October 2010

MORPHOLOGICAL VARIATION OF GALAPAGOS ISLAND POPULATIONS OF THE YELLOW WARBLER DENDROICA PETECHIA AUREOLA

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SUMMARY

Culmen (beak) length and width, wing length and body mass varied significantly among six Galapagos island populations of the Yellow Warbler *Dendroica petechia aureola*. Culmen length and body mass were also significantly different between Galapagos and North American populations of *D. petechia*. Morphological differences among island populations of *D. p. aureola* may be related to resource variability and the presence of different bird species on different islands.

RESUMEN

Variación morfológica de las poblaciones del Canario María *Dendroica petechia aureola* **de las islas de Galápagos.** El largo y el ancho del pico, y la masa corporal, variaron significativamente entre las poblaciones del Canario María *Dendroica petechia aureola* de seis islas de Galápagos. El largo del pico y la masa corporal también fueron significativamente distintos entre las poblaciones de *D. petechia* de Galápagos y de Norte-América. Las diferencias morfológicas entre las poblaciones de *D. p. aureola* en las diferentes islas podrían relacionarse con la variabilidad de los recursos y la presencia de diferentes especies de aves en las diferentes islas.

INTRODUCTION

Studies of Galapagos birds have made significant contributions to our understanding of speciation and evolutionary processes, beginning with Darwin's observations and hypotheses to a series of modern investigations centered on finches Geospizinae (Grant 1999, Sato et al. 1999, Burns et al. 2002, Grant & Grant 2006). Key aspects of the Galapagos Islands as a model system to examine genetic divergence and genetic structure are their remoteness, fragmentation and age. The Galapagos Archipelago is c. 1100 km southwest of Central America, 1000 km from continental South America, and 720 km from Cocos Island (Costa Rica). Potassium-argon aging indicates a maximum age for currently emergent islands of less than six million years (Bailey 1976, Geist 1996), although a series of now submerged islands in this region may have formed more than 10 million years ago (Christie et al. 1992, Cox 1983, Geist 1996).

The Yellow Warbler *Dendroica petechia* occupies all major Galapagos Islands and many of the islets, where it is found in a variety of habitats but most commonly in littoral zone vegetation (Harris 1974). The diet is mainly arthropods, although fleshy fruit are also eaten (Castro & Phillips 2000, Guerrero-Gutiérrez 2002). Based on the rusty crown of mature males (Harris 1974, Castro & Phillips 2000), Yellow Warblers from the Galapagos Islands and Cocos Island have been recognized as a separate subspecies, *D. p. aureola* (Browning 1994, Lowther

et al. 1999). There appears to be little genetic structure in the Galapagos Yellow Warbler population, with a number of identical mtDNA haplotypes occurring on numerous islands dispersed throughout the archipelago (Browne *et al.* 2008). Although Yellow Warblers were previously thought to have colonized the Galapagos in historical times (Snow 1966, Steadman 1986) recent molecular evidence suggests that the Galapagos and mainland American populations diverged more than 37,000 years ago (Browne *et al.* 2008).

In this study, variation in culmen (beak) length, culmen width, wing length, and body mass are used to estimate morphological divergence among six Galapagos island populations. Divergence is also investigated between the *D.p. aureola* from the Galapagos Archipelago and *D. petechia* from three previously reported sites: Manitoba River delta (Canada), MacKenzie River delta, Alaska (U.S.A.) and northern South America (Lowther *et al.* 1999).

In addition, we present limited data on beak morphology for Galapagos populations of the Large-billed Flycatcher *Myiarchus magnirostris* and Grey Warbler Finch *Certhidia fusca*. The presence or absence of other competing species can result in morphological change in as short a period as a year, as demonstrated among species of Darwin's finches (Grant & Grant 2006). *M. magnirostris* and *C. fusca* are both potential competitors for food resources with *D. petechia* (Grant & Grant 1989, Tonnis *et al.* 2004). Although *D. petechia* are currently abundant on Floreana Island they are absent from the fossil record (Steadman

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1986). It has been suggested that they are relatively recent arrivals to that island and may have thereby contributed to the apparent recent extinction of *C. fusca* from Floreana (Grant *et al.* 2005). However the two species coexist in the same habitat on other Galapagos islands (Lack 1947, Bowman 1961, Grant & Grant 2002).

METHODS

Adult D. p. aureola in the Galapagos were captured for morphological measurements in mist nets at the same locations on six islands where they were captured for a genetic study (Browne et al. 2008): Punta Cevallos (Española Island), 1°23.47'S, 89°37.15'W; Puerto Ayora (Santa Cruz), 0°40.12'S, 90°10.16'W; Post Office Bay (Floreana), 1°13.37'S, 90°27.37'W: Espumilla Beach (Santiago), 0°10.30'S, 90°30.32'W; Punta Pitt (San Cristóbal), 1°42.30′S, 89°14.90′W; Darwin Bay (Genovesa), 0°18.75′N, 89°56.45'W (study area 1 depicted in Fig. 3.1 of Grant & Grant 1989). All individuals were captured in May 2001 except those from Española which were captured in January 2001. On Santa Cruz, in addition to the ten individuals captured in 2001, eight additional adult birds from the highlands (Tortoise Reserve) were mist-netted in December 1981 by DJA. Morphological measurements were recorded only on adult males and females that could be confidently sexed. Morphological measurements consisted of culmen length measured from the anterior edge of the nostril to tip, culmen width measured at the anterior edge of the nostril, flattened wing chord (distance from bend of wrist to tip of ninth primary, with radiusulna and manus held at right-angle), and body mass for all individuals with the exception of those sampled on Española, the first island visited, where only wing length and body mass were measured. Body mass was measured by weighing a bird in a mesh bag with a spring scale and the mass of the bag was recorded after the removal of the bird. Since DJA captured the individuals in 1981 and trained the other authors of this study, there was continuity in measurement techniques for the 1981 and 2001 collections. M. magnirostris and C. fusca that were captured incidentally in mist nets when sampling *D*. *p*. aureola were measured for culmen length, culmen width, wing length and mass. Morphological measurements are presented as means \pm SD.

RESULTS

Males and females in the combined Galapagos population (all individuals sampled, not weighted by island) were not significantly different in culmen length (males 9.36 ± 0.55, n = 19; females 9.38 ± 0.32, n = 18; $F_{1,35} = 0.05$, P = 0.64), culmen width (males 1.98 ± 0.18 , n = 19; females 2.11 ± 0.17 , n = 18; $F_{1,35} = 1.00$, P = 0.33) or mass (males 12.1 ± 1.06 , n = 35; females 11.9 ± 0.86 , n = 26; $F_{1,59} = 0.22$, P = 0.33), but were significantly different in wing length (males 64.07 ± 2.19 , n = 35; females 62.18 ± 2.14 , n = 26; $F_{1,59} = 11.06$, P = 0.002).

There were no significant differences in any of the measured variables between Santa Cruz *D. p. aureola* collected in 1981 and those collected in 2001.

Measurements of *D. p. aureola* (sexes combined) are presented in Table 1. Three of the four characters varied significantly among subpopulations (culmen length, $F_{4,32}$ = 7.9, *P* < 0.001; culmen width, $F_{4,32}$ = 21.3, *P* < 0.001; mass, $F_{5,56}$ = 9.5, *P* < 0.001). Although wing length was not significantly different between islands for males and females combined ($F_{5,56}$ = 1.0, *P* = 0.44), when separated by sex, wing length differed between islands for males ($F_{4,30}$ = 3.20, *P* = 0.027) but not for females ($F_{3,22}$ = 3.20, *P* = 0.169). Santa Cruz individuals had the shortest and narrowest beaks. Individuals from Española weighed the least, while individuals from Genovesa weighed the most and had the widest beaks.

There were no significant correlations among culmen length, culmen width, wing length and mass among island populations.

Comparable mean and variance measures for other *D. petechia* subspecies have only been reported for *D. p. amnicola* from Manitoba and *D. p parkesi* from the MacKenzie River delta (Lowther *et al.* 1999). Combining all Galapagos populations, *D. p aureola* were significantly larger than *D. p amnicola* in male culmen length ($t_{76} = 11.9$, *P* < 0.001), female culmen length ($t_{38} = 19.4$, *P* < 0.001), male mass ($t_{194} = 11.9$, *P* < 0.001) and female mass ($t_{156} = 11.6$, *P* < 0.001), with no significant differences for male or female wing length. *D. p aureola* were significantly larger than *D. p. parkesi* in culmen length (the only variable reported by Lowther *et al.* 1999) ($t_{53} = 16.3$, *P* < 0.0001). Additional culmen length means (without measurements of variance) have been reported for *D. p rubiginosa* from Alaska and *D. p banksi* from Yukon (Canada) (Browning 1994). The data from these

Table 1. Measurements (mean ± SD) of Dendroica petechia aureola from six Galapagos Islands.

	Culmen length (m	m) n	Culmen width (mi	m) n	Mass (g)	n	Wing length (mm)	n
Genovesa	9.23 ± 0.51	4	2.27 ± 0.12	4	13.45 ± 1.04	4	63.00 ± 3.19	4
Santiago	9.88 ± 0.55	4	2.17 ± 0.06	4	12.38 ± 0.85	4	64.38 ± 1.38	4
Santa Cruz	9.06 ± 0.25	18	1.87 ± 0.10	18	12.27 ± 0.71	21	63.73 ± 1.97	21
San Cristóbal	9.62 ± 0.35	7	2.13 ± 0.11	7	12.21 ± 0.79	7	63.00 ± 2.22	7
Floreana	9.72 ± 0.23	4	2.14 ± 0.01	4	13.15 ± 1.30	4	63.20 ± 1.96	4
Española					11.20 ± 0.57	21	62.38 ± 2.73	21

five sites indicate that culmen is 13–25 % longer in *D*. *p*. *auroela* than in *D*. *petechia* from northern Canada or Alaska.

No significant differences were found in culmen length, culmen width, mass and wing length between three island populations of *M. magnirostris* (Table 2). *M. magnirostris* are only vagrants to Genovesa (Castro & Phillips 2000, DJA pers. obs.) and no *M. magnirostris* were captured there or on San Cristóbal or Española. Culmen length and width of *C. fusca* for Genovesa (n = 16) were 7.51 ± 0.23 and 2.15 ± 0.13 , respectively; the mass was 9.43 ± 0.29 and wing length was 53.9 ± 1.41 . *C. fusca* were not captured on the other islands. These measurements indicate that *M. magnirostris* is 16 % heavier than Galapagos *D. p. aureola*, with a 12 % longer wing and a culmen that is 18 % longer and 29% wider. In contrast, *D. p. aureola* is 28 % heavier than *C. fusca*, with a 17 % longer wing and a culmen that is 25% longer but differs < 1 % in width.

DISCUSSION

Although no inter-island correlation occurred between any of the four measurements, statistical power was low since a maximum of six populations were measured. In a more extensive analysis of 617 skins of more than 40 breeding D. petechia populations from near the Arctic Circle to the equator, Wiedenfeld (1991) found a significant negative correlation between body mass and latitude, with the largest individuals in the equatorial region, but reported only summarized statistics and did not include data from individual populations. Wing length, however, did not follow the overall size trend; although the longest wings occurred in the south, the shortest also occurred in the tropics (on Caribbean islands). Variation in wing length appears to be related to migratory distance. Although Wiedenfeld (1991) did not give supporting data, he characterized Galapagos D. p. aureola as having a long tail and tarsus and proportionately short wing and bill. In general, body mass for *D. petechia* mass fluctuates seasonally and diurnally and in females is affected by presence of an egg in the oviduct (Baldwin & Kendeigh 1938, Wiedenfeld 1991).

The pattern found in *D. p. aureola* of low levels of interisland genetic variation (Browne *et al.* 2008), combined with significant differences in culmen length, culmen width and body mass on different islands, is also seen in Darwin's finches (Petren *et al.* 2005), land iguanas *Conolophus subcristatus* (Rassman 1997), giant tortoises *Geochelone* spp. (Caccone *et al*. 1999, 2002) and *Opuntia* cacti (Browne *et al*. 2003, Helsen *et al*. 2009), all of which have distinct phenotypes among islands with shallow but significant levels of genetic divergence. In other organisms, including Galapagos mockingbirds *Nesomimus* spp. (Arbogast *et al*. 2006), land snails *Bulimulus* spp. (Parent & Crespi 2006) and darkling beetles *Stomion* spp. (Finston & Peck 2004) distinct morphological differences among islands are accompanied by more pronounced genetic differences.

The evolutionary origin of the observed differences in culmen length, culmen width and body mass for *D*. *p*. aureola on different islands might be due to chance (founder effects or genetic drift), possibly in combination with selection. Chance effects become less important with increasing movement of individuals among islands, accompanied by a decrease in genetic structure. The distribution of the same mtDNA haplotype on more than one island and the low level of genetic structuring among islands (Browne et al. 2008) suggest that effects other than chance influence beak morphology and body mass. Selection on trophic structures (bill dimensions) may result in character displacement, as shown for Darwin's finches (Grant 1999). The presence or absence of M. magnirostris or C. fusca could lead to character displacement in D. p. aureola, since all three species specialize on arthropods and eat at least small amounts of fruit (Grant & Grant 1989, Guerrero-Gutiérrez 2002). M. magnirostris is absent from some islands where D. p. aureola is present, such as Genovesa (Harris 1974, Castro & Phillips 2000). However, C. fusca is extremely common on Genovesa (Castro & Phillips 2000) and was the most common bird caught in our nets there (whereas in all other locations D. *p. aureola* was the most common bird caught). These differences in potential competitors may cause directional $selection on trophic structures of {\it D. p. aureola}. On Genovesa,$ where the smaller *C. fusca* is common and the larger *M*. magnirostris is absent, displacement in some morphological traits of *D. p. aureola* toward a larger size might be predicted. This was not the case for wing length and culmen length (D. p. aureola on Genovesa had shorter culmens and wings than most other Galapagos subpopulations), but was found for culmen width and body mass (Genovesa birds had the highest values among all island subpopulations). A possible interpretation is that selection on Genovesa has favored "stouter" individuals, with more mass per unit of wing length and a thicker beak per unit of length, a morphotype that approximates that

Table 2. Measurements of Myiarchus magnirostris captured on Santa Cruz, Santiago and Floreana islands.

	n	Culmen length (mm)	Culmen width (mm)	Wing length (mm)	Mass (g)
Santa Cruz	11	10.93 ± 0.38	2.71 ± 0.14	70.23 ± 4.22	13.76 ± 0.71
Santiago	7	11.03 ± 0.41	2.72 ± 0.16	71.53 ± 4.69	13.92 ± 0.42
Floreana	3	11.14 ± 0.30	2.74 ± 0.11	72.09 ± 2.33	14.07 ± 0.39
Above combined	21	10.99 ± 0.37	2.72 ± 0.15	70.93 ± 4.74	13.86 ± 0.57

of the absent *M. magnisrostris*, which deviates more from *D. p. aureola* in body mass than in wing length and more in culmen width than length.

The mtDNA data (Browne et al. 2008) indicate significant genetic divergence between Galapagos D. petechia and populations from the American continents. The rusty crown of Galapagos D. p. aureola clearly separates it from other D. petechia populations. Our results show that Galapagos D. p. aureola are also significantly larger than at least some North American populations in culmen length, culmen width and body mass. Passerines on islands usually have larger bodies and bills than mainland populations of the same species (Grant 1965, Lack 1971, Clegg & Owens 2002). A larger bill may permit use of a wider range of resources, and an increase in body size may reflect a more "generalist" strategy (Scott et al. 2003). However, Galapagos D. p. auroela appear to have similar mass and bill size to those from the Pacific coast of South America (Wiedenfeld 1991).

Our study was based on small samples from each island and should be considered preliminary. Additional studies will be necessary before robust conclusions can be made about inter-island variation of *D. p. auroela* or differences between Galapagos birds and continental populations of *D. petechia*.

ACKNOWLEDGMENTS

Kathryn Huyvaert, Paola Espinosa, John Colavincenzo, Travis Vesel and Jenny Trucano provided field assistance. The Charles Darwin Research Station and TAME airline provided logistical support and the Servicio Parque Nacional Galápagos provided research permits. Peter Grant and an anonymous reviewer provided constructive suggestions. This paper is based upon work supported by the National Science Foundation under grant no. DEB 98-06606 to D.J.A. and by the Richter Foundation.

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FIRST INVENTORY OF ANTS (HYMENOPTERA: FORMICIDAE) ON BALTRA ISLAND, GALAPAGOS

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SUMMARY

Baltra island is vulnerable to ant invasions because it is one of the principal ports of entry to the Galapagos archipelago. In spite of this, little was known about its ant fauna. We present 13 new records of ants for Baltra collected during 2005 and 2006: *Tapinoma melanocephalum*, *Camponotus planus*, *Paratrechina longicornis*, *Paratrechina* sp., *Monomorium destructor*, *M. floricola*, *Pheidole* sp., *Solenopsis geminata*, *S. globularia pacifica*, *Tetramorium bicarinatum*, *T. lanuginosum* and *T. simillimum*. In addition to this, we report a new species for Galapagos: *Monomorium* sp. nr. *pharaonis*. *S. geminata* and *M. destructor* are considered threats to native fauna

RESUMEN

Primer inventario de las hormigas (Hymenoptera: Formicidae) en la Isla Baltra, Galápagos. La isla de Baltra es uno de los puntos vulnerables a la introducción de hormigas invasivas ya que es uno de los puertos principales del archipiélago de Galápagos. Pese a ello durante mucho tiempo la isla ha permanecido poco conocida en cuanto a su myrmecofauna. Presentamos 13 registros nuevos de hormigas para Baltra colectados durante 2005 y 2006; *Tapinoma melanocephalum, Camponotus planus, Paratrechinalongicornis, Paratrechina sp., Monomorium destructor, M. floricola, Pheidole sp., Solenopsis geminata, S. globularia pacifica, Tetramorium bicarinatum, T. lanuginosum and T. simillimum. Incluimos al resultado un nuevo registro de hormiga para Galápagos: <i>Monomorium sp. c. pharaonis*. Identificamos a *S. geminata* y *M. destructor* como las especies de mayor amenaza a la fauna nativa.

INTRODUCTION

Baltra is a small island (25.1 km²) that lies north of the island of Santa Cruz. The vegetation is similar to that of northern Santa Cruz and is dominated by native and endemic plants such as *Bursera malacophylla* B.L. Rob, *Chamaesyce punctulata* (Andersson) D.G. Burch, *Cordialutea* Lam., *Crotalaria pumila* Ortega, *Opuntia echios var. echios*

Howell, *Panicum alatum var. minus* (Andersson) Zuloaga & Morrone, *Parkinsonia aculeata* L., and *Scalesia crockeri* Howell, and with important introduced elements such as *Cleome viscosa* L. (Wiggins & Porter 1971). Baltra has also been altered by human activities including the introduction of exotic animals. During the Second World War, Baltra was converted into a U.S. military base and in 1946 was placed under the jurisdiction of the armed forces of