1 **Parasite Assemblages of Double-crested Cormorants as Indicators of Host** 2 **Populations and Migration Behavior**

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4 Kate L. Sheehan^{1,3}, David W. Tonkyn², Greg K. Yarrow¹, Ron J. Johnson¹

5 ¹Department of Forestry and Environmental Conservation, 261 Lehotsky Hall, Clemson
6 University, Clemson, SC 29634-0317

7 ²Department of Biological Sciences, Clemson University, Clemson, SC 29634-0315

8 ³Corresponding author: Scripps Institution of Oceanography, University of California, San Diego,
9 La Jolla, CA 92093-0218

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11 **ABSTRACT:** The Double-crested Cormorant (*Phalacrocorax auritus*) is culled in many
12 states because of the real and presumed damages it inflicts on farmed and recreational
13 fisheries and other ecosystem services. Resident cormorant colonies breeding in the
14 southeastern United States are protected in some areas, so it is important to distinguish
15 these from co-occurring but unprotected migratory cormorants. Migratory *P. auritus* are
16 likely to contain helminthic parasite communities that differ from those of non-migratory,
17 resident birds, because they will encounter a wider variety of habitats and intermediate
18 host communities during migrations. Here, we document five distinct assemblages of
19 helminth parasites collected from 218 *P. auritus* culled from 11 sites in Alabama,
20 Minnesota, Mississippi, and Vermont. The assemblages of *P. auritus* parasites are
21 distinct among many sampling locations and can be used to correctly predict where a host
22 cormorant has been feeding. We provide evidence for mixing of cormorants at a regional
23 scale using discriminant analysis, which suggests there is a single population of
24 migratory cormorants. Furthermore, our models strongly differentiate between migratory

and resident *P. auritus* in the southeastern United States. In conjunction with species-by-species latitudinal and longitudinal trends, our models could serve as effective tools for managers interested in both the population control of migratory cormorants and the conservation of non-migratory, resident birds. Finally, parasite counts per host are notoriously variable with many zeros and a few large numbers, leading many researchers to use simple prevalence in their analyses. We show that at an intermediate level of data resolution, species occurrence ranks within individuals, behaves well statistically and provides the greatest discrimination among distinct host groupings.

1. Introduction

To reduce human-wildlife conflicts in the United States, legislative acts have given authority to state and federal wildlife managers to control mammal and bird populations that pose a threat to human health, safety, and apparent wellbeing (50 CFR 21.47 eCFR, 2013; FGC 4181, 2014; and 14 CCR 401, 2008). Consequently, programs to limit the colony sizes of the Double-crested Cormorant, *Phalacrocorax auritus*, through culling and egg-oiling programs (Bedard et al., 1995; DeVault et al., 2012; SCDNR News Release, 2013 accessible at http://dnr.sc.gov/news/yr2013/nov21/nov21_cormorant.html) are widespread throughout the United States.

P. auritus is a colonial, pursuit diving waterbird that primarily consumes forage fish (Brugger, 1995; Fenech et al., 2004). Large colonies of *P. auritus* are conspicuous

and have been suggested to deplete fish stocks from lakes, rivers, reservoirs, estuaries, and coasts in addition to farmed (aquaculture) aquatic ecosystems (Brugger, 1995, DeVault et al., 2012). Colony numbers and densities of *P. auritus* are higher today than at any time in the last 50 years (Jackson and Jackson, 1995), and colonies are commonly culled to reduce presumed effects to ecosystem services such as decreased sport fisheries, diminished water quality, impacts to co-nesting species, and fouling of nesting islands that could serve as sites for human recreation (Coleman and Richmond, 2007; Wires and Cuthbert, 2010; Boutin et al., 2011). Cormorants are subject to many laws that allow for both protection and management, including lethal control to limit impacts to aquatic resources (Wires and Cuthbert, 2006; Dorr and Somers, 2012). We used these management programs to acquire the carcasses of culled cormorants for parasite assessments.

Five distinct subspecies of *P. auritus* have been described: *P. a. cincinnatus* in Alaska; *P. a. albociliatus* in coastal California; *P. a. hueritas* in the Bahamas, *P. a. floridanus* in the southeastern United States (Audubon, 1840-1844; Bent, 192; Wires and Cuthbert, 2006); and *P. a. auritus* occurring throughout the interior and east coast of North America south to the Caribbean and Mexico (Palmer, 1962; Dolbeer, 1991; Watson et al. 1991, Hatch, 1995; Wires et al., 2001; Dorr et al., 2014). Based on winter sightings of banded birds, Dolbeer (1991) suggested that *P. a. auritus* consists of two distinct populations, one that breeds in the interior (migrating along the Mississippi flyway) and one on the Atlantic coast. However, molecular studies do not support the existence of multiple populations for any of the cormorant subspecies (Waits et al.,

2003). Furthermore, molecular assessments suggest that only three subspecies exist (Alaskan, Pacific coast, and interior/eastern North America; Mercer et al., 2013).

Like many other avian top-predators, *P. auritus* experienced population bottlenecks in the middle of the 20th century, with its geographic distribution shrinking dramatically (Kirsch, 1995; Krohn et al., 1995; Wires and Cuthbert, 2006). Double-crested Cormorants of the interior and Atlantic coast continue to migrate between breeding seasons with notable exceptions in the southeastern United States where resident cormorants are present year-round, including at newly-created freshwater reservoirs and aquaculture facilities. Aquaculture facilities also provide opportunities for wintering birds to reduce migration distances and, in some cases, encourage year-round inhabitation. Some suggest that these ‘new’ resident colonies are the expanding Florida subspecies rather than *P. a. auritus* (Wires et al., 2001; Wires and Cuthbert, 2006). Although Audubon (1840-1844 available online <https://www.audubon.org/birds-of-america/florida-cormorant>) considered resident cormorants to be a separate species (*Phalacrocorax floridanus*), they were downgraded to subspecies and molecular assessments have not differentiated migratory *P. a. auritus* from resident birds in Florida and the southeastern U.S. (Green et al., 2006; Waits et al., 2003).

In this study, we examine whether intestinal helminthic parasites differ among foraging groups of *P. auritus* and, if so, whether they can be used to identify the regional breeding locations (interior vs. coastal) and migratory status (northern vs. southern breeding) of individual hosts. Examination for parasites of culled birds from 11 sites in 4

states allowed us to assess the spatial distribution of parasite communities in relation to geographically distinct populations, and resident and migratory status. Using free-living multi-species indices is not uncommon in habitat assessments (Mawdsley and O'Malley 2009; Ogden et al., 2014) and here we test whether parasite assemblages differ enough among host groups for use as ecological indicators. If parasite assemblages differ for specific sampling sites, management plans for specific foraging groups could be developed. If assemblages differ among breeding regions, this might indicate the existence of distinct populations of coastal and interior *P. a. auritus*. If parasite assemblages differ among resident and migratory birds, then parasites can be used to assign migratory status of cormorants. This would be of basic interest, but could also benefit managers seeking to control one cormorant group while protecting another. For example, a management program for *P. auritus* that includes culling has been developed in South Carolina, where both migratory and breeding resident birds occur (SCDNR News Release, 2013 accessible at http://dnr.sc.gov/news/yr2013/nov21/nov21_cormorant.html) and additional culls are projected for other states where resident and migratory cormorants co-occur. We first describe the sampling methodology and assessment of parasite communities, then define distinct assemblages of parasites, and use predictive models to assign hosts to a site, region, migration status, and parasite assemblage. Finally, we test our models based on predicted (when known) versus actual characteristics of each host.

2. Methods

2.1 Sample Collection and Processing

The USDA/APHIS Wildlife Service of Minnesota, the Leech Lake Natural Resource Division, and the USDA/APHIS National Wildlife Research Center collected and assisted in preparation of frozen intestines of *P. auritus*, which were obtained from 11 sites from 2010 to 2012 (see Supplemental Interactive Map and Table S.3). Two of the southern sites had previously been reported to support breeding colonies of resident *P. auritus* (Swamp Roost, Mississippi (n=20) and Lake Guntersville, Alabama, U.S.A. (n=37); Hanson et al., 2010; B. S. Dorr, USDA APHIS/WS, personal communication), and four sites were known to support breeding colonies of migratory *P. auritus* (three in Minnesota [n=89] and one in Vermont, U.S.A. [n=25]). The remaining five locations had not been documented as *P. auritus* breeding sites (four in Mississippi [n=35] and one in Alabama, U. S. A. [n=22]).

(Insert Figure of map with KML file here).

We based our migratory status assignments of birds from information provided by managers familiar with site-specific breeding and wintering activities (K. Hanson-Dorr USDA APHIS/WS, personal communication). Because some birds were culled during winter months when both resident and migrant birds could be present (Glahn and

McCoy, 1995; Farley et al., 2001), all birds from Mississippi (n=35) and Cat Island, AL (n=22) were excluded from migratory model development. Thus, we did not include cormorants where the migration status might be contended (Dorr et al., 2014; Farley et al. 2001, Wires et al., 2001, Wires and Cuthbert 2006).

Intestines were frozen prior to parasite assessment and defatted before the contents were removed by cutting down the length of the intestine and stripping the contents and lining of the intestine from the tissue by hand (Rae 2003). We assessed 218 cormorant intestines (from base of proventriculus to cloaca) for presence of helminthic parasites. We washed intestinal contents in a 64µm sieve and fixed parasites either in 70% ethanol or 10% buffered formalin. Parasites were identified to the lowest possible taxonomic level based on previously reported parasites of the *Phalacrocorax* genus in North America (K.L. Sheehan, unpublished data).

We analyzed parasite data at three levels of resolution: raw counts (abundance) of each of the parasites within individual birds, ranks of relative abundance within individual birds (from 1 – most common, to 7), and presence or absence (prevalence). Raw counts are complete data for analysis, but include many zeros and some very large numbers, making parametric analyses challenging. Prevalence (presence/absence) contains the least information, but can be simplest to analyze. Rank data provide a useful, intermediate alternative that can be analyzed using parametric tests. It was important that we establish the appropriate level of resolution of parasite data in determining whether parasites could be used as biomarkers of host identities and movement.

2.2 Geographic Trends of Parasite Abundance

To assess changes in parasite distribution over the geographic range of *P. auritus* sampled in this study (see Supplemental Interactive Map), we used regression analyses to test for linear and quadratic associations between parasite intensity and prevalence with latitude and longitude. Note that these are the highest and lowest resolution measures that we considered. Positive correlation coefficients for latitudinal data indicated higher parasite numbers in the North and for longitude (using negative values for all sites west of the Prime Meridian) indicated higher parasite numbers in the East.

2.3 Parasite Community Assessments

We used a 1,000-permutation iterated multivariate Analysis of Variance (Adonis in the vegan package of R© version 2.0-9; Anderson, 2001; McArdle and Anderson, 2001; Oksanen et al., 2013) on the raw abundance data to test for significant differences in parasite assemblages among 11 sites. Using abundance data ensured that the analysis incorporated differences in the number as well as identity of parasites present. To determine how parasite assemblages differed, we then ran pairwise tests for all sites using the same methodology as the whole-system test (1,000-permutation Adonis; McArdle and Anderson, 2001; Anderson, 2001). This technique includes correlation matrices of response variables (parasite data) and sampling information (latitude and longitude, sample year, etc.; Supplementary Table S.1); thus, it accounts for autocorrelation among sites. Results of the Adonis analysis were confirmed with a Mantel test (Oksanen et al., 2013). Significant differences among pairwise tests were compiled into a binary matrix using the more conservative (highest) p-value of the Mantel and Adonis analyses. The

binary matrix was used in a Cluster Analysis (Average Hierarchical method using JMP® Pro 10. 0. 0) to combine sites into distinct parasite assemblages (Little et al., 2010). Assemblages identified as clusters were assessed qualitatively for confirmation of similarities or differences. Sites that did not differ (at an alpha level of 0. 05) from at least 4 other sites were not assigned to specific assemblages.

2.4 Predictive Models Using Parasite Data

We performed regularized discriminant function analyses (DA; lambda shrinkage to common covariance = 1, gamma shrinkage to diagonal = 1) with stepwise selection using JMP® Pro 12 to find axes that discriminate among pre-defined *P. auritus* groups (sample site, region, migratory status, parasite assemblage) based on their parasite assemblages (Higham and Jayne, 2004, Williams et al., 2008). We performed this assessment on each resolution of data (abundance, ranked abundance, and prevalence); however, ranked data yielded the greatest point separation and we will present only those results here.

Ranked data are more likely to meet or successfully transform to meet assumptions of parametric statistical tests than are raw counts (Kanno and Vokoun, 2008). Nonetheless, having many rare species in computations will ultimately skew the distribution of a dataset by introducing many unranked zero counts. To overcome this issue, we removed uncommon species from our ranking system if they met two criteria: 1) they occurred in $\leq 1\%$ of all hosts examined, and 2) were never the most abundant

194 parasite in any host. These criteria allowed us to exclude five uncommon parasites,
195 leaving eleven types of helminthes for our assessments using ranked data.

196 3 Results and Discussion

197 3.1 Parasites Recovered from Cormorant Intestines

198 Nine taxa of digenetic trematodes (see Supplemental Tables S.3 and S.4) occurred
199 in a combined 87% of the intestinal tracts examined. We also observed dilepidid cestodes
200 (65% prevalence), two taxa of nematodes (combined 53% prevalence), and two
201 acanthocephalans (combined 4% prevalence) in the intestines of *P. auritus* (see data
202 imbedded in Supplemental Interactive Map and Supplemental Table S.3).

203 3.2 Geographic Trends of Parasite Abundance

204 Four species of trematode changed significantly in intensity or prevalence with
205 latitude and/or longitude (Table S.1). *Drepanocephalus spathans* intensity was highest in
206 the north and west, and prevalence was highest in the west. *Hysteromorpha triloba*
207 increased in prevalence to the south. Three other species, *Neodiplostomum* sp.,
208 *Echinochasmus* sp., and *Austrodiplostomum ostrowskiae* increased in prevalence to the
209 south and west, while *Amphimerus* sp. increased in prevalence to the north. Cestode
210 prevalence and intensity increased to the north and east. The nematode *Contracaecum*
211 *rudolphi* was more prevalent in the east and north (Table S.1). Acanthocephalan
212 prevalence was highest in the east. The prevalences reported here are comparable to those
213 of cormorants in Florida (Hutton and Sogandares-Bernal, 1960; Hutton, 1964; Threlfall,
214 1982), Texas (Dronen, 2009), Mississippi (Overstreet and Curran, 2004; Doffitt et al.,

2009, O’Hear et al., 2014), central Canada (Chandler and Rausch, 1984; Kuiken et al., 1999; Robinson et al., 2008; Robinson et al., 2009; Wagner et al., 2012), and Mexico (Violante-Gonzalez et al., 2011; Garcia-Varela et al., 2012; see data imbedded in Supplemental Interactive Map and Table S.3). Because individual parasite species exhibit geographic gradients, and not all in parallel, the analysis of the parasite assemblage as a whole rather than of any one or few species will best discriminate populations from different sites, regions, or of different migration status.

3.3 Parasite Community Assemblage Analyses

In the full model with raw counts of parasites, multiple parasite assemblages of *P. auritus* emerged among the 11 sample sites ($p < 0.0001$). Cluster analysis of the resulting binary matrix from pairwise Adonis assessments (0 for significant differences, 1 for non-significant differences; Supplemental Table S.2) revealed five distinct parasite assemblages (Figure 1). Colonies from two sites, Wells Lake and Lake Waconia, MN, shared assemblages with all five groups and were not assigned to a distinct parasite assemblage. Although not presented, here, identification of parasites responsible for assemblage differences can be achieved by comparing prevalence and intensities between birds pooled within and among groupings.

232

233 Figure 1. Biplot of parasite assemblages grouped based on output of the Adonis Analysis
 234 illustrating the distribution of Double-crested Cormorant parasite assemblages in ordinate
 235 space. 50% contour lines are around each group mean. Group 1 represents Mossy
 236 Lake/Bee Lake, 2 = Leech Lake, 3 = Cat Island/Swamp Roost/Port of Columbus, 4
 237 =Lake Champlain/Whittington Channel, and 5 = Leech Lake/Lake, Guntersville.
 238 Canonical axis 1 explains 64.4% (eigenvalue=1.803, correlation=0.802, DF=32, $p<0.$
 239 0001) and axis 2 explains 24.8% (eigenvalue=0.695, correlation=0.447, DF=21, $p<0.$
 240 0001) of the separation of the means

241 With the Adonis analysis, we detected unique parasite assemblages for two year-
 242 round colonies of *P. auritus*: breeding birds from Lake Guntersville, AL and wintering
 243 birds at Swamp Roost, MS (Hanson et al., 2010). The parasite assemblage for Swamp
 244 Roost, MS was similar to those found at Port of Columbus, MS and Cat Island, AL,
 245 which provides nesting habitat to wading birds in summer and is a roosting site for *P.*
 246 *auritus* in winter (K. L. Sheehan, personal observation). The cormorants included in this

AL/MS assemblage were collected in winter, and we suggest this confirms accounts that some southern breeding cormorants disperse longitudinally along the Gulf of Mexico in winter (Audubon, 1840-1844, Johnsgard, 1993), and possibly that these sites attract previously migratory birds to southern breeding colonies. The strong delineation of multiple groups within a restricted geographic area might also result if foraging groups that developed on the breeding grounds persist on the wintering grounds. This geographic cohesion of breeding groups has been documented in some tagging studies of migratory cormorants (Dorr et al., 2012, King et al., 2012).

3.4 Predictive Models Using Parasite Community Data

Figure 2. Biplot of Double-crested Cormorant parasite assemblages based on ranked abundance data from different collection sites with mean confidence limit contour lines

259 around each group mean. Canonical axis 1 explains 53. 5% (eigenvalue=2. 008,
260 correlation=0. 817, DF=110, $p<0. 0001$) and Canonical axis 2 explains 25. 6%
261 (eigenvalue=0. 959, correlation=0. 700, DF = 90, $P<0. 0001$) of the separation of the
262 means.

263 Discriminant analysis models correctly assigned birds to their collection sites 37% of the
264 time using abundance data (Figure 2). The success rate rose to 46% and 49% when using ranked
265 data and prevalence, respectively. The success in assigning birds to their region of collection
266 increased to 60%, 73% and 71% for abundance, ranked data, and prevalence, respectively (Table
267 1). Finally, both ranked and prevalence data were more useful in distinguishing migration status
268 (both 78% successful) than were the abundance data (56%). In all three cases, analyses based on
269 the complete abundance data, with its huge variation, were less clear than were those based on
270 simple ranks and prevalence. We suspect this is why the Adonis analysis grouped migratory
271 birds from Minnesota to resident birds from Alabama. All of our models significantly
272 outperformed random classifications (equiprobable assignment $p < 0. 0001$; Table 2). Classifying
273 sites based on Adonis parasite assemblages improved the site prediction model (correct
274 prediction 70% of the time, $p < 0. 0001$, Figure 1) compared with grouping by site alone.
275 Reducing the number of collection sites based on the Adonis output allowed for coarse-scale
276 resolution of foraging grounds contributing to parasite assemblages. Pooling sampling sites in
277 this way could be informative for researchers in documenting the introduction of parasites into
278 aquatic systems as newly formed wintering and breeding colonies are established.

279 Many Lake Champlain, VT cormorants were misclassified by region. This was the only
280 site in the Northeast region and it shared parasite assemblage characteristics with birds from
281 Mississippi (South-central region). This overlap in northeastern and south-central parasite

communities is contrary to findings from banding recovery records (Dolbeer, 1991), and should be investigated further by assessing additional sites from New England and the Northcentral region of North America for confirmation.

Our models were most successful (78%) at classifying birds to migratory status (migratory vs. resident), confirming that parasite communities can be used to detect differences in the fish assemblages or feeding habits of migratory and resident *P. auritus*. This is independent evidence that may support the separation of subspecies that molecular studies have been unable to provide; however parasites of birds from Florida should also be assessed for further evidence. Many researchers have defined parasite communities based on host phylogeny (Arneberg et al., 1998; Price, 1989); here we use parasite communities to indicate host groupings.

Discriminate analysis models based on parasite communities are useful for the assignment of unknown host individuals to host groups, and we used this method to predict the migratory status of birds collected in winter. Birds collected in winter at Swamp Roost, a southern breeding site of *P. auritus*, were classified as a foraging group of migratory *P. auritus*. Another site in Mississippi, Bee Lake, was the only group of birds identified as having resident cormorants in winter. We received only 5 hosts from Bee Lake, and the unique classification of cormorants there might be a consequence of the small sample size, but it is likely that this is a winter foraging site for resident *P. auritus*. Here, we show how parasite data from only a few definitive hosts might indicate high species richness of intermediate host communities (fishes and invertebrates) that should be studied further for conservation considerations (Laurila-Pant et al., 2015).

Birds from the sites in Mississippi were often classified as migrants, confirming the results from the Adonis analysis which suggested that mixtures of migratory and resident birds yield distinct parasite community profiles. We believe the foraging groups collected during winter in Mississippi are indeed mixed colonies of migratory and resident cormorants and individual hosts maintain a large component of the parasite community acquired on summer foraging grounds through the winter season. Larger datasets of parasite assemblages from breeding colonies of resident and migratory *P. auritus* will help to determine the identity of wintering birds with more confidence.

4. Conclusions

Understanding characteristics that differentiate groups of animals can be informative for management and conservation initiatives. Parasite assemblages might be useful to distinguish individuals from different populations of the same species (Baldwin et al., 2012; Catalano et al., 2014), in the same way that genes (Frankham et al., 2010), genomics (Shafer et al., 2015), stable isotopes (Pekarsky et al., 2015), and other markers might. We suggest parasites be considered more readily for restoration and management applications (Shea et al., 2012) and could be used as indicators of population or ecosystem health (Costa et al., 2012). We found that some parasites of *P. auritus* showed clear geographic gradients in intensity or prevalence, suggesting that parasite species could be used to illustrate geographic gradients of parasitization for intermediate (invertebrate and fish) and avian definitive hosts. Moreover, we found that discriminant analyses based on parasite records could be used to assign *P. auritus* correctly to sites and regions of origin, and to migratory status. Parasite counts are notoriously variable from host to host, and we found that ranked abundance and even simple prevalence were more informative than were complete abundance data. These measures abstracted from the full counts

are less commonly used in community assessments (Kanno and Vokoun, 2008; Lennon et al., 2004; Mazaris et al., 2013), but in this study proved superior.

These results establish clear linkages between cormorant parasite assemblages and their associated migratory patterns. These results are particularly compelling given the disagreement on the status of different subspecies within *P. auritus* (Glahn and McCoy, 1995; Wires et al., 2001). As future research better clarifies how birds group in space and time, parasite assemblages could become a valuable tool for characterizing bird colony behavior as part of control or conservation management initiatives. For example, cormorants in South Carolina often inhabit distinct geographic areas, foraging and roosting in different locations. Managers might compare parasite assemblages of birds from these different locations to evaluate the degree to which resident cormorants integrate with migratory birds. Finally, the fact that regional populations of a widespread vertebrate host contain somewhat distinct parasite assemblages means that even local extinctions of some hosts may threaten parasite species, increasing conservation concerns (Colwell et al., 2012; Gomez and Nichols, 2013).

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Table 1. Model parameters and output comparing discriminant analyses model performance for three groupings (sampling site, geographic region, migration behavior) at three levels of resolution of the same parasite data (parasite abundance, prevalence, and ranked abundance). Optimum model (yielding the fewest misclassified hosts) output is given above that of the full model, which includes all parasites. Canonical estimation of point separation provides the number of significant axes, the cumulative variance explained by the significant axes, and a Wilk's Lambda p-value for model performance.

		Correct Classification			Sig. Axes	Cumulative Explanation	Wilk's p
		Parasites Included	Number	Percent			
Site	Abundance	11	98	37	3	81	<0.0001
		all	94	35	3	77	<0.0001
	Rank	10	100	46	4	93	<0.0001
		all	100	46	4	93	<0.0001
	Prevalence	15	107	49	3	82	<0.0001
		all	104	48	4	90	<0.0001
Region	Abundance	6	142	60	1	89	<0.0001
		all	133	55	1	88	0.0008
	Rank	6	160	73	2	100	<0.0001
		all	158	72	2	100	<0.0001
	Prevalence	8	154	71	2	100	<0.0001
		all	147	67	2	100	<0.0001
Migration	Abundance	12	134	56	4	93	<0.0001
		all	128	53	1	79	0.0032
	Rank	all	169	78	1	69	<0.0001
	Prevalence	all	1709	78	1	69	<0.0001

596 Table 2. Comparison of model performance (DA) for correctly classifying *P. auritus* by
 597 sample site, geographic region, or migration status (migratory or resident) when
 598 compared to null model (Null). Models built with all hosts (all) and subsets of hosts
 599 based on incomplete information (assemblages, known) are indicated with grouping
 600 descriptions. Performance of the discriminant analysis (DA) compared to the null (Sig.)
 601 derived with Chi-Square analysis.

Grouping	# Groups	Null	DA	Sig.
Site (all)	11	9%	43%	P<0. 0001
Site (assemblages)	5	20%	70%	P<0. 0001
Region	3	33%	74%	P<0. 0001
Migration (all)	2	50%	83%	P<0. 0001
Migration (known)	2	50%	84%	P<0. 0001

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