TERRITORIALITY VERSUS FLOCKING IN THE ZENAIDA DOVE (*ZENAIDA AURITA*): RESOURCE POLYMORPHISM REVISITED USING MORPHOLOGICAL AND GENETIC ANALYSES

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ABSTRACT.—The term "resource polymorphism" refers to the existence of alternative phenotypes in relation to resource use, as a result of disruptive selection. Evidence for resource polymorphism is widespread in fish but remains scarce in birds. Although Zenaida Doves (*Zenaida aurita*) usually defend year-round territories, doves on Barbados can also be observed foraging at seed-storage sites in large flocks with little, if any, inter-individual aggression. On the basis of morphological variation, it has been suggested (Sol et al. 2005) that this represents a case of resource polymorphism, primarily driven by competition for territories. Using new data, we revisited the evidence for resource polymorphism in Zenaida Doves on Barbados. In particular, we added replicates in time and space for territorial and flock-foraging birds and used molecular markers to assign sex to adults and juveniles. In addition, we used microsatellite markers to assess potential genetic differentiation between flock-feeding and territorial doves. Our results confirm previous observations that territorial adults were larger than flock-feeding ones, whereas the reverse was observed in juveniles. Contrary to previous observations, we found a significant excess of females among flock-feeding adults, whereas the sex ratio was balanced in territorial adults and in juveniles. In addition, we observed no significant difference in body condition and no genetic differentiation between territorial and flock-feeding individuals. Overall, our data question the existence of resource polymorphism in Zenaida Doves in Barbados. We suggest alternative, more parsimonious explanations, based on age- and sex-related differences in the relative benefits of holding a territory. *Received 30 November 2009, accepted 5 August 2010.*

Key words: alternative resource use, competition, genetic differentiation, metareplication, morphometrics, *Zenaida aurita*, Zenaida Dove.

Territorialité versus agrégation chez la tourterelle à queue carrée (Zenaida aurita) : hypothèse du polymorphisme de ressources revisitée par des analyses morphométriques et génétiques

RÉSUMÉ.—Le terme "polymorphisme de ressources" renvoie à l'existence de phénotypes alternatifs en relation avec l'utilisation des ressources résultant d'une sélection disruptive. Les preuves en faveur du polymorphisme de ressources sont multiples chez les poissons mais plus rare chez les oiseaux. Bien que, généralement, les tourterelles à queue carrée (*Zenaida aurita*) défendent leurs territoires tout au long de l'année, les individus présents à la Barbade ont également été observés se nourrissant en groupe avec peu ou pas de comportements agressifs entre eux. Sur la base de données morphométriques, il a été suggéré (Sol et al. 2005) que cette situation était un cas de polymorphisme de ressources, principalement généré par la compétition pour les territoires. En utilisant de nouvelles données, nous avons testé de nouveau cette hypothèse chez la tourterelle à queue carrée de la Barbade. En particulier, nous avons ajouté des réplicats dans le temps et l'espace pour les oiseaux territoriaux et ceux se nourrissant en groupe et des marqueurs moléculaires du sexe ont été utilisés pour sexer les adultes et les juvéniles. De plus, nous avons utilisé des marqueurs microsatellites afin d'évaluer le niveau de différenciation entre les tourterelles se nourrissant en groupe et celles défendant des territoires. Nos résultats confirment les observations précédentes sur le fait que les adultes territoriaux étaient plus grands que ceux se nourrissant en groupe mais l'inverse était observé chez les juvéniles. Contrairement aux observations précédentes, nous avons trouvé un excès significatif de femelles adultes chez les individus se nourrissant en groupe alors que la sex ratio était équilibrée chez les tourterelles capturées sur les sites territoriaux et les juvéniles des sites de nourrissage en groupe. Par ailleurs, aucune différence de condition corporelle ni de différenciation génétique n'a été observée entre individus territoriaux et ceux se nourrissant en groupe. Dans l'ensemble, nos résultats mettent en doute l'existence d'un polymorphisme de ressources chez les tourterelles à queue carrée de la Barbade. Nous suggérons ici une explication alternative plus parcimonieuse basée sur les différences en lien avec l'âge et le sexe dans les bénéfices relatifs que procure un territoire.

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Understanding how variation in resources influences morphological diversity and divergent natural selection is of primary interest in ecological and evolutionary research, because it may ultimately result in speciation (Schluter 2000, Bolnick and Fitzpatrick 2007). Various mechanisms may link resource use and morphology. In particular, both the invasion of "open" niches in a heterogeneous environment and the relaxation of inter- or intraspecific competition are thought to favor the evolution of resource (or trophic) polymorphism, which is defined as alternative phenotypes that evolved to use different resources through disruptive selection (Skúlason and Smith 1995, Smith and Skúlason 1996, Pfennig et al. 2007, Martin and Pfennig 2009). Although resource polymorphism may play an important role in population divergence and speciation in vertebrates (Smith and Skúlason 1996), the extent of empirical evidence varies among taxonomic groups. Reports of resource polymorphism are common in fish (Ruzzante et al. 2003, Proulx and Magnan 2004, Olsson et al. 2007, Parsons and Robinson 2007, Svanbäck et al. 2008) and, to a lesser extent, in amphibians (Maerz et al. 2006, Pfennig et al. 2007), but the importance of resource polymorphisms remains poorly documented in birds.

The few known examples of resource polymorphism in birds all involve the existence of discrete morphs based on bill size or shape (Smith and Temple 1982, Goss-Custard and Durell 1983, Smith 1990, Borrás et al. 2008, Clabaut et al. 2009) or plumage color (Rohwer 1990, Roulin 2004). One noticeable exception, however, is the resource polymorphism associated with continuous variation in body size reported by Lefebvre and collaborators (Carlier and Lefebvre 1996, 1997; Dolman et al. 1996; Lefebvre et al. 1996; Sol et al. 2005) in the Zenaida Dove (*Zenaida aurita*) on the island of Barbados, West Indies. Barbados hosts a very limited avifauna and has practically no pristine habitats left because of intensive agriculture and development. On the island, Zenaida Doves usually establish year-round feeding territories that they defend against conspecifics irrespective of their sex (F. Cézilly unpubl. data) and, to a lesser extent, other columbid species (*Columbina passerina* and *Columba squamosa*), while showing more tolerance toward unrelated avian species (*Loxigilla noctis*, *Molothrus bonariensis*, *Quiscalus lugubris*; Dolman et al. 1996; F. Cézilly unpubl. data). By contrast, where food availability is particularly high, Zenaida Doves gather in large numbers and feed in flocks with relatively little inter-individual aggression. This is especially the case at some isolated grain-storage facilities on the island, where large amounts of seed spillage attract Zenaida Doves and a few other bird species. On the basis of a comparison of morphological traits between flocking and territorial individuals and additional experiments, Sol et al. (2005) concluded that the existence of alternative foraging tactics by Zenaida Doves on Barbados was a case of resource polymorphism driven by competition for territories, where less competitive individuals, irrespective of age and sex, are forced to exploit a suboptimal resource. However, that study was limited to a 1-year comparison between a single population of territorial birds and a single population of flock-feeding ones, such that the absence of replications in time and space makes interpreting the results difficult (Hurlbert 1984; see also Oksanen 2001). In addition, Sol et al.'s (2005) conclusions on male and female differences, as well as the probable lack of genetic differentiation between territorial and flock-feeding populations (see Carlier and Lefebvre

1996, 1997; Dolman et al. 1996), were based on observational and morphological data. Sol et al. (2005) did not utilize genetic techniques that would be much more appropriate both to identify sex and to document the extent of genetic differentiation between individuals engaged in each of the two foraging tactics.

Here, we reexamine the evidence for resource polymorphism in Zenaida Doves on Barbados, as part of a long-term project on the behavioral ecology and population biology of the species. In particular, we expand on Sol et al.'s (2005) study by adding replications in space and time for each type of foraging tactic. We also used molecular makers to sex all adult and juvenile individuals captured at our four study sites. Finally, because recent evidence suggests that rapid niche expansion and resource polymorphism can be associated with genetic divergence at very small spatial scales in vertebrates (McCormack and Smith 2008, Bergek and Björklund 2009) even in the presence of gene flow (Señar et al. 2006), we measured the extent of genetic differentiation between territorial and flock-feeding Zenaida Doves using recently developed microsatellite markers (Monceau et al. 2009).

Methods

Zenaida Doves on Barbados.—The Zenaida Dove is widely distributed throughout the Caribbean (Raffaele et al. 1998). Although its primary habitat consists of woodlands and scrub thickets (Wiley 1991; Rivera-Milán 1997, 1999), on several islands, including Barbados, it has colonized open coastal areas and gardens. On Barbados, Zenaida Doves typically feed solitarily or as pairs on seeds on the ground (Lefebvre et al. 1996) but may opportunistically exploit alternative food sources such as leftover bread or cooked rice.

Territories provide Zenaida Doves with a presumably stable feeding resource and a place for nesting. In the Caribbean, Zenaida Doves can reproduce all year long and can make several breeding attempts per year, often using the same nest (Wiley 1991, F. Cézilly pers. obs.). Owning a territory might be crucial for successful reproduction, particularly when fledglings start to feed themselves on their parents' territory. Both males and females defend territories against conspecifics year-round by running or flying toward intruders of any sex, and eventually attacking them with wing slaps and pecks (F. Cézilly unpubl. data). Escalated contests between territory owners and intruders involve ritualized displays such as ground pecking and wing raising. During the latter display, birds typically flick one wing contra-lateral to the opponent while walking parallel to each other (Goldberg et al. 2001).

Males are slightly larger than females, but the sexes are otherwise similar in appearance (Wiley 1991, F. Cézilly unpubl. data). We used the absence of iridescent patches on each side of the neck (Sol et al. 2005), the presence of grayish first feathers, and high-pitched vocalizations to distinguish juveniles from adults.

Study area.—For each foraging tactic (i.e., territorial feeding or flock-feeding), we sampled two distinct sites over two consecutive years (2007 and 2008), thus generating replications in space and time. We studied territorial birds at the Bellairs Research Institute (St. James Parish, 13°11′30.87″N, 59°38′21.55″W) and the adjacent Folkestone Park (hereafter collectively referred to as "Bellairs"), and in the Sunset Crest area (13°10′55.06″N, 59°38′11.80″W), a residential location consisting of small to medium-sized villas surrounded by gardens and parks (hereafter "Sunset Crest").
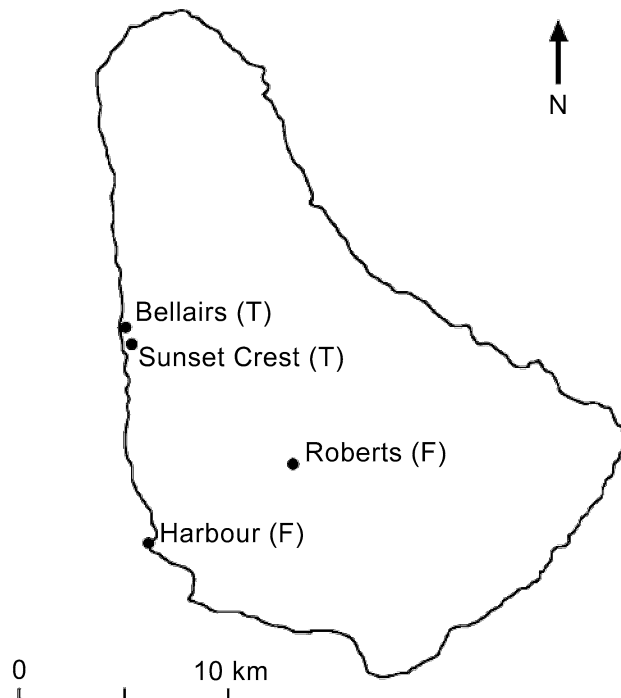
Fig. 1. Map of Barbados indicating the location of study areas. "T" specifies areas where Zenaida Doves hold territories, and "F" stands for flock-feeding sites.

Although the distance between the two sites is only ~1,500 m, data from intensive banding and resightings indicate that the exchange of birds between the two sites is limited (only ~10% of the birds banded at one site have been seen at the other site between 2007 and 2010; F. Cézilly unpubl. data). We studied flock-feeding birds at the Barbados Mills compound in Deep Water Harbour (St. Michael Parish, 13°6′38.99″N, 59°37′46.06″W; hereafter "Harbour"), and at Roberts Manufacturing Company (Lower Estate, St. Michael Parish, 13°7′52.46″N, 59°34′48.66″W; hereafter "Roberts"). Both sites include large facilities for storage of animal feed and grain. The territorial sites are ~8 km north of Harbour and northwest of Roberts, whereas the distance between the two latter sites is ~5 km (Fig. 1). Our study thus includes the two sites studied by Sol et al. (2005), Bellairs and Harbour, plus a replicate for each foraging tactic. Contrary to Sol et al. (2005), we did not distinguish between territory holders and floaters at the Bellairs and Sunset Crest sites, because our observations showed that territorial birds often engage in extraterritorial forays, alone or in pairs, up to several hundred meters from their own territory, which makes the distinction between floaters and territorial birds unreliable.

Captures.—We captured a total of 857 birds from March to May in both 2007 ($n = 586$) and 2008 ($n = 271$), all ages combined, using walk-in baited drop traps (as used by Sol et al. 2005) and single-catch closing net bird traps. We banded birds with a unique combination of color plastic bands (A.C. Hughes, Hampton Hill, United Kingdom) and one numbered aluminum ring from the Muséum National d'Histoire Naturelle de Paris. We then measured each banded bird (see below), weighed it to the nearest 0.1 g (using a Pesola digital pocket scale, MS 500), and drew a blood sample (see below). All birds were released at their capture locations.

Morphological Data

Repeatability and measurement error.—We took two measurements of each of the following morphological characters: bill length, depth and width at nostrils, tarsus length (left and right), and flattened wing chord (left and right). The same person (K.M.) took all measurements using a digital caliper (accuracy ±0.2 mm), except for wing chord, which was measured with a ruler (accuracy ±1 mm). We later assessed repeatability (R) and measurement error (ME) using two-way analysis of variance (ANOVA) with random effect (Lessells and Boag 1987, Bailey and Byrnes 1990). Because repeatability was high and measurement error was moderate for both adults (R range: 0.79–0.98; ME range: 2–11%, except bill depth 21%) and juveniles (R range: 0.76–0.99; ME range: 0.48–5.5 %, except bill depth 24%), we used the mean of the two measurements in the analyses. In addition, right and left measurements were significantly correlated for both tarsus length (Pearson's product-moment correlation, adults: $r = 0.85$, $P < 0.0001$, $n = 783$; juveniles: $r = 0.93$, $P < 0.0001$, $n = 74$) and wing chord (Spearman's correlation coefficient, adults: $r_s = 0.91$, $P < 0.0001$, $n = 783$; juveniles: $r_s = 0.92$, $P < 0.0001$, $n = 74$). Therefore, we used the means of the right and left measurements for analysis.

Testing for differences between replicates.—We used the first factor (PC1) of a principal component analysis (PCA) based on all measurements (bill length, depth, and width; mean tarsus length; mean wing chord; and body mass) as a global index of size and shape, separately for juveniles and adults. PC1 accounted for 51.8% and 39.1% of total variance in juveniles and adults, respectively. We then tested for the effects of year and site of capture within each foraging tactic and age class, using two-way ANOVA with fixed effects. We found no effect of year (territorial birds: $F = 0.02$, df = 1 and 51, $P = 0.88$; flock-feeding birds: $F = 0.16$, df = 1 and 21, $P = 0.69$) or of site (territorial birds: $F = 3.06$, df = 1 and 51, $P = 0.09$; flock-feeding birds: $F = 0.64$, df = 1 and 21, $P = 0.43$) on the morphology of juveniles. By contrast, we found significant differences in adult morphology between years (territorial birds: $F = 9.61$, df = 1 and 406, $P < 0.01$; flock-feeding birds: $F = 9.98$, df = 1 and 375, $P < 0.01$), but no difference between sites (territorial birds: $F = 0.09$, df = 1 and 406, $P = 0.78$; flock-feeding birds: $F = 0.46$, df = 1 and 375, $P = 0.50$). Therefore, only the year effect was included in the analyses of the association of foraging tactic and morphology. Comparisons between foraging tactics were also controlled for the effect of sex in order to avoid potential bias.

Morphological specialization for feeding.—Following Sol et al. (2005), we assessed the extent of morphological specialization for feeding from differences in bill shape between individuals engaged in the two foraging tactics. We performed a PCA on bill measurements (bill length, depth, and width), including tarsus length as an index of body size (see methods in Sol et al. 2005). Contrary to Sol et al. (2005), who used wing chord as an index of body size, we used tarsus length because it is not susceptible to wear and tear. In the adults, all bill measurements and tarsus length loaded positively and with roughly equal weight on factor 1 (Table 1), which indicated that PC1 was an overall measure of size: birds with positive scores had large bills. The only factor of

TABLE 1. Factor loadings of the three bill dimensions and tarsus length of Zenaida Doves on Barbados in 2007 and 2008 on the first (PC1) and the second (PC2) axes of the principal component analysis, with percentages of explained variance in juveniles and adults (after pooling data for sex, site, and year).

	Juveniles		Adults	
	PC1	PC2	PC1	PC2
Bill length	0.62	−0.18	0.49	−0.29
Bill width	−0.49	0.54	0.46	0.88
Bill depth	0.31	0.78	0.53	−0.21
Tarsus length	0.52	0.26	0.52	−0.30
Explained variance (%)	44.4	25.1	42.7	20.2

importance on PC2 was bill width: birds with positive scores had wide bills. We therefore used only PC1 for the analysis of adult bill morphology (Table 1). The PCA of juveniles identified slightly different patterns. Individuals with positive scores on PC1 were large and had long but narrow bills. Bill width and depth loaded positively on PC2 for juveniles, which indicates that, independently of body size, individuals with positive scores had robust (wide and deep) bills (Table 1). We retained PC1 to explain differences in bill length and PC2 to explain differences in bill depth and width in juveniles for subsequent analysis. Because homoscedasticity (Levene's test) was verified in both adults and juveniles, the influence of foraging tactic on bill morphology was analyzed using a two-way ANOVA with fixed effects.

Competitive ability and wing chord.—Because wing flicking appears to be an important component of territorial display (Sol et al. 2005), we assessed competitive ability from wing chord. Although this character was normally distributed in adults, variances for birds of the two foraging modes were not homogeneous, even after transformation. We thus used a generalized linear model (GLM) with a Gaussian link function to assess the effects of sex, year of capture, and foraging tactic on wing chord. Tarsus length was also included as a control for body size, and model assumptions were verified by analyzing the distribution of residuals. In juveniles, homoscedasticity was verified, and an analysis of covariance (ANCOVA) that used the same explanatory variables as for the adults was performed. In both cases, residuals from the regression of log (wing chord) against log (tarsus length) were used for post hoc tests and graphic representations.

Overall body-size comparison.—Following Sol et al. (2005), we computed a body size index (BSI) from PC1 of a PCA that included wing chord, tarsus length, and bill length. Contrary to Sol et al. (2005), however, we did not include body mass in the PCA, in order to be able to use the residuals from the regression of body mass on body size index as a measure of body condition (see next section). Factor loadings on PC1 for the juveniles (wing chord = 0.62, bill length = 0.57, and tarsus length = 0.54) and adults (wing chord = 0.61, bill length = 0.50, and tarsus length = 0.61) were all positive and accounted for 69.5% and 52.2%, respectively, of the overall variance in morphology. Because homoscedasticity (Levene's test) was verified for both adults and juveniles, the BSI was analyzed using a two-way ANOVA with fixed effects.

Differences in payoffs between foraging tactics: Body condition.—Following Sol et al. (2005), we assessed potential differences in payoffs between the two foraging tactics by comparing body condition. Body condition was defined as body mass controlled for body size (Jacob et al. 1996) and was analyzed with an ANCOVA using BSI as a covariate (García-Berthou 2001). Residuals from the regression of log (body mass) against log (BSI) were used for post hoc tests.

We analyzed the data using R software, version 2.10.0 (R Development Core Team 2008) and the packages "car" for Levene's test, "nlme" for two-way ANOVA with random effect, and "stats" and "multcomp" for GLM analyses and Tukey's HSD test. All PCAs were performed with the "prcomp" function included in the R basic version, using a singular value decomposition of the centered and scaled (standardized) data matrix (Crawley 2007) and reversing the rotated matrix of principal component scores. All the ANOVAs, ANCOVAs, and GLMs used for analyses were coupled with a stepwise backward procedure based on likelihood ratios comparison, in order to retain only the significant effects. We used Tukey's HSD test to identify significant differences between groups.

Molecular analyses of sex ratio.—We collected blood samples (~40 μL bird⁻¹) in sodium heparinized capillary tubes after puncturing the brachial vein. The samples were kept in 800 μL of storage buffer (70% ethanol and 30% Tris-EDTA buffer pH 8), and DNA was extracted using the standard phenol-chloroform method described in Monceau (2009).

We identified sex using size variation of introns of the Chromo-Helicase-DNA binding protein genes (CHD1-Z and CHD1-W), using 2550F/2718R primer pair and standard PCR and electrophoresis conditions (Fridolfsson and Ellegren 1999, Monceau 2009). Intron size variation was easily scored: CHD1-W = 450 pb and CHD1-Z = 750 pb. Deviation from a balanced sex ratio was assessed, in both adults and juveniles, using binomial tests and then compared between years, foraging tactics, and sites using chi-square tests or Fisher's exact test.

Microsatellite genotyping and genetic differentiation.—For genotyping, we randomly selected ~30 adults from each site for each year (247 individuals in total), which resulted in eight sampling units that allowed both spatial and temporal comparisons. We scored polymorphism at seven microsatellite markers (ZaD1, ZaD11, ZaD104, ZaD105, ZaD108, ZaD119, and ZaD121) specifically developed for the Zenaida Dove (Monceau et al. 2009).

We first investigated linkage disequilibrium between loci for each sampling unit and then assessed departure from Hardy-Weinberg equilibrium using Fisher's exact test, for each sampling unit as well as for the entire data set, to allow for detection of a possible Wahlund effect. We evaluated both pairwise and overall genetic differentiation between sampling units using Fisher's exact tests (Raymond and Rousset 1995) and F_{ST} statistics (Weir and Cockerham 1984). Following Wright (1969), we calculated an estimate of the effective migration rate among sampling units (Nm) from the equation Nm = $(1 - F_{ST})/4 F_{ST}$. All analyses were processed using ARLEQUIN, version 3.1 (Excoffier et al. 2005), and probabilities for Fisher's exact test were approximated by a Markov chain. We tested for departure from null values for F_{ST} by permuting genotypes between sampling units, and adjusted the 0.05 significant level using Bonferroni's correction for multiple comparisons. Finally, we evaluated whether genetic differentiation was more pronounced between sites where birds used a

TABLE 2. Percentage distribution of juvenile Zenaida Doves according to site and foraging tactic (after pooling data for sex and year) on Barbados in 2007 and 2008.

Foraging tactic, site	Juveniles (%)	Sample size
Territorial		
Bellairs	21.23	146
Sunset Crest	6.71	313
Flock-feeding		
Roberts	6.22	193
Harbour	4.88	205

different foraging tactic than between sites where birds used the same foraging tactic. To that end, we calculated F_{ST} values for all pairs of sites and compared them using the Osx statistic implemented in FSTAT software (Goudet 1995), after pooling data from the two years.

RESULTS

Differences in age and sex composition between foraging tactics.—At each site, age composition did not differ between years (Fisher's exact test: Bellairs: $P = 0.07$, Roberts: $P = 0.23$, Harbour: $P = 1.00$, and Sunset Crest: $P = 0.17$); therefore, we pooled the data from the two years for subsequent analyses (Table 2). The proportion of juveniles was significantly lower than that of adults at all sites (binomial test, $P < 0.0001$ for each site). The proportion of juveniles differed significantly between Bellairs and the three other sites ($\chi^2 = 37.06$, df = 1, $P < 0.0001$), whereas no difference was observed between the two flock-feeding sites (Fisher's exact test, $P = 0.66$).

We could not reject the null hypothesis of equal sex ratio between years in juveniles at any site (Fisher's exact test, Bellairs: $P = 0.15$, Sunset Crest: $P = 0.64$, Roberts: $P = 1.00$, and Harbour: $P = 0.07$), and therefore we pooled the data for subsequent analyses. We found a balanced juvenile sex ratio in both territorial and group-feeding sites (binomial test, $P > 0.19$ in all cases), with no difference between replicates for each foraging tactic (Fisher's exact test, territorial feeding: $P = 0.56$; flock-feeding: $P = 0.41$). There was no significant difference in sex ratio between juveniles foraging on territories or in flocks (Fisher's exact test, $P = 1$).

We could not reject the null hypothesis of equal sex ratio between years in adults at any site (Fisher's exact test, Bellairs: $P = 0.32$ Sunset Crest: $P = 0.72$, Roberts: $P = 0.05$, and Harbour: $P = 0.25$), and therefore we pooled the data for subsequent analysis. A balanced sex ratio was observed at the two territorial sites (binomial test, $P = 1.00$ and $P = 0.32$ for Bellairs and Sunset Crest, respectively), with no difference between them (Fisher's exact test, $P = 0.58$). By contrast, the sex ratio was significantly female-biased at both Roberts (binomial test, $P = 0.03$) and Harbour ($P = 0.002$), with no difference between sites (Fisher's exact test, $P = 0.60$). Overall, there was a significantly higher proportion of females among birds feeding in groups than among those feeding on territories (Fisher's exact test, $P < 0.001$).

Feeding specialization and bill morphology.—In juveniles, variation in bill length (PC1) was explained only by the foraging tactic: birds feeding in groups had longer bills than territorial ones

(sex: $F = 1.29$, df = 1 and 73, $P = 0.26$; year of capture: $F = 0.57$, df = 1 and 73, $P = 0.45$; foraging tactic: $F = 6.96$, df = 1 and 73, $P < 0.05$; Tukey's HSD test, $P < 0.01$; Fig. 2). Variation in bill width and depth (PC2) was not associated with sex, year of capture, or foraging tactic (sex: $F = 0.78$, df = 1 and 73, $P = 0.38$; year of capture: $F = 0.001$, df = 1 and 73, $P = 0.97$; foraging tactic: $F = 1.43$, df = 1 and 73, $P = 0.24$). In adults, males had larger and deeper bills than females ($F = 236.67$, df = 1 and 782, $P < 0.0001$; Tukey's HSD, $P < 0.0001$). There was no effect of year of sampling or foraging tactic (year: $F = 2.23$, df = 1 and 782, $P = 0.13$; foraging tactic: $F = 0.74$, df = 1 and 782, $P = 0.39$). Although a significant interaction between foraging tactic and year of sampling was detected ($F = 22.37$, df = 1 and 782, $P < 0.0001$), Tukey's HSD tests did not reveal any difference between territorial birds captured in 2007 and group feeders captured in 2008 or the reverse (in both cases $P > 0.05$). However, because of the strong sex effect, we performed de novo the analysis with only foraging tactic and year of sampling as explanatory variables. We found that territorial individuals had bigger bills than birds feeding in groups ($F = 22.37$, df = 1 and 782, $P = 0.02$), with no effect of year ($F = 1.13$, df = 1 and 782, $P = 0.29$). The interaction between foraging tactic and year of sampling was still significant ($F = 18.01$, df = 1 and 782, $P < 0.0001$): territorial birds had bigger bills than individual feeding in group, but only in 2007 (Tukey's HSD test, $P < 0.0001$; Fig. 2).

Competitive ability and wing chord.—Juvenile wing chord was independent of sex, year of capture and foraging tactic (sex: $F = 1.21$, df = 1 and 73, $P = 0.27$; year of capture: $F = 0.003$, df = 1 and 73, $P = 0.96$; foraging tactic: $F = 1.48$, df = 1 and 73, $P = 0.23$; Fig. 3). In adults, GLM and post hoc tests (Tukey's HSD test, all $P < 0.0001$) revealed that, within each foraging tactic and after controlling for body size, males had longer wings than females. Overall, territorial birds had longer wings than group-feeding ones (Table 3 and Fig. 3). The significant interaction between sex and foraging tactic (Table 3) corresponded to the fact that the wing chords of females on territories and males in flock-feeding areas did not differ ($P = 0.99$), whereas all others comparisons involving sex or foraging tactic effects were significant (Tukey's HSD test, all $P < 0.0001$). The significant interaction between sex and year existed because females captured in 2008 had longer wings than those captured in 2007 (Tukey's HSD test, females: $P < 0.05$; Table 3), whereas no such difference was observed in males ($P = 0.68$).

Overall morphological differentiation.—Juveniles feeding in groups were larger than those captured on territories ($F = 4.58$, df = 1 and 73, $P < 0.05$; Tukey's HSD test, $P < 0.05$; Fig. 4). In adults, males were larger than females ($F = 322.33$, df = 1 and 782, $P < 0.0001$; Tukey's HSD test, $P < 0.0001$; Fig. 4). Overall, adult territorial birds were larger than adults feeding in groups ($F = 6.17$, df = 1 and 782, $P < 0.05$; Tukey's HSD test, $P < 0.05$; Fig. 4), irrespective of sex ($F = 6.17$, df = 1 and 782, $P = 0.24$). ANOVA and Tukey's HSD test indicated that the significant interaction between site and year of capture was due to the larger body size of adult birds feeding in groups in 2008 compared with 2007 ($F = 16.48$, df = 1 and 782, $P < 0.0001$; Tukey's HSD test, $P < 0.001$; Fig. 4).

Tactic payoffs and body condition.—Overall, body condition (body mass corrected for body size) did not differ between birds of different foraging tactics, sex, or age. In juveniles, variation in body mass was independent of foraging tactic and sex (foraging tactic: $F = 0.07$, df = 1 and 73, $P = 0.79$; sex: $F = 0.84$, df = 1 and 73,
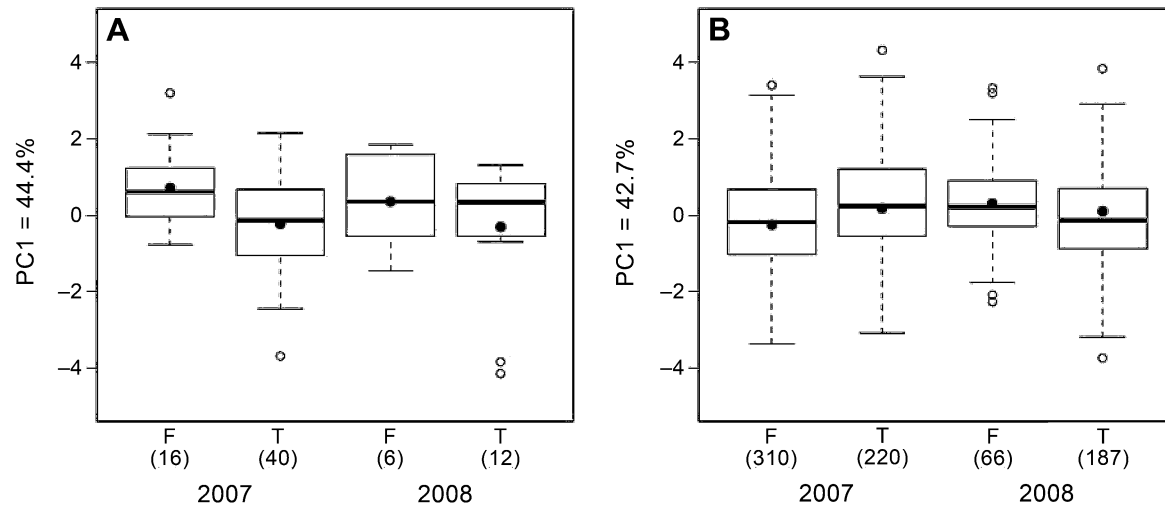
Fig. 2. Variation in bill morphology represented as the first factor of a principal component analysis according to foraging tactic and year of sampling in (A) juvenile and (B) adult Zenaida Doves (data pooled for sex). PC1 represented mainly variation in bill length in juveniles and overall bill morphology in adults. "F" stands for flock-feeders and "T" for territorial birds, with samples sizes in brackets. Boxes, plain line, black point, dashed lines, and open circles represent 50% of all values, medians, means, standard error, and extreme values, respectively.

$P = 0.36$). In adults, body mass varied with BSI ($F = 199.93$, df = 1 and 782, $P < 0.0001$) and, to a lesser extent, the interaction between year and site ($F = 4.71$, df = 1 and 782, $P < 0.05$). Post hoc tests failed to identify any difference between groups.

Genetic differentiation.—Genotyping at seven microsatellite loci for 30 individuals for each sampling site and year (resulting in eight sampling units) revealed a high level of polymorphism, with an average of 9.43 (6–14) alleles per locus (Appendix 1). We found no evidence of linkage disequilibrium in any sampling unit, and no multilocus deviation from Hardy-Weinberg equilibrium

(Appendix 1), whether we examined each sampling unit separately (Fisher's exact test, all $P \geq 0.60$) or pooled data from all sampling units (Fisher's exact test, $P = 1.00$). Furthermore, we found no difference in allele frequencies either in paired comparisons of sampling units (Fisher's exact test, all $P \geq 0.48$) or when all data were pooled (Fisher's exact test: $P = 0.70$) (Appendix 2). Similarly, pairwise F_{ST} values between sampling units (–0.006 to 0.011) were small and not significantly different from zero. A large (Slatkin 1985) absolute number of migrants was estimated between sites, with a minimum of 46.2 effective dispersers per generation
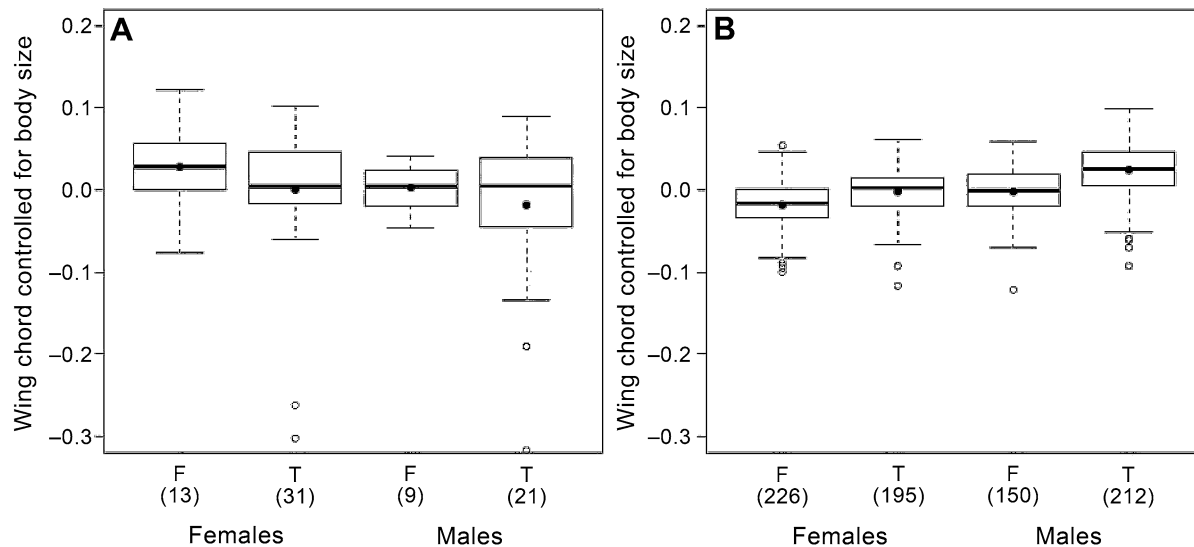

Fig. 3. Wing chord (controlled for body size) comparison between foraging tactic and sex in (A) juvenile and (B) adult Zenaida Doves (data pooled for year). "F" stands for flock-feeding areas and "T" for territorial sites, with samples sizes in brackets. Boxes, plain line, black point, dashed lines, and open circles represent 50% of all values, medians, means, standard error, and extreme values, respectively.

TABLE 3. General-linear-model summary of the analyses of sources of variation (sex, year, and foraging tactic) in wing chord in adult Zenaida Doves on Barbados in 2007 and 2008.

	Estimate ± SE	P
Intercept	14.65 ± 0.03	<0.0001
Tarsus length	0.12 ± 0.02	<0.0001
Sex	0.34 ± 0.05	<0.0001
Year	0.06 ± 0.05	0.20
Foraging tactic	0.22 ± 0.04	<0.0001
Sex * year	−0.15 ± 0.07	<0.05
Sex * foraging tactic	0.22 ± 0.06	<0.001

(Appendix 2). Our data thus suggest that the four sampled sites could be considered one genetically homogenous population in space and in time.

DISCUSSION

Despite its importance (Johnson 2002, McCaffery and Ruthrauff 2004, Kelly 2006), complete replication of studies that address the same phenomena in the same species (i.e., metareplication, *sensu* Johnson 2006) is scarce in ecology and ornithology. Indeed, revisiting the evidence for the existence of a resource polymorphism in Zenaida Doves from the same population in Barbados leads to different conclusions from those drawn by Sol et al. (2005). Although our results confirm that, irrespective of sex, territorial adults were larger than adults feeding in flocks, the reverse was observed in juveniles. Contrary to Sol et al. (2005), we found a significant excess of females among flock-feeding adults, whereas the sex ratio was balanced in territorial adults and in both territorial and flock-feeding juveniles. In addition, body condition did not differ between birds that fed in flocks or on territories. Finally, we found

no evidence for genetic differentiation between flock-feeders and territorial birds. Our results thus suggest that the patterns described by Sol et al. (2005) are not stable over time and do not provide a mechanism for the difference in foraging strategies between group-feeding and territorial Zenaida Doves.

The larger proportion of juveniles observed on territorial sites than in areas where birds fed in flocks was largely a consequence of the unusually high proportion of juveniles in Bellairs in 2007. Thus, the difference between the present study and that of Sol et al. (2005) might be simply explained by stochastic differences in productivity between years. Indeed, variation in breeding chronology in Zenaida Doves has been observed between Caribbean islands (Nellis et al. 1984, Wiley 1991) and between years for the same island (Nellis et al. 1984).

Consistency in female-biased sex ratio in areas where birds feed in flocks over two consecutive years indicates that the phenomenon was not spurious (i.e., due to random fluctuations). The difference between the present study and that of Sol et al. (2005) may, then, be due to the method used for sexing birds. Sol et al. (2005) relied on differences in the color of the back, supposedly less reddish in females than in males. By contrast, we used more reliable (Griffiths and Tiwari 1993, van de Pol et al. 2009) molecular markers to assign a sex.

Assessment of body condition suggested that territorial and flock-feeding doves were in equivalent condition. The observed discrepancy between the present study and that of Sol et al. (2005) in the comparison of payoffs between the two foraging strategies could, however, be due to the fact that unlike Sol et al. (2005), we did not include body mass in the calculation of BSI (see above).

Anthropogenic flock-feeding sites like Roberts and the Harbour are, however, likely to produce unstable conditions for birds. On one hand, occasional pest-management operations result in the removal of some of the individuals from these sites (L. Lefebvre pers. comm.), but in their absence, birds at Roberts and the Harbour
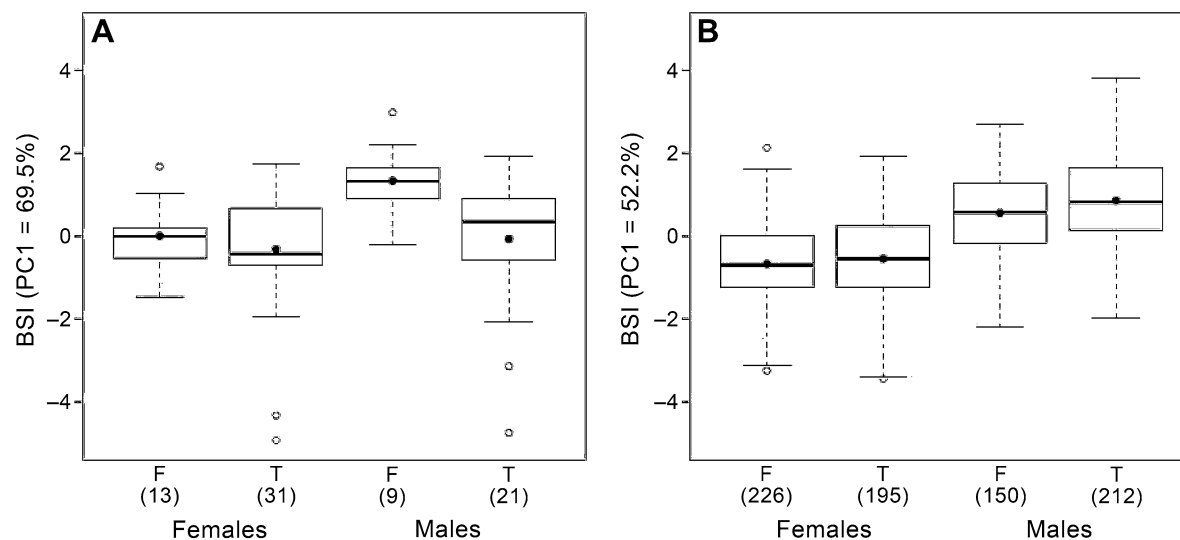

FIG. 4. Body size index (BSI) comparison between foraging tactic and sex in (A) juvenile and (B) adult Zenaida Doves (data pooled for year). "F" stands for group-feeding areas and "T" for territorial sites, with samples sizes in brackets. Boxes, plain line, black point, dashed lines, and open circles represent 50% of all values, medians, means, standard error, and extreme values, respectively.

have unrestricted access to very large quantities of cereal, legume, and maize seeds, the latter of which have very high digestibility and are readily stored in the body of columbid species as fat (Hullar et al. 1999, Sales and Janssens 2003). Birds in large flocks may also be less vulnerable to predators than individuals feeding alone or in pairs on territories (Hamilton 1971, Pulliam 1973) and may even achieve higher rates of food acquisition (Phelan 1987, Cézilly and Brun 1989, Sadedin and Elgar 1998, Dias 2006). Indeed, we never saw any Indian Mongoose (*Herpestes javanicus*) or feral cats (*Felix catus*) at the two sites where doves forage in flocks, whereas both predators are frequently seen in areas where doves defend territories and have been seen attacking and capturing doves (F. Cézilly pers. obs., J. Moreau pers. comm.; see also Nellis et al. 1984).

Finally, our genetic analyses did not reveal any level of genetic differentiation between individuals feeding on territories and individuals feeding in groups. Sol et al. (2005) hypothesized that genetic differentiation of territorial and flock-feeding birds might exist, despite casual observations of movements of birds between territorial and flock-feeding sites. Given the large sample size, the number of microsatellite loci, and the degree of polymorphism in our study, we are confident that even a low level of genetic differentiation would have been detected if present. Studies on resource polymorphism have revealed a variable amount of gene flow among sympatric morphs (Smith and Skúlason 1996, Dynes et al. 1999). However, there is some evidence that variation in spatial distribution linked to variation in feeding habits can promote partial reproductive isolation, nonrandom mating, and genetic differentiation in vertebrates (Dynes et al. 1999, Gíslason et al. 1999, Bergek and Björklund 2009). In Citril Finches (*Serinus citrinella*), for instance, a strong genetic and morphological differentiation has been observed at a small geographic sale (<5 km), in spite of current gene flow (Señar et al. 2006).

Sol et al. (2005) mentioned observations of doves roosting and nesting at the Harbour, suggesting that the presence of birds at that site did not correspond to short visits by floaters or birds defending territories elsewhere and instead represented a true behavioral option that included reproduction. By contrast, we found no evidence that doves nested at the Harbour or at Roberts during our 2007 and 2008 field seasons. Although we did not actively look for nests, we never observed any, nor did we observe any fledgling alone or with its parents at any of the two flock-feeding sites. By contrast, we regularly observed territorial birds with nests and parents feeding or escorting fledglings.

Taken together, our results suggest that the existence of alternative foraging tactics in Zenaida Doves in Barbados does not conform to the concept of resource polymorphism (Skúlason and Smith 1995, Smith and Skúlason 1996). Confirming earlier results (Sol et al. 2005), we found no evidence for the existence of discrete morphs linked to each foraging strategy in Zenaida Doves, as often reported in true cases of resource polymorphism (Skúlason and Smith 1995, Smith and Skúlason 1996, Whiteley 2007; but see Maerz et al. 2006). In addition, neither Sol et al. (2005) nor we were able to test for disruptive selection on body size, as would be expected in the case of resource polymorphism (Martin and Pfennig 2009).

More importantly, the assumption that floating is an inferior strategy compared with holding a territory deserves further consideration (Brown and Long 2007). Freed from spatial constraints, floaters may be better able than sedentary birds to find and exploit patchily distributed food resources. Thus, an alternative explanation is that flock-feeding by Zenaida Doves on Barbados is simply a facultative strategy, conditioned by local food availability and by sex- and age-related variation in the benefits of holding, or ability to hold, a territory. Juveniles and young adults with low resource-holding potential and poorly developed parental abilities may benefit more in the short term from exploiting a rich and predictable resource than from attempting to defend a territory. Adult females may also be less able to defend a territory when unpaired and may engage more than males in flock-feeding, which would explain the larger proportion of females among flock-feeders. Difference in body size between birds captured when feeding alone or in pairs and birds captured when feeding in flocks may, then, reflect not only variation in competitive ability but also differences in age between adult birds. Indeed, evidence shows that wing chord can increase significantly with age for several years in birds (Pienkowski and Minton 1973, Merom et al. 1999, Pérez-Tris and Telleria 2001). If flock-feeding is a particularly rewarding alternative strategy for young adults, we would expect that a significant proportion of flock-feeding birds would later become territorial. Nine of 400 birds ringed at Roberts or Harbour were resighted one or two years later on territorial sites (7 on one occasion, and 2 on two occasions).

In conclusion, our results indicate that the existence of two, not necessarily mutually exclusive, foraging tactics in Zenaida Doves in Barbados is more representative of a continuous intrapopulation variation in resource use than of resource polymorphism. Our study illustrates both the importance of metareplication (Johnson 2002) and the value of molecular tools in population biology and behavioral ecology (Hughes 1998, Parker et al. 1998). In addition, it suggests that caution should be exerted when referring to well-defined ecological concepts such as "resource polymorphism" to interpret intrapopulation variation in foraging strategy.

Literature Cited

Bailey, R. C., and J. Byrnes. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Systematic Zoology 39:124–130.

Bergek, S., and M. Björklund. 2009. Genetic and morphological divergence reveals local subdivision of perch (*Perca fluviatilis* L.). Biological Journal of the Linnean Society 96:746–758.

Bolnick, D. I., and B. M. Fitzpatrick. 2007. Sympatric speciation: Models and empirical evidence. Annual Review of Ecology, Evolution, and Systematics 38:459–487.

Borrás, A., J. Cabrera, and J. C. Señar. 2008. Local divergence between Mediterranean Crossbills occurring in two different species of pine. Ardeola 55:169–177.

Brown, D. R., and J. A. Long. 2007. What is a winter floater? Causes, consequences, and implications for habitat selection. Condor 109:548–565.

Carlier, P., and L. Lefebvre. 1996. Differences in individual learning between group-foraging and territorial Zenaida Doves. Behaviour 133:1197–1207.

Carlier, P., and L. Lefebvre. 1997. Ecological differences in social learning between adjacent, mixing, populations of Zenaida Doves. Ethology 103:772–784.

Cézilly, F., and B. Brun. 1989. Surveillance et picorage chez la tourterelle rieuse, *Streptopelia risoria*: effets de la présence d'un congénère et de la dispersion des graines. Behaviour 110:146–160.

Clabaut, C., A. Herrel, T. J. Sanger, T. B. Smith, and A. Abzhanov. 2009. Development of beak polymorphism in the African seedcracker, *Pyrenestes ostrinus*. Evolution and Development 11:636–646.

Crawley, M. J. 2007. The R Book. Wiley, Chichester, United Kingdom.

Dias, R. I. 2006. Effects of position and flock size on vigilance and foraging behaviour of the Scaled Dove *Columbina squammata*. Behavioural Processes 73:248–252.

Dolman, C. S., J. Templeton, and L. Lefebvre. 1996. Mode of foraging competition is related to tutor preference in *Zenaida aurita*. Journal of Comparative Psychology 110:45–54.

Dynes, J., P. Magnan, L. Bernatchez, and M. A. Rodríguez. 1999. Genetic and morphological variation between two forms of lacustrine brook charr. Journal of Fish Biology 54:955–972.

Excoffier, L., G. Laval, and S. Schneider. 2005. ARLEQUIN, version 3.0: An integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1:47–50.

Fridolfsson, A., and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30:116–121.

García-Berthou, E. 2001. On the misuse of residuals in ecology: Testing regression residuals vs. the analysis of covariance. Journal of Animal Ecology 70:708–711.

Gíslason, D., M. M. Ferguson, S. Skúlason, and S. S. Snorrason. 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences 56:2229–2234.

Goldberg, J. L., J. W. A. Grant, and L. Lefebvre. 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida Dove. Behavioral Ecology 12:490–495.

Goss-Custard, J. D., and S. E. A. Le. V. dit Durell. 1983. Individual and age differences in the feeding ecology of oystercatchers *Haematopus ostralegus* wintering on the Exe Estuary, Devon. Ibis 125:155–171.

Goudet, J. 1995. FSTAT (version 1.2): A computer program to calculate *F*-statistics. Journal of Heredity 86:485–486.

Griffiths, R., and B. Tiwari. 1993. The isolation of molecular genetic markers for the identification of sex. Proceedings of the National Academy of Sciences USA 90:8324–8326.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Hughes, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: A revolution results. Ecology 79:383–399.

Hullar, I., I. Meleg, S. Fekete, and R. Romvar. 1999. Studies of the energy content of pigeon feeds I. Determination of digestibility and metabolizable energy content. Poultry Science 78:1757–1762.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Jacob, E. M., S. D. Marshall, and G. W. Uetz. 1996. Estimating fitness: A comparison of body condition indices. Oikos 77:61–67.

Johnson, D. H. 2002. The importance of replication in wildlife research. Journal of Wildlife Management 66:919–932.

Johnson, D. H. 2006. The many faces of replication. Crop Science 46:2486–2491.

Kelly, C. D. 2006. Replicating empirical research in behavioral ecology: How and why it should be done but rarely ever is. Quarterly Review of Biology 81:221–236.

Lefebvre, L., B. Palameta, and K. K. Hatch. 1996. Is group-living associated with social learning? A comparative test of gregarious and a territorial columbid. Behaviour 133:241–261.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: A common mistake. Auk 104:116–121.

Maerz, J. C., E. M. Myers, and D. C. Adams. 2006. Trophic polymorphism in a terrestrial salamander. Evolutionary Ecology Research 8:23–35.

Martin, R. A., and D. W. Pfennig. 2009. Disruptive selection in natural populations: The roles of ecological specialization and resource competition. American Naturalist 174:268–281.

McCaffery, B. J., and D. R. Ruthrauff. 2004. Spatial variation in shorebird nest success: Implications for inference. Wader Study Group Bulletin 103:67–70.

McCormack, J. E., and T. B. Smith. 2008. Niche expansion leads to small-scale adaptive divergence along an elevation gradient in a medium-sized passerine bird. Proceedings of the Royal Society of London, Series B 275:2155–2164.

Merom, K., R. McCleery, and Y. Yom-Tov. 1999. Age-related changes in wing-length and body mass in the Reed Warbler *Acrocephalus scirpaceus* and Clamorous Reed Warbler *A. stentoreus*. Bird Study 46:249–255.

Monceau, K. 2009. Biologie des populations de tourterelles à queue carrée sur l'île de la Barbade—Apport de l'outil moléculaire. Ph.D. dissertation, Université de Bourgogne, Dijon, France.

Monceau, K., M. Gaillard, E. Harrang, D. Santiago-Alarcon, P. Parker, F. Cézilly, and R. Wattier. 2009. Twenty-three polymorphic microsatellite markers for the Caribbean endemic Zenaida Dove, *Zenaida aurita*, and its conservation in related *Zenaida* species. Conservation Genetics 10:1577–1581.

Nellis, D. W., R. A. Dewey, M. A. Hewitt, S. Imsand, R. Philibosian, and J. A. Yntema. 1984. Population status of Zenaida Doves and other columbids in the Virgin Islands. Journal of Wildlife Management 48:889–894.

Oksanen, L. 2001. Logic of experiments in ecology: Is pseudoreplication a pseudoissue? Oikos 94:27–38.

Olsson, J., R. Svanbäck, and P. Eklöv. 2007. Effects of resource level and habitat type on behavioral and morphological plasticity in Eurasian perch. Oecologia 152:48–56.

Parker, P. G., A. A. Snow, M. D. Schug, G. C. Booton, and P. A. Fuerst. 1998. What molecules can tell us about populations: Choosing and using a molecular marker. Ecology 79:361–382.

Parsons, K. J., and B. W. Robinson. 2007. Foraging performance of diet-induced morphotypes in Pumpkinseed Sunfish (*Lepomis gibbosus*) favours resource polymorphism. Journal of Evolutionary Biology 20:673–684.

Pérez-Tris, J., and J. L. Telleria. 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. Journal of Avian Biology 32:207–213.

Pfennig, D. W., A. M. Rice, and R. A. Martin. 2007. Field and experimental evidence for competition's role in phenotypic divergence. Evolution 61:257–271.

Phelan, J. P. 1987. Some components of flocking behavior in the Rock Dove (*Columba livia*). Journal of Field Ornithology 58:135–143.

Pienkowski, M. W., and C. D. T. Minton. 1973. Wing length changes of the knot with age and time since moult. Bird Study 20:63–68.

Proulx, R., and P. Magnan. 2004. Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis* M.). Evolutionary Ecology Research 6:503–522.

Pulliam, H. R. 1973. On the advantages of flocking. Journal of Theoretical Biology 38:419–422.

R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. [Online.] Available at www.R-project.org.

Raffaele, H., J. Wiley, O. Garrido, A. Keith, and J. Raffaele. 1998. A Guide to the Birds of the West Indies. Helm, London.

Raymond, M., and F. Rousset. 1995. An exact test for population differentiation. Evolution 49:1280–1283.

Rivera-Milán, F. F. 1997. Seasonal and annual changes in the population density of Zenaida Doves in the xerophytic forest of Guanica, Puerto Rico. Journal of Field Ornithology 68:259–272.

Rivera-Milán, F. F. 1999. Population dynamics of Zenaida Doves in Cidra, Puerto Rico. Journal of Wildlife Management 63:232–244.

Rohwer, S. 1990. Foraging differences between white and dark morphs of the Pacific Reef Heron *Egretta sacra*. Ibis 132:21–26.

Roulin, A. 2004. Covariation between plumage colour polymorphism and diet in the Barn Owl *Tyto alba*. Ibis 146:509–517.

Ruzzante, D. E., S. J. Walde, V. E. Cussac, P. J. Macchi, M. F. Alonso, and M. Battini. 2003. Resource polymorphism in a Patagonian fish *Percichthys trucha* (Percichthyidae): Phenotypic

evidence for interlake pattern variation. Biological Journal of the Linnean Society 78:497–515.

Sadedin, S. R., and M. A. Elgar. 1998. The influence of flock size and geometry on the scanning behaviour of Spotted Turtle Doves, *Streptopelia chinensis*. Australian Journal of Ecology 23:177–180.

Sales, J., and G. P. J. Janssens. 2003. Methods to determine metabolizable energy and digestibility of feed ingredients in the Domestic Pigeon (*Columba livia domestica*). Poultry Science 82:1457–1461.

Schluter, D. 2000. The Ecology of Adaptive Radiation. Oxford University Press, Oxford, United Kingdom.

Señar, J. C., A. Borrás, J. Cabrera, T. Cabrera, and M. Björklund. 2006. Local differentiation in the presence of gene flow in the Citril Finch *Serinus citrinella*. Biology Letters 2:85–87.

Skúlason, S., and T. B. Smith. 1995. Resource polymorphisms in vertebrates. Trends in Ecology & Evolution 10:366–370.

Slatkin, M. 1985. Gene flow in natural populations. Annual Review of Ecology and Systematics 16:393–430.

Smith, T. B. 1990. Resource use by bill morphs of an African finch: Evidence for intraspecific competition. Ecology 71:1246–1257.

Smith, T. B., and S. Skúlason. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annual Review of Ecology and Systematics 27:111–133.

Smith, T. B., and S. A. Temple. 1982. Feeding habits and bill polymorphism in Hook-billed Kites. Auk 99:197–207.

Sol, D., M. Elie, M. Marcoux, E. Chrostovsky, C. Porcher, and L. Lefebvre. 2005. Ecological mechanisms of a resource polymorphism in Zenaida Doves of Barbados. Ecology 86:2397–2407.

Svanbäck, R., P. Eklöv, R. Fransson, and K. Holmgren. 2008. Intraspecific competition drives multiple species resource polymorphism in fish communities. Oikos 117:114–124.

van de Pol, M., K. Oosterbeek, A. L. Rutten, B. J. Ens, J. M. Tinbergen, and S. Verhulst. 2009. Biometric sex discrimination is unreliable when sexual dimorphism varies within and between years: An example in Eurasian Oystercatchers *Haematopus ostralegus*. Ibis 151:171–180.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population-structure. Evolution 38:1358–1370.

Whiteley, A. R. 2007. Trophic polymorphism in a riverine fish: Morphological, dietary, and genetic analysis of mountain whitefish. Biological Journal of the Linnean Society 92:253–267.

Wiley, J. W. 1991. Ecology and behavior of the Zenaida Dove. Ornitologia Neotropical 2:49–75.

Wright, S. 1969. Evolution and the Genetics of Populations, vol. 2: The Theory of Gene Frequencies. University of Chicago Press, Chicago, Illinois.

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APPENDIX 1. Genetic data summary of adult Zenaida Doves on Barbados. Sample size (n), number of alleles A (with total number), observed (H_o) and expected (H_e) heterozygosity and P value from Fisher's exact test of Hardy Weinberg equilibrium (p HWE) are presented for each locus and population for the two sampling years (data pooled for sex). Significant values after Bonferroni's correction are in bold ($P = 0.007$).

		2007				2008			
		Bellairs (30)	Sunset Crest (30)	Roberts (32)	Harbour (32)	Bellairs (32)	Sunset Crest (32)	Roberts (29)	Harbour (30)
ZaD1									
	A (8)	8	8	7	7	6	6	8	7
	H_o	0.87	0.83	0.75	0.84	0.87	0.81	0.86	0.76
	H_e	0.84	0.84	0.81	0.81	0.82	0.82	0.84	0.76
	p HWE	0.41	0.80	0.88	0.85	0.87	**0.007**	0.86	0.27
ZaD11									
	A (8)	7	6	7	5	7	7	6	6
	H_o	0.81	0.81	0.83	0.90	0.80	0.69	0.78	0.79
	H_e	0.80	0.73	0.77	0.78	0.82	0.79	0.79	0.77
	p HWE	0.82	0.87	0.73	0.07	0.26	0.67	0.49	0.52
ZaD104									
	A (10)	7	8	8	7	8	7	8	6
	H_o	0.93	0.90	0.91	0.72	0.85	0.81	0.79	0.78
	H_e	0.83	0.84	0.80	0.79	0.79	0.83	0.84	0.78
	p HWE	0.79	0.90	0.33	0.57	0.86	0.06	0.58	0.65
ZaD105									
	A (6)	6	4	5	6	5	5	5	5
	H_o	0.73	0.57	0.65	0.56	0.63	0.43	0.64	0.46
	H_e	0.65	0.59	0.66	0.56	0.59	0.53	0.62	0.63
	p HWE	0.69	0.88	0.83	0.67	0.57	0.18	0.39	0.09
ZaD108									
	A (10)	9	9	9	9	9	10	9	9
	H_o	0.79	0.79	0.75	0.93	0.69	0.77	0.86	0.79
	H_e	0.87	0.82	0.84	0.86	0.87	0.88	0.86	0.86
	p HWE	0.06	0.81	0.46	0.73	0.17	**0.003**	0.52	0.34
ZaD119									
	A (10)	7	8	9	8	7	9	10	9
	H_o	0.79	0.79	0.77	0.93	0.59	0.74	0.76	0.83
	H_e	0.77	0.81	0.75	0.77	0.80	0.80	0.81	0.75
	p HWE	0.87	0.63	0.85	0.15	0.04	0.22	0.39	1.00
ZaD121									
	A (14)	10	11	10	9	10	10	11	10
	H_o	0.83	0.83	0.90	0.87	0.87	0.63	0.93	0.80
	H_e	0.91	0.84	0.88	0.86	0.88	0.82	0.89	0.88
	p HWE	0.19	0.99	0.13	0.87	0.57	0.04	1.00	0.22
All loci									
	Mean H_o	0.82	0.79	0.79	0.82	0.76	0.70	0.80	0.74
	Mean H_E	0.81	0.78	0.79	0.78	0.80	0.78	0.81	0.78
	p HWE	1.00	1.00	1.00	0.60	1.00	1.00	1.00	1.00

APPENDIX 2. Pairwise genetic differentiation between populations of Zenaida Doves (adults only, data pooled for sex): exact test/F_{ST} value (above diagonal) and absolute number of migrants (below diagonal). Significant level after Bonferroni's correction $P = 0.002$. None of the F_{ST} values was significant.

		2007				2008			
		Bellairs	Sunset Crest	Roberts	Harbour	Bellairs	Sunset Crest	Roberts	Harbour
2007	Bellairs	—	1.00/0.002	1.00/0.001	0.54/0.007	1.00/−0.010	1.00/−0.006	1.00/−0.002	1.00/0.003
	Sunset Crest	266.45	—	1.00/0.008	0.48/0.008	1.00/0.004	1.00/−0.011	1.00/0.003	1.00/0.011
	Roberts	500.88	63.47	—	0.50/0.002	1.00/0.0001	1.00/0.004	1.00/0.002	1.00/0.005
	Harbour	72.25	70.15	208.40	—	0.54/0.004	0.51/0.002	0.59/0.001	0.58/0.0005
2008	Bellairs	∞	113.71	3,553.21	111.09	—	1.00/−0.002	1.00/−0.003	1.00/0.008
	Sunset Crest	∞	∞	120.77	304.49	∞	—	1.00/0.004	1.00/0.006
	Roberts	∞	149.8	241.28	820.63	∞	134.02	—	1.00/0.009
	Harbour	146.51	46.18	107.2	1,014.05	62.83	88.44	53.29	—