# ECOLOGICAL MECHANISMS OF A RESOURCE POLYMORPHISM IN ZENAIDA DOVES OF BARBADOS

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Abstract. Despite the important place of resource polymorphisms in ecological and evolutionary theories, the reason why a group of individuals sharing a common environment should diverge in the use of the resources remains poorly known. Given the existence of distinct open niches and the relaxation of interspecific competition, niche theory suggests two possible mechanisms: resource competition between conspecifics and trade-offs in resource use efficiency. We investigated the importance of these explanations in a foraging polymorphism recently developed by Zenaida Doves (Zenaida aurita) on the West Indian island of Barbados. In this polymorphism, individuals either aggressively defend feeding territories from conspecifics or feed in large unaggressive groups with conspecifics. Combining field observations and a cage experiment, we found no evidence that the polymorphism is primarily driven by age- or sex-related differences, or that it results from morphological feeding specializations or dietary preferences. Instead, our results support the hypothesis that individual specializations arise from contest competition. In the study area, competition for territories was intense, with very little undefended space left between territories and owners frequently involved in territorial contests. Replacement of territory holders from year to year was low compared to the number of potential recruits, implying that many doves were incapable of securing a territory. Approximately half the doves at territorial sites did not hold a territory but wandered between them as floaters. Compared with territory holders, floaters were smaller and had shorter wings, traits that in this species mediate territory defense. Yet floaters did not differ from group feeding doves on these morphological traits. This suggests that group feeders are floaters that shift to an alternative resource. The new resource appears to be suboptimal, as indicated by the fact that group feeders were in worse body condition than doves from the territorial sites. Taken together, our results suggest that the resource polymorphism in Zenaida Doves is primarily driven by competition for territories, which forces less competitive individuals to use alternative, subobtimal resources.

Key words: competition; ecomorphology; foraging specialization; social learning.

# INTRODUCTION

Resource polymorphisms, the occurrence of discrete intraspecific differences in niche use, are widespread and diverse in vertebrates (Skúlason and Smith 1995, Smith and Skúlason 1996). Classic examples include the benthivory vs. planktivory habits in fish (Ehlinger 1990, Skúlason et al. 1999), the feeding on soft vs. hard seeds in Seedcrackers (Smith 1987, 1990), and the "stabber" vs. "hammerer" techniques to open mussels in oystercatchers (Goss-Custard and Le V. Dit Durell 1983). Resource polymorphisms are increasingly recognized as important in resource partitioning and competitive avoidance within populations (Skúlason and Smith 1995, Smith and Skúlason 1996). They are

<sup>1</sup> Present address: Centre de Recerca Ecologica i Aplicacions Forestals (CREAF), Universitat Autònoma de Barcelona, E-08193 Bellaterra, Catalonia, Spain. E-mail: d.sol@creaf.uab.es also thought to be a major diversifying force by promoting the initial stages of evolutionary divergence (Skúlason and Smith 1995, Smith and Skúlason 1996). Thus, understanding the ecological factors that maintain a polymorphism, and may also have been involved in its origin, is of broad interest (Smith 1990, Andersson 2003).

Smith and Skúlason (1996) suggested two fundamental conditions that promote resource polymorphisms: the existence of distinct open niches and the relaxation of interspecific competition. Provided that these conditions hold, why should a group of individuals sharing a common environment diverge in the use of the resources? There are two possible answers to this question (Le V. Dit Durell 2000, Bolnick et al. 2003). One is the existence of a trade-off in resource use such that individuals that are more efficient at exploiting one resource are less efficient at exploiting another ("trade-off" hypothesis). These trade-offs may reflect individual differences in the morphological, behavioral, or physiological capacity to exploit alterna-

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PLATE 1. Zenaida Dove (Zenaida aurita) from the Island of Barbados. Photo credit: D. Sol.

tive resources, as well as differences in previous experience with the resources (Le V. Dit Durell 2000, Bolnick et al. 2003). In the oystercatcher *Haematopus ostralegus* for example, specialization on a prey capture technique is determined by a combination of functional variation in bill morphology and individual limitations in learning a small repertoire of handling behaviors (Sutherland et al. 1996).

Alternatively, resource polymorphisms might be driven by competition in which the strongest competitors monopolize the most rewarding resources, forcing the poorest competitors to adopt alternative resources ("competition" hypothesis). In the case of oystercatchers, the different feeding sources do not provide equal fitness payoffs; subdominant and juvenile birds are then restricted to suboptimal diets that differ from the ones they would choose in the absence of competition (Goss-Custard and Le V. Dit Durell 1983, 1987). The "tradeoff" and "competition" hypotheses are not mutually exclusive, and may be linked to both age and/or sex differences (see also Temeless and Kress 2003).

The importance of the "trade-off" and "competition" hypotheses on the initial establishment of resource polymorphisms has been the subject of few empirical tests. To contrast these alternatives, one needs to study resource polymorphisms when they are at the early stage of development. In more advanced stages, alternative processes such as frequency-dependent and divergent selection may gain greater importance (Smith and Skúlason 1996), leading to new trade-offs and altering the competitive conditions. This may obscure the ecological processes that have initially driven the polymorphism. Unfortunately, there are few well-documented examples of polymorphisms that are known to be in their early stages.

Here, we test the alternative hypotheses that tradeoffs and contest competition may have driven a foraging polymorphism shown by Zenaida Doves (Zenaida aurita; see Plate 1) on the West Indian island of Barbados. In this polymorphism, individuals either aggressively defend feeding territories from conspecifics or feed in large unaggressive groups with conspecifics (see the following section). The second strategy has been possible since the appearance of a resource opportunity associated with human activities, the building in the mid 1960s of grain storage facilities in a landfilled harbor (Haverschmidt 1969). The new resource is predominantly used by Zenaida Doves, who represent 86% of the birds seen there (Dolman et al. 1996), on an island that has a very low avian diversity overall (Evans 1990). Thus, niche expansion of Zenaida Doves is a recent phenomenon little constrained by ecological pressures from heterospecifics, providing a good system to investigate the early stages of development of a resource polymorphism. In addition, because the effects of the polymorphism on learning have been well studied in Barbados Zenaida Doves (Carlier and Lefebvre 1996, 1997, Dolman et al. 1996, Lefebvre et al. 1996, Seferta et al. 2001), it not only provides an interesting test case for ecological theory, but a chance to study the role of cognition in the maintenance, and possible accentuation, of divergent behavioral strategies.

# THE RESOURCE-BASED POLYMORPHISM OF ZENAIDA DOVES IN BARBADOS

In most areas of Barbados, Zenaida Doves aggressively defend, either alone or in mated pairs, year-round territories against conspecifics (Lefebvre et al. 1996). In sharp contrast, at isolated sites where large amounts of seed spillage are available, for example the Barbados Mills compound at the Deep Water Harbor, Zenaida Doves feed in large, unaggressive aggregations (Carlier and Lefebvre 1996, Dolman et al. 1996). These very different social foraging conditions are reflected in differences in cognition. Experiments in captivity have shown that group-feeding doves are less neophobic and faster at individual learning than are territorial doves (Carlier and Lefebvre 1997, Seferta et al. 2001). In line with their social foraging experience in the field, groupfeeding doves also learn more readily from a conspecific than from a heterospecific demonstrator, while territorial doves learn poorly from conspecifics (Lefebvre et al. 1996), but more readily from the bird they most often feed with, the Carib Grackle, Quiscalus lugubris (Dolman et al. 1996). Territorial doves also use grackles as sources of information on predation risk, responding to their alarm calls with increased vigilance (Griffin et al., in press).

Previous work indicates that the shift between territorial aggression and unaggressive group feeding is controlled by the density and spatio-temporal predictability of food (Goldberg et al. 2001), in line with the predictions of both resource-defense and game theory (Grant 1997, Dubois et al. 2003). Territorial doves exploit predictable, low-density seeds and legumes, while group-feeding doves exploit large ephemeral patches of spilled grain and animal feed provided by factories (Dolman et al. 1996, Goldberg et al. 2001). Experimental manipulations of food supply have shown that when food becomes "defendable" (i.e., less abundant and more predictable in time and space) group-feeding doves increase their aggressiveness and exclude conspecifics from the patches. In normal conditions, however, territorial and group feeding are highly specialized in their own strategy, with 96% fidelity to sites that feature different foraging modes (Carlier and Lefebvre 1997).

# **TESTED PREDICTIONS**

The "trade-off" hypothesis makes two predictions particularly amenable for empirical testing. First, if

morphology improves performance in using one resource at the expense of the other, then we predict differences in morphology between solitary and groupfeeding doves. In particular, we expect differences in bill morphology, as this character is associated with feeding performance in birds (e.g., Smith 1987, 1990, Sutherland et al. 1996). We tested this prediction through a morphometric comparison of solitary and group-feeding doves. Second, if there are trade-offs in resource efficiency between morphs, whether associated with differences in morphology, behavior, or physiology, this would be reflected in differences between them in food type preferences. We consequently designed a food preference experiment to assess this prediction.

The "competition" hypothesis makes three main predictions (Fretwell and Lucas 1970, Goss-Custard and Le V. Dit Durell 1983, Petit and Petit 1996). First, alternative resources should differ in their payoffs. Second, competition for resources should be strong in the most rewarding habitat. Finally, the poorest competitors should preferentially use the less rewarding habitat. We tested these predictions by examining the dynamics of territory acquisition in the dove population.

# STUDY AREA

We studied Zenaida Doves in two sites located 9 km apart on the island of Barbados: one where doves are territorial (the Bellairs Research Institute of McGill University and the adjacent grounds of Folkestone Park, St-James Church, and the Coral Reef Club Hotel; hereafter termed "Bellairs"), and the other where they are group feeders (Barbados Mills compound, Deep Water Harbor; hereafter termed "Harbor"). The Bellairs site consists of a coastal stretch that provides abundant arboreal cover (palm, manchineel, casuarina, and mahogany) and includes beaches, hotel and restaurant grounds, public parks, and private residences (Dolman et al. 1996). The Harbor includes docking, grain-loading, milling, and storage operations for animal feed and grain. It is situated in an industrial zone created by land filling in 1961, joining the small Pelican Island to the southwest coast of Barbados. Haverschmidt (1969) reports that in 1965, he saw only 15-20 doves at the harbor, with numbers increasing to 75-80 in 1968 and >200 in recent years (Goldberg et al. 2001; this study). The area has no arboreal cover but often provides large, ephemeral patches of spilled grains (wheat and maize) and soybean as a result of transport and storage operations (Dolman et al. 1996).

#### GENERAL METHOD

Zenaida Doves were caught using walk-in baited drop traps at the Bellairs and Harbor sites. Upon capture, doves were fitted with colored plastic leg bands to identify them individually. Juveniles were identified for the presence of distinctive, unmolted great cover feathers and lack of iridescent patches on the neck (Del Hoyo et al. 1997, Gibbs et al. 2001). Sex of adults was determined from the color of the back, less reddish in females than in males (Del Hoyo et al. 1997, Gibbs and Cox 2001).

To examine morphological differences between birds, 302 Zenaida Doves (100 at Bellairs and 202 at the Harbor) were captured between 15 May and 3 June 2001. After ringing, the following measurements were taken by a single experimenter: length of the right third primary feather; length of the right tarsus; bill length; bill depth; bill width; tail length; and mass. Sample sizes vary slightly for some measures because we did not measure traits affected by injuries or feather molting. Measurements were taken using an electronic caliper ( $\pm$  0.01 mm), except for wing and tail variables, which were measured with a ruler ( $\pm$  1 mm). Mass was measured with a 300-g Pesola spring scale ( $\pm 0.5$ g). Comparison of 15 birds captured twice indicated high repeatability of all our measures (Pearson's r, range 0.70-0.92) except body mass (0.57). In birds, the repeatabilities of body mass tend to be lower than that of other traits because it may fluctuate according to the food ingested between captures. After all morphological measures were taken, banded doves were released at their capture site.

During two months after banding and release, individuals captured at the Bellairs site were intensively monitored through standardized surveys to assess temporal and spatial patterns of site attendance. A route was selected such that it included all parts of the study site. To avoid biasing data gathering to some periods of the day, we divided it into four periods and a similar number of surveys were carried out within each period. Each survey took  $\sim$ 30 minutes, and a maximum of two surveys at different periods were done per day. During a survey, we noted the position of each marked bird on a grid, the main behavior it showed in the five minutes after sighting, and the eventual presence of a mate. Although Bellairs Zenaida Doves are extremely tame around humans (Lefebvre 1996), all observations were carried out at a distance of at least 10 m to avoid disturbance. We carried out a total of 41 surveys. In addition, we periodically surveyed more distant areas with a less standardized method to determine whether some of the banded doves held territories outside the study area.

A dove was considered territorial if it was observed for several weeks attacking and driving away other doves from the same area. Territorial displays are very obvious in Zenaida Doves. The resident patrols its territory by walking slowly on the ground, and it responds to the presence of any conspecific intruder by running towards it, performing a raised-wing, ground-pecking display at the territory boundary, and attacking the other bird with wing slaps if it does not retreat (see photographs in Lefebvre 1996). Mated pairs were defined as different-sex birds that were repeatedly seen feeding or walking unaggressively within 5 m of each other in the same area, showing a characteristic wing vibration display when encountering each other on the ground, as well as occasional allogrooming and mating behaviors.

In May 2002, we captured, marked, and measured the wing length of 90 new doves at Bellairs. This information was used to increase sample size in comparisons of doves within this study site. From 1 May to 15 August we also carried out 6 hours of randomized focal observations on banded individuals. These observations were used to estimate territory boundaries and study changes in territory owners between years, as well as further identify the few presumed territorial birds or mates from 2001 for which insufficient information was available. In addition, we made focal observations of mated pairs seen simultaneously (30 minutes maximum) so that we could examine sex-specific differences in time devoted to territorial behavior.

To test for differences in food preference, nine adult individuals were caught at the Bellairs site and eight at the Harbor. They were housed individually in 30 imes $30 \times 30$  cm cages in an outdoor aviary at the Bellairs Research Institute, out of visual contact with the other doves. After capture and housing, the birds were given a commercial dove seed mixture and water ad libitum for two days. On day 3, they were food deprived overnight and offered four uncovered Petri dishes that each contained a single seed type, randomly chosen from eight types (millet, milomaize, wheat, cracked maize, safflower, canary seed, oats, and shelled sunflower). Water was available ad libitum in a cup situated just outside the cage. Before presentation to the birds, each dish was filled with  $\sim 15$  g of its designated seed type and weighed to the nearest 0.01 g on a digital scale. Each dish was then placed under the wire mesh bottom of the dove's cage. Food dishes presented outside or inside a Zenaida Dove cage lead to extensive spillage, which the wire bottom of the cage prevented. Birds were given four hours every day to feed, after which the dishes were removed and the seed remaining in the dishes carefully weighed; whatever minimal spillage had occurred was added to the remaining seed in its dish before weighing. Control dishes were set out on a adjacent table to assess any changes in mass due to drying or humidity. On the next day, the birds were offered four dishes each containing the food types not given the day before. The presentation of all eight food types was repeated eight times in this manner over 16 days. After the experiment, all 17 doves were offered mixed seed and water for 24 hours and released at their point of capture.

#### RESULTS

#### Sex and age differences

In many animals, feeding specializations are related to sex, age, or both, but this does not seem to be the case in Barbados Zenaida Doves. Among the 302 wild-



FIG. 1. Percentages of Zenaida Doves trapped at Bellairs and the Harbor according to (A) their age and (B) their sex.

caught birds, neither the proportion of juveniles (test of proportions: P = 0.293) nor the proportion of females (P = 0.376) differed between the sites where doves are territorial and where they feed in groups (Fig. 1).

#### Morphological specializations for feeding

We described the bill morphology of adult doves in terms of size and shape, and tested for differences between Harbor and Bellairs doves. Shape was studied through a principal components analysis (PCA; see Sneath and Sokal 1973) on standardized values of bill measures (bill length, depth, and width), including a measure of overall body size (wing length). The first factor (44% of the total variance explained), which was positively correlated with bill depth and width, may be interpreted as variation in bill size that does not covary with body size. The second principal component (32% of the total variance explained) was positively associated with bill length and wing length; it thus does not describe bill shape per se but overall size of the

TABLE 1. Correlations of morphological traits of Zenaida Doves with the two main factors extracted from a principal component analysis with a varimax rotation.

Trait	Factor 1	Factor 2	
Wing length	0.120	0.798	
Bill length	-0.124	0.798	
Bill depth	<b>0.932</b>	0.021	
Bill width	<b>0.938</b>	-0.025	
Explained variance	0.44	0.32	

*Note:* Variables with the highest weightings on the factors are shown in boldface type.

individual. Bellairs and Harbor birds did not significantly differ on either of the three bill size measures or on the first factor of the PCA (Tables 1 and 2). Harbor males tended to have deeper bills than Bellairs males ( $t_{90} = 2.32$ , P = 0.023), but this difference was not significant under Bonferroni standards.

# Dietary preferences

We found no evidence that doves from Bellairs and the Harbor differed in their food choices in our cage experiment. Birds from the two sites showed uncorrelated choices in the first three trials, but converged on highly correlated choices in later trials (P < 0.05, n = 8; average amount of each seed type eaten per trial for all birds from each site; Fig. 2B). A repeated-trials ANOVA revealed significant effects of food type ( $F_{7, 120}$ = 10.33, P < 0.001) and repeated trials ( $F_{7,840} = 6.75$ , P < 0.001), as well as a significant food-by-trial interaction ( $F_{49,840} = 2.54, P < 0.001$ ). However, there was no effect of site, either as a main effect ( $F_{1, 120} =$ 0.15, P = 0.701) or a between- ( $F_{7, 120} = 1.11$ , P =363) or within-subjects ( $F_{7,840} = 0.57, P = 0.770$ ) interaction. Over the eight repeated trials, doves showed a marked increase in their total consumption of seed (71%), but birds from the two sites did not differ in this increase (Fig. 2A; site by repeated trials ANOVA on total consumption: site effect:  $F_{1,15} = 0.45$ , P =0.511; trial effect:  $F_{7,105} = 10.89$ , P < 0.001; interaction:  $F_{7,105} = 0.90, P = 0.508$ ).

#### Competition for territories

Having found no evidence for age, sex, bill morphology, and food preferences, we asked whether the

TABLE 2. Differences in bill morphology (mm, mean  $\pm$  SD) between Zenaida Doves trapped at the Bellairs and Harbor sites (see *Morphological specializations for feeding* for details). Factor 1 and 2 values are from a principal component analysis.

	Sexes pooled		Females		Males	
Trait	Harbor	Bellairs	Harbor	Bellairs	Harbor	Bellairs
Bill length Bill depth Bill width Factor 1 Factor 2	$\begin{array}{c} 22.81 \pm 0.84 \\ 5.38 \pm 0.42 \\ 5.76 \pm 0.37 \\ 0.46 \pm 0.55 \\ -0.24 \pm 0.94 \end{array}$	$\begin{array}{c} 22.96 \pm 0.90 \\ 5.31^* \pm 0.39 \\ 5.76 \pm 0.48 \\ 0.35 \pm 0.53 \\ 0.16^* \pm 0.99 \end{array}$	$\begin{array}{c} 22.62 \pm 0.72 \\ 5.33 \pm 0.40 \\ 5.71 \pm 0.31 \\ 0.36 \pm 0.47 \\ -0.51 \pm 0.70 \end{array}$	$\begin{array}{r} 22.72 \pm 0.88 \\ 5.27 \pm 0.39 \\ 5.71 \pm 0.60 \\ 0.21 \pm 0.55 \\ -0.26 \pm 1.02 \end{array}$	$\begin{array}{c} 23.05 \pm 0.80 \\ 5.56 \pm 0.39 \\ 5.86 \pm 0.39 \\ 0.68 \pm 0.56 \\ 0.17 \pm 0.87 \end{array}$	$\begin{array}{c} 23.19 \pm 0.94 \\ 5.36 \pm 0.42 \\ 5.82 \pm 0.38 \\ 0.51 \pm 0.51 \\ 0.63^* \pm 0.87 \end{array}$

\*P < 0.05.



FIG. 2. (A) Total amount of food (g) eaten per day by doves from Bellairs (circles) and from the Harbor (triangles); the error bar indicates  $\pm$ SEM. (B) Correlation between the average amount of each food type eaten per day per bird from Bellairs and from the Harbor. The horizontal line represents the threshold of significance for the correlation coefficients. Correlations between food types above this threshold are significantly different from zero at P < 0.05. (See the *General Method* section for further details.)

resource-based polymorphism in Zenaida Doves could be driven by competition for territories. To validate this possibility, we predicted (1) differences in payoff between alternative foraging habitats, (2) high levels of competition for resources in the most rewarding foraging habitat, and (3) the use of the less rewarding habitat by the poorest competitors. Evidence for all these predictions is presented in the next sections.

# Differences in payoff between habitats

We evaluated differences in the payoff among foraging areas by comparing the body condition of birds caught at the two sites (Sherry and Holmes 1996). Body condition was estimated as body mass controlled for body size, a method widely used and reliable in birds and other vertebrates (Jakob et al. 1996, Garcia-Berthou 2001). All other things being equal, an individual whose mass is inferior to that of another for equal body size can be considered in worse condition. Body size for each individual was expressed as its factor score on a PCA, which included wing length, tarsus length, bill length, and mass (all previously log-transformed and standardized). This size factor score was then used as a covariate in an ANCOVA comparing body mass between Bellairs and Harbor doves (see Garcia-Berthou 2001) and including sex. Despite the fact that the body mass of an individual may weakly oscillate between days, we found clear patterns of variation across study sites and sexes. Doves from the Harbor had lower mass for their size than those from Bellairs ( $F_{1,188} = 7.32$ , P = 0.007; Fig. 3). Males had lower mass for their size than females ( $F_{1,188} = 21.98$ , P < 0.0001), but the interaction between sex and morph was not significant ( $F_{2,188} = 1.00$ , P = 0.32).

# Is there a shortage of territories at Bellairs?

If there is a shortage of suitable territories in the Bellairs area, we would expect some individuals there to be floaters (i.e., individuals without a given territory that attempt to feed on the territories of others). We studied the daily attendance rate of marked individuals by counting the number of days in which a bird was seen, divided by the total number of survey-days between their first and last sighting (Senar et al. 1992, Sol and Senar 1995). This method allowed us to assess how often individuals were observed, excluding the effects of emigration or death. The pattern of days in attendance at the study site was bimodal: some individuals were rarely observed at the site for long periods, whereas others occurred in a more regular fashion (Fig. 4). Behavioral observations during surveys revealed that these rarely observed individuals never succeeded in chasing other birds from a feeding area and never performed territorial displays or wing-slapping fights, either within or outside the study area. Their sighting patterns were also widely distributed in space. In contrast, birds that were regularly seen showed a concentrated spatial pattern of sightings and were often observed defending the same area. The latter type of Bellairs dove can be considered a territory holder, while the former can be characterized as a floater. In our Bellairs area sample, 53% of birds were con-



FIG. 3. Differences in body condition between doves from Bellairs and the Harbor. Body condition is measured as the residuals of a log-log regression of body mass against body size (first factor of a PCA; see details in *Differences in payoff between habitats*). Error bars represent  $\pm$ SE.



FIG. 4. Pattern of daily attendance of doves at the Bellairs site. Attendance is estimated as the number of days in which a bird was seen divided by the total number of survey days between the first and last observation.

sidered floaters in the summer of 2001 and 51% in the summer of 2002.

There were significant age- and sex-specific differences between floaters and territory owners. First, while juveniles were frequent among floaters (31.5% of the total, years pooled), all territorial individuals were adults ( $\chi^2 = 31.9$ , df = 1, P < 0.0001). Second, the tertiary sex ratio (males / males + females) in floaters was female-biased (0.28;  $\chi^2 = 8.39$ , df = 1, P < 0.0037) and significantly lower than that of territorial doves (0.60;  $\chi^2 = 10.1$ , df = 1, P < 0.002).

Further evidence for the existence of strong competition for territories comes from the analysis of territorial behavior. The mapping of the territories at the Bellairs site revealed very few vacant zones between defended areas (Fig. 5). Similar to the pattern reported by Dolman et al. (1996; up to 70 aggressive acts per bird per hour), territorial encounters were frequent in our study (14.7  $\pm$  10.5% [mean  $\pm$  sD] of all behaviors observed per individual; Fig. 6). Males were more often involved in defense than females (Fig. 7), initiating most attacks and territorial displays (Wilcoxon matched pairs test, z = 3.62, P = 0.0003, N = 17 mated pairs monitored together on their territory).

New territories become available when the owners die, and hence survival rates may be critical in determining settlement dynamics in the population. In territorial doves, the resighting rate of banded birds from 2001 to 2002 was 75%. This implies that in 2002, an insufficient number of vacant territories were created to recruit all the floaters. Indeed, only three new individuals were able to obtain a territory in 2002, two of which had been observed as floaters the previous year. The proportion of adult floaters marked in 2001 that were resignted in 2002 (43.3%) was significantly lower than that for territorial doves ( $\chi^2 = 10.9$ , df =



FIG. 5. Map of territories for 20 male doves from the Bellairs site estimated as 75% convex polygons. Maps were drawn with the program Range 5 (Kenward and Hodder 1996). Shaded areas represent buildings.

1, P < 0.001). This low value is likely to reflect emigration from the Bellairs area as well as death.

# Do poorer competitors use the less rewarding habitat?

We finally asked if Bellairs territory owners differed from floaters and Harbor group feeders in their ability for contest competition. Wild-caught Zenaida Doves do not interact or defend food sources when they are caged together (L. Lefebvre, *personal observation*), so we could not conduct experimental encounters. We looked instead for differences in the main morphological traits used in territorial displays and fights, wing (Lefebvre 1996) and body size (Johnston and Janiga 1995). We predicted that Bellairs territory holders



FIG. 6. Time allocated to different activities by the 21 adult doves most often observed (i.e., those with 15 or more observations) in the transects on marked individuals at the Bellairs site. Each number along the *x*-axis represents a single banded individual.



FIG. 7. Sexual differences in the frequency of territorial behaviors (actual numbers of chases, fights, and territorial displays) initiated by males and females on their territory, based on simultaneous observations (up to 30 min. of continuous monitoring) of both members of the pair. The dashed line represents the isometric line, points below this line indicating that the male defended the territory more often than the female.

should have larger wings and bigger bodies than do Bellairs floaters and group-feeding birds, but we expected no differences between the latter groups. We also predicted these differences to be more accentuated in males compared to females, given that territory defense is more often done by males (see Is there a shortage of territories at Bellairs?; Fig. 7). We focused on adults, as juveniles did not hold territories. As predicted, territory-holding males had a larger body size  $(F_{2.74} = 8.96, P = 0.0003)$  and longer wings  $(F_{2.101} =$ 8.42, P = 0.0004) than both Bellairs floaters and groupfeeding birds from the Harbor (Fig. 8), but they did not differ in any other morphological trait (P > 0.05in all cases). In females, differences in body size ( $F_{2.83}$ = 2.4, P = 0.09) and wing length ( $F_{1,116} = 2.19, P =$ (0.12) were in the same direction as those seen in males, but were not significant. Bellairs floaters and birds from the Harbor did not show any differences, either in males or females (P > 0.86 always).

# DISCUSSION

Our results reveal that the resource polymorphism in Zenaida Doves is not primarily caused by age or sex-related differences in the use of alternative resources. Then why have Barbados Zenaida Doves diverged in the use of the resources despite sharing a common environment? Doves from the territorial and group-feeding sites showed no differences either in bill morphology or food type preference. In our cage experiment, birds from the two sites converged on very similar seed preferences after only three encounters with the eight seed types. There is thus no evidence for the "trade-off" hypothesis.

Instead, our results provide support for the "competition" hypothesis. Intraspecific competition is considered a major driver of resource specializations, as it increases the pressure on individuals that do poorly on the preferred resource to switch to alternative ones (Bolnick et al. 2001). In a territorial bird, contest competition may result in pressures on territory size, in the presence of a large number of floaters and/or in the use of alternative habitats (Sutherland 1996). Evidence for all these effects was found in Barbados Zenaida Doves. Territories covered most of the Bellairs area, competition for them was intense, particularly in males, and replacement of holders from year to year was low compared to the number of potential recruits. The ability to secure a territory was partially dependent on age and sex, and was strongly associated with wing morphology and body size. Territory holders were all adults, tended to be males, and had significantly heavier bodies and longer wings than did floaters. In pigeons and doves, age, sex, and morphology are all defining characters of social dominance (Johnston and Janiga 1995). The wing is particularly relevant in the case of Zenaida Doves, as it is used both in attacks and territorial displays. In displays, where opponents walk parallel to each other along the territory boundary, pecking at the ground and raising the contralateral wing, length of the wing may serve as an honest indicator of resourceholding potential. In fights, the extra reach provided



FIG. 8. Differences in wing length and body size (first factor of a PCA) between group-feeding (gregarious) doves from the Harbor and floater and territorial doves from Bellairs. Error bars represent standard errors.

by the difference in wing length means that the blows of the longer winged bird hit the opponent more often than those of the shorter winged bird.

While floaters from Bellairs had shorter wings and were smaller than territorial individuals, they did not differ on these traits from group feeding doves from the Harbor. Many group feeders may thus be floaters that settle in the alternative habitat provided by the Harbor. The body condition of group-feeding doves, estimated as body mass adjusted by body size, was worse than that of Bellairs birds, indicating that the Harbor was a suboptimal habitat compared to Bellairs (see Sherry and Holmes 1996 for a similar situation). The lack of arboreal cover, the stress and frequent feeding interruptions caused by mechanical operations and human movement, and the pressure from pest-control programs (Carlier and Lefebvre 1996) might all contribute to the decrease in body condition. Taken together, the results suggest that intraspecific competition is the major factor affecting the spatial distribution of Zenaida Doves in Barbados, leading smaller, shorter winged doves to use the lower rewarding feeding habitat of the Harbor.

Systems like the one we describe are common in vertebrates (e.g., Krebs 1971, Marra 2000) but do not, by themselves, produce polymorphisms (Griffith 1996). For a polymorphism to develop, the presence of alternative, suitable resources that are underutilized by other species is also indispensable (Smith and Skúlason 1996). In Barbados Zenaida Doves, the use of spilled grain at the harbor may have been facilitated by low competition from other species. Feral pigeons, who exploit harbor warehouses in other countries (Murton et al. 1972, Lévesque and McNeil 1985), occur only in small numbers in Barbados (Dolman et al. 1996). Shiny Cowbirds (Molothrus bonariensis) and Carib Grackles (Q. lugubris), the other avian species present, are also relatively scarce (Dolman et al. 1996). Overall, there is a very low avian species diversity in Barbados compared to other West Indian islands (Evans 1990). Thus, on this island, the benefit of niche expansion due to high intraspecific competition is not constrained by ecological pressures from other species. This does not appear to be the case on all Caribbean islands. On Mona, a small island near Puerto Rico that also has a low species diversity, it is the Common Ground-Dove, Columbina passerina, practically absent from Barbados Harbor (Dolman et al. 1996), that seems to have expanded its niche, despite the fact that the Zenaida Dove is a common resident there (Terborgh and Faaborg 1973).

Although the territorial vs. group-feeding polymorphism appears to be particular to Barbados, Zenaida Doves are known to show opportunistic shifts in behavior in at least two other areas of the Caribbean. In Puerto Rico, Rivera-Milán and colleagues (Rivera-Milán 1992, 1997, 1999, Rivera-Milán and Schaffner 2002, Rivera-Milán and Vazquez 2002) report seasonal hab-

itat and foraging shifts from xerophytic forests to agricultural zones, where doves join mixed species aggregations at animal feeding stations. In the neighboring Culebra archipelago, Zenaida Doves switch from arboreal to ground nesting on small islands that lack predators (Burger et al. 1989a, b, 1991). This behavioral flexibility seems to have played a prominent role in the establishment of the polymorphism in Barbados, as suggested by the numerous behavioral adjustments that accompany the shift from conspecific exclusion to group foraging. These include a reduction in conspecific aggression and neophobia, as well as an enhancement of individual and conspecific social learning (Carlier and Lefebvre 1996, 1997, Dolman et al. 1996, Lefebvre et al. 1996). In Barbados, Zenaida Doves might show higher levels of flexibility than they do on other islands. Pinchon (1963) and Bond (1979) have underlined the high degree of urbanization of Zenaida Doves in Barbados compared to other Caribbean islands. In documenting the increase in the Zenaida Dove harbor population between 1965 and 1968, Haverschmidt (1969) points out that he did not see any birds of this species exploiting similar conditions in neighboring Georgetown harbor, Grenada. The apparent differences in flexibility shown by Zenaida Doves in Mona, Culebra, Puerto Rico and Barbados constitute an interesting "natural experiment" to study the role of behavior in facilitating niche expansion.

The ability of Zenaida Doves to adjust their behavior to the specific foraging conditions is nevertheless limited. For example, it is easy to make normally unaggressive group-feeding doves defend clumped food patches that are predictable in space and time at the Harbor (Goldberg et al. 2001), but the reverse does not hold. Over the time span that led to a sharp behavioral shift in the Harbor birds, doves from Bellairs maintained high rates of aggression despite experimental manipulations of resource density and unpredictability that made food defense uneconomical (Goldberg et al. 2001). Such limitations in behavioral change may have a negative effect on a dove's ability to shift strategies and thus reinforce the polymorphism. For example, learned reliance on conspecifics for feeding information (Carlier and Lefebvre 1997) would not be useful in a territorial context, where other doves are aggressive competitors. The fact that proximity to humans inhibits feeding in Harbor doves more than it does in territorial birds (Seferta et al. 2001) would pose a further problem if group feeders were to move to areas like Bellairs. The parks, residences, hotels, and restaurants where territorial birds feed imply a high tolerance to human proximity (Dolman et al. 1996, Lefebvre 1996); if Harbor birds avoid humans, this would reduce their foraging success in many of the situations available to Bellairs birds. Similar effects of learning may also accentuate the foraging specialization of territorial birds. Bellairs doves join feeding grackles in the field, learn from them in captivity (Dolman et al. 1996), and

use their alarm calls as danger signals while foraging (Griffin et al., *in press*). This reliance on grackles would be of little use by doves at the Harbor, where that species is rare and high background noise levels would drown out any eventual grackle alarm calls. Thus, behavioral trade-offs might increase the value of specialization and hence help maintain the polymorphism.

In sum, the resource polymorphism in Barbados Zenaida Doves appears to have been driven by intraspecific competition, made possible by the existence of alternative resources underutilized by other species, facilitated by behavioral adjustments, and reinforced by behavioral trade-offs. Evolutionary processes such as frequency-dependent and disruptive selection are also known to be important in the maintenance of resource polymorphisms (Skúlason and Smith 1995, Smith and Skúlason 1996), but the fact that the Zenaida polymorphism is so recent and that there are no morphological differences in bill characters between morphs despite differences in diet and habitat suggests that the population has not yet reached this stage. Moreover, although many group feeder doves breed in the harbor, movement of individuals between the harbor and territorial areas still occurs (Carlier and Lefebvre 1997, Goldberg et al. 2001; this study). Thus, gene flow may at present be a major difficulty for genetic differentiation in Barbados Zenaida Doves. This is not to say that evolutionary divergence is impossible. Recent evidence indicates that genetic differentiation may occur even in very close populations, provided that divergent selection is strong (e.g., Blondel et al. 2002). Whether or not the resource polymorphism in Zenaida Doves may eventually drive evolutionary divergence is an intriguing possibility.

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