1   **RRH: *E. T. Yang et al.*** • "Oregon" Dark-eyed Junco color

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3   **Dorsal color variation among subspecies of the "Oregon" Dark-eyed Junco**

4   **complex**

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14   **Abstract —** Initial descriptions of avian subspecies were based on expert opinions of geographic

15   variation in phenotypes and are inherently subjective. Although best practices for subspecies

16   delimitation continue to be debated, reassessing subspecies limits with current, quantitative

17   methods is important toward refining and improving taxonomic treatments. Plumage coloration

18   is the basis of many subspecies diagnoses, but is potentially problematic because of the historical

19   lack of quantitative methods to quantify color. Recently developed methods, such as colorimetry,

20   provide repeatable measurements of color variation that can be used to reassess subspecies

21   limits. In this study, we reassess color variation among subspecies of the Oregon Dark-eyed

22   Junco (*Junco hyemalis [oreganus Group]*) complex, in which differences in back and hood color

23   were established as diagnostic characters. We measured back and hood brightness and hue in 206

24   museum specimens among five Oregon Dark-eyed Junco subspecies using a colorimeter. We

25   then compared mean measurements among subspecies and conducted a discriminant function

26   analysis to assess how well dorsal color predicted subspecies. Our data correctly classified only

27   67.9% of males and 82.5% of females to their presumed subspecies. Furthermore, no adjacent

28   subspecies pairs passed the "75% rule" due to extensive overlap in plumage characters. Thus,

29   back color alone is not as effective in diagnosing Oregon Dark-eyed Junco subspecies as

30   originally described, suggesting a possible taxonomic revision. Specifically, similarity in

31   phenotypic and genetic data suggests that some combination of *thurberi*, *montanus*, and *shufeldti*

32   may be lumped to recognize broad, clinal variation in dorsal color alongside clinal variation in

33   other phenotypes and extensive gene flow.

34   **Keywords:** classification, color, Passerellidae, subspecies delimitation, taxonomy.

35   Avian subspecies delimitation is a controversial taxonomic practice that has been debated

36   and refined since its initial conceptualization (Mayr 1943; Wilson & Brown 1953; Zink 2004;

37   Patten 2010, 2015; Remsen 2010; Winker 2010). In birds, subspecies are generally thought to

38   represent phenotypically and/or genotypically differentiated populations within a species that

39   occupy a geographic region (Patten & Remsen 2017). However, original subspecies descriptions

40   were based mostly on expert opinions of geographic variation in phenotypes, resulting in

41   subjective classifications that often fail to meet current best practices (James 2010). Today,

42   delimiting subspecies is still far from straightforward: taxonomists continue to differ on what

43   subspecies represent and optimal criteria for delimitation (Fitzpatrick 2010; Gill 2014; Cronin et

44   al. 2015; Weckworth et al. 2015; Vinarski 2015). Nonetheless, the development and

45   implementation of quantitative metrics and statistical analyses promote a more consistent and

46   standardized subspecies classification system (Patten 2010). Many subspecies described prior to

47   the development of current practices are equivocal and would benefit from reassessments using

48   modern approaches. Such reassessments are important for current applied and basic research

49   initiatives, many of which use subspecies as units of biodiversity and indices of ecological and

50   evolutionary processes (Phillimore & Owens 2006; Haig & D'Elia 2010).

51   Phenotypic variation guided initial subspecies descriptions and remains important in

52   infraspecific taxonomy, even as genetic data play a growing role in subspecies delimitation

53   (Winker 2009; Patten & Remsen 2017). Coloration in particular has played a prominent role in

54   avian taxonomy for multiple reasons. First, plumage coloration and patterning is influenced by

55   selective pressures, such as natural selection favoring coloration that promotes camouflage or

56   sexual selection favoring bright, showy colors that promote mate choice (Hill & McGraw 2006;

57   Mason & Bowie 2020). Thus, differences among populations may represent evolutionary

58   changes in response to local conditions (Zink & Remsen 1986; Zamudio et al. 2016). Second,

59   differences in coloration are readily observable by the human eye and were easily detected by

60   early taxonomists (Endler 1990). However, historical assessments of color differences relied on

61   individual assessment of matches between plumage patches and color swatches (Ridgway 1912),

62   which may introduce qualitative, subjective differences among observers (Zuk & Decruyenaere

63   1994; Butler et al. 2011). Today, colorimetry, spectrophotometry, and digital photography offer

64   affordable ways to accurately measure color variation in a consistent, quantitative manner (Burns

65   et al. 2017). Recently, colorimetry has been used to quantify color variation and reexamine

66   subspecific taxonomy in various groups, including Willow Flycatchers (*Empidonax trailli*;

67   Paxton et al. 2010), Least Terns (*Sternula antillarum*; Johnson et al. 1998), and Sagebrush /

68   Bell's Sparrows (*Artemisiospiza sp.*; Patten & Unitt 2002). Nonetheless, many subspecies

69   groups are still in need of quantitative reevaluations of color variation and diagnosability among

70   taxa.

71   Among the subspecies groups that would benefit from a reexamination of how coloration

72   differences correspond to subspecies is the Oregon Dark-eyed Junco (*Junco hyemalis*) complex.

73   Dark-eyed Juncos exhibit pronounced intraspecific plumage variation, with seven 'groups' of

74   subspecies that have recently diversified across North America (Milá et al. 2007; Friis et al.

75   2016; Clements et al. 2019). In western North America, from Baja California north to Alaska,

76   seven subspecies comprise the "Oregon" Dark-eyed Junco group (Clements et al. 2019; Nolan et

77   al. 2020). Following comprehensive analyses of Oregon Junco subspecies by early taxonomists

78   (Ridgway 1901; Dwight 1918), Miller (1941) further established the current taxonomy of the

79   genus *Junco* by matching the specimens' hoods and backs with graded color samples and

80   examining pigments under a microscope (see Table 1 for subspecies descriptions). Despite the

81   widespread, longstanding use of Miller's (1941) classification, it is still unknown whether these

82   subspecies represent diagnosable taxa that meet current guidelines for subspecies delimitation.

83   In this study, we reevaluated Miller's (1941) classification of the Oregon Dark-eyed

84   Junco complex using colorimetry. We compared back and hood color variation between five

85   subspecies from the Oregon Dark-eyed Junco complex (*pinosus*, *thurberi*, *shufeldti*, *montanus*,

86   and *oreganus*), and excluded two subspecies from Mexico (*pontillis*, *townsendi*) for which we

87   lacked adequate sample sizes. We compared mean values of brightness and hue measurements

88   among sexes, age classes, and subspecies. We also quantified subspecies diagnosability of males

89   and females using a discriminant function analysis. Finally, we tested the "75% rule" (Amadon

90   1949; Patten & Unitt 2002) to see if quantitative color variation among subspecies passed a

91   widely used 'yardstick' of diagnosability. In doing so, we reassessed the validity of back color as

92   a diagnostic character for Oregon Dark-eyed Junco subspecies, and reconsidered subspecies

93   limits within the complex.

94

Methods

96   We measured plumage reflectance from 206 specimens of Oregon Dark-eyed Junco

97   (Figure 1; Appendix A). Our sampling was drawn from specimens housed in three collections:

98   the San Diego Natural History Museum (SDNHM), Natural History Museum of Los Angeles

99   County, Los Angeles (LACM), and the University of Los Angeles, California (UCLA). We

100 measured a minimum of 15 individuals from 5 subspecies, including (from north to south) *J. h.*

101 *oreganus* (16), *J. h. montanus* (29), *J. h. shufeldti* (17), *J. h. thurberi* (125), *J. h. pinosus* (n =

102 19). Specimens were selected based on the ranges described by Miller. Individuals falling out of

103   the range of their labeled subspecies were removed. Wintering individuals in subspecies with

104   nonbreeding ranges overlapping the range of other subspecies were also removed.

105   We did not include specimens with significantly worn plumage nor those that had faded

106   or missing feathers. We also omitted juveniles with irregular streaking, diffuse brown dorsal

107   plumage, obvious truncations in tail or greater coverts or completely unossified skulls. Immature

108   birds were identified whenever possible via known aging criteria, tag labels noting partially

109   ossified skulls, or labels noting developing ovaries. Birds for which none of this information was

110   obvious or available were labeled as adult. Thus, each individual included in the study was

111   classified as either immature or adult.

112   We measured the coloration of the center of the hood and the back of each specimen

113   using a Konica Minolta CR-300 Chroma Meter (Ramsey, New Jersey, USA). We recorded three

114   measurements: (1) L^*, or brightness, in which higher values corresponding to brighter plumage;

115   (2) a^*, or redness, in which lower values correspond to greener hues and higher values

116   correspond redder hues; and (3) b^*, or yellowness, in which lower values correspond to bluer

117   hues and higher values correspond to yellower hues. We repeated each measurement three times

118   and subsequently averaged those measurements.

119   We constructed separate generalized linear models (GLMs) for each of the six dorsal

120   color measurements (hood L, hood a, hood b, back L, back a, and back b) with a Gaussian

121   distribution of error using the glm() function in the R programming environment (R Core Team

122   2020). We included subspecies, sex, age class, days since molt, and years since collection as

123   main effects in each model. Dark-eyed Juncos undergo two body molts per year: an alternate

124   plumage molt from February to April and a basic molt from July to October (Pyle 1997).

125   Definitive basic and alternate plumages are nearly identical in Dark-eyed Juncos (Nolan et al.

126   2020), but color may change as freshly molted feathers wear and abrade over time (Tökölyi et al.

127   2008). We therefore incorporated the number of days since molt into our GLMs as the difference

128   between the collection date and the most recent molt event of either March 15th or September

129   1st. Furthermore, because specimens can fade and change color over years since their initial

130   collection (Doucet & Hill 2009), we also incorporated the number of years since collection into

131   our GLMs. We examined the distribution of residuals for each model to ensure that they

132   approximated a normal distribution (Supplementary Figure SF1). We subsequently performed a

133   series of Tukey's Honestly Significant Difference (HSD) tests to quantify differences in the

134   mean values of each plumage metric among sexes, age classes, and subspecies using the R

135   package agricolae v1.3.1 (de Mendiburu 2019).

136   We also performed a discriminant function analysis (DFA) on adult males (n=91) and

137   females (n=83) separately to determine the diagnosability of Oregon Junco subspecies based on

138   hood and mantle coloration using the MASS package (Venables & Ripley 2002) in R. We

139   subsequently performed a 'leave-one-out' (i.e., jackknifed) cross validation on our DFA to

140   predict the subspecies of each individual specimen and test the diagnosability of each subspecies

141   for both sexes (i.e., quantify the proportion of individuals that were correctly predicted as their

142   identified subspecies based on colorimetry data).

143   Finally, we implemented a widely-used diagnosability test commonly referred to as the

144   "75% rule" (Amadon 1949; Patten & Unitt 2002). In brief, the "75% rules" involves a pair-wise

145   test that determines whether 75% of the distribution of a single trait for one subspecies falls

146   outside of 99% of another subspecies' distribution for the same trait. The derivation of the test

147   statistic is described in detail in Patten and Unitt (2002) and is shown here.

148

149   Equation 1: $D_{ij} = \bar{x}_i - S_i(t_{0.25,df_i}) - \bar{x}_j - S_j\left(t_{0.99,df_j}\right)$

150

151   In this equation, $\bar{x}_i$ the mean and S_j is the standard deviation of a given trait for

152   subspecies i. If the D_{ij} statistic is greater than 1, then subspecies i is diagnosable from subspecies

153   j. For the "75% rule" to be met, the converse has to be true such that both subspecies are

154   diagnosable from each other. The second statistic (D_{ji}) can be calculated by swapping the critical

155   t values in the equation above. In our case, we tested pairwise diagnosability via the "75% rule"

156   for each subspecies pair with overlapping ranges. We only included adults and considered each

157   sex separately. This resulted in five diagnosability tests (from northernmost to southernmost): (1)

158   *oreganus* and *montanus*, (2) *oreganus* and *shufeldti*, (3) *montanus* and *shufeldti*, (4) *shufeldti* and

159   *thurberi*, and (5) *thurberi* and *pinosus*. We conducted a DFA for each subspecies pair and then

160   used scores from the first DFA axis to calculate the two summary statistics, D_{ij} and D_{ji} for adult

161   males and females.

162

163   **Results**

164   We uncovered variation in hood and mantle coloration among sexes, age classes, and five

165   subspecies within the "Oregon" Dark-eyed Junco complex. When we compared hood and back

166   color among males and females, we found that females had higher hood L and hood b values, but

167   lower hood a values (Fig. 2, Table 2). Among back measurements, females had higher back L,

168   back a, and back b values compared to males (Fig. 2, Table 2). Overall, this indicates that

169   females typically have lighter hoods and backs compared to males, while female hoods and

170   backs are typically 'buffier' with higher red and yellow reflectance than males. Although average

171   values differed between males and females, there was still substantial overlap in the range of

172   plumage coloration measurements between sexes.

173   Age classes also differed in dorsal color. Hood a was higher in immatures compared to

174   adults, while immatures also had higher back L, a, and b measurements (Fig. 3, Table 2).

175   Together, these results confirm that immature birds included in our study tended to have lighter,

176   more 'buffy' backs compared to adult juncos.

177   We also documented differences in coloration among subspecies of the "Oregon" Dark-

178   eyed Junco group (Fig. 4, Table 2). We observed greater differentiation among subspecies in the

179   mean values of hood measurements than back measurements. Using the Tukey's HSD test, we

180   identified as many as four groups of mean hood coloration values among subspecies (Fig. 4A,

181   Fig. 4B, Fig 4C). The northernmost subspecies, *J. h. oreganus*, had the lowest average hood

182   reflectance, or L values, while *J. h. Thurberi* had the highest average L values. The resident

183   subspecies, *J. h. pinosus*, had the highest average hood a values, or 'redness', while *J. h.*

184   *montanus* had the lowest average hood a values. Patterns for hood b values, or 'yellowness',

185   followed a similar pattern to hood a values, but exhibited more overlap among subspecies.

186   Although average hood measurements varied substantially among subspecies, differences

187   in back coloration were less pronounced (Fig. 4, Table 2). The maximum number of back

188   groupings we recovered via Tukey's HSD was two (Fig. 4D, Fig. 4E, Fig 4F). Differences

189   among subspecies in average back L values, or reflectance, were similar to that observed among

190   hoods, albeit with greater overlap among subspecies.

191   The number of days since molt did not exhibit any associations with any back or hood

192   measurements. The number of years since collection exhibited positive correlations with hood b,

193   back *a*, and back *b* values (Table 3), consistent with a pattern of 'foxxing', or increasing red and

194   yellow with years collection among the specimens studied here.

195   The discriminant function analysis using the colorimetry data on adult specimens

196   correctly assigned 55 out of 81 males to their identified subspecies (67.90%; Fig. 4A) and 66 out

197   of 80 females (82.50%; Fig. 4B). Diagnosability varied among subspecies. For males, hood and

198   back color successfully categorized (from north to south) 69.23% of *oreganus* (9/13), 75.00% of

199   *montanus* (9/12), 20.00% of *shufeldti* (2/10), 82.86% of *thurberi* (29/35), and 54.55% of *pinosus*

200   (6/11). For females, hood and back color correctly categorized 50.00% of *oreganus* (1/2),

201   66.66% of *montanus* (8/12), 0% of *shufeldti* (0/3), 92.86% of *thurberi* (52/56), and 71.43% of

202   *pinosus* (5/7).

203   Among all pairs of subspecies and sexes for which we tested the "75% rule", only two

204   compairisons were diagnosable with D_{ij} *values* ≥ 0: female *J. h. oreganus* were diagnosable from

205   female *J. h. montanus* ($D_{ij} = 1.68$; Table 3) and female *J. h. thurberi* were diagnosable from *J. h.*

206   *pinosus* ($D_{ij} = 0.06$; Table 3) . In both these cases, the converse comparisons did not meet the

207   requirements of the "75% rule". All other pairwise comparisons had largely overlapping

208   distributions of discriminant function scores and therefore failed to meet the "75% rule"

209   threshold of diagnosability.

210

Discussion

212   Using a colorimeter, we documented variation in the coloration of hoods and backs

213   between subspecies, sexes, and age classes within the "Oregon" Dark-eyed Junco complex

214   (Table 2; Fig. 2; Fig. 3; Fig. 4). Diagnosability of Oregon Junco subspecies on the basis of back

215   and hood coloration was limited for both sexes. Only two subspecies pairwise comparisons —

216   male *oreganus* and *montanus* and female *oreganus* and *montanus* — passed the '75% rule' often

217   used to delimit intraspecific taxonomy in birds (Table 2; Patten & Unitt 2002). Furthermore,

218   cross-validation of our DFA was only able to accurately predict the subspecies grouping of

219   67.90% of males and 82.50% of females (Figure 4). In contrast, Miller (1941) claimed that back

220   color allows a 90% "separation rate" between *shufeldti* and *thurberi* in interior ranges and a 75%

221   separation rate along the coast, a 92% separation rate between *oreganus* and *shufeldti,* and a 97%

222   separation between *oreganus* and *montanus*. Similarly high separation rates are reported for

223   other subspecies pairs. When comparing *montanus* and *shufeldti*, Miller (1941) reported a 75%

224   to 80% separation rate, but acknowledged that *shufeldti* is variable enough to "include the

225   original *montanus* series." It is unclear the methodology Miller (1941) used when generating this

226   output and whether the numbers represent the extent of overlap, correct identification rate based

227   on back color, or another method of differentiation. The most direct interpretation is that they

228   represent the percentage of species that were able to be identified to subspecies by back color

229   alone. In this case, our diagnosability rates fell short of what Miller (1941) reported, suggesting

230   that subspecies of Oregon Dark-eyed Juncos exhibit weaker differentiation in dorsal coloration

231   than has been heretofore assumed. Importantly, we had low sample sizes for females in a few

232   subspecies, most notably the non-migratory *pinosus* ($n_{male} = 11$, $n_{female} = 7$), which has a

233   restricted geographic range and correspondingly few specimens in most collections. We also had

234   low sample sizes for *oreganus* ($n_{male} = 13$, $n_{female} = 2$), which decreased our statistical power to

235   detect diagnosable differences for these taxa and contributed to the output of the "75% rule" tests

236   involving *oreganus* and *pinosus*.

237   Beyond dorsal coloration, many subspecies in the Oregon Dark-eyed Junco complex

238   exhibit broadly overlapping, clinal variation in other phenotypes. For example, many subspecies

239   exhibit substantial overlap in morphological characters, such as tail length, wing length, and the

240   extent of white on rectrices (Ferree 2013). Furthermore, four out of five of the Oregon Dark-eyed

241   Junco subspecies included in this study (*thurberi*, *shufeldti*, *montanus*, and *oreganus*) exhibit

242   little to no genetic population structure based on genomic analyses involving thousands of loci

243   (Friis et al. 2018). *Pinosus*, however, exhibits pronounced genomic differentiation (Friis et al.

244   2018), is non-migratory, and has the shortest wings of all Oregon Dark-eyed Junco subspecies

245   (Ferree 2013), and is therefore a valid subspecies. Although *oreganus* exhibits less genomic

246   differentiation than *pinosus*, *oreganus* is also distinct in its darker plumage and partially

247   geographically isolated range, suggesting it too may be a valid subspecies. On the other hand,

248   *montanus*, *shufeldti*, and *thurberi* are less distinct: while *montanus* is duller than either *shufeldti*

249   or *thurberi*, the broadly overlapping ranges between *shufeldti* with both *thurberi* and *montanus*

250   and low genomic differentiation suggest a potential taxonomic revision for the three subspecies.

251   Based on observed similarity in phenotype and genotype, one taxonomic solution may be to treat

252   *montanus, shufeldti, and thurberi* as a single, widely distributed taxon with broad clinal variation

253   across its range. Another solution would be to either lump *shufeldti* and *thurberi* together or to

254   lump *thurberi* and *montanus*. Finally, a fourth option would be to retain all existing taxonomic

255   classifications and continue to recognize *montanus, shufeldti*, and *thurberi* as distinct subspecies.

256   In summary, our quantitative, colorimetric analysis of dorsal values do not support

257   preexisting assertions of subspecies diagnosability within the Oregon junco complex. Miller

258   (1941)'s method for assessing pigmentary characters, which consisted of matching color effect in

259   a given area of plumage with a graded series of color swatches and microscopic examination of

260   pheomelanin and eumelanin, yielded results that are inconsistent with our colorimetry data. Our

261   findings suggest a possible taxonomic revision of the Oregon Dark-eyed Junco group whereby

262 fewer subspecies are recognized in light of broadly overlapping phenotypic and genetic

263 variation. Revising subspecies limits in light of an improved understanding of geographic

264 variation among populations promotes a more accurate and functional taxonomic classification

265 of birds, which has broad implications across ornithology.

266

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274

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373

374

375   Table 1: Phenotypic descriptions of the five subspecies' appearances and breeding ranges

376   (following Miller (1941)) included in this study.

377

Subspecies	Plumage color description	Breeding Range
J. h. oreganus	Dark reddish brown back Dark brown flanks Black hood in male Gray hood in female	Southeast Alaska to south-central British Columbia
J. h. shufeldti	Grayer, browner, less red than oreganus Cinnamon flanks Black hood in male Gray hood in female	Southwest British Columbia through western Washington and Oregon
J. h. montanus	Cinnamon brown flanks Dark gray brown back Blackish to slate hood in male Gray hood in female	Central interior British Columbia and Southwest Alberta through Northwest Montana, Western Idaho, Eastern Washington, Eastern Oregon
J. h. thurberi	Sides cinnamon brown Back rich coffee brown,	Southern Oregon to coastal California, interior California

	lighter and more pinkish than *J. h. shufeldti* Hood as *J. h. shufeldti*	
J. h. pinosus	Ruddier back and flanks than thurberi, sides and flanks bright cinnamon brown, bright russet back, grayer hood than thurberi - blackish to slate in male, gray in female	Resident central coastal California

378

379

380

381   Table 2: Results from generalized linear model (GLM) analyses for each of six response

382   variables: hood *L*, hood *a*, hood *b*, back *L*, back *a*, back *b*. Significant model effects (P < 0.05)

383   are displayed with a bold font for the P value. GLMs were generated with a Gaussian distribution

384   of error. Categorical terms are compared to a base model with male sex, adult age class, and

385   *oreganus* subspecies. Days since molt Specimen age displays change in parameter values per

386   year.

387

Hood L	**β** ± SE	t value	P value
(Intercept)	27.183 ± 0.617	44.036	**>0.0001**
Sex Female	0.768 ± 0.267	2.875	**0.0045**
Age Class Immature	-0.772 ± 0.314	-2.463	**0.0146**
Subspecies *montanus*	4.118 ± 0.589	6.991	**>0.0001**
Subspecies *shufeldti*	3.4 ± 0.641	5.302	**>0.0001**
Subspecies *thurberi*	5.861 ± 0.53	11.05	**>0.0001**
Subspecies *pinosus*	3.826 ± 0.627	6.103	**>0.0001**
Days Since Molt	0.002 ± 0.003	0.798	0.4261
Specimen Age	-0.004 ± 0.004	-1.012	0.3126
Hood a	**β** ± SE	t value	P value
(Intercept)	5.156 ± 0.259	19.928	**>0.0001**
Sex Female	-0.243 ± 0.112	-2.168	**0.0313**

Age Class Immature	0.458 ± 0.131	3.485	**0.0006**
Subspecies *montanus*	-1.401 ± 0.247	-5.676	**>0.0001**
Subspecies *shufeldti*	-0.683 ± 0.269	-2.543	**0.0117**
Subspecies *thurberi*	0.014 ± 0.222	0.065	0.9483
Subspecies *pinosus*	1.555 ± 0.263	5.92	**>0.0001**
Days Since Molt	-0.001 ± 0.001	-0.974	0.3312
Specimen Age	0.002 ± 0.002	1.075	0.2837

Hood b	$\beta \pm SE$	t value	P value
(Intercept)	13.171 ± 0.436	30.195	**>0.0001**
Sex Female	0.542 ± 0.189	2.869	**0.0046**
Age Class Immature	0.194 ± 0.222	0.874	0.383
Subspecies *montanus*	-1.867 ± 0.416	-4.485	**>0.0001**
Subspecies *shufeldti*	-0.333 ± 0.453	-0.734	0.4639
Subspecies *thurberi*	1.123 ± 0.375	2.996	**0.0031**
Subspecies *pinosus*	2.466 ± 0.443	5.566	**>0.0001**
Days Since Molt	-0.002 ± 0.002	-1.047	0.2966
Specimen Age	0.016 ± 0.003	6.128	**>0.0001**

Back L	$\beta \pm SE$	t value	P value
(Intercept)	15.892 ± 1.102	14.416	**>0.0001**

	$\beta \pm SE$	t value	P value
Sex Female	5.988 ± 0.477	12.555	**>0.0001**
Age Class Immature	2.839 ± 0.56	5.068	**>0.0001**
Subspecies *montanus*	2.112 ± 1.052	2.007	**0.0461**
Subspecies *shufeldti*	1.207 ± 1.145	1.054	0.2933
Subspecies *thurberi*	1.242 ± 0.947	1.312	0.1912
Subspecies *pinosus*	1.548 ± 1.12	1.383	0.1682
Days Since Molt	0.006 ± 0.005	1.261	0.2087
Specimen Age	0.007 ± 0.007	1.082	0.2804
Back a	$\boldsymbol{\beta} \pm SE$	t value	P value
(Intercept)	1.296 ± 0.203	6.396	**>0.0001**
Sex Female	0.417 ± 0.088	4.757	**>0.0001**
Age Class Immature	0.627 ± 0.103	6.089	**>0.0001**
Subspecies *montanus*	-0.187 ± 0.193	-0.967	0.3348
Subspecies *shufeldti*	0.154 ± 0.211	0.732	0.4647
Subspecies *thurberi*	0.158 ± 0.174	0.907	0.3657
Subspecies *pinosus*	0.537 ± 0.206	2.609	**0.0098**
Days Since Molt	-0.001 ± 0.001	-1.651	0.1004
Specimen Age	0.008 ± 0.001	6.251	**>0.0001**
Back b	$\boldsymbol{\beta} \pm SE$	t value	P value

(Intercept)	4.053 ± 0.582	6.959	**>0.0001**
Sex Female	2.196 ± 0.252	8.713	**>0.0001**
Age Class Imature	2.11 ± 0.296	7.132	**>0.0001**
Subspecies *montanus*	-0.768 ± 0.556	-1.382	0.1687
Subspecies *shufeldti*	0.375 ± 0.605	0.619	0.5364
Subspecies *thurberi*	0.32 ± 0.5	0.64	0.5231
Subspecies *pinosus*	1.29 ± 0.591	2.182	0.0303
Days Since Molt	-0.003 ± 0.003	-1.366	0.1736
Specimen Age	0.019 ± 0.003	5.488	**>0.0001**

388

389   Table 3: Results from diagnosability tests of the "75% rule" formalized by Patten and Unitt

390   (2002) using the first two axes of the discriminant function analysis with all five subspecies

391   included. When the test statistic (D) is greater than zero, then 75% of the distribution for the first

392   subspecies lies outside of 99% of the other subspecies.

393

394

		Male		Female	
Subspecies 1	Subspecies 2	D_{12}	D_{21}	D_{12}	D_{21}
oreganus	*montanus*	0.00	-0.61	**1.68**	-66.93
oreganus	*shufeldti*	-1.67	-1.09	-6.57	-9.55
montanus	*shufeldti*	-1.11	-0.81	-6.85	-0.20
shufeldti	*thurberi*	-0.71	-0.86	-1.02	-1.99
thurberi	*pinosus*	-1.04	-0.75	-0.98	**0.06**

395

396

397   **Figure Headings**

398   Figure 1: Sampling map of vouchered specimens included in our study of plumage reflectance

399   among subspecies of the "Oregon" Dark-eyed Junco. Plates of male and female "Oregon" Dark-

400   eyed Junco are shown on the left. Approximate breeding ranges of each subspecies are shown in

401   different colors and have been modified following the descriptions of Miller (1941). As our

402   study included wintering as well as breeding birds, some circles fall outside of their expected

403   range due to non-breeding seasonal movements. Sampling localities are indicated with circles

404   with subspecies indicated by the fill color of the circle. Some dots may represent more than one

405   individual sampled from the same locality. Illustrations are provided courtesy of Lynx Edicions.

406

407   Figure 2: Boxplots of hood and back coloration measurements among males and females of the

408   "Oregon" Dark-eyed Junco complex. For the back and hood, "L" corresponds to brightness with

409   higher values indicating brighter colors; "a" corresponds to redness, in which higher values

410   correspond to more red coloration; and "b" corresponds to yellowness, in which higher values

411   correspond to more yellow coloration. Shown above each box is the group classification

412   following a Tukey's HSD test for pairwise differences in mean values with the alphabetical order

413   of groupings corresponding to descending differences in mean values among groups.

414

415   Figure 3: Boxplots of hood and back coloration measurements among immature and adult

416   individuals of the "Oregon" Dark-eyed Junco complex. For the back and hood, "L" corresponds

417   to brightness with higher values indicating brighter colors; "a" corresponds to redness, in which

418   higher values correspond to more red coloration; and "b" corresponds to yellowness, in which

419   higher values correspond to more yellow coloration. Shown above each box is the group

420   classification following a Tukey's HSD test for pairwise differences in mean values with the

421   alphabetical order of groupings corresponding to descending differences in mean values among
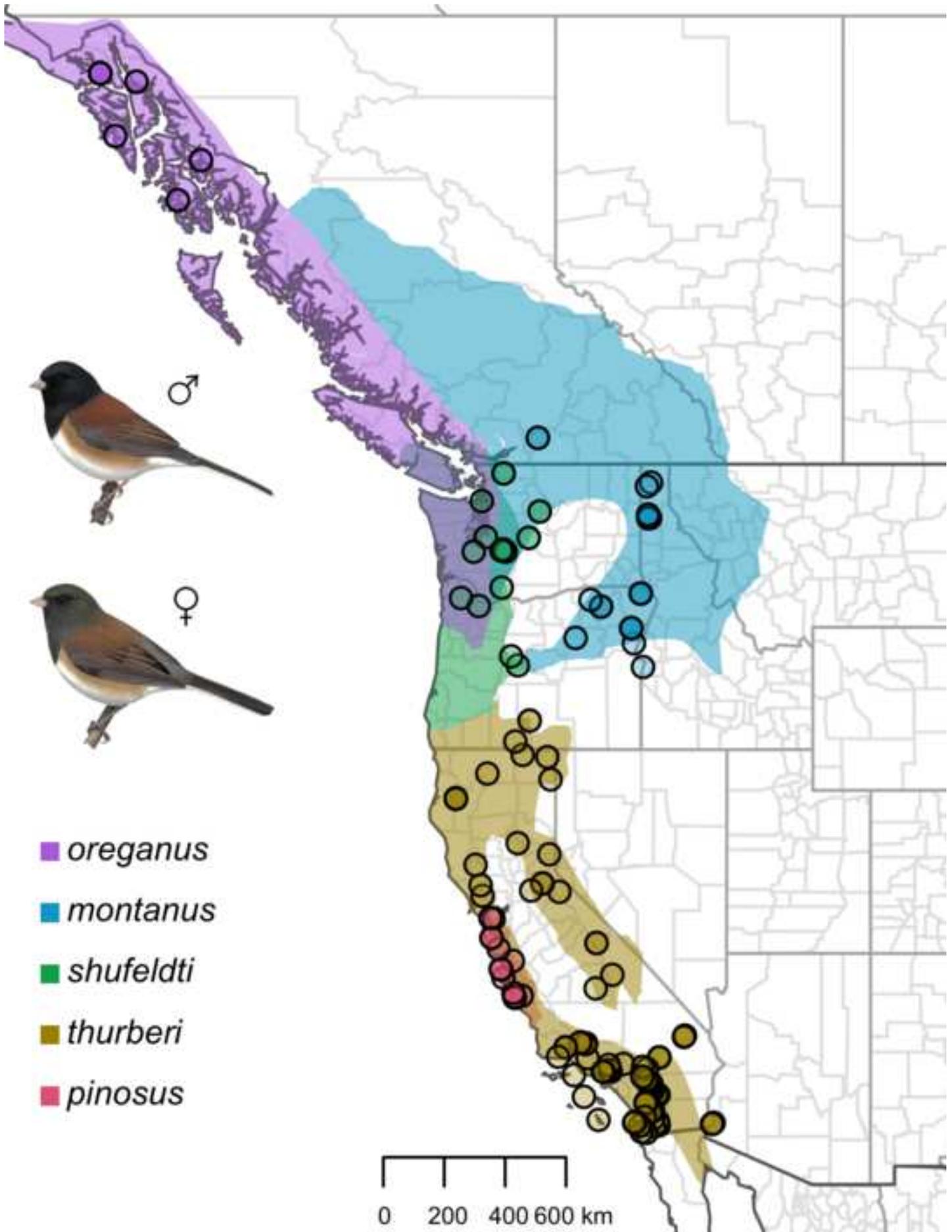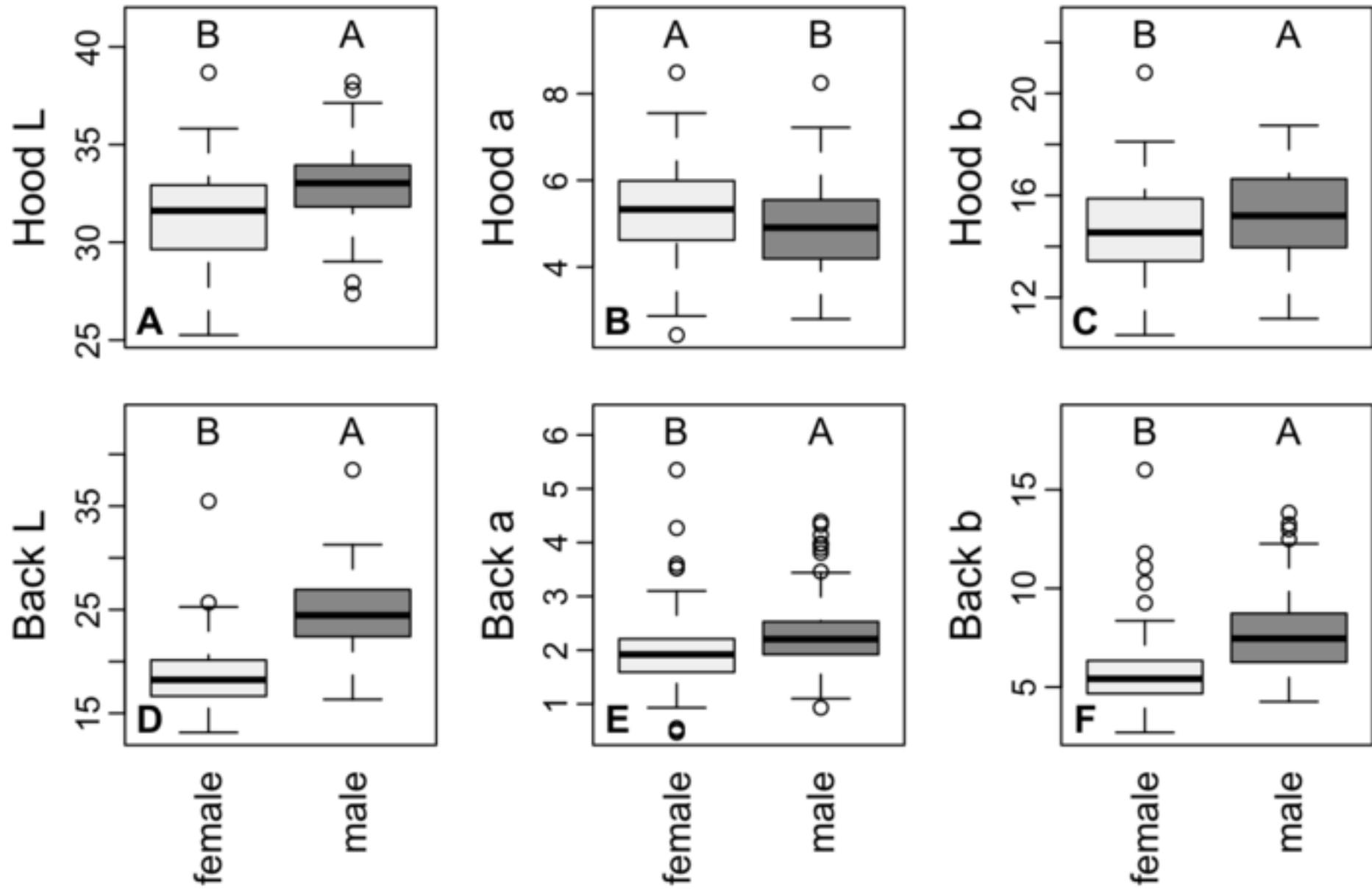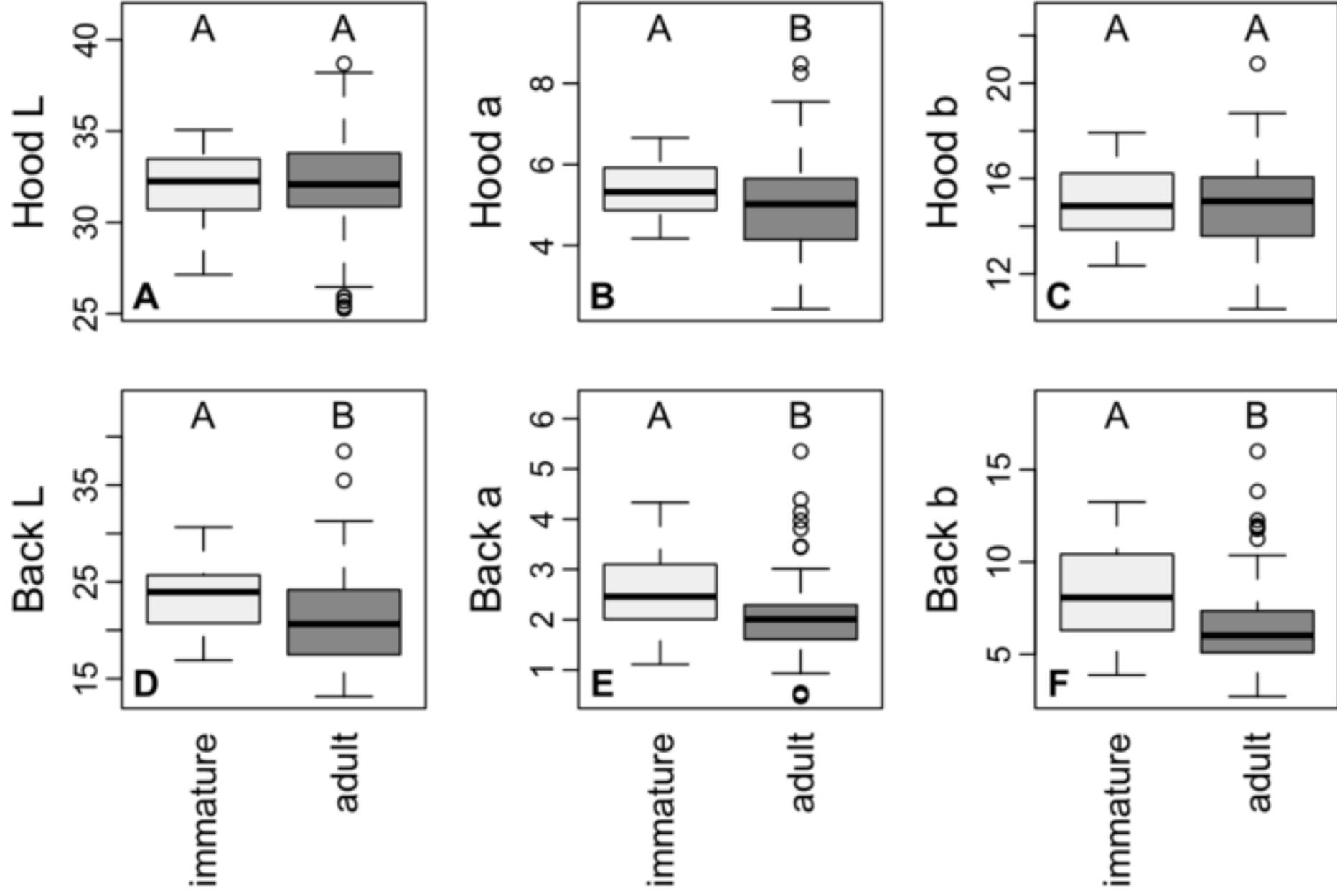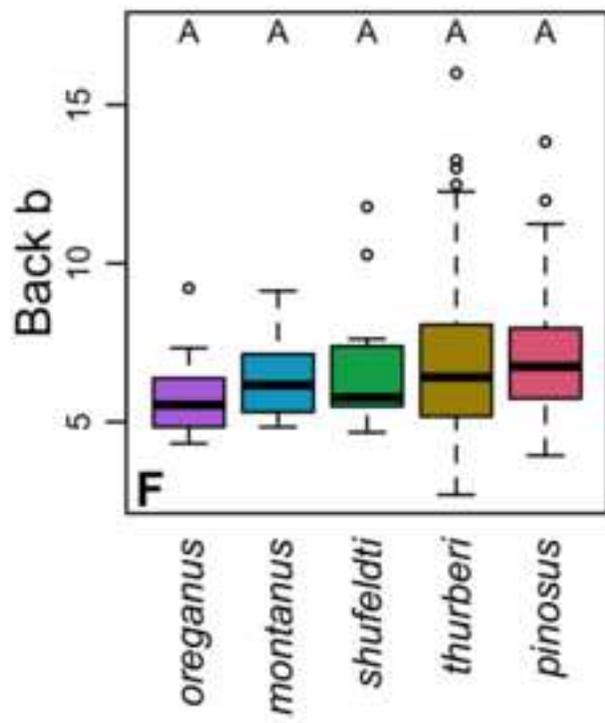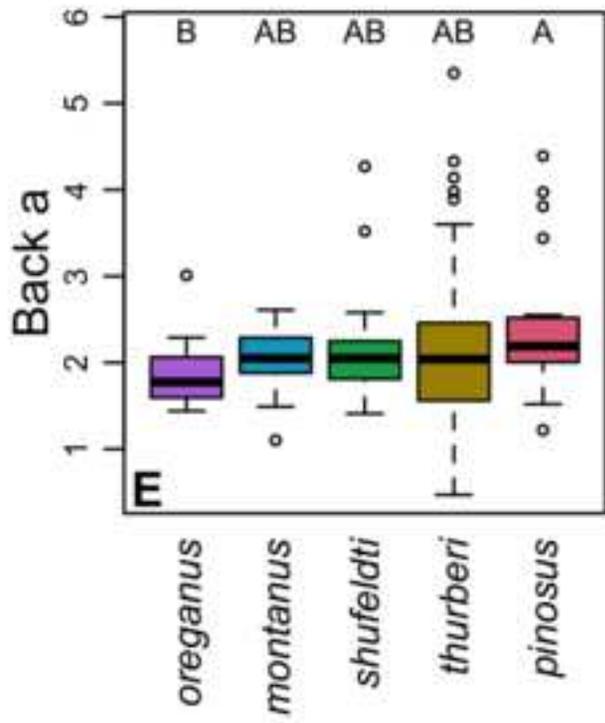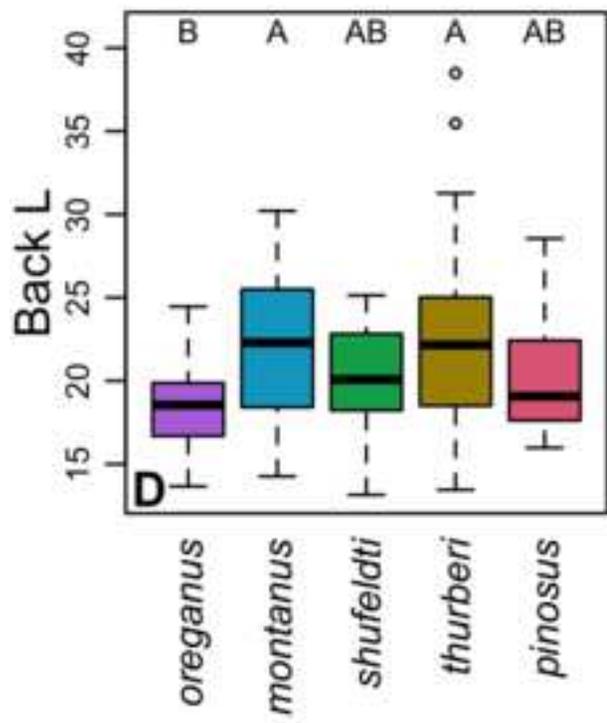
422   groups.

423

424   Figure 4: Boxplots of hood and back coloration among subspecies of the "Oregon" Dark-eyed

425   Junco complex. For the back and hood, "L" corresponds to brightness with higher values

426   indicating brighter colors; "a" corresponds to redness, in which higher values correspond to more

427   red coloration; and "b" corresponds to yellowness, in which higher values correspond to more

428   yellow coloration. Shown above each box is the group classification following a Tukey's HSD

429   test for pairwise differences in mean values with the alphabetical order of groupings

430   corresponding to descending differences in mean values among groups.
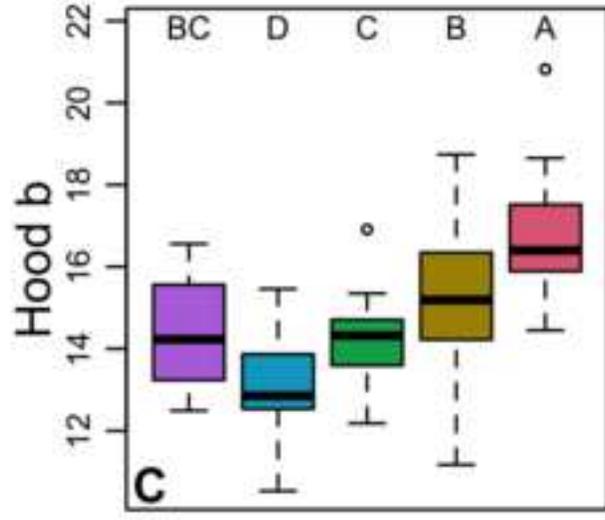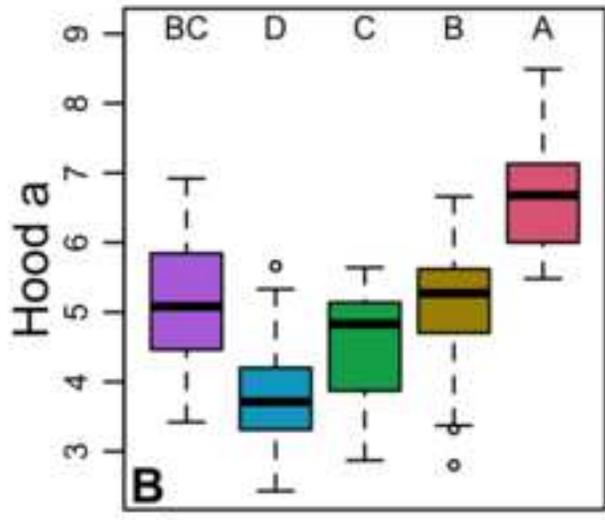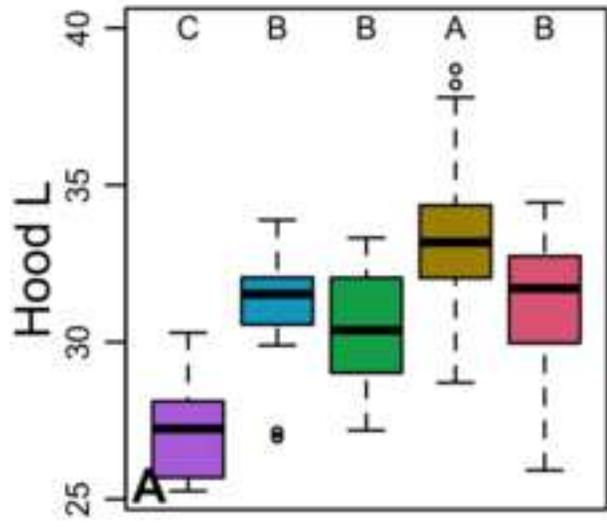
431

432   Figure 5: Discriminant function analysis and cross-validation analyses based on hood and back

433   coloration for adult (A) males and (B) females among subspecies within the "Oregon" Dark-eyed

434   Junco complex. The percentage of total correct classifications across subspecies is shown at the

435   top of each plot. Within each plot, the center of each point corresponds to the subspecies identity

436   associated with the metadata of each specimen, while the outside ring of each point corresponds

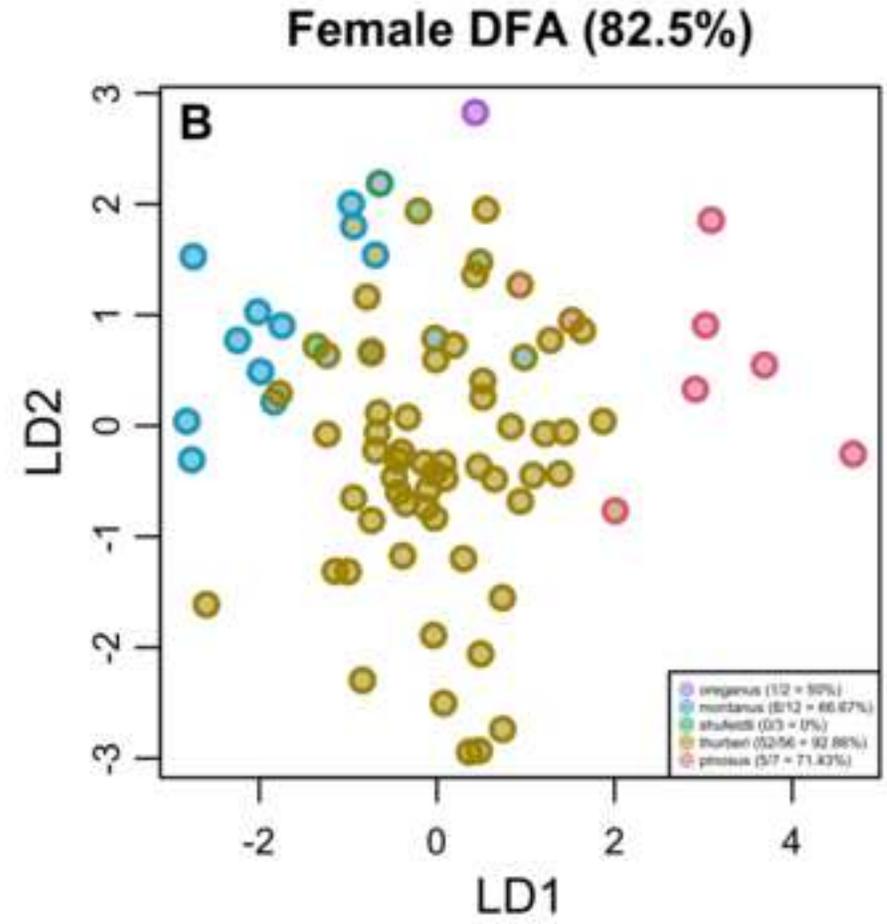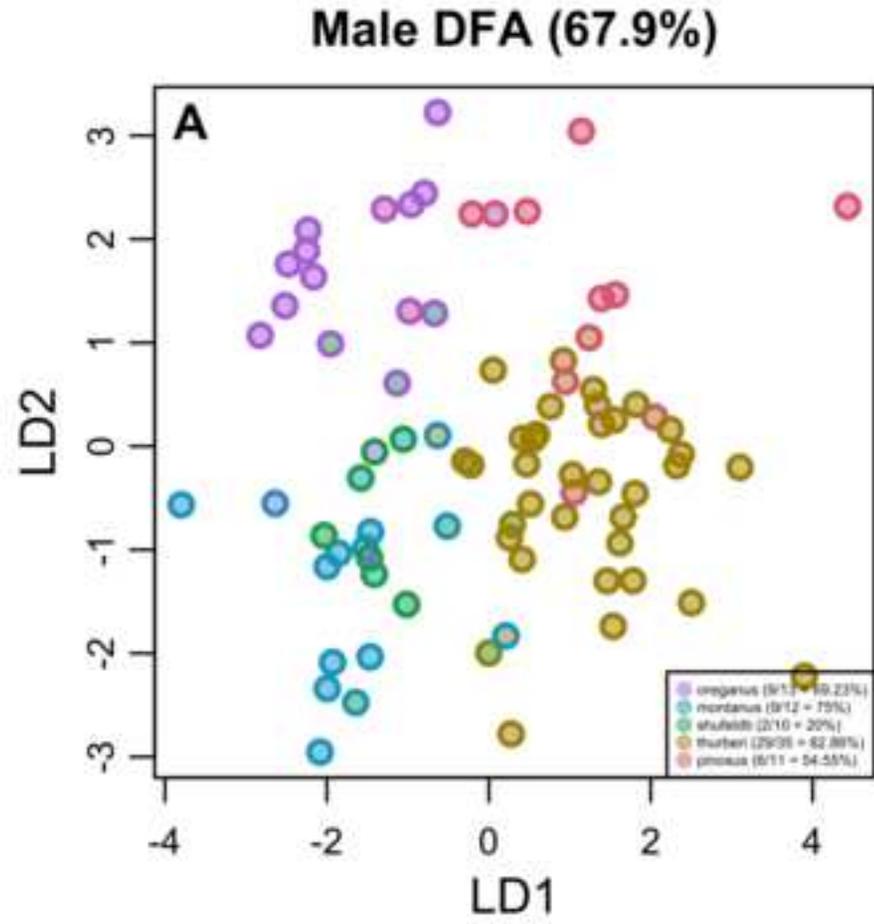437   to the predicted subspecies of each individual.

438

oreganus

montanus

shufeldti

thurberi

pinosus

Figure 2

Figure 3

Figure 4

Figure 5

Male DFA (67.9%)

Female DFA (82.5%)

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Supplemental Material

Yang_Juncos_SupplementaryInformation_v1.docx