

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

95 **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: $D_{ij} = \bar{x}_i - S_i(t_{0.25,df_i}) - \bar{x}_j - S_j(t_{0.99,df_j})$

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. oregonus*, 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 comparisons were diagnosable with D_{ij} values ≥ 0 : female *J. h. oregonus* 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

211 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* ($n_{\text{male}} = 11$, $n_{\text{female}} = 7$), which has a
233 restricted geographic range and correspondingly few specimens in most collections. We also had
234 low sample sizes for *oreganus* ($n_{\text{male}} = 13$, $n_{\text{female}} = 2$), 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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- 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
<i>J. h. oregonus</i>	Dark reddish brown back Dark brown flanks Black hood in male Gray hood in female	Southeast Alaska to south-central British Columbia
<i>J. h. shufeldti</i>	Grayer, browner, less red than oregonus Cinnamon flanks Black hood in male Gray hood in female	Southwest British Columbia through western Washington and Oregon
<i>J. h. montanus</i>	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
<i>J. h. thurberi</i>	Sides cinnamon brown Back rich coffee brown,	Southern Oregon to coastal California, interior California

	lighter and more pinkish than <i>J. h. shufeldti</i> Hood as <i>J. h. shufeldti</i>	
<i>J. h. pinosus</i>	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	$\beta \pm SE$	t value	P value
(Intercept)	27.183 \pm 0.617	44.036	>0.0001
Sex Female	0.768 \pm 0.267	2.875	0.0045
Age Class Immature	-0.772 \pm 0.314	-2.463	0.0146
Subspecies <i>montanus</i>	4.118 \pm 0.589	6.991	>0.0001
Subspecies <i>shufeldti</i>	3.4 \pm 0.641	5.302	>0.0001
Subspecies <i>thurberi</i>	5.861 \pm 0.53	11.05	>0.0001
Subspecies <i>pinosus</i>	3.826 \pm 0.627	6.103	>0.0001
Days Since Molt	0.002 \pm 0.003	0.798	0.4261
Specimen Age	-0.004 \pm 0.004	-1.012	0.3126
Hood a	$\beta \pm SE$	t value	P value
(Intercept)	5.156 \pm 0.259	19.928	>0.0001
Sex Female	-0.243 \pm 0.112	-2.168	0.0313

Age Class Immature	0.458 ± 0.131	3.485	0.0006
Subspecies <i>montanus</i>	-1.401 ± 0.247	-5.676	>0.0001
Subspecies <i>shufeldti</i>	-0.683 ± 0.269	-2.543	0.0117
Subspecies <i>thurberi</i>	0.014 ± 0.222	0.065	0.9483
Subspecies <i>pinosus</i>	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 <i>montanus</i>	-1.867 ± 0.416	-4.485	>0.0001
Subspecies <i>shufeldti</i>	-0.333 ± 0.453	-0.734	0.4639
Subspecies <i>thurberi</i>	1.123 ± 0.375	2.996	0.0031
Subspecies <i>pinosus</i>	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

Sex Female	5.988 ± 0.477	12.555	>0.0001
Age Class Immature	2.839 ± 0.56	5.068	>0.0001
Subspecies <i>montanus</i>	2.112 ± 1.052	2.007	0.0461
Subspecies <i>shufeldti</i>	1.207 ± 1.145	1.054	0.2933
Subspecies <i>thurberi</i>	1.242 ± 0.947	1.312	0.1912
Subspecies <i>pinosus</i>	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	$\beta \pm SE$	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 <i>montanus</i>	-0.187 ± 0.193	-0.967	0.3348
Subspecies <i>shufeldti</i>	0.154 ± 0.211	0.732	0.4647
Subspecies <i>thurberi</i>	0.158 ± 0.174	0.907	0.3657
Subspecies <i>pinosus</i>	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	$\beta \pm SE$	t value	P value
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(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 <i>montanus</i>	-0.768 ± 0.556	-1.382	0.1687
Subspecies <i>shufeldti</i>	0.375 ± 0.605	0.619	0.5364
Subspecies <i>thurberi</i>	0.32 ± 0.5	0.64	0.5231
Subspecies <i>pinosus</i>	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

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
<i>oreganus</i>	<i>montanus</i>	0.00	-0.61	1.68	-66.93
<i>oreganus</i>	<i>shufeldti</i>	-1.67	-1.09	-6.57	-9.55
<i>montanus</i>	<i>shufeldti</i>	-1.11	-0.81	-6.85	-0.20
<i>shufeldti</i>	<i>thurberi</i>	-0.71	-0.86	-1.02	-1.99
<i>thurberi</i>	<i>pinosus</i>	-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.

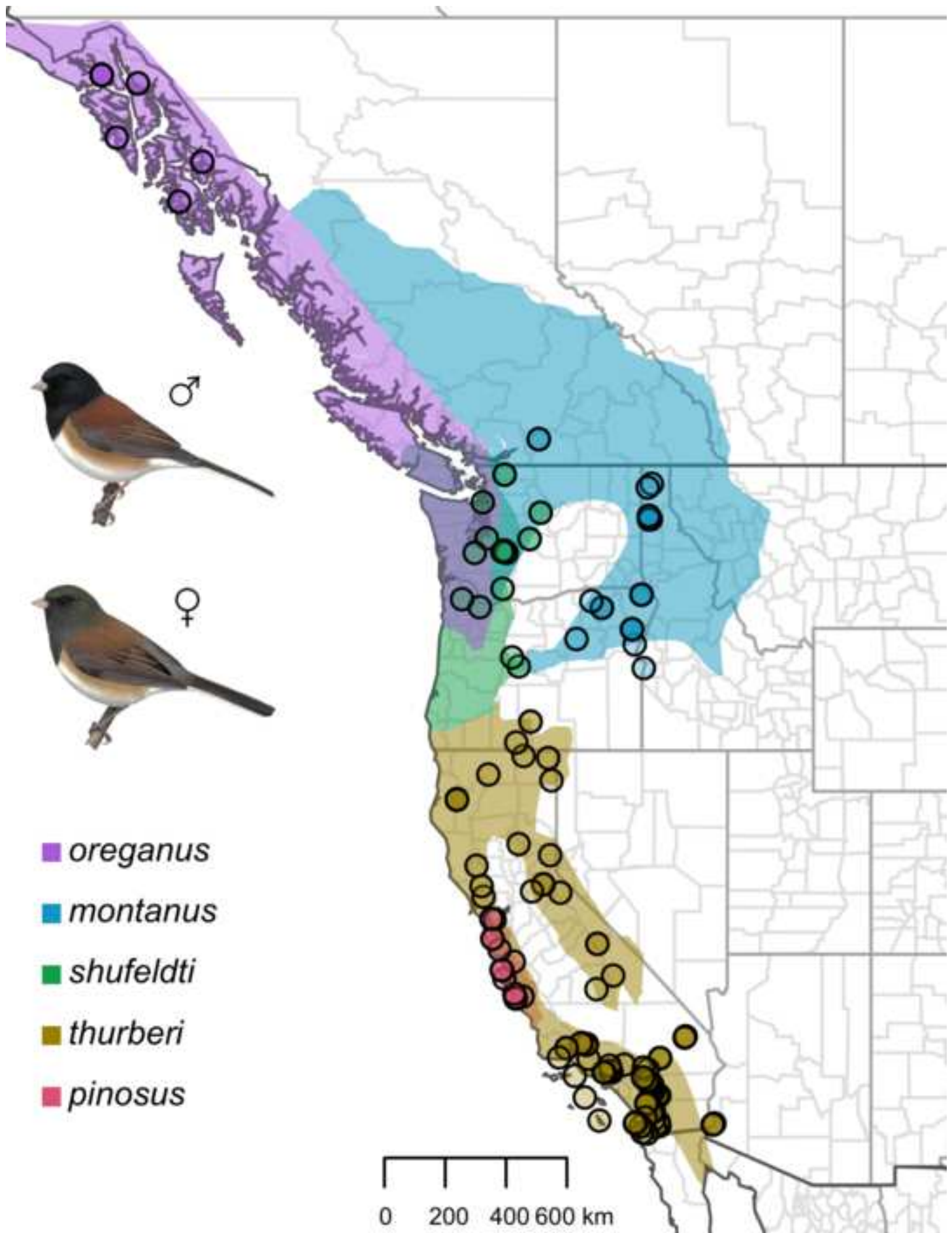
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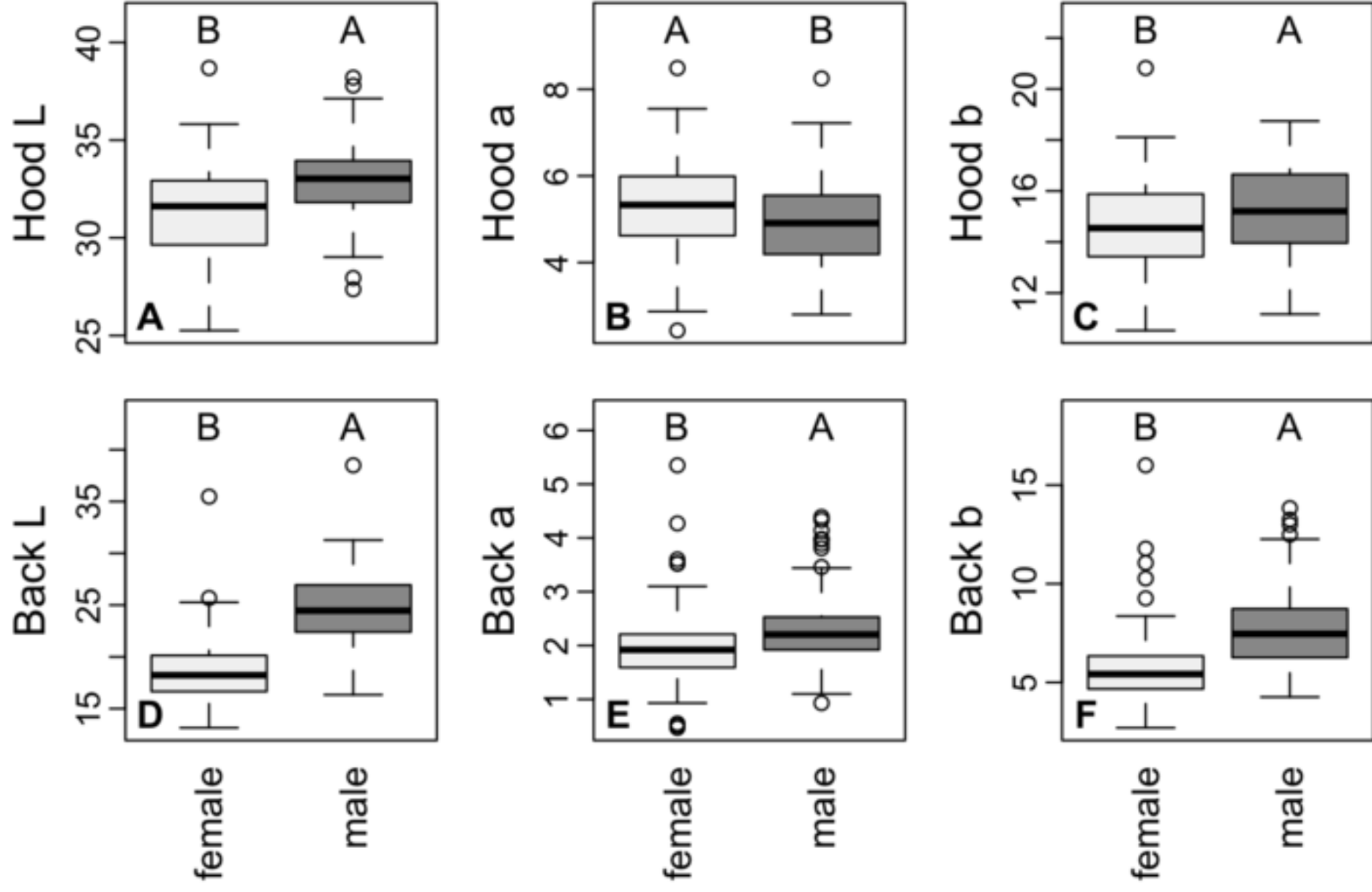
424 Figure 4: Boxplots of hood and back coloration among subspecies of the “Oregon” Dark-eyed
425 Junco complex. For the back and hood, “L” corresponds to brightness with higher values
426 indicating brighter colors; “a” corresponds to redness, in which higher values correspond to more
427 red coloration; 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





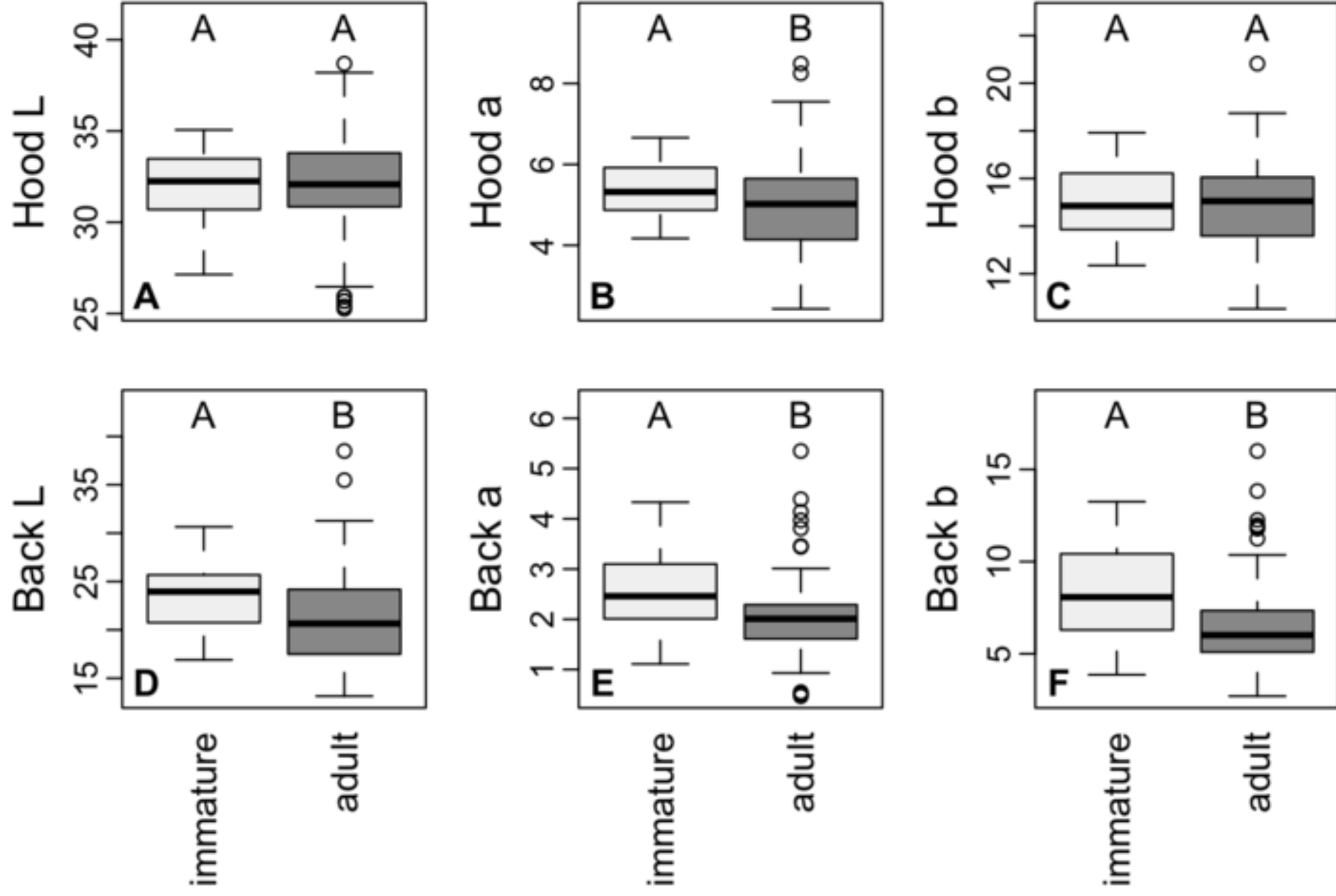
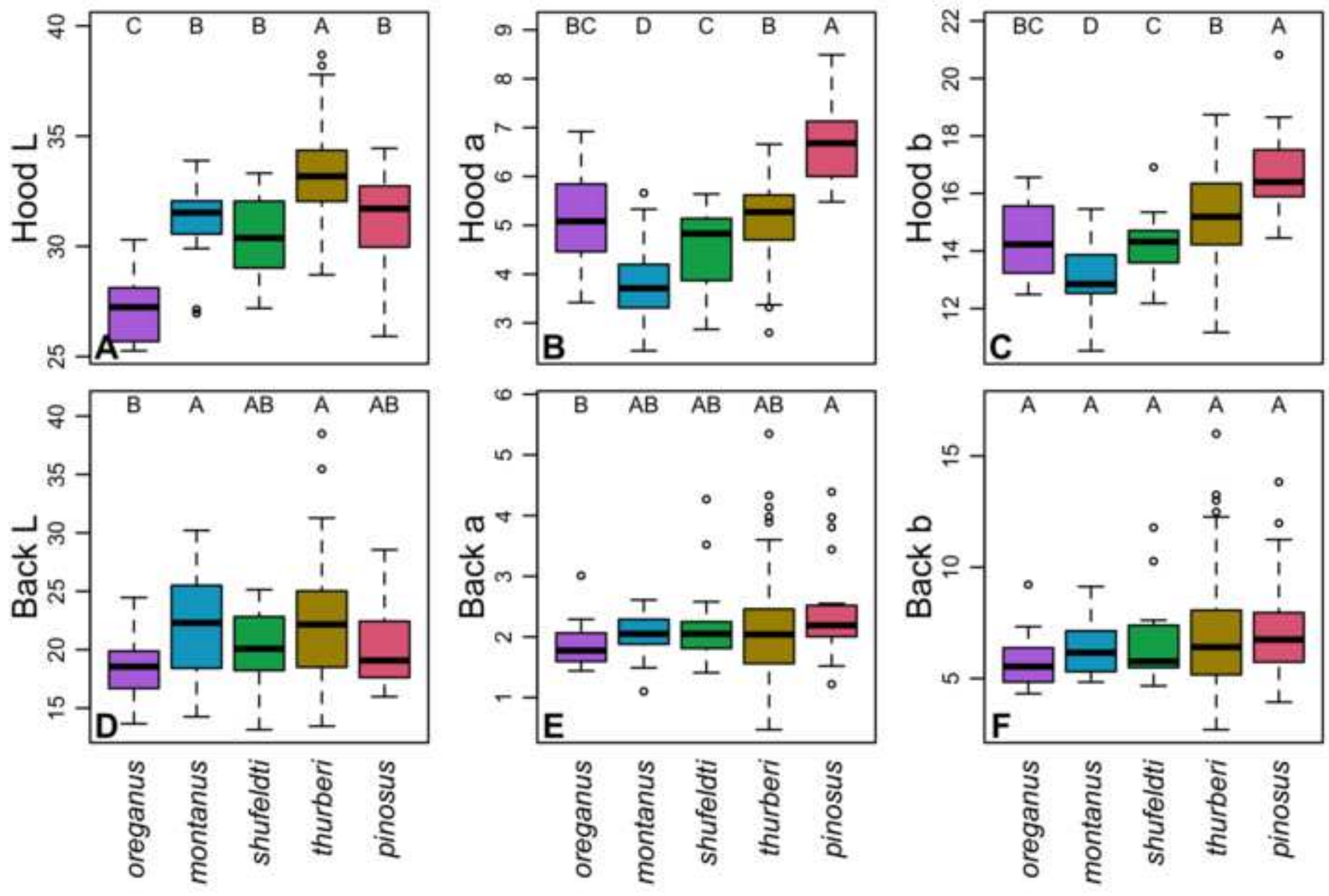
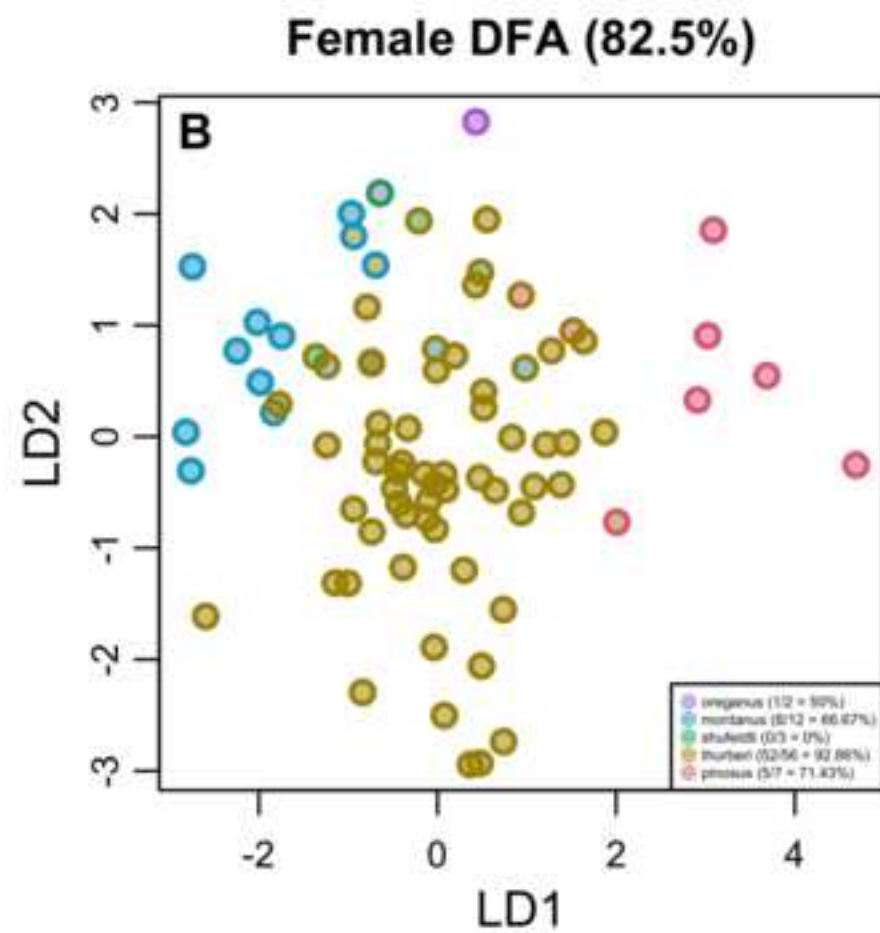
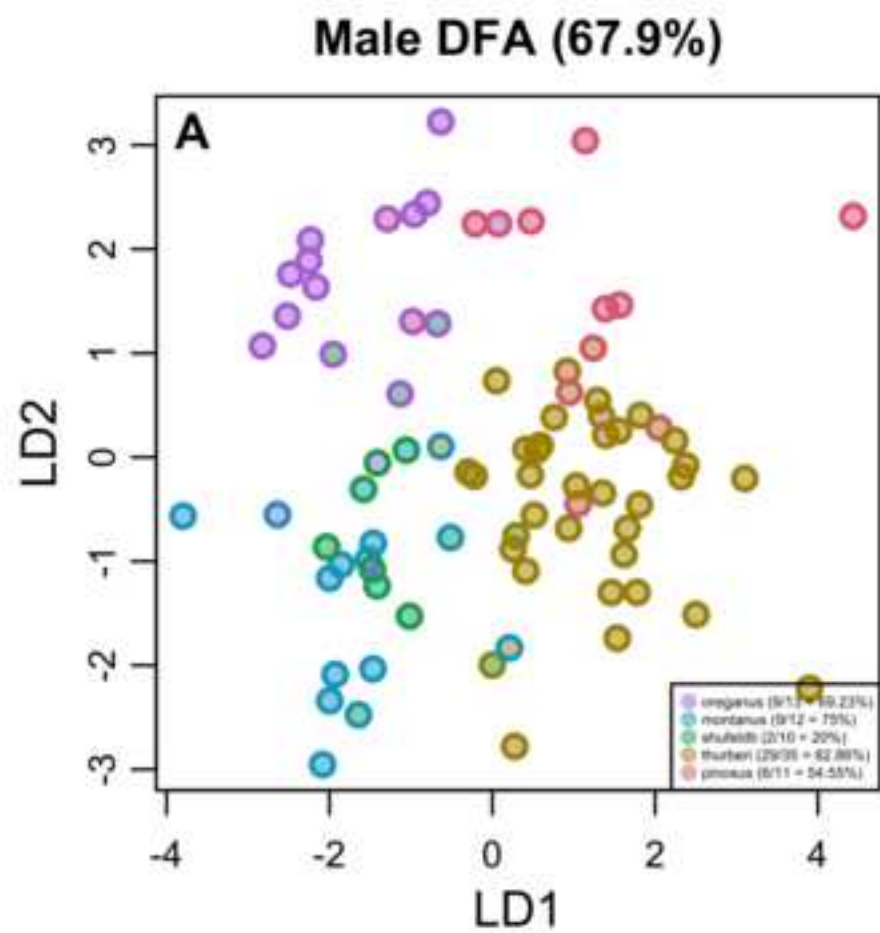
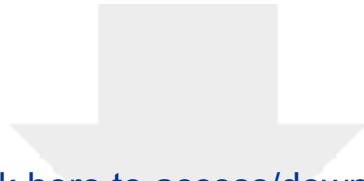


Figure 4

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Supplemental Material

Yang_Juncos_SupplementaryInformation_v1.docx

