

SEXUAL SIZE DIMORPHISM AND MORPHOLOGICAL EVIDENCE SUPPORTING THE RECOGNITION OF TWO SUBSPECIES IN THE GALÁPAGOS DOVE

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Abstract. Sexual size dimorphism is a conspicuous trait of many wild bird species. Differences in body size between the sexes might reflect selective pressures and trade-offs to optimize performance. Here, we analyze the size dimorphism of the Galápagos Dove (*Zenaida galapagoensis*) using principal component and discriminant analyses with samples obtained from six islands: Santiago, Santa Fe, Santa Cruz, Española, Genovesa, and Wolf. We also reanalyze published morphological data but also including additional samples from Wolf Island to account for morphological differences among islands. Males were significantly larger than females. Discriminant analyses correctly classified 98% of males and 100% of females, and cross-validation of the model correctly classified 97% of males and 98% of females. We created two sexual size dimorphism indices using wing chord and tarsus as body-size surrogates. Significant differences were found in the sexual size dimorphism index for both measurements among islands. Significant differences in sexual size dimorphism among islands might indicate the role of different selective pressures acting on individual islands (e.g., competition, predation, resources, sexual selection), which might result in life history variation of the species among islands. For the first time, we provide significant morphological evidence supporting the classification of the Galápagos Dove into two subspecies: *Z. g. galapagoensis* and *Z. g. exsul*.

Key words: Galápagos, morphology, sexual size dimorphism, *Zenaida galapagoensis*.

Dimorfismo Sexual de Tamaño y Evidencia Morfológica que Apoya la Separación de *Zenaida galapagoensis* en Dos Subespecies

Resumen. El dimorfismo sexual de tamaño es una característica común de muchas especies de aves. Las diferencias en el tamaño corporal entre machos y hembras puede reflejar la acción de factores de selección y soluciones de costo-beneficio que actúan para optimizar el rendimiento de las aves en su ambiente. Analizamos el dimorfismo de tamaño de *Zenaida galapagoensis* por medio de análisis de componentes principales y análisis de discriminación utilizando muestras colectadas en seis islas: Santiago, Santa Fe, Santa Cruz, Española, Genovesa y Wolf. También reanalizamos información morfológica previamente publicada, en donde incluimos muestras provenientes de la isla Wolf la cual no estuvo comprendida en el estudio anterior, para analizar diferencias morfológicas entre las islas. Los machos fueron significativamente más grandes que las hembras. El análisis de discriminación clasificó correctamente el 98% de los machos y el 100% de las hembras, el análisis de validación del modelo de discriminación clasificó correctamente el 97% de los machos y el 98% de las hembras. Creamos un índice de dimorfismo sexual de tamaño utilizando la cuerda alar y el tarso como medidas de tamaño corporal. Se encontraron diferencias significativas en el dimorfismo sexual de tamaño entre algunos pares de islas para ambas medidas. Diferencias significativas en el dimorfismo sexual de tamaño pueden indicar la acción de diferentes presiones selectivas en diferentes islas (e.g., competición, depredación, recursos, selección sexual), lo cual puede crear variaciones en la biología de la especie entre las distintas islas. Por primera vez, proveemos resultados morfológicos significativos que apoyan la separación de *Z. galapagoensis* en dos subespecies: *Z. g. galapagoensis* y *Z. g. exsul*.

INTRODUCTION

Animal life-history traits are strongly influenced by body size. Sexual dimorphism within

species (e.g., plumage color or body size) is a widespread phenomenon throughout the animal kingdom (Butler et al. 2000). Different body sizes reflect trade-offs and selective pressures (e.g., environmental conditions, sexual selection) acting on different populations and between the sexes (Wikelski and Trillmich 1997,

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Owens and Hartley 1998). In general, there is a strong positive association between sexual size dimorphism and individual body size (Fairbairn 1997, Wikelski and Trillmich 1997). Apparently, this relationship results from the advantage of being large, with the sexes benefiting in different ways as size increases. Males may acquire priority access to food resources, better territories, and increased mating success; females may acquire higher fertility (Fairbairn 1997, Wikelski and Trillmich 1997).

Geographic isolation of populations is expected to influence differentiation of both morphological and genetic characters, due to drift or different selective regimes (Slatkin 1985, Hutchison and Templeton 1999, Coleman and Abbott 2003). Santiago-Alarcon et al. (2006) showed that males and females of the Galápagos Dove (*Zenaida galapagoensis*) are morphologically similar among five islands of the Galápagos archipelago (Santa Fe, Santa Cruz, Santiago, Española, and Genovesa). High gene flow is apparent among these islands (Santiago-Alarcon et al. 2006); hence, significant differences in sexual size dimorphism among islands would not be expected. However, as Wikelski and Trillmich (1997) showed in lava lizards of the archipelago, sexual size dimorphism may vary significantly among populations located within the same island group and in close geographical proximity, possibly due to high variation in microclimatic conditions on different islands (Wikelski and Trillmich 1997).

The Galápagos Dove is an endemic species whose biology is poorly known. Our knowledge about this species is restricted to taxonomic relationships (Goodwin 1977, Johnson and Clayton 2000), morphological records (Ridgway 1897, Gifford 1913, Prestwich 1959), and some aspects of its breeding and feeding ecology on Genovesa Island (Grant and Grant 1979). Morphological and ecological studies of birds in the Galápagos archipelago have been confined to few species, including Darwin's finches (Bowman 1961, Boag 1981, 1983, Grant et al. 1985, Grant 2001), Galápagos mockingbirds (*Nesomimus* spp.; Curry 1988, 1989, Curry and Grant 1989), and the Galápagos Hawk (*Buteo galapagoensis*; Bollmer et al. 2003, 2005). Measurements and general descriptions of Galápagos Doves are given by Ridgway (1897), Gifford (1913), and Swarth (1931).

These authors provide measurements for a limited number of individuals and do not present any rigorous statistical analysis in support of their claims for two different subspecies of the dove. Color patterns in this species are the same for both sexes, although females tend to be duller than males. However, differences in color intensity are not obvious and can vary individually, making sex difficult to determine. Juveniles have a different color pattern than adults and are easily distinguished. Some aspects of the biology of sexually monochromatic bird species (i.e., the same or very similar plumage coloration between the sexes) are difficult to study in the wild because sexes are identical (Winker et al. 1996).

We analyzed the sexual size dimorphism of the Galápagos Dove using principal component and discriminant analyses, created two sexual size dimorphism indices, and evaluated whether there were significant differences across islands by reanalyzing the morphological data in Santiago-Alarcon et al. (2006) but including samples from Wolf Island, individuals from which represent what is considered a different subspecies of the Galápagos Dove (Swarth 1931, Grant and Grant 1979). The specific questions addressed in this study are: (1) whether there is sexual dimorphism in body size of the endemic Galápagos Dove; (2) whether there are differences among island populations in the degree of sexual dimorphism; and (3) whether there are morphological differences that separate the two subspecies.

METHODS

FIELD METHODS

We conducted this study in the Galápagos archipelago from May through July 2002, from June through July 2004, and during July 2005. We sampled individuals using hand nets and mist nets following the guidelines in Ralph et al. (1996). We took blood samples (50 μ l) by venipuncture from 25 birds each from Santa Cruz (15 males, 10 females), Santa Fe (15 males, 10 females), and Española Islands (11 males, 14 females), 30 each from Santiago (18 males, 12 females) and Genovesa Islands (20 males, 10 females), and 29 from Wolf Island (13 males, 16 females; Fig. 1). Samples were mixed with 500–700 μ l of Longmire's lysis buffer (Longmire et al. 1988). We used a PCR-based

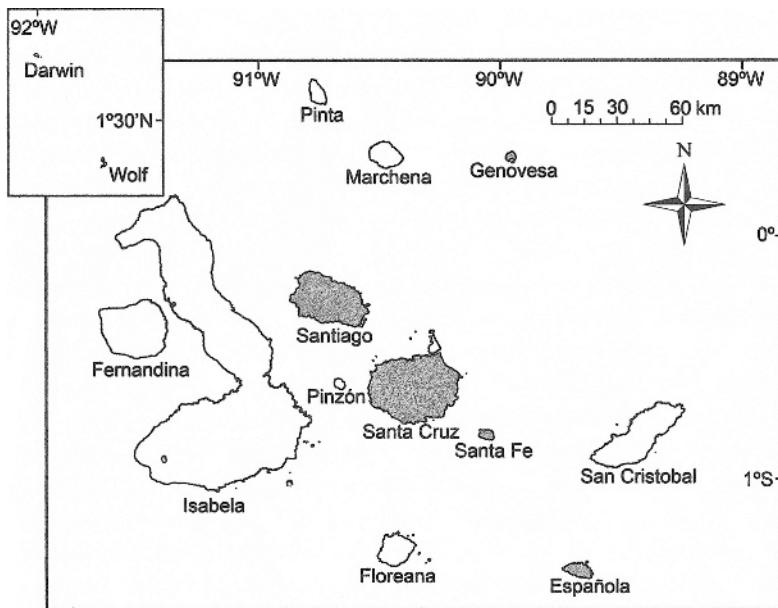


FIGURE 1. Map of the Galápagos archipelago, with islands on which Galápagos Doves were measured shaded in gray. Wolf and Darwin islands are located 186 km and 239 km, respectively, northwest of the northern tip of Isabela Island.

technique for sexing individuals (Fridolfsson and Ellegren 1999). We visited San Cristobal during 2002 and Darwin during 2005, but due to small sample sizes ($n = 2$ and 4, respectively) these islands were not included in our analysis. To quantify intersexual differences in morphology, we took the following measurements to the nearest 0.1 mm from the right side of each individual: (1) tarsus (from the joint between the tibiotarsus and the tarsometatarsus to the bent joint between the tarsometatarsus and metatarsals); (2) tail (posterior base of uropygial gland to tip of central rectrices); (3) exposed culmen (from the tip of the feathering to the bill's tip); (4) bill width (calipers were oriented at a 90° angle to the axis of the bill and measurement was taken at the tip of the feathering); (5) bill depth (at the tip of the feathering and at 90° angle to the axis of the bill); and (6) wing chord, to the nearest 0.5 mm, using a ruler with a brass perpendicular stop (unflattened, from carpal joint to the tip of the longest primary). Mass was measured to the nearest 0.1 g using Pesola scales (100 g and 300 g). Raw morphological measurements can be obtained by request from DS-A. Measurements were taken by DS-A on all the islands but Santa Fe, where

Jennifer Bollmer (JB) conducted the sampling. Although JB worked with DS-A on other islands and was instructed in dove measurement by DS-A, measurement error due to observer variability could create false differences among islands. Hence, both DS-A and JB measured Rock Pigeon (*Columba livia*) and Mourning Dove (*Zenaida macroura*) individuals at the Saint Louis Zoo to assess observer variability. There were no significant differences between these observers in any of the measured variables (same variables as measured in this study; $Z \geq 0.3$, $P \geq 0.44$). Wild birds were released within 40 m of their capture location.

STATISTICAL ANALYSES

We used principal component analysis (PCA) to describe morphological variation between the sexes. We used SPSS v. 11.0.1 for Windows (SPSS 2001) in all analyses. Although all variables were normally distributed (Kolmogorov-Smirnov test, $P \geq 0.09$) and had the same scale and dimension (except mass), they were log-transformed to examine the proportional contributions of large and small measurements equally. Principal component (PC) scores were normally distributed (Kolmogorov-

Smirnov test, $P \geq 0.86$). All components with eigenvalues ≥ 1 were retained for subsequent analyses. Eigenvectors were rotated using varimax rotation. We retained rotated eigenvectors when the explained variance was higher than that of unrotated components or when the interpretation of principal components was easier. We used t -tests for group comparisons of PC scores (males vs. females); t -tests were independent and two-tailed. Variances of PC scores were homogeneous among groups (Levene's test, $P > 0.32$). In addition to the dimorphism analysis, we conducted two PCAs, one for males and one for females, to examine morphological variation among islands. These analyses used previously published data (Santiago-Alarcon et al. 2006) with the addition of samples from Wolf Island, which were not available for analysis in the previous study. Individuals from Wolf Island represent what is considered a different subspecies of the Galápagos Dove (*Z. g. exsul*), which is restricted to the northern islands of Darwin and Wolf. We conducted the analyses describing morphological variation among islands separately by sex to prevent any variance due to sexual dimorphism from masking variation among populations. Bill depth was excluded from the PCA for females because only one individual was measured for this variable on one of the islands (Santiago). We used ANOVAs to test for differences among islands. We used Tukey post-hoc tests any time an ANOVA was significant.

We used discriminant analysis (DA) to create a discriminant function that complemented the PCA analysis for sexual dimorphism. Because doves from Wolf Island are significantly larger (see results) than those of the southern islands, we conducted separate discriminant analyses for the southern subspecies (*Z. g. galapagoensis*) and the northern subspecies (*Z. g. exsul*). Samples from Genovesa Island were taken two years (2004) after the rest of the samples (2002), thus we decided to compute two discriminant analyses for the southern subspecies. One analysis excluded Genovesa samples, which subsequently were used to validate the model; the other analysis used all individuals from the five sampled islands. This second model was validated using the U -method (leave-one-out; McGarigal et al. 2000). In addition to the normality and variance assumptions fulfilled for PCA and detection of outliers, we

checked for equality of variance-covariance matrices using Box's test for the two DA analyses ($M = 5.5$, $df = 6$, $P = 0.51$ and $M = 7.1$, $df = 6$, $P = 0.33$, respectively). Multicollinearity was checked by conducting pairwise correlations (culmen vs. tarsus: $r = 0.82$, $P = 0.01$; culmen vs. wing chord: $r = 0.77$, $P = 0.01$; and wing chord vs. tarsus: $r = 0.82$, $P = 0.01$; only correlations ≥ 0.7 are shown). We retained wing chord and tarsus and excluded culmen from the analysis because wing chord and tarsus explained most of the variance between groups ($F_{1,5} = 304.8$, $P < 0.001$, and $F_{1,5} = 448.2$, $P < 0.001$, respectively). Even though tarsus and wing chord were highly correlated, they presented high tolerance during the variable selection process. In addition, we checked for agreement between standardized canonical coefficients and structure coefficients; variable weights were in the same rank order and had equal signs, thus proving the adequacy of the generated models. Prior probabilities were assumed to be equal because our sample included similar numbers of males and females, both when the discriminant analysis model included all samples and when Genovesa individuals were excluded. We conducted stepwise backward discriminant function analysis using Wilk's lambda as the optimization criterion.

We validated the discriminant analysis from Wolf Island using the U -method (leave-one-out) and we also used the four individuals (two males and two females) from Darwin Island, although we recognize the need for a much larger and independent data set to validate this model. We checked for equality of variance-covariance matrices using Box's test ($M = 0.8$, $df = 1$, $P = 0.35$). Multicollinearity was checked by conducting pairwise correlations (only mass vs. tail had a correlation > 0.7 and both variables were excluded from the analysis). Prior probabilities were assumed to be equal because our sample included a similar number of males and females.

We calculated a sexual size dimorphism index (Smith 1999) as:

$$(\text{male size/female size}) - 1.$$

Wing chord and tarsus were used as surrogates for body size to test whether there were significant differences in degree of sexual size

TABLE 1. Principal component (PC) scores and proportion of variance extracted (communalities) from each variable for the analysis of morphological differences between male and female Galápagos Doves. PC scores represent the correlation of each variable with the principal component and communalities are the sums of squares of the correlation coefficients on the first two components or the proportion of variance extracted from each variable.

Variable	PC1	PC2	Communalities
Culmen	0.88	0.19	0.81
Bill width	0.75	0.48	0.79
Tarsus	0.89	0.18	0.84
Tail	0.82	-0.44	0.87
Wing chord	0.93	-0.02	0.87
Mass	0.85	-0.37	0.86

dimorphism among islands. Wing chord and tarsus proved to be the two variables that best predicted body size according to the principal component analysis (high PC score and high extracted variance). Additionally, they were the variables that most reduced Wilk's lambda during discriminant analyses (DA). To increase sample sizes among islands for the calculation of the sexual size dimorphism index we used the PopTools 2.5.4 (Hood 2003) add-in for Microsoft Excel to generate 100 randomizations for each population before the index was calculated. We took all individual measurements made on males and females from each island and used them as source data to generate 100 randomized measurements for each sex. We next calculated the sexual size dimorphism index as shown by the above formula for each of the 100 measurement pairs and finally calculated the average of the 100 pairs. Because variances were not homogeneous across populations, we conducted a Kruskal-Wallis test to evaluate differences among islands in the degree of sexual size dimorphism. Values are reported as means \pm SD.

RESULTS

We retained the first component from the PCA conducted to compare the sexes for statistical analysis. PC1 explained 73% of the variance whereas PC2 explained 11%. PC1 described overall body size and the variance extracted from each variable was $>79\%$ (Table 1). Males were significantly larger than females (PC1: $t_{155} = -9.3$, $P < 0.001$; Fig. 2).

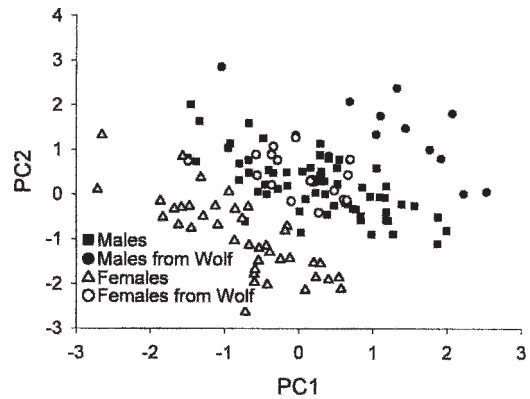


FIGURE 2. Morphological ordination space between males and females of the Galápagos Dove. PC1 is an axis of overall body size and PC2 is a vector of bill and tail size and mass. Males are larger than females, and birds of both sexes are larger on Wolf Island (northern subspecies) than on the other islands (southern subspecies).

For statistical analysis of females, we also retained the first component of the PCA. PC1 explained 66% of the variance and described overall body size. PC2 explained 14% of the variance and was a compound size component defined mainly by bill width, tail, and mass (Table 2). The variance extracted from each variable was $>76\%$ (Table 2). We found significant differences among islands ($F_{5,61} = 20.4$, $P < 0.001$). Genovesa Island females were significantly smaller than females on Santa Cruz and Santiago Islands (Tukey test, HSD = 0.9 and 1.1, respectively, $P \leq 0.01$ for both comparisons); however, there was overlap among individuals of these islands (Fig. 3A). Wolf Island females were significantly larger than females from the other islands, clearly forming a separate group in ordination space from the rest of the female doves (Tukey test, $2.2 > \text{HSD} > 1.2$, $P < 0.001$ for all comparisons; Fig. 3A).

For males, we retained the first component from the PCA for statistical analysis. PC1 explained 60% of the variance and PC2 explained 12%. PC1 described overall body size and PC2 was a compound size component defined mainly by bill width, tail, and mass (Table 2). The variance extracted from each variable was $>63\%$ (Table 2). We found significant differences among islands ($F_{5,73} = 9.4$, $P < 0.001$). Males from Genovesa Island were significantly larger than doves on Santa Fe

TABLE 2. Principal component (PC) scores and communalities (proportion of variance extracted) from the analysis of morphological differences of male and female Galápagos Doves among six islands of the Galápagos archipelago. PC scores represent the correlation of each variable with the principal component and communalities represent the sums of squares of the correlation coefficients on the first two principal components or the proportion of variance extracted from each variable.

Variable	Males			Females		
	PC1	PC2	Communalities	PC1	PC2	Communalities
Culmen	0.79	0.07	0.64	0.84	-0.26	0.78
Bill width	0.59	0.67	0.81	0.74	-0.45	0.76
Bill depth	0.80	0.37	0.77	Not included	Not included	Not included
Tarsus	0.79	-0.04	0.63	0.84	-0.26	0.78
Tail	0.77	-0.36	0.73	0.72	0.54	0.82
Wing chord	0.85	-0.21	0.77	0.89	0.02	0.79
Mass	0.77	-0.33	0.71	0.80	0.45	0.85

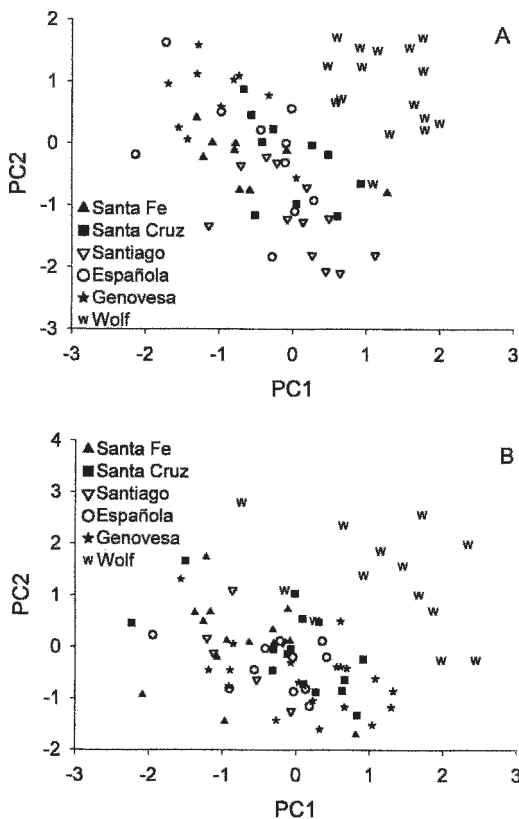


FIGURE 3. (A) Morphological ordination space between islands for adult female Galápagos Doves. PC1 is an axis of overall body size and PC2 is a vector reflecting bill size and tarsus length. (B) Morphological ordination space between islands for male Galápagos Doves. PC1 is an axis of overall body size and PC2 is a composite vector reflecting bill size and tarsus length. Note that the y axes of A and B have different scales. Birds from Wolf Island (northern subspecies, *Z. g. galapagoensis*) are significantly larger than birds on the southern islands (southern subspecies, *Z. g. exsul*). There is broad overlap among birds of the southern islands.

Island (Tukey test, HSD = 0.9, $P = 0.02$); however, as in the case of females, there was overlap among individuals of these islands (Fig. 3B). Male doves on Wolf Island were significantly larger than males on the other islands (Tukey test, $1.9 > HSD > 1.1$, $P \leq 0.006$ for all comparisons; Fig. 3B). As in the case of females, Wolf males also formed a separate group in ordination space (Fig. 3B).

The discriminant analysis that excluded Genovesa individuals retained wing chord (W), tarsus (T), and tail (Ta) as significant variables discriminating between males and females ($\lambda = 0.17$, $\chi^2_3 = 105.9$, $P < 0.001$). Tarsus had the highest discriminating power ($\lambda = 0.22$), followed by wing chord ($\lambda = 0.19$), and tail ($\lambda = 0.17$). The discriminant function was:

$$D = -41.08 + T(0.689) + W(0.123) + Ta(0.08).$$

Individuals that scored zero or positive values were classified as males and those that scored negative values were classed as females. Canonical correlation was high ($r = 0.90$). The model correctly classified 94% of males and 100% of females (Fig. 4). Cross-validation by the *U*-method yielded 94% correct classification for males and 100% for females. When discriminant scores for Genovesa individuals were computed with the above function, we obtained 100% correct classification for both males and females.

The discriminant model including all samples from the southern islands retained wing chord (W), tarsus (T), and bill width (BW) as significant variables discriminating between groups

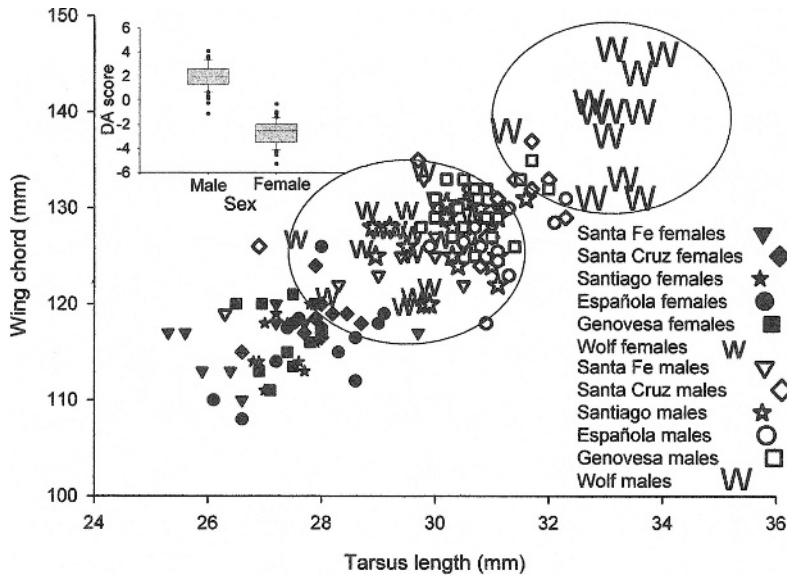


FIGURE 4. Scatter plot showing the two variables with the highest discriminating power (tarsus length and wing chord) for both males and females of the Galápagos Dove by island. Ellipses indicate individuals from Wolf Island. Inset is the box-plot of discriminant (DA) scores for males and females for the model that included all samples of the southern subspecies (*Z. g. galapagoensis*) of the Galápagos Dove. Birds from Wolf Island are larger than birds on the southern islands for both males and females. This result is supported by the discriminant analyses, which suggests that tarsus length and wing chord measurements are enough to confidently separate males from females.

($\lambda = 0.15$, $\chi^2_3 = 161.4$, $P < 0.001$). As in the former model, tarsus was the variable that best discriminated between groups ($\lambda = 0.19$), followed by wing chord ($\lambda = 0.16$), and bill width ($\lambda = 0.15$). The discriminant function was:

$$D = -45.24 + T(0.826) + W(0.14) + BW(0.722).$$

Individuals that scored zero or positive values were classified as males and those that scored negative values were categorized as females. Canonical correlation was high ($r = 0.92$). The model correctly classified 98% of males and 100% of females (Fig. 4). Cross-validation by the *U*-method yielded 97% correct classification for males and 98% for females.

The discriminant analysis for individuals sampled on Wolf Island retained only tarsus (T) as a significant variable discriminating between males and females ($\lambda = 0.14$, $\chi^2_1 = 52.6$, $P < 0.001$). The discriminant function was:

$$D = -141.27 + T(94.77).$$

Individuals with scores of zero or positive values were classified as males and those scoring negative values were classed as females. Canonical correlation was high ($r = 0.93$). The model correctly classified 100% of males and 100% of females. Cross-validation by the *U*-method yielded 100% correct classification for males and females. When discriminant scores for Darwin individuals were computed with the above function, we obtained 100% correct classification for both males and females. After conducting a discriminant analysis that included the samples from all six islands, the correct classification of males and females by the model decreased to around 80%. This result was due to the inclusion of individuals from Wolf Island, which are significantly larger than individuals from other islands, as shown by the PCA.

We found significant differences among island populations in the degree of sexual size dimorphism for both wing chord (Kruskal-Wallis test: $\chi^2_4 = 37.8$, $P < 0.001$) and tarsus (Kruskal-Wallis test: $\chi^2_4 = 29.3$, $P < 0.001$) indices. Differences for the wing chord index

were identified between Genovesa and all the other islands (Genovesa = 0.116 ± 0.036 , Santiago = 0.083 ± 0.034 , Santa Cruz = 0.095 ± 0.030 , Española = 0.090 ± 0.041 , Santa Fe = 0.098 ± 0.042 , Wolf = 0.088 ± 0.053). In the case of the tarsus index, differences were found between Santiago and Wolf Islands, and between Santa Cruz vs. Santa Fe, Genovesa, and Wolf Islands (Genovesa = 0.120 ± 0.028 , Santiago = 0.108 ± 0.029 , Santa Cruz = 0.100 ± 0.044 , Española = 0.115 ± 0.042 , Santa Fe = 0.120 ± 0.060 , Wolf = 0.129 ± 0.040). We plotted sexual size dimorphism vs. body size for both males and females by island (Fig. 5) and found no positive correlations between the two measurements. The sample from Wolf Island, in particular, had low sexual size dimorphism relative to individual size.

DISCUSSION

Our finding of significant morphological differences between the sexes is in agreement with morphological records for other *Zenaida* species, in which males are generally larger than females (Baptista et al. 1997). The three discriminant models developed in this study supported the results obtained by the principal component analysis. Importantly, the efficiency of the discriminant model was reduced when samples from Wolf Island (northern subspecies) were included in the analysis, which supports observed morphological differences between

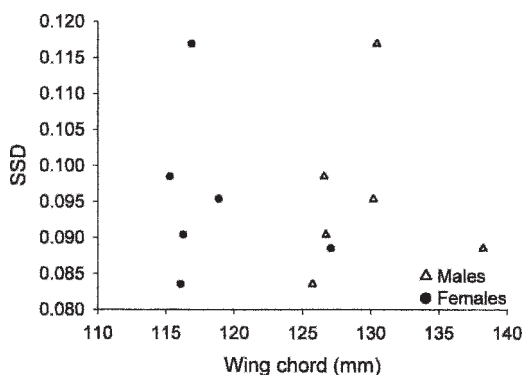


FIGURE 5. Scatter plot showing the sexual size dimorphism (SSD) wing index against the average wing chord (body size surrogate) for both male and female Galápagos Doves. The lack of a positive relationship between SSD and body size might reflect differences in selection pressures for both males and females on the different islands.

individuals from Wolf and from the other islands.

This is the first study to provide statistically significant morphological evidence that supports the separation of the Galápagos Dove into two subspecies, as has been previously suggested by other authors (Ridgway 1897, Gifford 1913, Swarth 1931). This result suggests that populations on Wolf and Darwin islands might be somewhat isolated from the other islands, which is supported by significant positive F_{ST} values (based on five microsatellite loci; see Santiago-Alarcon et al. [2006] for an explanation of the molecular and genetic analyses used) and lower gene flow between northern and southern islands as estimated with program MIGRATE (DS-A and PGP, unpubl. data). In contrast, there is evidence of high gene flow among populations of the southern subspecies based on microsatellite markers (Santiago-Alarcon et al. 2006).

The sexual size dimorphism wing chord index calculated for Genovesa doves was significantly higher than indices calculated for the other islands. Because of high gene flow among southern island populations of the Galápagos Dove (Santiago-Alarcon et al. 2006), morphological differences between the sexes on this island might be the result of phenotypic plasticity in response to different local conditions (Wikelski and Trillmich 1997). Genovesa Island is unique in the Galápagos archipelago in that the top predator, the Galápagos Hawk, has been replaced by the Short-eared Owl (*Asio flammeus galapagoensis*). Thus, variation in predation regimes on Genovesa due to different hunting strategies and other life history traits of the Short-eared Owl compared to the Galápagos Hawk, coupled with abiotic conditions, might be generating different pressures on the dove population of Genovesa.

In addition, we identified significant differences between some island pairs for the sexual size dimorphism tarsus index. It has been suggested that tarsus size depends on the foraging strategy of a species (Miles and Ricklefs 1984). If the two sexes of a species have different ecological roles, some of their morphological traits might vary. Thus, differences in this sexual size dimorphism index between some islands might be due to differences in habitat structure and ecological interactions. For example, inhabited islands such as Santa Cruz

have been altered and are composed of habitats not found on other uninhabited islands. These differences among islands might represent areas of strong selection pressure for endemic doves. Nonetheless, because of high gene flow among southern island populations, observed differences are more likely the result of phenotypic plasticity.

The ecological causes of sexual size dimorphism in the Galápagos Dove are difficult to identify because there are limited data for this species (Grant and Grant 1979). However, morphological differences are likely not the result of a single factor, but rather the result of multiple interacting factors (Moore 1990, Owens and Hartley 1998, Clegg and Owens 2002).

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