, W-T = 8.48mm
 JP635, Alberta: SLAVE LAKE, Lores-weak, W-T = 8.54mm, Song type - MO9
 JP637, Alberta: SLAVE LAKE, Lores-weak, W-T = 12.36mm
 JP645, Alberta: SLAVE LAKE, Lores-weak, W-T = 10.93mm
 JP636, Alberta: SLAVE LAKE, Lores-weak, W-T = 9.92mm, Song type - MO6
 JP640, Alberta: SLAVE LAKE, Lores-weak, W-T = 10.35mm
 JP646, Alberta: SLAVE LAKE, Lores-weak, W-T = 8.63mm
 JP688, Alberta: WHITECOURT, Lores-strong, W-T = 9.77mm, Song type - MO6
 JP687, Alberta: WHITECOURT, Lores-weak, W-T = 9.20mm
 JP690, Alberta: WHITECOURT, Lores-weak, W-T = 8.64mm
 JP691, Alberta: WHITECOURT, Lores-weak, W-T = 9.79mm
 JP689, Alberta: WHITECOURT, Lores-weak, W-T = 12.76mm
 JP683, British Columbia: FORT NELSON, Lores-strong, W-T = 11.54mm
 JP686, British Columbia: FORT NELSON, Lores-strong, W-T = no data
 JP684, British Columbia: FORT NELSON, Lores-strong, W-T = 8.44mm

JP682, British Columbia: FORT NELSON, Lores-strong, W-T = 9.90mm

JP679, British Columbia: FORT NELSON, Lores-strong, W-T = 10.46mm

JP680, British Columbia: FORT NELSON, Lores-strong, W-T = 10.77mm

JP681, British Columbia: FORT NELSON, Lores-weak, W-T = 10.91mm

JP131, Ontario: CALSTOCK-HEARST, Lores-weak, W-T = 14.00mm, Song type - MO1

JP128, Ontario: CALSTOCK-HEARST, Lores-weak, W-T = 13.00mm, Song type - MO1

JP133, Ontario: CALSTOCK-HEARST, Lores-weak, W-T = no data, Song type - MO1

JP126, Ontario: CALSTOCK-HEARST, Lores-weak, W-T = 12.00mm

JP115, Ontario: COCHRANE, Lores-strong, W-T = no data

JP116, Ontario: COCHRANE, Lores-strong, W-T = 12.00mm

JP124, Ontario: COCHRANE, Lores-weak, W-T = 14.00mm, Song type - MO1

JP192, Ontario: DORION, Lores-weak, W-T = 13.00mm

JP177, Ontario: DORION, Lores-weak, W-T = 11.00mm, Song type - MO1

JP181, Ontario: DORION, Lores-weak, W-T = 12.00mm, Song type - MO6

JP182, Ontario: DORION, Lores-weak, W-T = 9.00mm

JP199, Ontario: DORION, Lores-weak, W-T = 13.00mm, Song type - MO5

JP197, Ontario: DORION, Lores-weak, W-T = 10.00mm, Song type - MO6

JP195, Ontario: DORION, Lores-weak, W-T = 13.00mm, Song type - MO6

JP185, Ontario: DORION, Lores-weak, W-T = 11.00mm, Song type - MO6

JP178, Ontario: DORION, Lores-weak, W-T = 15.00mm

JP148, Ontario: GERDTON, Lores-weak, W-T = 13.00mm

JP147, Ontario: GERDTON, Lores-weak, W-T = 13.00mm

JP171, Ontario: MINITAKI, Lores-strong, W-T = 11.00mm
 JP167, Ontario: MINITAKI, Lores-strong, W-T = 12.00mm
 JP176, Ontario: MINITAKI, Lores-weak, W-T = 12.00mm, Song type - MO6
 JP63, Quebec: DESMARAISVILLE, Lores-strong, W-T = no data
 JP72, Quebec: LEBEL-SUR-QUEVILLION, Lores-strong, W-T = 11.00mm
 JP88, Quebec: LEBEL-SUR-QUEVILLION, Lores-strong, W-T = 12.00mm,
 Song type - MO1
 JP82, Quebec: LEBEL-SUR-QUEVILLION, Lores-strong, W-T = 13.00mm
 JP74, Quebec: LEBEL-SUR-QUEVILLION, Lores-strong, W-T = 13.00mm
 JP70, Quebec: LEBEL-SUR-QUEVILLION, Lores-strong, W-T = no data
 JP66, Quebec: LEBEL-SUR-QUEVILLION, Lores-weak, W-T = 15.00mm
 JP69, Quebec: LEBEL-SUR-QUEVILLION, Lores-weak, W-T = 11.00mm
 JP67, Quebec: LEBEL-SUR-QUEVILLION, Lores-weak, W-T = 14.00mm
 JP81, Quebec: LEBEL-SUR-QUEVILLION, Lores-weak, W-T = 10.00mm, Song
 type - MO1
 JP68, Quebec: LEBEL-SUR-QUEVILLION, Lores-weak, W-T = 14.00mm
 JP37, Quebec: ST. PAULE, Lores-weak, W-T = 16.00mm
 JP36, Quebec: ST. PAULE, Lores-weak, W-T = 14.00mm
 JP35, Quebec: ST. PAULE, Lores-weak, W-T = 11.00mm
 JP91, Quebec: VAL PARADIS, Lores-strong, W-T = 11.00mm, Song type - MO1
 JP89, Quebec: VAL PARADIS, Lores-weak, W-T = 12.00mm
 JP92, Quebec: VAL PARADIS, Lores-weak, W-T = 13.00mm
 JP103, Quebec: VAL PARADIS, Lores-weak, W-T = 11.00mm
 JP1, Maine: CASTLE HILL, Lores-weak, W-T = 11.00mm
 JP19, Maine: ST. FRANCIS, Lores-weak, W-T = 10.00mm

JP778, New York: CHAZY, Lores-strong, W-T = 8.60mm

JP779, New York: CHAZY, Lores-strong, W-T = 11.20mm

JP781, New York: CHAZY, Lores-strong, W-T = 9.50mm

JP793, New York: CHAZY, Lores-strong, W-T = 10.40mm

JP795, New York: CHAZY, Lores-strong, W-T = 12.40mm

JP796, New York: CHAZY, Lores-strong, W-T = 9.10mm

JP798, New York: CHAZY, Lores-strong, W-T = 11.80mm

JP782, New York: CHAZY, Lores-weak, W-T = 8.60mm

JP794, New York: CHAZY, Lores-weak, W-T = 10.30mm

***Oporornis philadelphia* SPECIMENS WITH W-T < 11.00mm
(all males)**

JP3, Maine: ST. FRANCIS, W-T = 9.00mm, Song type - MO 1

JP16, Maine: ST. FRANCIS, W-T = 9.00mm

JP19, Maine: ST. FRANCIS, W-T = 10.00mm

JP25, Maine: ST. FRANCIS, W-T = 9.00mm

JP44, Quebec: GIRARDVILLE, W-T = 9.00mm

JP49, Quebec: GIRARDVILLE, W-T = 10.00mm

JP81, Quebec: LEBEL-SUR-QUEVILLION, W-T = 10.00mm, Song type - MO1

JP118, Ontario: COCHRANE, W-T = 8.00mm, Song type - MO1

JP120, Ontario: COCHRANE, W-T = 10.00mm

JP130, Ontario: COCHRANE, W-T = 10.00mm

JP137, Ontario: CALSTOCK-HEARST, W-T = 10.00mm, Song type - MO1

JP156, Ontario: GERALDTON, W-T = 10.00mm, Song type - MO1

JP162, Ontario: MINITAKI, W-T = 9.00mm, Song type - MO 5

JP182, Ontario: DORION, W-T = 9.00mm

JP183, Ontario: DORION, W-T = 10.00mm, Song type - MO1
JP184, Ontario: DORION, W-T = 10.00mm, Song type - MO1
JP197, Ontario: DORION, W-T = 10.00mm, Song type - MO6
JP200, Ontario: DORION, W-T = 10.00mm
JP631, Alberta: SLAVE LAKE, W-T = 8.77mm
JP632, Alberta: SLAVE LAKE, W-T = 10.54mm, Song type - MO88
JP633, Alberta: SLAVE LAKE, W-T = 10.61mm, Song type - MO13
JP634, Alberta: SLAVE LAKE, W-T = 10.44mm, Song type - MO6
JP635, Alberta: SLAVE LAKE, W-T = 8.54mm, Song type - MO9
JP636, Alberta: SLAVE LAKE, W-T = 9.92mm, Song type - MO6
JP638, Alberta: SLAVE LAKE, W-T = 10.68mm
JP640, Alberta: SLAVE LAKE, W-T = 10.35mm
JP642, Alberta: SLAVE LAKE, W-T = 8.48mm
JP643, Alberta: SLAVE LAKE, W-T = 10.13mm
JP645, Alberta: SLAVE LAKE, W-T = 10.93mm
JP646, Alberta: SLAVE LAKE, W-T = 8.63mm
JP647, Alberta: SLAVE LAKE, W-T = 10.51mm
JP648, Alberta: SLAVE LAKE, W-T = 9.59mm
JP649, Alberta: SLAVE LAKE, W-T = 9.54mm
JP679, British Columbia: FORT NELSON, W-T = 10.46mm
JP680, British Columbia: FORT NELSON, W-T = 10.77mm
JP681, British Columbia: FORT NELSON, W-T = 10.91mm
JP682, British Columbia: FORT NELSON, W-T = 9.90mm
JP684, British Columbia: FORT NELSON, W-T = 8.44mm
JP685, British Columbia: FORT NELSON, W-T = 10.39mm

JP687, Alberta: WHITECOURT, W-T = 9.20mm

JP688, Alberta: WHITECOURT, W-T = 9.77mm, Song type - MO6

JP690, Alberta: WHITECOURT, W-T = 8.64mm

JP691, Alberta: WHITECOURT, W-T = 9.79mm

JP714, Alberta: BATTLE LAKE, W-T = 8.60mm

JP778, New York: CHAZY, W-T = 8.60mm

JP781, New York: CHAZY, W-T = 9.50mm

JP782, New York: CHAZY, W-T = 8.60mm

JP792, New York: CHAZY, W-T = 10.50mm

JP793, New York: CHAZY, W-T = 10.40mm

JP794, New York: CHAZY, W-T = 10.30mm

JP796, New York: CHAZY, W-T = 9.10mm

***Oporornis tolmiei* SPECIMENS WITH W-T > 10.00mm
(males and females)**

JP462, British Columbia: BALFOUR (Sex - female), W-T = 11.00mm

JP464, British Columbia: BALFOUR, (Sex - male), W-T = 11.00mm

JP702, British Columbia: KANANASKIS (Sex - male), W-T = 15.35mm

JP673, British Columbia: LIARD RIVER (Sex - male), W-T = 10.12mm

JP432, Washington: LOOMIS (Sex - male), W-T = 11.00mm

JP375, Oregon: MT. HOOD (Sex - male), W-T = 12.00mm

APPENDIX J
Geographic Distribution of MO Syllables and Syllable Variants

MO1

Maine: ST. FRANCIS; Quebec: ST. PAULE, GIRARDVILLE, LEBEL-SUR-QUEVILLION, DESMARAISVILLE, VAL PARADIS; Ontario: COCHRANE, CALSTOCK-HEARST, GERALDTON, MINITAKI; Alberta: SLAVE LAKE, WHITECOURT

MO1A

Maine: ST. FRANCIS; Quebec: ST. PAULE, LEBEL-SUR-QUEVILLION, GIRARDVILLE, VAL PARADIS; Ontario: COCHRANE, CALSTOCK-HEARST, GERALDTON; Alberta: SLAVE LAKE

MO1B

Maine: ST. FRANCIS; Quebec: LEBEL-SUR-QUEVILLION; Ontario: COCHRANE, CLASTOCK-HEARST

MO1D

Quebec: GIRARDVILLE, LEBEL-SUR-QUEVILLION; Ontario: COCHRANE

MO1E

Quebec: ST. PAULE, VAL PARADIS

MO1F

Maine: ST. FRANCIS

MO5

Ontario: MINITAKI

MO6

Ontario: MINITAKI; Alberta: SLAVE LAKE, WHITECOURT, OBED, LODGEPOLE,
BATTLE LAKE; British Columbia: STEAMBOAT, FORT NELSON

MO6A

Ontario: MINITAKI; Alberta: SLAVE LAKE, WHITECOURT, OBED; British
Columbia: STEAMBOAT, FORT NELSON

MO6B

Alberta: SLAVE LAKE, BATTLE LAKE; British Columbia: STEAMBOAT, FORT
NELSON

MO6C

SLAVE LAKE

MO6D

Alberta: WHITECOURT, OBED, LODGEPOLE; British Columbia: FORT
NELSON

MO8

Alberta: SLAVE LAKE, WHITECOURT, EDSON

MO9

Alberta: SLAVE LAKE, LODGEPOLE

MO10

Alberta: SLAVE LAKE

MO14

Alberta: LODGEPOLE

MO16

Ontario: MINITAKI; Alberta: SLAVE LAKE, WHITECOURT, OBED, LODGEPOLE

MO16A

Alberta: SLAVE LAKE

MO16B

Alberta: WHITECOURT, OBED, LODGEPOLE

MO16C

Alberta: SLAVE LAKE

MO17

Alberta: SLAVE LAKE

MO18C

Newfoundland: ST. ANTHONY, PORT SAUNDERS, CAPE BONAVISTA,
STEPHENVILLE

MO19

Newfoundland: ST. ANTHONY, PORT SAUNDERS

MO19B

Newfoundland: PORT SAUNDERS, RODDICKTON

MO19C

Newfoundland: ST. ANTHONY, PORT SAUNDERS

MO60

Maine: ST. FRANCIS; Alberta: SLAVE LAKE

MO86

Alberta: SLAVE LAKE, OBED; British Columbia: FORT NELSON

MO89

Alberta: SLAVE LAKE

MO90, 90A, B

Ontario: MINITAKI

MO91, 91A, C, D

Ontario: MINITAKI

MO94

Maine: ST. FRANCIS; Quebec: LEBEL-SUR-QUEVILLION, VAL PARADIS;
Ontario: COCHRANE

MO99

Maine: ST. FRANCIS; Quebec: GIRARDVILLE, LEBEL-SUR-QUEVILLION, ST.
PAULE, DESMARSAISVILLE, VAL PARADIS; Ontario: COCHRANE,
CALSTOCK-HEARST, GERALDTON, MINITAKI

MO99A

Quebec: ST. PAULE, GIRARDVILLE, VAL PARADIS; Ontario: COCHRANE,
CALSTOCK-HEARST, GERALDTON, MINITAKI

MO99C

Maine: ST. FRANCIS; Quebec: LEBEL-SUR-QUEVILLION, GIRARDVILLE,
ST. PAULE, VAL PARADIS; Ontario: COCHRANE, GERALDTON

MO99F

Maine: ST. FRANCIS; Quebec: ST. PAULE, VAL PARADIS

MO99G

Maine: ST. FRANCIS; Quebec: GIRARDVILLE

MO99H

Quebec: ST. PAULE, LEBEL-SUR-QUEVILLION, GIRARDVILLE,
DESMARAISVILLE

MO99I

Quebec: LEBEL-SUR-QUEVILLION; Ontario: COCHRANE, CALSTOCK-
HEARST

MO99Z

Ontario: COCHRANE

APPENDIX K
Geographic Distribution of MA Syllables and Syllable Variants

MA1

Washington: SEARS CREEK, PACKWOOD, Oregon: , FORT KLAMATH, MT. HOOD, California: CEDARVILLE, Alberta: KANANASKIS, Idaho: TWIN FALLS, POCATELLO, Nevada: JARBIDGE, PARADISE VALLEY, Wyoming: ALLRED FLATS

MA1A

Washington: SEARS CREEK, PACKWOOD, Oregon: MT. HOOD, California: CEDARVILLE, Idaho: TWIN FALLS, Nevada: JARBIDGE

MA1B

Nevada: PARADISE VALLEY

MA1D

California: CEDARVILLE, Wyoming: ALLRED FLATS

MA2

British Columbia: MCBRIDE, BALFOUR, Washington: CONCONULLY, California: CEDARVILLE, Idaho: TWIN FALLS, POCATELLO, Nevada: PARADISE VALLEY, Wyoming: ALLRED FLATS

MA2A

Washington: CONCONULLY, Idaho: POCATELLO

MA2B

Idaho: POCATELLO

MA2C

California: CEDARVILLE, Wyoming: ALLRED FLATS

MA2D

Washington: CONCONULLY

MA2E

British Columbia: BALFOUR

MA2F

California: CEDARVILLE

MA2G

British Columbia: MCBRIDE

MA2H

Nevada: PARADISE VALLEY

MA2I

Idaho: TWIN FALLS

MA2J

Idaho: POCATELLO

MA4

Idaho: TWIN FALLS, Nevada: JARBIDGE

MA5

Nevada: JARBIDGE

MA6

British Columbia: MCBRIDE, Washington: CONCONULLY, SEARS CREEK,
PACKWOOD, Oregon: FORT KLAMATH, Alberta: HINTON, Idaho:
POCATELLO, Nevada: JARBIDGE

MA6A

Nevada: JARBIDGE

MA6B

British Columbia: MCBRIDE, Washington: PACKWOOD, Idaho: POCATELLO

MA6C

British Columbia: MCBRIDE, Washington: CONCONULLY, Oregon: FORT
KLAMATH

MA6D

Washington: CONCONULLY

MA6G

Washington: PACKWOOD

MA7

California: CEDARVILLE, Nevada: PARADISE VALLEY

MA8

Idaho: TWIN FALLS, POCATELLO

MA8A

Alberta: KANANASKIS, Idaho: TWIN FALLS

MA8B

Nevada: PARADISE VALLEY

MA8C

Washington: PACKWOOD

MA8D

Washington: PACKWOOD

MA8E

Washington: PACKWOOD

MA8Z

Idaho: TWIN FALLS, Nevada: PARADISE VALLEY

MA10

Nevada: PARADISE VALLEY

MA11

Nevada: PARADISE VALLEY

MA12

Washington: CONCONULLY, PACKWOOD, Oregon: MT. HOOD, Nevada:
PARADISE VALLEY

MA14

Nevada: PARADISE VALLEY

MA15

Nevada: PARADISE VALLEY

MA17

Alberta: CYPRESS HILLS, Idaho: POCA TELLO

MA18

Idaho: TWIN FALLS

MA19

California: CEDARVILLE

MA20

California: CEDARVILLE

MA21

California: CEDARVILLE, Nevada: PARADISE VALLEY

MA22

California: CEDARVILLE

MA23

British Columbia: MCBRIDE, Oregon: MT. HOOD, Alberta: KANANASKIS,

California: CEDARVILLE

MA223A

California: CEDARVILLE, Alberta: KANANASKIS

MA26

Alberta: KANANASKIS, CYPRESS HILLS

MA27

British Columbia: MCBRIDE

MA28

British Columbia: MCBRIDE, Washington: SEARS CREEK

MA29

British Columbia: MCBRIDE

MA31

British Columbia: MCBRIDE, Oregon: MT. HOOD, FORT KLAMATH

MA32

British Columbia: LIARD RIVER

MA33

British Columbia: LIARD RIVER, Washington: CONCONULLY

MA34

Alberta: HINTON

MA35

Washington: PACKWOOD, Oregon: FORT KLAMATH

MA35A

Washington: PACKWOOD

MA36

Oregon: MT. HOOD

MA37

Oregon: MT. HOOD

MA38

Washington: SEARS CREEK, PACKWOOD, Oregon: MT. HOOD

MA39

Oregon: MT. HOOD

MA42

Washington: PACKWOOD

MA44

Washington: SEARS CREEK, PACKWOOD

MA44A

Washington: SEARS CREEK

MA45

Washington: PACKWOOD

MA46

Washington: SEARS CREEK

MA47

Washington: CONCONULLY, SEARS CREEK

MA48

Washington: SEARS CREEK

MA50

Washington: CONCONULLY

MA57

Washington: CONCONULLY

MA58

Washington: SEARS CREEK

MA59

Washington: SEARS CREEK

MA60

Washington: PACKWOOD

MA61

Washington: PACKWOOD

MA61A

Washington: PACKWOOD

MA63

Washington: PACKWOOD, Oregon: MT. HOOD

MA63A

Washington: PACKWOOD

MA65

Oregon: MT. HOOD

MA67

Oregon: MT. HOOD

MA68

Washington: SEARS CREEK, PACKWOOD, Oregon: MT. HOOD, FORT
KLAMATH, Idaho: TWIN FALLS

MA68A

Washington: SEARS CREEK, Oregon: MT. HOOD

MA68B

Washington: SEARS CREEK

MA68C

Washington: PACKWOOD

MA68D

Washington: PACKWOOD, Oregon: MT. HOOD

MA68Q

Washington: SEARS CREEK, Oregon: MT. HOOD

MA68T

Oregon: MT. HOOD

MA68U

Washington: PACKWOOD, Oregon: MT. HOOD

MA68Y

Oregon: MT. HOOD

MA68Z

Oregon: MT. HOOD

MA69

British Columbia: LIARD RIVER, Oregon: MT. HOOD

MA69A

Oregon: MT. HOOD

MA70

British Columbia: MCBRIDE

MA71

British Columbia: MCBRIDE, Washington: SEARS CREEK, PACKWOOD,
Oregon: MT. HOOD

MA71A

Washington: SEARS CREEK

MA71B

Washington: SEARS CREEK

MA71D

Oregon: MT. HOOD

MA71Z

Washington: SEARS CREEK

MA73

Washington: SEARS CREEK, PACKWOOD, Oregon: MT. HOOD, Alberta:
CYPRESS HILLS,

MA73A

Oregon: MT. HOOD

MA73Z

British Columbia: LIARD RIVER, Nevada: JARBIDGE

MA74

Alberta: KANANASKIS

MA77

California: CEDARVILLE

MA80

Idaho: TWIN FALLS

MA81

Idaho: TWIN FALLS

MA85

Idaho: POCA TELLO

MA87

Nevada: PARADISE VALLEY

MA88

British Columbia: BALFOUR, Washington: CONCONULLY, SEARS CREEK,
California: CEDARVILLE, Nevada: PARADISE VALLEY

MA88A

California: CEDARVILLE, Nevada: PARADISE VALLEY

MA89

Nevada: PARADISE VALLEY

MA91

Nevada: PARADISE VALLEY

MA91A

Nevada: PARADISE VALLEY

MA92

Washington: PACKWOOD, Nevada: PARADISE VALLEY, JARBIDGE

MA92A

Washington: PACKWOOD

MA94

Nevada: JARBIDGE

MA95

Nevada: JARBIDGE

MA95A

Nevada: JARBIDGE

MA96

Nevada: JARBIDGE

MA97

Nevada: JARBIDGE

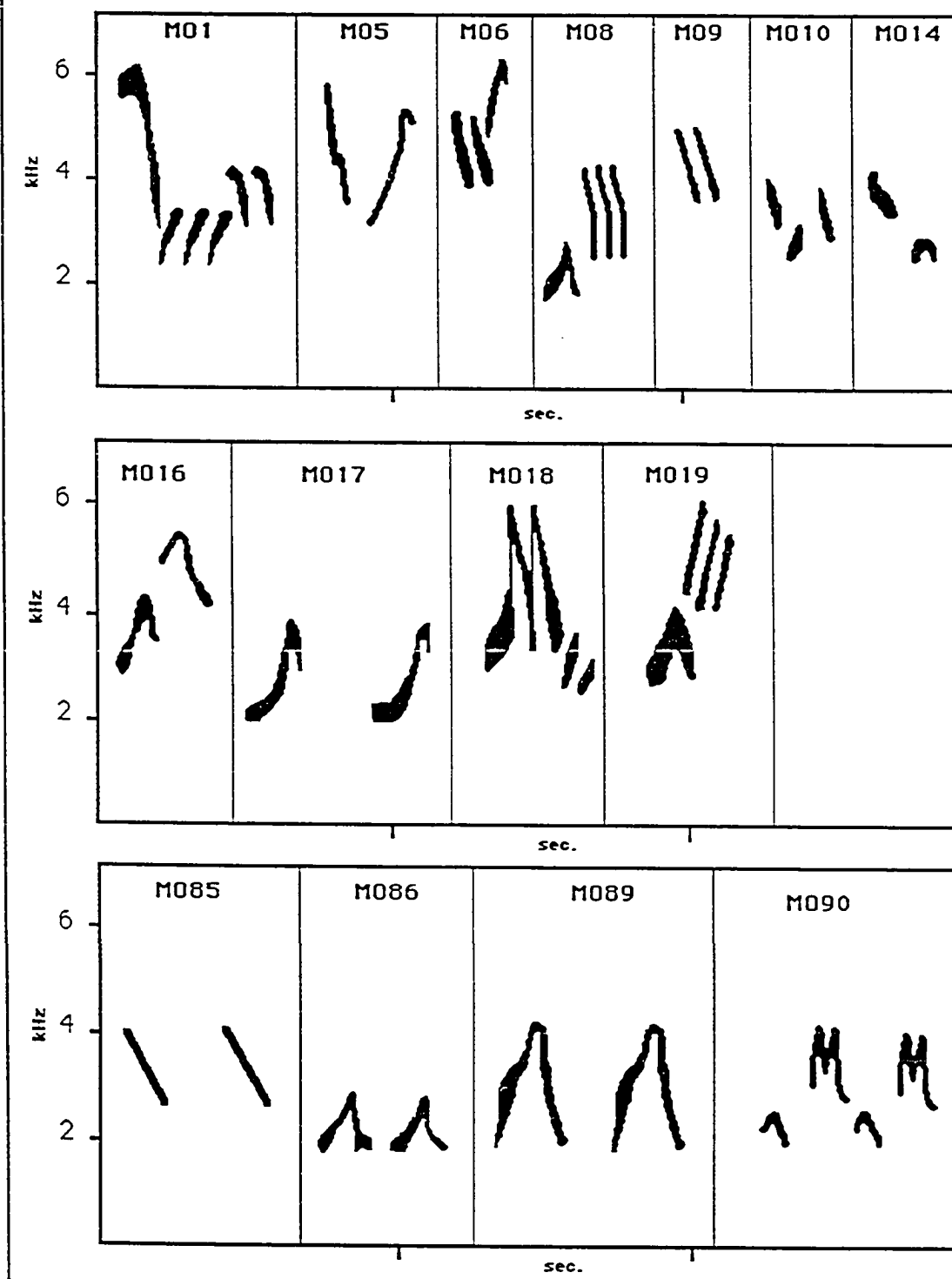
MA98

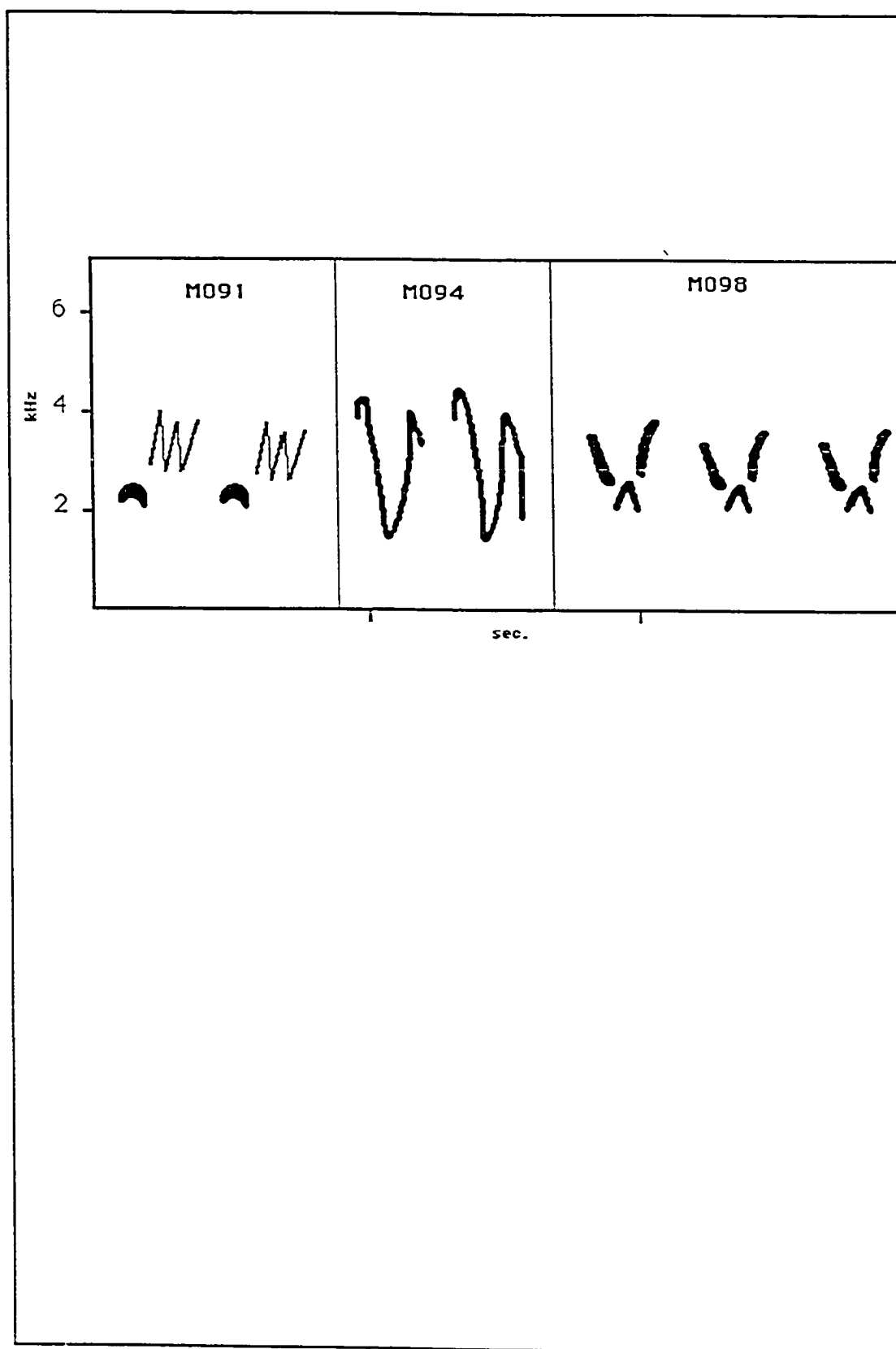
Idaho: POCA TELLO, Wyoming: ALLRED FLATS

PA98A

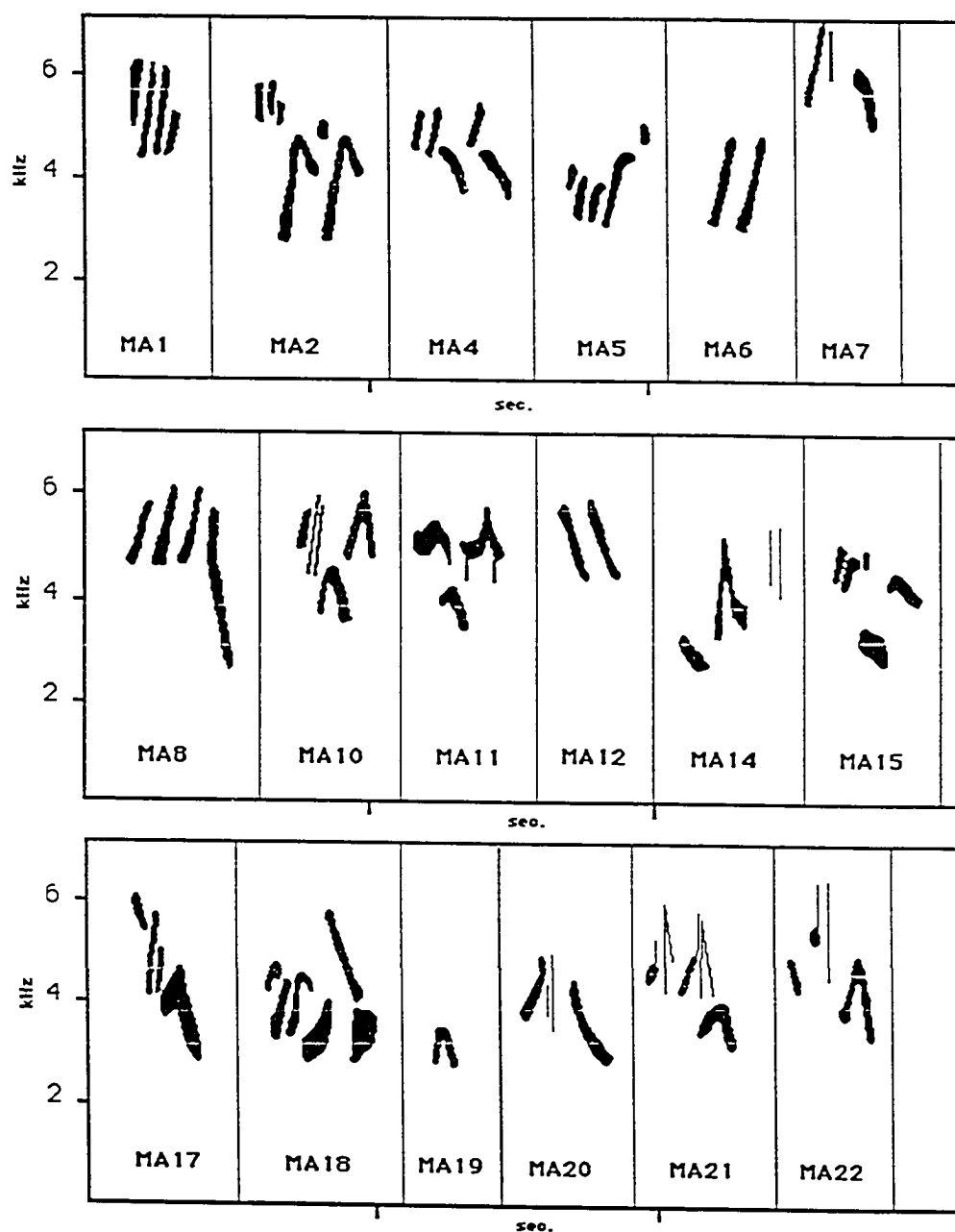
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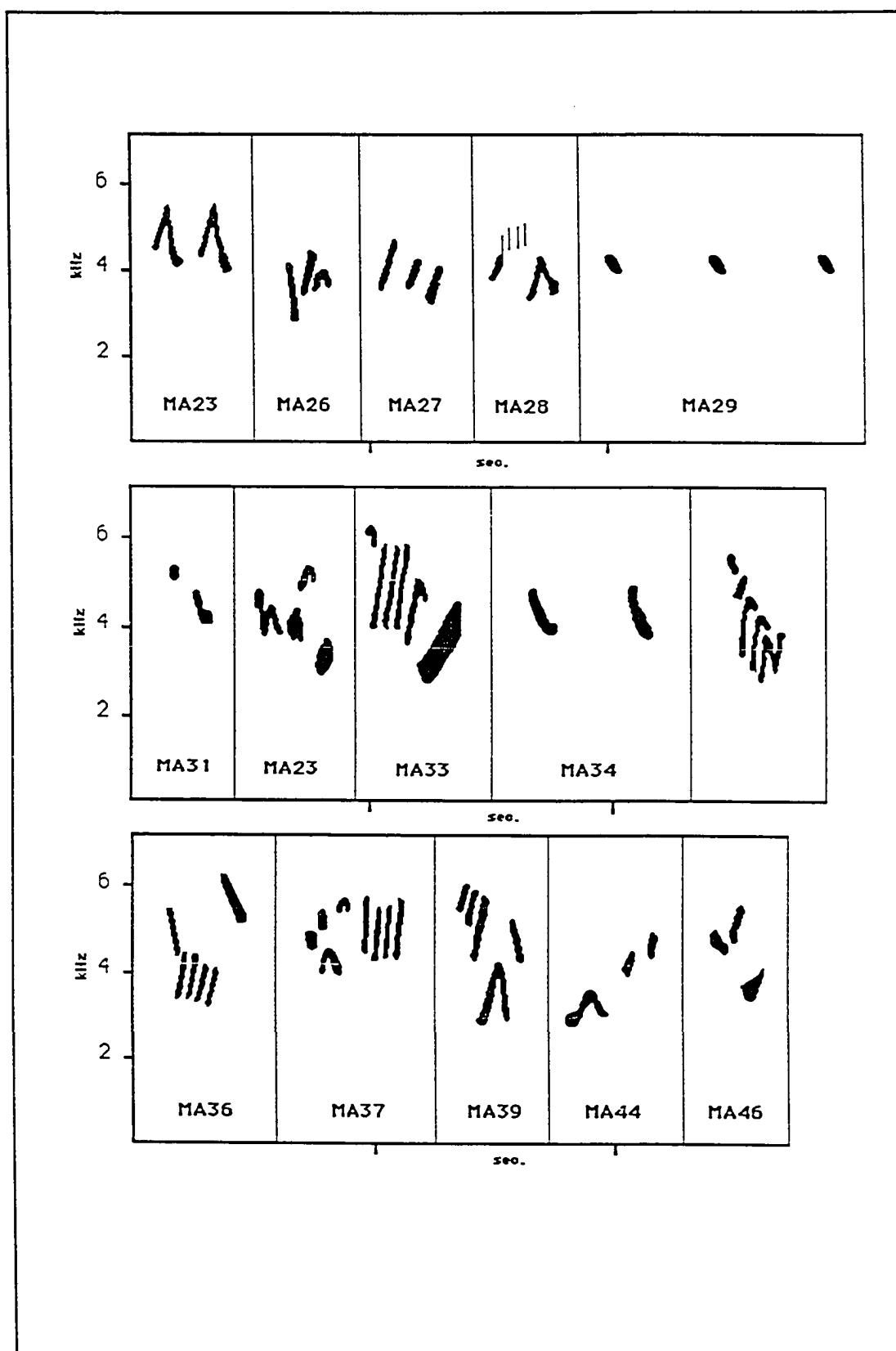
APPENDIX L
O. philadelphia Syllable Catalogue

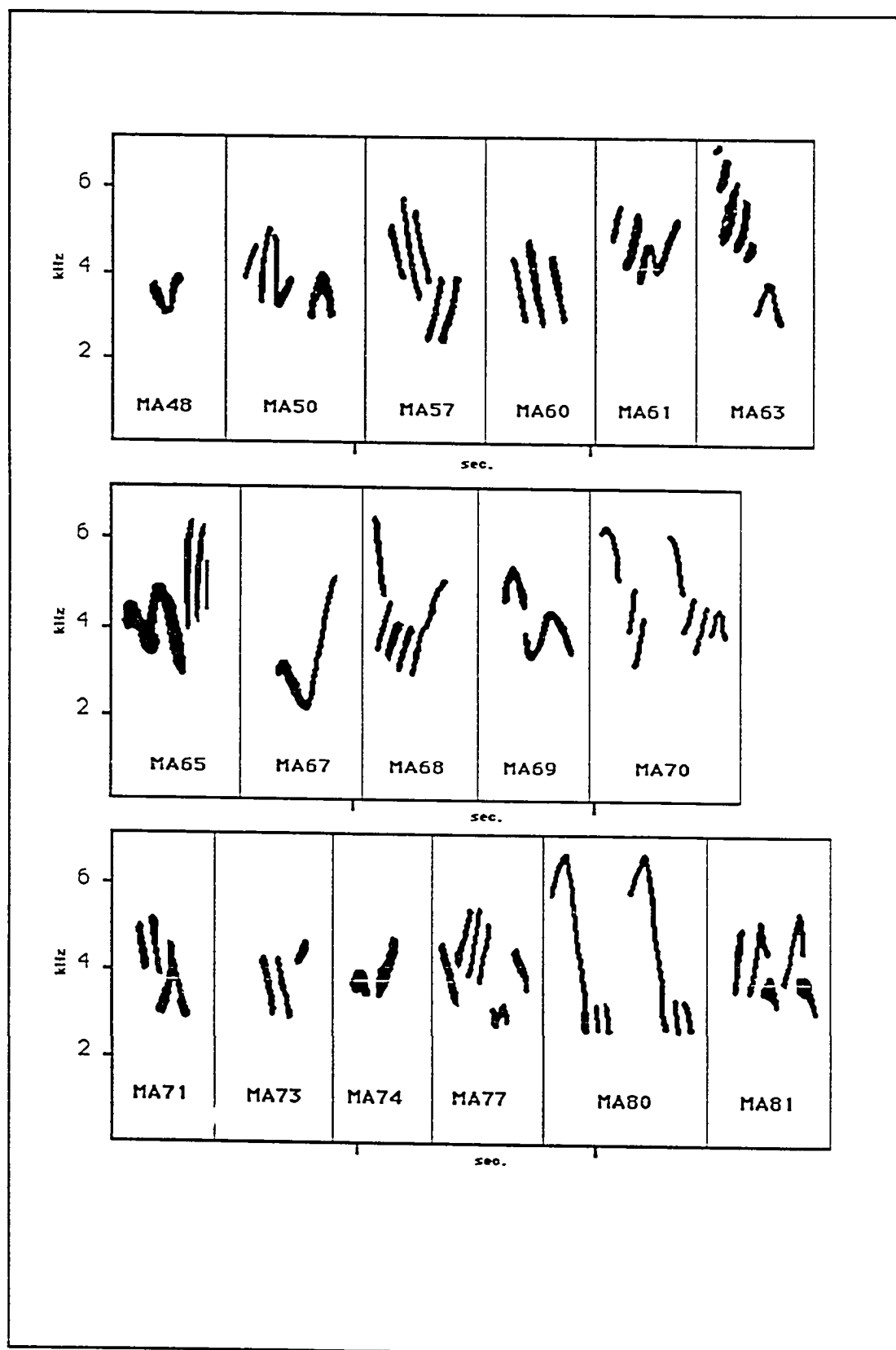


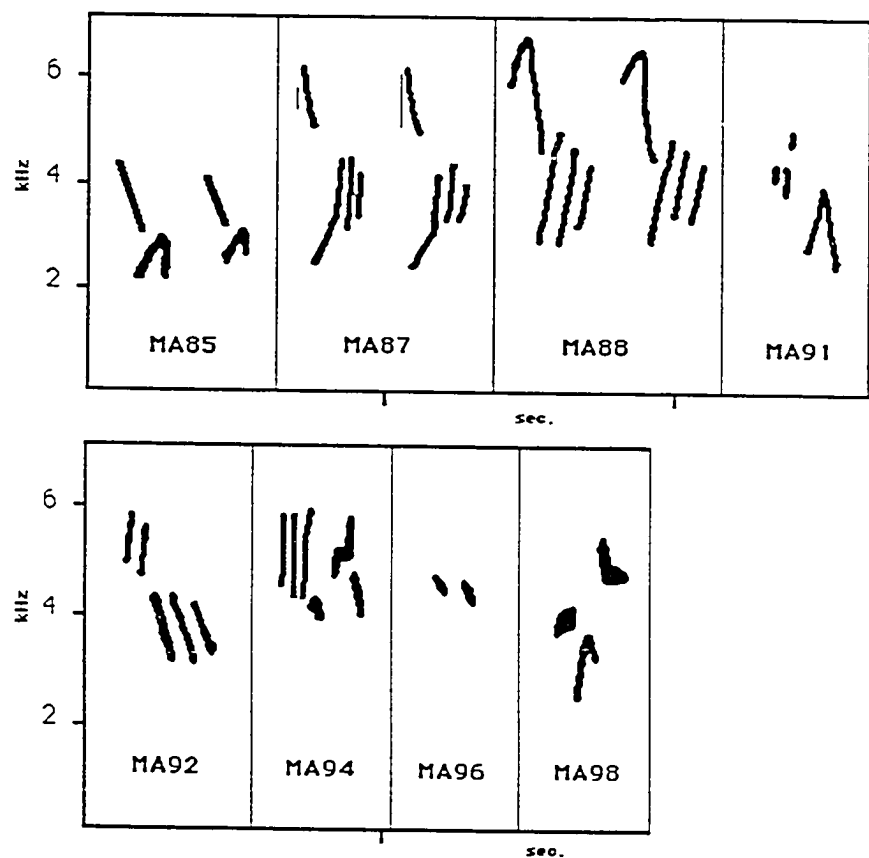


APPENDIX M
O. tolmiei Syllable Catalogue









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