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Community ecology and phylogeography of bird assemblages in arid zones of northern Venezuela: Implications for the conservation of restricted-range birds

Adriana Rodriguez-Ferraro
University of Missouri-St. Louis, arppf@umsl.edu

University of Missouri-St. Louis
Department of Biology
Graduate Program in Ecology, Evolution, and Systematics

Community ecology and phylogeography of bird assemblages in arid zones of northern Venezuela: Implications for the conservation of restricted-range birds

A Dissertation submitted to the Graduate School of the University of Missouri – St. Louis in partial fulfillment of the requirements for the Degree Doctor of Philosophy in Biology

by

Adriana Rodríguez-Ferraro
M.S. Biology, University of Missouri-St. Louis, 2004
B.S. Biology, Universidad Simón Bolívar, Caracas, Venezuela, 1994

Advisory Committee

John G. Blake, Ph. D. (Advisor)
Robert E. Ricklefs, Ph. D.
Bette A. Loiselle, Ph. D.
Robert M. Zink, Ph. D.

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Deserts are special places, with a unique beauty.

To do serious ecological studies in deserts is difficult and often uncomfortable, but the rewards, in both science and aesthetics are great.

John A. Wiens
The Ecology of Desert Birds (1991)

GENERAL ABSTRACT

Aridlands of northern Venezuela are important from an ornithological perspective because of the occurrence of habitat specialist birds that depend exclusively on desert scrubs for their survival and are almost all endemic to this single zoogeographic region. Currently, long-term survival of habitat specialists is threatened by ongoing changes in vegetation structure and composition but the effects of such changes on bird assemblages are unknown. Limited baseline information on bird assemblages that inhabit aridlands in the Neotropics precludes the implementation of appropriate conservation plans. The goal of this study was to characterize bird assemblages found in six arid zones in northern Venezuela at both ecological and genetic levels, and to generate information relevant for conservation planning in these regions. The study involved assessments of patterns of avian species richness, abundance, community composition and genetic diversity, as well as specific bird-habitat associations.

Through systematic surveys, 96 bird species were recorded throughout the study areas. Even though the six areas support a homogeneous habitat type, species richness, composition, and abundance varied among them. The most abundant birds in all six areas were mainly widespread generalist species, and only one of the habitat specialists had high densities in all areas. Species richness was not a good indicator of an area's conservation value, because the protection of the area with highest number of species does not guarantee the effective conservation of all habitat specialist birds. Conservation initiatives for arid zone birds should not only consider species richness and representativeness, but also other factors such as abundance patterns and complementarity between eastern and western areas.

Vegetation analyses indicated differences in mean values of both floristic and structural vegetation variables among the six study areas but, overall, the six areas had relatively similar vegetation. Vegetation variables explained more variation in distributions of habitat specialists and generalists when groups were considered separately than when they were combined in a single analysis. Habitat specialists, however, differed in their responses to vegetation variables, which may be related to differences in foraging strategies. Even though habitat specialists did not respond strongly to vegetation variables, results of this study suggest that some structural attributes are important for the survival of this particular group of species. Thus, conservation programs devoted to protect these birds should focus on the maintenance of the structural integrity of the habitat.

Molecular techniques were used to investigate patterns of genetic diversity in three codistributed specialist birds (Yellow-shouldered Parrot, Buffy Hummingbird, and Vermilion Cardinal). Multiple analyses indicated geographic structure in the three species, but the extent of geographic structure varied among them as a result of different levels of population isolation during historical times and recent demographic expansions into some of the study areas. The assessment of genetic diversity and geographic structure of these three restricted birds showed incongruent patterns, which evidence different evolutionary histories. Conservation efforts should focus not only on the preservation of genetic diversity in each species but also on the maintenance of the diverse set of processes that generated such patterns.

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CHAPTER I

DIVERSITY PATTERNS OF BIRD ASSEMBLAGES IN ARID ZONES OF NORTHERN VENEZUELA

INTRODUCTION

The study of bird assemblages has contributed significantly to the field of community ecology, but not all bird communities have been equally well studied. In general, bird assemblages of arid regions or deserts have been neglected at least in part because of their lower species richness (see Wiens 1991) compared with wooded areas and forests. Additionally, of the few studies done on the structure and dynamics of these bird communities in the Americas, most have been conducted in temperate deserts (Dixon 1959, Raitt and Maze 1968, Tomoff 1974, Szaro and Jackle 1985).

In the Neotropics arid scrublands harboring distinctive avian communities are located in six main regions: 1) the lowlands and slopes of the Greater Antilles; 2) the Pacific arid slope of Central America, which extends from northwestern Mexico to northwestern Costa Rica; 3) the northern Yucatán peninsula; 4) the Caribbean lowlands of Colombia and Venezuela; 4) the Pacific coast of South America; and 6) the lowlands of central and southern South America, which include the Brazilian Caatinga, the Chaco of Paraguay and northern Argentina, the Monte of western Argentina, and Patagonia (Stotz et al. 1996). Despite the very few studies that have been conducted in the Neotropics, general descriptions of these communities characterize them as having a low overall diversity, but differing considerably in their regional species composition (Stotz et al. 1996). It has been suggested that no single arid formation in the Neotropics contains even a third of the

total arid-region species pool; most adjacent pairs of regions share fewer than 10% of their species, whereas adjacent humid-forest regions can share as many as 85% of their species (Stotz et al. 1996). Further, level of endemism is high, comparable to or higher than that of humid forests, and increases with the level of dependence on the habitat (Stotz et al. 1996, Brawn et al. 1998). These characteristics illustrate the distinctiveness of the species pools found in arid regions, and the need to study these areas and formulate regional conservation strategies to conserve this avifauna as a whole.

Our current knowledge about bird community structure in Neotropical arid regions is based on limited studies at two single localities in northern Venezuela (Bosque 1984, Poulin et al. 1992, 1993, 1994), one locality in Mexico (Arizmendi and Espinoza de los Monteros 1996), and two areas in Argentina, the Chaco (López de Casenave et al. 1998, López de Casenave 2001, Codesido and Bilenca 2004, Derlindati and Caziani 2005) and the Monte desert (Marone 1992, Blendinger 2005). These studies concur with the general description that bird communities in arid regions have low species richness and they also suggested that species composition is constant over time and dominated by year-round resident species (Poulin 1993, Arizmendi and Espinoza de los Monteros 1996, Codesido and Bilenca 2004, Blendinger 2005). However, the main focus of most of these studies has been the seasonal variation in bird abundances related to breeding and feeding guilds (Bosque 1984, Marone 1992, Poulin et al. 1992, 1993, 1994; Codesido and Bilenca 2004, Blendinger 2005) or the variation of bird communities in relation to vegetation differences associated with habitat gradients (Bosque 1984, López de Casenave et al. 1998). Here I present a different approach to the previous studies conducted in Neotropical arid zones by analyzing spatial variation of diversity attributes (richness,

composition, and abundance) of bird communities inhabiting Venezuelan arid zones to generate information for conservation planning in these areas. This is particularly relevant because most Neotropical arid regions are currently subject to habitat modification (Janzen 1988, Stotz et al. 1996, Fajardo et al. 2005).

Venezuelan arid zones constitute an especially well-suited region for the study of avian assemblages for several reasons: 1) they belong to the "peri-Caribbean arid belt", one of the six Neotropical arid regions; 2) this habitat is currently represented in the country by isolated remnants (Fig. 1) of a much broader expanse that was covered by xerophytic vegetation during past glacial times (Nassar et al. 2002); 3) these arid lands are considered an Endemic Bird Area (EBA) (*sensu* Stattersfield et al. 1998) because of the occurrence of restricted-range and habitat specialist birds; and 4) arid scrublands are represented only marginally in the Venezuelan system of protected areas (less than 5% of this habitat is protected even on paper) (Stattersfield et al. 1998), and conservation efforts to preserve those and their avifaunas are scarce. Currently, the long-term survival of habitat-specialist birds is threatened by ongoing changes in vegetation structure and composition (Stattersfield et al. 1998, pers. observ.).

In this study, I quantified avian diversity in six arid zones located in northern Venezuela, which vary in size and degree of isolation. First, I conducted surveys to characterize the six areas in terms of species richness and composition, because comparisons of these variables are widely used in conservation to assess the status of different areas and to identify potential reserves (e.g., Conroy and Noon 1996, Kerr 1997, Su et al. 2004, Steinitz et al. 2005). Second, I used distance-sampling (Buckland et al. 2001) to determine density of bird species in the six sampling areas. Finally, I assessed

the relative importance of each area from a conservation perspective based on total species richness as well as the presence and abundance of habitat specialists.

METHODS

Study Sites. Field work was conducted in arid zones in northern Venezuela, characterized by the presence of thorn scrubs that are dominated by species belonging to Cactaceae, Mimosaceae, and Capparidaceae (Sarmiento 1972). Mean annual temperature is 28°C and annual rainfall ranges between 300 and 700 mm, with the presence of a long and severe dry season and two brief rainy peaks in July-August and December (Sarmiento 1976).

Study sites encompassed six arid zones in northern Venezuela (Fig. 1) that differ in extent and geological origin:

- Paraguaná Peninsula (PP) is located in northwestern Venezuela and stretches over 2,500 km^2. It was an island during the Pliocene that was joined to the mainland approximately 10,000 years ago when the isthmus of Médanos de Coro was formed (Ochsenius 1983, Feo-Codecido [1968] in Bosque 1984).

- Falcón (FL) and Lara (LL) lowlands represent the most extensive arid zone in Venezuela with an approximate area of 16,000 km^2. The valleys of the Lara and Falcón depression in western Venezuela include areas with intermediate or transitional relief between the two great mountain systems of Venezuela, the Andes and the Coastal Mountain Range.

- Clarines-Píritu (CP) extends for about 4,500 km^2 in north-eastern Venezuela, and covers the Unare depression, between the central and eastern portions of the Coastal Mountain

Range.

- Araya Peninsula (AP) occupies 900 km^2 in north-eastern Venezuela, and comprises the lowlands to the north of the eastern Coastal Mountain Range.

- Macanao Peninsula (MP), about 300 km^2, constitutes the westernmost portion of Margarita Island. Geologically, Margarita is an island that was connected to the Araya Peninsula from the end of the Eocene until the Miocene, when the sea level rose and separated the island from mainland (Jam and Méndez Arocha 1962).

Bird Surveys. Bird counts were conducted from September 2004 to August 2005 using point-transect distance sampling (Buckland et al. 2001). In each site, three 50-ha plots (500 m x 1000 m), located at least 3 km apart, were established in thorn-scrub vegetation. Within each plot, 10 point counts were selected. I randomly established the first point, and then the other nine points were systematically located keeping a separation of at least 250 m between consecutive points (Fig. 2), and a distance of 100 m from vegetation borders and roads. Bird surveys were conducted from 6:00 am to 10:00 am during three consecutive days (one day in each plot) every two months in each study site. The sequence in which point counts in each plot were visited was alternated among sampling periods to compensate for effects of hourly variation in bird activity.

After the arrival at a point, a minute was allowed for birds to resume normal behavior and then, during 10 min, the identity and number of individuals of all species seen or heard were recorded. Distance from the point to each bird detected was measured using a laser range-finder, as suggested by Buckland (2006). Simultaneous records (either visual or auditory) were noted to reduce the possibility of counting the same individual more than once. Species not included in the surveys were those observed flying over the point

counts but that do not use thorn scrub vegetation, such as vultures (Cathartidae), herons and egrets (Ardeidae), and swallows (Hirundinidae), as well as nocturnal species, such as owls (Strigidae) and nightjars (Caprimulgidae).

Analyses of Diversity Patterns. Species richness, community composition and species abundance were examined and compared among the six study sites and over time.

Species Richness. As the number of individuals differed among the six sites, I estimated rarefaction curves using a Monte Carlo simulation procedure run with EcoSim Version 7.0 (Gotelli and Entsminger 2001) to compare species richness on the basis of the same number of individuals. Simulations were run 1,000 times and statistical significance was based on the simulated 95% confidence intervals generated by EcoSim. The variation of the total rarefied species richness among the six arid zones over the whole period was analyzed using a repeated-measures ANOVA, with time (six sampling periods) and study sites (six arid zones) as the explanatory variables and rarefied species richness as the response variable. Three plots (each combining data from 10 points) per study site were used as replicates for this analysis. This analysis was conducted using SPSS, Ver. 15.0 (SPSS 2006).

As not all species might be detected during surveys, I also estimated the total species richness for each of the six study areas. I computed the Chao 1 estimator (Chao 1984) using EstimateS v5 (Colwell 1997). Chao 1 estimates species richness by taking into account species that are not recorded by the researcher but whose presence can be inferred from the pattern of observed species occurrences in a set of samples, particularly by the number of rare species recorded (Chao 1984).

Community Composition. An initial approximation of differences in community composition among the six sites was assessed using pairwise comparisons of the observed number of species shared by any two of the sites and by calculation of a Bray-Curtis Similarity Index for each pair of arid zones. Both values were calculated using EstimateS (Colwell 1997).

Variation in community composition among study sites was subsequently tested for significance with an analysis of similarity (ANOSIM, Clarke and Warwick 2001), included in the software PRIMER v5.2.9 (Clarke and Gorley 2001). ANOSIM is a non-parametric analysis, which tests if differences among samples within pre-defined groups (points within study sites) are less than expected when compared to differences among samples across the six study sites. Non-metric Multidimensional Scaling (NMS, Clarke and Warwick 2001) was also conducted in PRIMER to graphically represent the results of ANOSIM.

Finally, an Indicator Species Analysis (Dufrêne and Legendre 1997) was conducted in PC-ORD (McCune and Mefford 1999) to identify which species were significantly associated with one or more study sites. This analysis provides indicator values (ranging from 0 to 100) for all the species and uses a Monte Carlo test to evaluate the statistical significance of the maximum indicator value of each species. A species was considered as indicator of a given site if its indicator value was $\geq 25\%$, following Dufrêne and Legendre (1997), and it was significant in the Monte Carlo test ($P < 0.05$).

Species Abundance. Detection functions for species with at least 80 observations were modeled using Distance 5.0 (Thomas et al. 2005). Detection probabilities for each species were assumed to be the same among sites and across sampling periods. Thus, I developed

individual detection functions for each species by pooling all observations in all the study sites. I also assumed that detection probabilities were similar among related or similar species (in terms of size, plumage coloration, and behavior). Thus, when the number of observations for a species was < 80 and a similar species was also detected during surveys, data for both species were pooled and a common detection function was modeled. Based upon recommendations by Buckland et al. (2001), observations far from the point, representing 5% of the total, were excluded from the analyses. In the case of some species recorded aurally, when the probability of detection at close distances was uncertain, left truncation at 20 m was applied to the data set following recommendations of Buckland et al. (2001). The detection function chosen for a given species was the model with the smallest Akaike's Information Criterion (AIC) from a set of six possible models that included the combination of three key functions (Half Normal, Hazard-Rate, and Uniform) and three series expansion terms (Cosine, Simple Polynomials, and Hermite Polynomials), as suggested by Buckland et al. (2001). Based on the estimated detection functions, Distance 5.0 was also used to estimate species densities independently for each of the sites using post-stratification. All results are presented as means ± SE and accompanied by 95% confidence intervals calculated assuming a log-normal distribution for the estimated density.

RESULTS

Species Richness. A total of 21,228 individuals representing 96 bird species and 26 families (Appendix I) was recorded across all study sites. Ten species were recorded only once (*Geranospiza caerulescens*, *Buteo brachyurus*, *Herpethoteres cachinnans*,

Anthracothorax nigricollis, *Chlorostilbon gibsoni*, *Picumnus squamulatus*, *Machetornis rixosus*, *Setophaga ruticilla*, *Parula pitiayumi*, *Carduelis psaltria*); 19 species had 2 to 5 records for the entire sampling period.

The number of species recorded at each site ranged from 37 at MP to 82 at CP (Table 1). The asymptote in the accumulation curves (Fig. 3) indicated that bird sampling was thorough. Species richness based on 2,170 individuals (fewest number of individuals recorded at any site in PP) was also significantly greater in CP (Table 1). Estimated species richness for the six areas is shown in Table 1. All estimations per study area are greater than the observed species richness, indicating that some new species could still be recorded both at local and regional levels.

Mean species richness varied temporally across sites, with an important effect of time of year (rm ANOVA, $F_{5,60} = 21.60$, $P < 0.001$) and of site (rmANOVA, $F_{5,12} = 16.75$, $P < 0.001$). A significant interaction effect (time x site; rmANOVA, $F_{25,60} = 2.86$, $P = 0.001$) indicated differences in patterns of temporal variation among sites (Fig. 4). Pairwise comparisons showed that two different patterns can be distinguished. CP and LL had more species than the other four sites and a similar temporal variation pattern (Tukey HSD Post Hoc test, $P = 0.681$), which differed from the pattern seen in the other four sites (Tukey HSD Post Hoc test, $P < 0.001$ in all cases). The other four sites (FL, PP, AP, and MP) did not differ in the number of species over time (Tukey HSD Post Hoc test, $P > 0.05$ in all cases).

Community Composition. Four main groups of birds were recognized from the species-pool in the study sites. Thirty-five species (36%) were widely-distributed ones that occupy a broad range of environments across the Neotropics; 38 (40%) were widely-

distributed species that occupy open areas and dry habitats across the Neotropics; 16 (17%) were species restricted to northern and central Venezuela and Colombia that occupy desert scrubs, dry and deciduous forests; and 6 (6%) were arid-scrub specialists of relatively limited distribution in northern Venezuela and Colombia. One species (1%), *Tiaris bicolor*, does not nicely fit in any of these four groups, because it is an arid-scrub specialist but it has a wide distribution that includes coastal Colombia and Venezuela, as well as most of the Caribbean islands. For analytical purposes, *Tiaris bicolor* was included in the last group of the arid-scrub specialists. There were no significant differences in the proportion of the four groups present in each site (Fig. 5; $G = 7.74$, df = 15, $0.95 > P > 0.90$). FL was the site where the proportion of arid-scrub specialists was highest (14%), and it was also the only site where all seven arid-scrub specialists (*Amazona barbadensis*, *Leucippus fallax*, *Synallaxis candei*, *Inezia tenuirostris*, *Todirostrum viridanum*, *Cardinalis phoeniceus*, and *Tiaris bicolor*) were present.

Migrants constituted a relatively small group of species within the arid-scrub bird communities. Eight long-distance migrants, representing 8% of the total species-pool, were recorded during surveys. Based on Hayes' (1995) classification of Neotropical migrants, 3 were Nearctic migrants (*Coccyzus americanus*, *Dendroica striata*, and *Setophaga ruticilla*), 3 were Austral migrants (*Coccyzus melacoryphus, Elaenia parvirostris,* and *Tyrannus savana*), and 2 were intratropical migrants (*Chrysolampis mosquitus* and *Sporophila bouvronides*). An important difference between Nearctic migrants and the other two migrant types is that species in the first group are transients in Venezuelan arid zones whereas species of the other two groups remain for 5-6 months per year, when numbers of some of them, such as *Tyrannus savana,* can be exceptionally

high (see Species Abundance). Two other species, *Patagioenas corensis* and *Zenaida auriculata*, occurred seasonally throughout the study sites. These latter species move locally between the coastal arid zones and the Venezuelan llanos.

From the 96 species recorded during surveys, 28 (29%) were recorded in only one site (Appendix I). CP was the site with the greatest number of unique species (21), which represented 26% of the observed species richness for that site and 22% of the overall number of species. As a result, although CP shared the largest absolute number of species (45) with two other sites, FL and LL (Table 2A), it had the lowest pairwise similarity values (Table 2B). Pairwise comparisons indicated that two of the eastern sites (AP and MP) were the most similar, based on the number of shared species (Table 2B).

The six study sites differed in overall community composition based on species presence/absence. This was the case both when the three plots per site were used as replicates (ANOSIM Global R = 0.81, $P = 0.001$; number of permuted statistics [out of 5000] ≥ R was 0) and when the 30 point-counts per site were treated as replicates (ANOSIM Global R = 0.68, $P = 0.001$; number of permuted statistics [out of 5000] ≥ R was 0). Pairwise comparisons, based only on point counts as replicates, showed significant differences in species composition for all the site pairs (range R: 0.52 [AP vs MP] – 0.96 [LL vs MP], $P < 0.001$ for all cases; number of permuted statistics [out of 5000] ≥ R was 0 for all cases).

The NMS indicated that species composition in each of the sites was distinctive and consistent when plots were used as replicates within each site (Fig. 6A). When using point counts as replicates, however, the pattern was less clearcut (Fig. 6B). At the plot scale, FL and LL showed higher similarity in species composition, but at the point-count

scale, similarities among MP, PP, and AP were evident. CP uniqueness in species composition was evident at both scales of analysis but the difference was slightly less when point counts were used as replicates.

The indicator species analysis determined that 26 species were significantly associated ($P < 0.05$) with one or more of the study sites (Table 3). Eleven species were good indicators of CP, and two more (*Thraupis glaucocolpa* and *Volatinia jacarina*) were perfect indicators. Three species (*Forpus passerinus*, *Campylorhynchus griseus*, and *Euphonia trinitatis*) were good indicators of LL. Only two of the arid-scrub specialists were significantly associated with a specific site. *Inezia tenuirostris* was an equally good indicator of LL and FL, and *Cardinalis phoeniceus* was a good indicator of MP.

Species Abundance. Densities were estimated for 21 species based on visual observations (Table 4), and for 24 species based on auditory detections (Table 5); detection functions are shown in Appendixes II and III, respectively. Enough data were collected for 12 species to allow density estimations based on both visual and on auditory detections. Although the absolute density values differed between the two estimations, the pattern of relative abundance among the six study sites was maintained in all cases. The most abundant birds in all six sites were mainly widely-distributed species, such as *Columbina passerina*, *Polioptila plumbea*, and *Mimus gilvus* (Table 4). Only one of the restricted-range arid-scrub specialists, *Leucippus fallax*, had high densities throughout all the study sites (Table 4), and one, *Inezia tenuirostris,* was very abundant in two of the three study sites which are considered part of its distributional range. Densities of two other arid-scrub specialists, *Amazona barbadensis* and *Cardinalis phoeniceus*, differed

considerably among sites as a consequence of anthropogenic factors, such as habitat modification and illegal poaching.

Limitations in the number of detections precluded the estimation of species density per sampling period per site. This type of estimation would be important in the case of migrants, because density estimations reported in Table 4 are based on the whole sampling period even though the presence of such species was strongly seasonal in some of the sites. This was true for three species: *Zenaida auriculata*, *Patagioenas corensis*, and *Tyrannus savana*. The first two species migrate locally in Venezuela, and even though individuals were found year-round, a significant part of the population spent the dry season (November-April) in the llanos and moved north to the arid zones during the llanos' wet season (May-October). In some of the study sites, such as Lara lowlands, the mean number of individuals of *Zenaida auriculata* recorded per point-count increased considerably from May to August (Fig. 7A). The abundance of *Tyrannus savana*, an Austral migrant, in terms of the mean number of individuals recorded per point count, was augmented in the three eastern study sites (Clarines-Píritu, Araya Peninsula, and Macanao Peninsula) from May to August, and this increase was more dramatic in Clarines-Píritu (Fig. 7B).

DISCUSSION

Although the six study sites support a homogeneous habitat type (unpub. data), important differences in bird species richness, community composition, and species abundance were evident.

Species Richness. Differences in species richness among study sites may reflect the effects of area, geological history, historical colonization patterns, and degree of isolation. Although the influence of all these factors is difficult to tease apart, my data suggest that area and degree of isolation might play an important role in shaping bird assemblages in Venezuelan arid zones. Larger sites that are surrounded by other habitat types, such as CP, FL, and LL, harbored more species, whereas the smallest and most isolated sites, such as PP and MP, had fewer species.

Compared to other Neotropical habitats, species richness in the Venezuelan arid zones is low, as had been noted previously in general descriptions of arid-zone bird communities (Wiens 1991, Stotz at al. 1996). The species pool found in the present study (96 species) is, however, larger than the species richness reported (63 species) for the lowland arid scrubs of northern South America (Stotz at al. 1996). CP included several species that were solely recorded at that site. Many of these were not included by Stotz et al. (1996), and this may explain the above-mentioned differences. Similar numbers of species to the ones found in this study were reported in previous evaluations of avian diversity in two Venezuelan arid zones. For the Paraguaná Peninsula, I detected 39 species and both Barnes and Phelps (1940), in a one-month collecting trip, and Bosque (1984), during a two-year study, reported 37 species (vultures and nocturnal species such as owls and nightjars were excluded for comparison purposes). Poulin et al. (1993) reported 39 species captured in mist-nets during a one-year period in a single locality on the Araya Peninsula. These authors did not include raptors, doves, pigeons, and psittacids in their list. When these groups are excluded from my own data, species richness in AP

is reduced from 47 to 36 species, a similar number to that reported by Poulin et al. (1993).

When compared at a regional level, the low species richness found in Venezuelan arid zones seems to be similar to patterns reported for other arid and semiarid areas in the Neotropics. Studies in the Argentinean Chaco using point-counts or point-counts combined with mist-nets recorded 96 (including vultures, nocturnal species, and swallows) and 74-91 species, respectively (López de Casenave et al. 1998, Codesido and Bilenca 2004, Derlindati and Caziani 2005). Another study in the Argentinean Monte desert found 60 species < 90 g body mass (Blendinger 2005). Although interesting, these comparisons are not enough to propose a general pattern of species richness in Neotropical arid regions because those are still based on too few studies, conducted using different methodologies, in a small number of localities, in only two Neotropical countries.

Community Composition. Although poor in species, bird assemblages in Venezuelan arid zones have a unique composition. Most of the species (69%) present were birds primarily associated with other habitats that also occurred in arid zones, as previously described for desert scrub habitats in California (Wiens 1991). The remaining species, however, represent a well-delimited group, with 24% being geographically restricted to northern Venezuela and Colombia, and 7% of the total number of species being restricted to arid scrubs. Previous general descriptions of bird assemblages underestimated the number of habitat-restricted and habitat endemics for the arid scrubs of northern South America (Stotz et al. 1996), and even failed to recognize *Amazona barbadensis*, *Inezia tenuirostris*, and *Todirostrum viridanum* as indicator species of this Neotropical habitat.

Twenty four species (25% of the total species pool) found in arid zones of northern Venezuela have been reported in the Argentinean Chaco (data taken from Codesido and Bilenca 2004) and the percentage increases to 40% when the comparison is done at the genus level. This similarity, however, is low if compared with similarities in species composition in other habitats, such as tropical rainforests (see Stotz et al. 1996, Blake 2007), highlighting the distinctiveness of bird communities in Neotropical arid zones in terms of species composition.

Migrant species constituted a minor component of the community, and the presence of different migrants in the arid zones varied. Bosque and Lentino (1987) reported that Nearctic migrants used the desert scrub of the western coast of Venezuela mainly during the fall migration and that these species stayed there briefly (≈ 1-2 months) in their passage towards other habitats inland. All three Nearctic migrants recorded in this study showed the same pattern described above; they were recorded only during the fall migration (October-November) and in only one sampling period in each site. Conversely, intratropical and Austral migrants arrived in large numbers, mainly to the three study sites in eastern Venezuela, and stayed there for the whole Austral winter (May-June to October).

Differences in species composition among study sites can be partially explained, as in the case of species richness, by degree of isolation or area, as well as by the proximity of other habitat types. The species composition of the two more isolated sites, PP and MP, are subsets of the species pools of the nearby sites FL and AP, respectively. Most of the species that colonized PP probably arrived from FL when the island joined the mainland during the Holocene (Ochsenius 1983). Similarly, a major group of

colonizers to MP came from AP and moved to Margarita Island when the sea level decreased during the Eocene and Miocene (Jam and Méndez Arocha 1962). Bird community composition in a given habitat is influenced by species composition and density in adjacent habitats (Shurcliff 1980, Szaro and Jackle 1985). CP's proximity to other habitat types (i.e., forest edges, dry forests) may have favored the colonization by species typical of other habitats that are not usually present in arid scrubs. This explains why CP has a high number of species that are not found in any other arid zone in northern Venezuela. Additional evidence of the peculiarity of CP in species composition was provided by the indicator species analysis, which showed that CP was the area with the highest number of indicator species (11). When considering the identity of these species, however, 7 (*Tapera naevia*, *Camptostoma obsoletum*, *Myiozetetes similis*, *Tyrannus melancholicus*, *Troglodytes aedon*, *Sicalis flaveola*, and *Volatinia jacarina*) of the 11 were classified as species indicators of disturbed habitats by Stotz et al. (1996), and are common residents of open areas.

Changes in species composition seem to have occurred over time in some of the sites, at least partially as a consequence of human activities. *Amazona barbadensis*, for example, has been extirpated from LL since the mid 1980's (Hilty 2003) due to illegal poaching. This same factor is responsible for the lack or very low number of records of *Amazona barbadensis* in PP, *Icterus icterus* in CP and AP, and *Aratinga pertinax* in AP; local extinctions for these species are not yet confirmed. Some other changes in species composition, however, seem to be the result of natural processes. In PP, the only site where studies on bird diversity have been conducted at three different time periods, some colonization and extinction events are evident. Barnes and Phelps (1940) reported two

species, *Campylorhynchus griseus* and *Volatinia jacarina*, which were not recorded either by Bosque (1984) or by this study. Conversely, one species that was common during this study, *Quiscalus lugubris*, was not recorded in either of the two previous studies. This is an interesting case, because it is a noisy species frequently found nearby human settlements, and it appears unlikely that it would have been undetected if present. In fact, this species seems to be expanding its range, and it was detected in PP in the early 1990's (C. Bosque pers. com.) and has reached Aruba (Netherland Antilles) very recently (J. Wells pers. com).

Species Abundance. The most abundant species tended to be the ones with wide distributions in the Neotropics. The same pattern has been reported by avian studies both in other habitats within the Neotropics and in the temperate zones (see Gaston 1996, Thiollay 2002). This relationship, however, may be influenced by several factors. First, as this was a multispecies survey, the variety of behaviors exhibited by different species makes it difficult to detect all the species with the same accuracy, and the high detectability of the common species might have masked the presence of rare species (Buckland 2006). Second, the abundance of some restricted species is reduced considerably because of illegal trapping in some of the study sites. This factor was already known to be the main cause of decline for *Amazona barbadensis* (Rodríguez and Rojas-Suárez 1995, Sanz and Rodríguez-Ferraro 2006) but based on this study it also is evident that, trapping has affected the abundance of *Icterus icterus* and *Cardinalis phoeniceus.* These two species were common in sites where poaching does not occur but their densities were low in sites where poaching is common, such as CP and AP (pers. observ.). Finally, in the case of *Amazona barbadensis,* as well as in all other psittacids,

the point-count method is not the most appropriate survey method for these birds because it tends to underestimate abundance in open areas (Casagrande and Beissinger 1997).

Differences in density estimates based on visual and auditory detections were significant, and have been reported before for other bird species (Jiménez et al. 2003). In the present study, such differences might be caused by the violation of one of the fundamental assumptions of distance sampling when using auditory detections. Distance sampling assumes that all the species located at the center of the point count (0 m) will be detected with a probability of 1 (Buckland et al. 2001). Generally, all the individuals located at the point-count or very close to it (≈ 20-25 m) were usually either observed or confirmed visually, producing a low number of detections at small distances from the center of the point, and as a consequence, causing an underestimation of the density.

Conservation Implications. Current land practices in Venezuelan arid zones pose a severe threat to the long-term survival of the habitat specialist birds restricted to these areas. Information compiled in this study can contribute to conservation priority schemes that target the identification of conservation areas within Venezuelan arid zones. Species richness and the presence of rare species are the most frequently used criteria for the selection of conservation areas. For the Venezuelan arid zones, species richness was not a good indicator of a site's conservation value, because the protection of the most species rich site (CP) will not guarantee the effective conservation of the restricted-range habitat specialist birds. This is not an uncommon result as studies across different taxa, such as birds, butterflies, mammals, and plants (see Prendergast et al 1993, Reyers et al. 2000), have shown that approaches to prioritize conservation areas that use species richness as the criterion were not effective in representing rare and endemic species (Catry et al.

2000), because spatial patterns of richness and endemism do not necessarily correspond (Reid 1998, Fleishman et al. 2006).

Community composition is also relevant for the selection of conservation areas, specifically when areas being compared differ in the degree of disturbance or human alteration (Nichols et al. 1998). As this type of difference does exist among Venezuelan arid zones, community composition should be incorporated in any initiative to protect the restricted-range birds. Data on community composition are particularly important to ensure that a conservation area contains as many species of this characteristic avifauna as possible. One of the study areas (FL) is representative of all Venezuelan arid zones, because it harbors the seven habitat specialist birds. Thus, its protection will allow the protection of the maximum number of the target species in a single site.

Relative abundance of target species is also an important parameter that must be considered when zones with similar species assemblages are considered for the selection of a conservation area. When economic resources for conservation are limited, as is the case of all the Neotropical countries, areas where target species are common or abundant should be valued more, to ensure viable populations in the long-term. Densities of two habitat specialists, *Amazona barbadensis* and *Cardinalis phoeniceus*, varied among the study sites as a consequence of illegal poaching and trade. Because of the high incidence of poaching in all the Venezuelan areas where the species is present, *Amazona barbadensis* is considered Endangered and Vulnerable at the national (Rodríguez and Rojas-Suárez 1995) and global (BirdLife International 2000) levels, respectively. The two largest populations of the species in Venezuela are located in two of the study sites (FL, MP), but the protection of one or both of these areas will not benefit this species

unless this measure is accompanied by efforts to control poaching. Conversely, the lack of up to date information on the effect of poaching on the abundance of *Cardinalis phoeniceus* precludes any evaluation of its conservation status. The information presented here indicates that populations of this species are reduced in three (LL, CP, AP) of the six Venezuelan arid zones sampled because of the cage-bird trade. Therefore, the long-term survival of this species will depend on the protection of at least one of the sites (FL, PP, MP) where the species is still abundant and it is not threatened by illegal poaching.

Mid- and long-term diversity studies of avian communities in the Neotropics are scarce, especially for species-poor habitats, such as the arid zones and deserts. Studies describing basic diversity patterns are in great need in the Neotropics because they provide baseline information that is relevant for both in-depth ecological studies on ecosystem dynamics and for conservation planning.

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TABLE 1. Total number of observations, observed and estimated species richness for each of the study sites. Study sites are the following: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

	PP	**FL**	**LL**	**CP**	**AP**	**MP**
Total count periods	6	6	6	6	6	6
Observed number of individuals	2,170	3,371	4,656	4,877	2,596	3,558
Individuals per count period	362	562	776	813	433	593
Observed species richness	39	51	50	82	47	37
Rarefied species richness (95% CI) (based on 2,170 individuals)	39.0 (39.0 – 39.0)	48.6 (46.0 – 51.0)	47.1 (44.0 – 50.0)	73.7 (69.0 – 78.0)	45.8 (44.0 – 47.0)	34.3 (32.0 – 37.0)
Estimated mean species richness (95% CI) Chao 1 estimator	40.5 (39.2 – 50.9)	51.3 (51.0 – 55.4)	50.3 (50.0 – 54.8)	89.5 (83.8 – 113.7)	48.9 (47.3 – 58.5)	42.0 (37.9 – 63.2)

TABLE 2. (A) Observed number of shared species among sampling areas computed using EstimateS. (B) Similarity index (Bray-Curtis) based on number of shared species computed using EstimateS. Study sites are the following: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

(A)

Area	PP	FL	LL	CP	AP	MP
PP	**39**					
FL	34	**51**				
LL	32	39	**50**			
CP	34	45	45	**82**		
AP	31	35	32	43	**47**	
MP	29	31	27	35	34	**37**

(B)

Area	PP	FL	LL	CP	AP	MP
PP	**1**					
FL	0.558	**1**				
LL	0.473	0.657	**1**			
CP	0.386	0.397	0.447	**1**		
AP	0.667	0.534	0.467	0.513	**1**	
MP	0.577	0.563	0.514	0.532	0.692	**1**

TABLE 3. Indicator values (% of perfect indication) for species in the study sites and results of Monte-Carlo tests (based on 1,000 permutations) of significance of observed maximum indicator values. Only species with indicator values significant at least at $P < 0.05$ are included.

Species	**Indicator values based on study sites**						***P***
	PP	**FL**	**LL**	**CP**	**AP**	**MP**	
Zenaida auriculata	5	23	47	7	7	11	0.022
Scardafella squammata	8	11	25	19	16	21	0.008
Leptotila verreauxi	28	1	36	18	6	8	0.043
Forpus passerinus	0	8	63	29	0	0	0.021
Tapera naevia	0	0	1	73	15	0	0.020
Chlorostilbon mellisugus	11	4	0	15	2	55	0.026
Formicivora intermedia	12	1	1	22	23	40	0.045
Camptostoma obsoletum	0	19	10	62	2	0	0.023
Elaenia parvirostris	0	5	0	77	3	0	0.017
Inezia tenuirostris	0	57	43	0	0	0	0.043
Euscarthmus meloryphus	0	10	0	71	0	0	0.036
Hemitriccus margaritaceiventer	0	2	0	81	2	2	0.032

TABLE 3. Continued

Species	Indicator values based on sampling areas						*P*
	PP	**FL**	**LL**	**CP**	**AP**	**MP**	
Myiozetetes similis	0	0	22	67	0	0	0.044
Tyrannus melancholichus	1	3	4	73	6	1	0.010
Tyrannus savana	0	0	0	73	9	18	0.012
Hylophilus flavipes	0	0	0	95	1	1	0.009
Campylorhynchus griseus	0	0	73	17	1	0	0.007
Troglodytes aedon	0	0	19	81	0	0	0.012
Coereba flaveola	19	0	3	20	39	18	0.039
Thraupis glaucocolpa	0	0	0	100	0	0	0.012
Euphonia trinitatis	0	2	66	26	4	0	0.018
Cardinalis phoeniceus	22	12	7	4	1	52	0.008
Volatinia jacarina	0	0	0	100	0	0	0.012
Sicalis flaveola	0	0	5	86	0	0	0.027
Icterus icterus	23	33	14	0	0	29	0.009
Icterus nigrogularis	14	10	45	16	3	11	0.013

TABLE 4. Mean densities ± SE (ind/ha) and 95% confidence intervals of arid zone birds based on visual records in the six study sites: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

Species	**STUDY SITE**					
	PP	**FL**	**LL**	**CP**	**AP**	**MP**
Patagioenas corensis	0.38 ± 0.10 (0.23 – 0.64)	0.64 ± 0.11 (0.46 – 0.88)	0.54 ± 0.09 (0.38 – 0.76)	0.77 ± 0.13 (0.56 – 1.06)	0.60 ± 0.11 (0.42 – 0.87)	0.66 ± 0.12 (0.46 – 0.96)
Zenaida auriculata	1.77 ± 0.29 (1.29 – 2.44)	3.76 ± 0.55 (2.82 – 5.00)	10.47 ± 1.58 (7.77 – 14.00)	2.04 ± 0.35 (1.47 – 2.85)	2.64 ± 0.41 (1.96 – 3.58)	1.89 ± 0.35 (1.32 – 2.73)
Scardafella squammata	0.37 ± 0.15 (0.17 – 0.78)	0.84 ± 0.21 (0.51 – 1.34)	3.30 ± 0.50 (2.45 – 4.43)	2.51 ± 0.45 (1.58 – 3.56)	2.15 ± 0.36 (1.55 – 2.98)	2.61 ± 0.45 (1.86 – 3.66)
Columbina passerina	3.65 ± 0.55 (2.72 – 4.89)	1.82 ± 0.34 (1.27 – 2.62)	5.94 ± 0.88 (4.44 – 7.95)	1.56 ± 0.31 (1.06 – 2.30)	3.86 ± 0.65 (2.78 – 5.36)	7.92 ± 1.04 (6.13 – 10.25)
Aratinga pertinax	0.00	3.56 ± 0.65 (2.49 – 5.09)	4.19 ± 0.55 (3.24 – 5.43)	1.36 ± 0.32 (0.78 – 2.06)	0.00	2.67 ± 0.42 (1.96 – 3.64)
Aratinga acuticaudata	0.00	0.30 ± 0.14 (0.12 – 0.72)	0.00	0.32 ± 0.26 (0.07 – 1.49)	0.00	0.00
Forpus passerinus	Out of range	0.41 ± 0.15 (0.20 – 0.82)	4.23 ± 0.69 (3.08 – 5.81)	1.83 ± 0.46 (1.13 – 2.98)	0.00	Out of range
Amazona barbadensis	0.00	0.05 ± 0.02 (0.03 – 0.11)	0.00	0.04 ± 0.02 (0.02 – 0.10)	0.10 ± 0.09 (0.02 – 0.58)	0.10 ± 0.04 (0.05 – 0.19)
Leucippus fallax	6.73 ± 0.89 (5.19 – 8.71)	3.15 ± 0.60 (2.17 – 4.56)	4.88 ± 0.84 (3.49– 6.82)	8.89 ± 1.15 (6.90 – 11.46)	9.22 ± 1.14 (7.23 – 11.75)	11.06 ± 1.28 (8.82 – 13.88)
Melanerpes rubricapillus	0.33 ± 0.10 (0.19 – 0.59)	1.10 ± 0.20 (0.78 – 1.57)	1.06 ± 0.19 (0.75 – 1.50)	0.69 ± 0.13 (0.47 – 1.00)	0.94 ± 0.17 (0.66 – 1.35)	0.16 ± 0.06 (0.08 – 0.31)

TABLE 4. Continued

Species	STUDY SITE					
	PP	**FL**	**LL**	**CP**	**AP**	**MP**
Xiphorhynchus picus	0.92 ± 0.26 (0.52 – 1.60)	0.58 ± 0.19 (0.32 – 1.07)	0.75 ± 0.23 (0.42 – 1.34)	0.71 ± 0.23 (0.38 – 1.31)	0.58 ± 0.19 (0.31 – 1.11)	0.21 ± 0.10 (0.08 – 0.51)
Sublegatus arenarum	1.86 ± 0.33 (1.32 – 2.63)	1.24 ± 0.26 (0.82 – 1.87)	1.97 ± 0.35 (1.40 – 2.78)	1.47 ± 0.30 (0.99 – 2.17)	1.92 ± 0.35 (1.34 – 2.75)	1.47 ± 0.30 (0.99 – 2.17)
Myiarchus tyrannulus	0.33 ± 0.10 (0.18 – 0.59)	0.28 ± 0.09 (0.16 – 0.51)	0.54 ± 0.13 (0.33 – 0.87)	0.52 ± 0.13 (0.32 – 0.83)	0.61 ± 0.14 (0.39 – 0.96)	0.75 ± 0.17 (0.48 – 1.18)
Tyrannus savana	0.00	0.24 ± 0.17 (0.07 – 0.85)	0.00	11.58 ± 2.89 (7.14 – 18.77)	6.97 ± 2.33 (3.67 – 13.23)	4.73 ± 1.37 (2.70 – 8.28)
Polioptila plumbea	8.23 ± 0.98 (6.52 – 10.39)	6.44 ± 0.84 (4.99 – 8.31)	4.65 ± 0.68 (3.50 – 6.18)	2.52 ± 0.49 (1.72 – 3.70)	5.11 ± 0.73 (3.87 – 6.76)	3.65 ± 0.60 (2.65 – 5.03)
Mimus gilvus	2.81 ± 0.25 (2.36 – 3.35)	2.80 ± 0.25 (2.35 – 3.33)	2.25 ± 0.22 (1.86 – 2.73)	1.86 ± 0.21 (1.48 – 2.32)	3.76 ± 0.30 (3.21 – 4.40)	4.46 ± 0.32 (3.87 – 5.16)
Coereba flaveola	3.74 ± 0.54 (2.82 – 4.95)	0.14 ± 0.09 (0.04 – 0.49)	0.14 ± 0.14 (0.03 – 0.72)	3.39 ± 0.53 (2.50 – 4.60)	5.81 ± 0.74 (4.53 – 7.46)	2.35 ± 0.39 (1.69 – 3.27)
Cardinalis phoeniceus	1.45 ± 0.26 (1.02 – 2.05)	0.57 ± 0.14 (0.36 – 0.91)	0.35 ± 0.11 (0.19 – 0.64)	0.10 ± 0.05 (0.04 – 0.26)	0.22 ± 0.08 (0.11 – 0.46)	4.09 ± 0.54 (3.17 – 5.29)
Tiaris bicolor	2.28 ± 0.40 (1.62 – 3.21)	0.12 ± 0.09 (0.04 – 0.43)	3.08 ± 0.49 (2.26 – 4.21)	5.86 ± 0.72 (4.60 – 7.46)	5.43 ± 0.72 (4.19 – 7.03)	5.86 ± 0.77 (4.53 – 7.57)
Icterus icterus	0.43 ± 0.11 (0.26 – 0.69)	0.66 ± 0.15 (0.42 – 1.04)	0.43 ± 0.12 (0.25 – 0.72)	0.02 ± 0.02 (0.003 – 0.08)	0.00	0.53 ± 0.13 (0.33 – 0.84)
Icterus nigrogularis	0.36 ± 0.13 (0.18 – 0.70)	0.21 ± 0.08 (0.10 – 0.45)	0.95 ± 0.25 (0.57 – 1.58)	0.41 ± 0.14 (0.21 – 0.77)	0.05 ± 0.04 (0.01 – 0.17)	0.21 ± 0.08 (0.10 – 0.45)

TABLE 5. Mean densities ± SE (ind/ha) and 95% confidence intervals of arid zone birds based on auditory records in the six study sites: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

Species	**STUDY SITE**					
	PP	**FL**	**LL**	**CP**	**AP**	**MP**
Colinus cristatus	0.22 ± 0.08 (0.12 – 0.40)	0.09 ± 0.03 (0.04 – 0.18)	0.31 ± 0.09 (0.18 – 0.54)	0.19 ± 0.06 (0.10 – 0.36)	0.12 ± 0.04 (0.06 – 0.15)	0.18 ± 0.06 (0.10 – 0.33)
Leptotila verreauxi	2.45 ± 0.45 (1.71 – 3.50)	0.35 ± 0.12 (0.18 – 0.69)	2.72 ± 0.49 (1.92 – 3.86)	1.55 ± 0.33 (1.03 – 2.35)	0.54 ± 0.19 (0.28 – 1.05)	0.66 ± 0.19 (0.38 – 1.14)
Scardafella squammata	0.54 ± 0.09 (0.39 – 0.76)	0.69 ± 0.12 (0.49 – 0.97)	1.41 ± 0.22 (1.04 – 1.92)	1.07 ± 0.18 (0.78 – 1.48)	0.92 ± 0.15 (0.67 – 1.28)	1.16 ± 0.18 (0.85 – 1.58)
Columbina passerina	0.84 ± 0.18 (0.56 – 1.27)	0.25 ± 0.08 (0.14 – 0.45)	0.36 ± 0.12 (0.19 – 0.68)	0.17 ± 0.07 (0.08 – 0.36)	0.25 ± 0.08 (0.04– 0.13	0.21 ± 0.07 (0.11 – 0.41)
Leucippus fallax	0.29 ± 0.09 (0.15 – 0.55)	0.54 ± 0.16 (0.31 – 0.95)	0.22 ± 0.08 (0.11 – 0.46)	0.79 ± 0.20 (0.49 – 1.29)	0.69 ± 0.17 (0.43 – 1.12)	0.48 ± 0.14 (0.27 – 0.83)
Hypnellus rufucollis	0.10 ± 0.02 (0.07 – 0.16)	0.03 ± 0.01 (0.01 – 0.07)	0.07 ± 0.02 (0.05 – 0.12)	0.04 ± 0.01 (0.01 – 0.07)	0.13 ± 0.03 (0.09 – 0.20)	0.10 ± 0.02 (0.06 – 0.15)
Melanerpes rubricapillus	0.72 ± 0.09 (0.57 – 0.92)	1.22 ± 0.12 (1.01 – 1.48)	0.76 ± 0.09 (0.60 – 0.96)	0.36 ± 0.07 (0.25 – 0.52)	0.92 ± 0.10 (0.74 – 1.14)	0.32 ± 0.06 (0.23 – 0.46)
Synallaxis albescens	0.49 ± 0.06 (0.38 – 0.63)	0.29 ± 0.05 (0.21 – 0.39)	0.35 ± 0.05 (0.27 – 0.47)	0.14 ± 0.03 (0.09 – 0.22)	0.33 ± 0.05 (0.25 – 0.45)	0.05 ± 0.02 (0.03 – 0.11)
Synallaxis candei	0.08 ± 0.03 (0.04 – 0.17)	0.27 ± 0.04 (0.19 – 0.37)	0.27 ± 0.07 (0.16 – 0.45)	Out of range	Out of range	Out of range
Xiphorhynchus picus	0.43 ± 0.05 (0.34 – 0.54)	0.34 ± 0.04 (0.26 – 0.43)	0.26 ± 0.04 (0.20 – 0.35)	0.43 ± 0.05 (0.34 – 0.54)	0.30 ± 0.04 (0.23 – 0.40)	0.19 ± 0.03 (0.14 – 0.26)

TABLE 5. Continued

Species	STUDY SITE					
	PP	**FL**	**LL**	**CP**	**AP**	**MP**
Sakesphorus canadensis	0.47 ± 0.11 (0.30 – 0.74)	0.19 ± 0.07 (0.10 – 0.37)	0.44 ± 0.11 (0.27 – 0.70)	0.06 ± 0.03 (0.20 – 0.17)	0.00	0.00
Formicivora intermedia	0.14 ± 0.04 (0.08 – 0.25)	0.02 ± 0.01 (0.01 – 0.08)	0.03 ± 0.02 (0.01 – 0.09)	0.36 ± 0.07 (0.24 – 0.54)	0.40 ± 0.08 (0.27 – 0.58)	0.64 ± 0.11 (0.46 – 0.88)
Inezia tenuirostris	0.00	3.70 ± 0.39 (3.02 – 4.54)	2.53 ± 0.29 (2.01 – 3.17)	Out of range	Out of range	Out of range
Myiarchus tyrannulus	0.13 ± 0.04 (0.07 – 0.25)	0.26 ± 0.06 (0.16 – 0.40)	0.12 ± 0.04 (0.07 – 0.23)	0.19 ± 0.05 (0.12 – 0.32)	0.35 ± 0.07 (0.24 – 0.52)	0.40 ± 0.07 (0.27 – 0.56)
Pitangus sulphuratus	0.01 ± 0.006 (0.001 – 0.03)	0.02 ± 0.01 (0.01 – 0.06)	0.30 ± 0.05 (0.22 – 0.41)	0.34 ± 0.05 (0.25 – 0.45)	0.01 ± 0.01 (0.001 – 0.03)	0.00
Campylorhynchus griseus	0.00	0.00	0.98 ± 0.12 (0.78 – 1.24)	0.35 ± 0.06 (0.25 – 0.49)	0.04 ± 0.02 (0.01 – 0.09)	Out of range
Polioptila plumbea	1.11 ± 0.13 (0.88 – 1.39)	1.99 ± 0.18 (1.67– 2.37)	0.95 ± 0.13 (0.72 – 1.25)	0.86 ± 0.11 (0.66 – 1.10)	1.67 ± 0.15 (1.39 – 1.99)	1.20 ± 0.13 (0.97 – 1.49)
Mimus gilvus	1.60 ± 0.20 (1.25 – 2.03)	1.41 ± 0.18 (1.09 – 1.82)	0.66 ± 0.10 (0.49 – 0.90)	0.58 ± 0.09 (0.42 – 0.81)	1.32 + 0.17 (1.02 – 1.71)	0.93 ± 0.14 (0.70 – 1.24)
Coereba flaveola	0.29 ± 0.08 (0.17 – 0.49)	0.00	0.17 ± 0.06 (0.08 – 0.33)	0.44 ± 0.09 (0.28 – 0.67)	0.95 ± 0.15 (0.70 – 1.31)	0.52 ± 0.11 (0.35 – 0.77)
Saltator coerulescens	0.46 ± 0.12 (0.28 – 0.77)	0.20 ± 0.07 (0.11 – 0.38)	0.52 ± 0.13 (0.32 – 0.85)	0.85 ± 0.18 (0.57 – 1.28)	0.07 ± 0.04 (0.03 – 0.19)	Out of range
Saltator orenocensis	Out of range	0.16 ± 0.04 (0.10 – 0.26)	0.32 ± 0.06 (0.22 – 0.46)	0.20 ± 0.04 (0.13 – 0.31)	Out of range	Out of range
Cardinalis phoeniceus	0.28 ± 0.05 (0.20 – 0.39)	0.20 ± 0.04 (0.14 – 0.29)	0.12 ± 0.03 (0.07 – 0.18)	0.09 ± 0.02 (0.05 – 0.13)	0.07 ± 0.02 (0.03 – 0.11)	0.50 ± 0.06 (0.39 – 0.64)

TABLE 5. Continued

Species	STUDY AREA					
	PP	**FL**	**LL**	**CP**	**AP**	**MP**
Tiaris bicolor	0.30 ± 0.10 (0.17 – 0.56)	0.05 ± 0.04 (0.01 – 0.18)	0.20 ± 0.08 (0.10 – 0.42)	0.51 ± 0.14 (0.29 – 0.88)	0.51 ± 0.13 (0.31 – 0.83)	0.43 ± 0.12 (0.25 – 0.75)
Icterus icterus	0.28 ± 0.03 (0.32 – 0.33)	0.38 ± 0.03 (0.32 – 0.44)	0.14 ± 0.02 (0.11 – 0.19)	0.01 ± 0.01 (0.01 – 0.02)	0.00	0.34 ± 0.03 (0.29 – 0.40)

FIGURE 1. Location of arid zones (shaded) in northern Venezuela. Study sites include the following: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

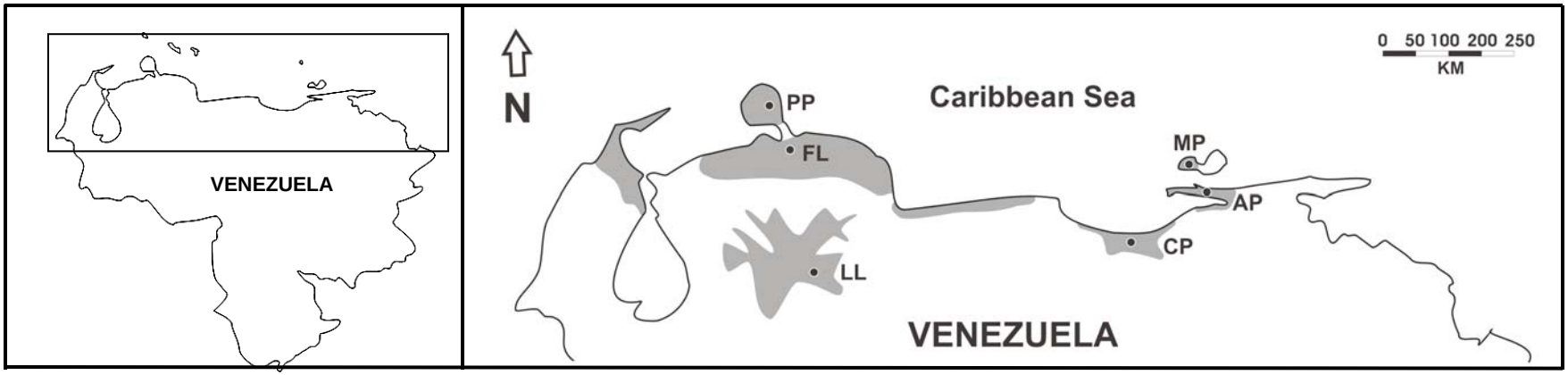


FIGURE 2. Schematic representation of the sampling plots and distribution of point counts.

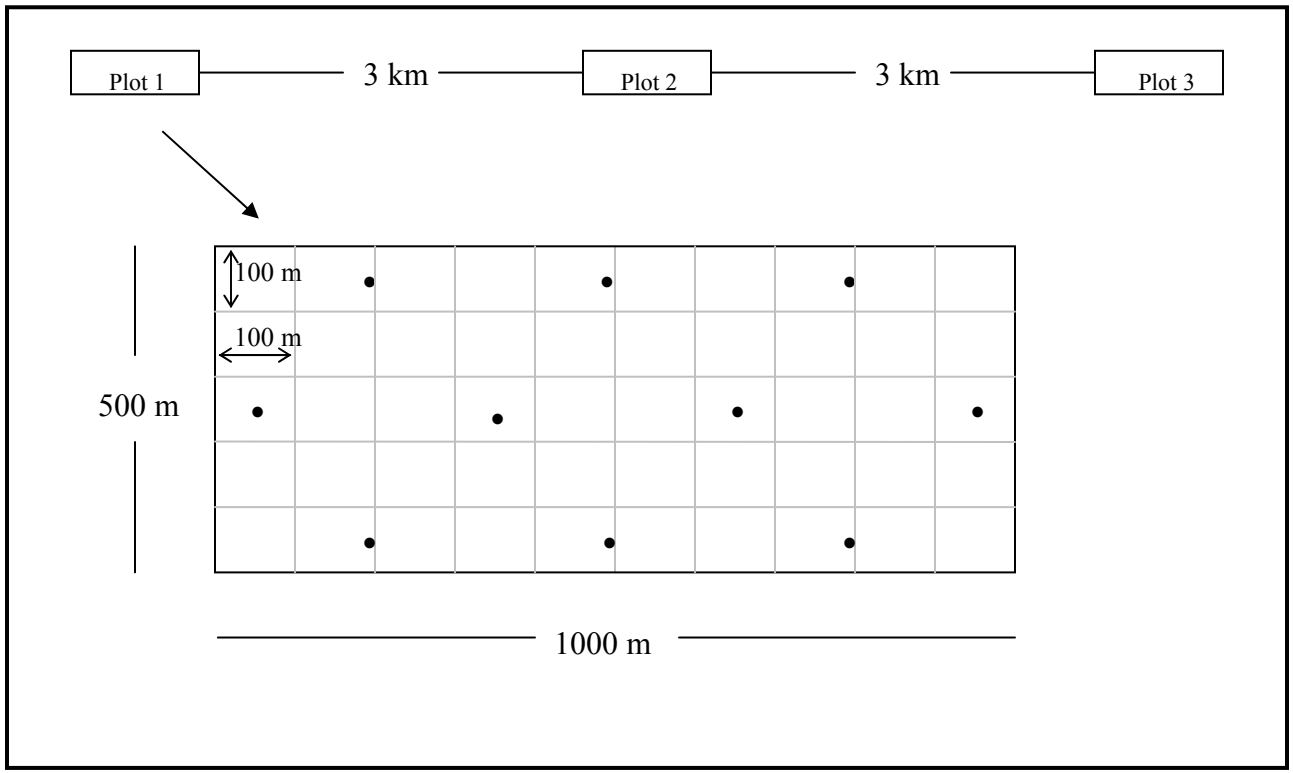


FIGURE 3. Species accumulation curves for the six study sites: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

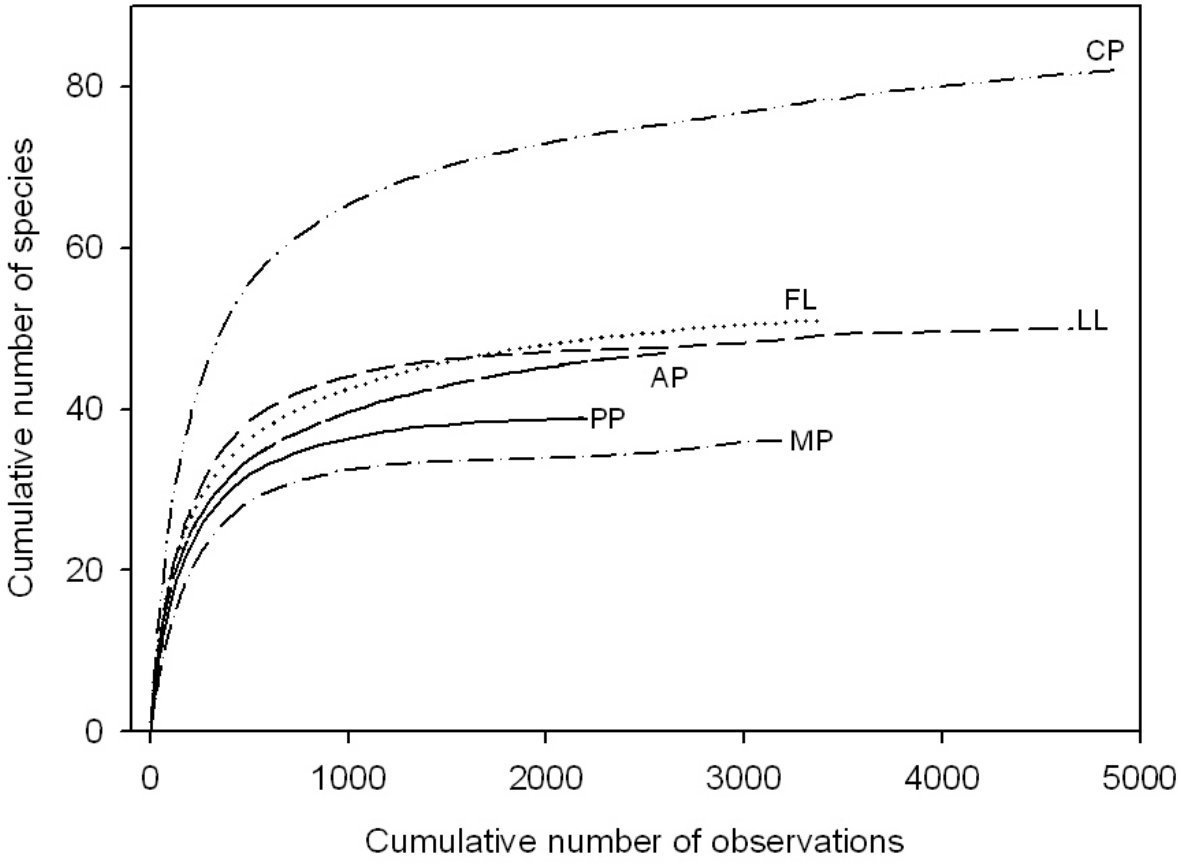


FIGURE 4. Temporal variation in the mean (± SE) number of species observed in each of the study sites: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

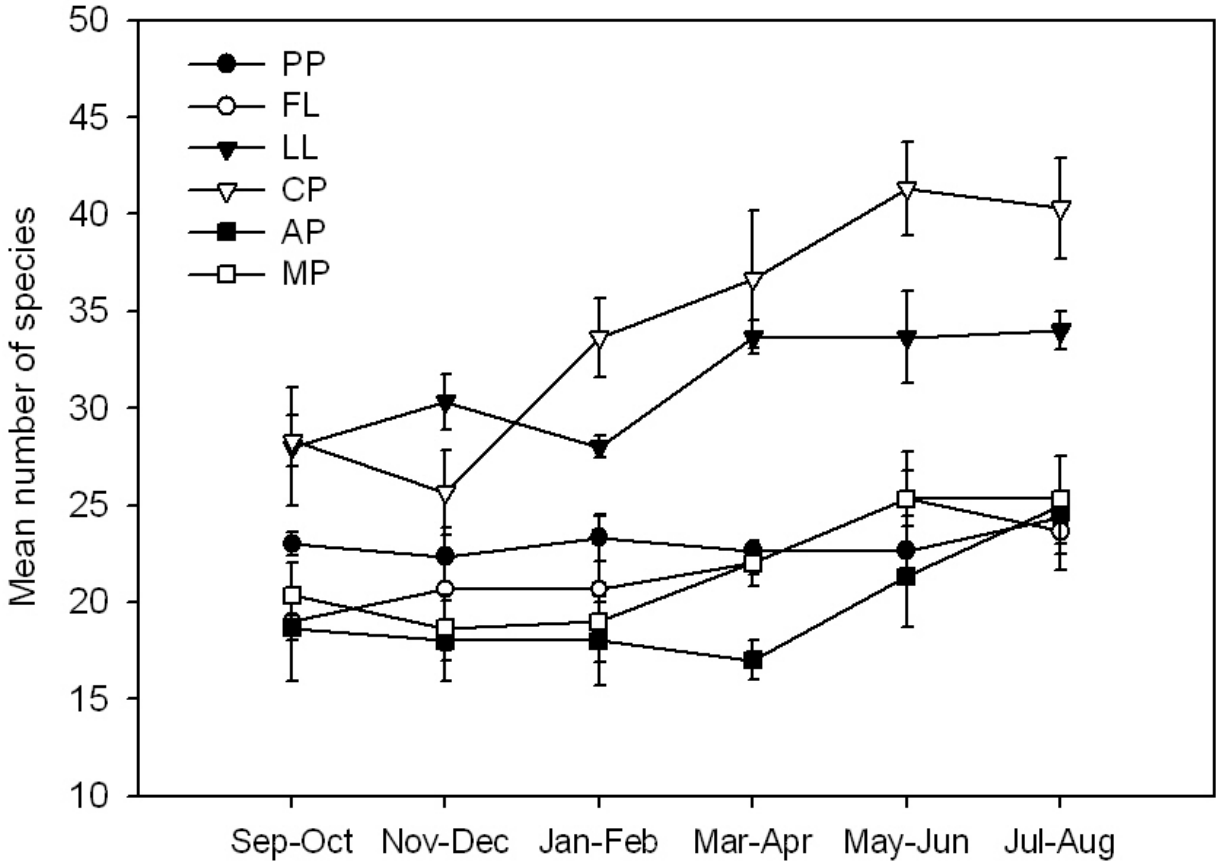


FIGURE 5. Proportion of different groups of species in each of the study sites. WD-G: widely-distributed that occupy a broad range of environments across the Neotropics; WD-DOH: widely-distributed that occupy open areas and dry habitats across the Neotropics; R-DOH: species restricted to northern and central Venezuela and Colombia that occupy open areas and dry habitats; and R-DSS: arid-scrub specialists of relatively limited distribution in northern Venezuela and Colombia. Study sites are the following: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

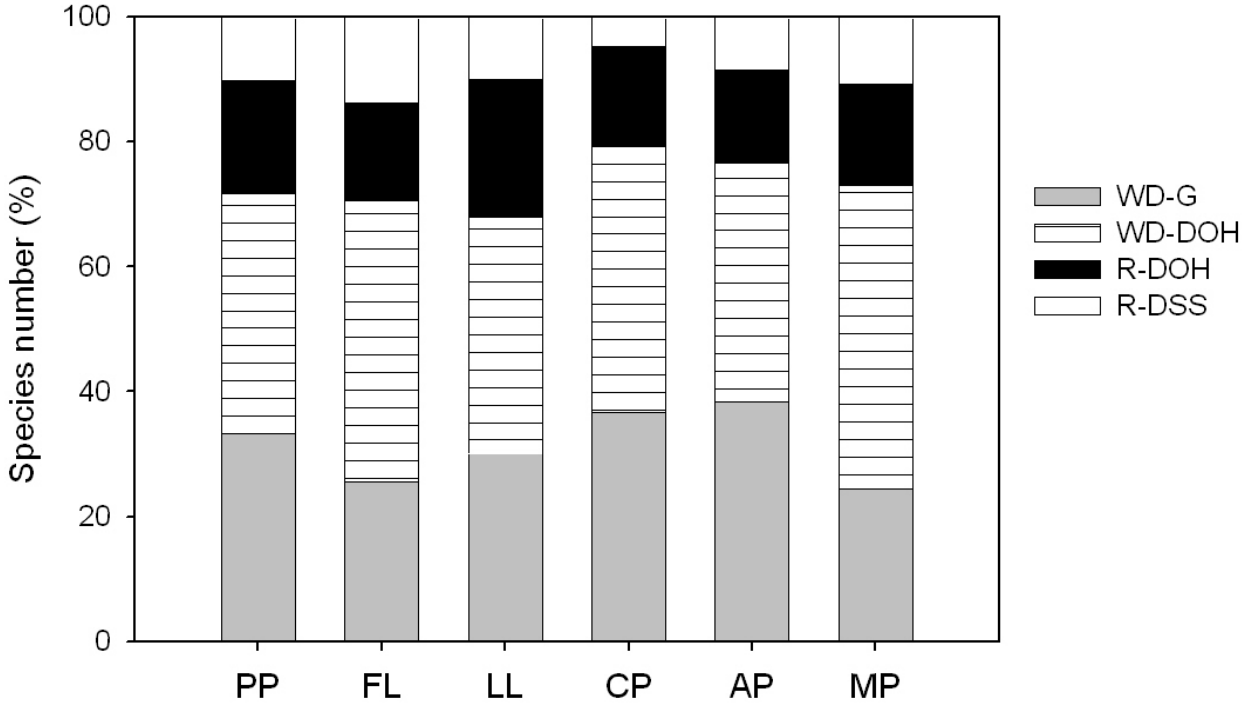


FIGURE 6. NMS configuration of species composition among study sites. (A) Each symbol represents a sampling plot and includes data from 10 point counts. (B) Each symbol represents a point count. Species showing high correlations with the two axes are indicated. Study sites are the following: PP = Paraguaná peninsula (filled triangles), FL = Falcón lowlands (open triangles), LL = Lara lowlands (filled squares), CP = Clarines-Píritu (open circles), AP = Araya peninsu circles), MP = Macanao peninsula (open squares).

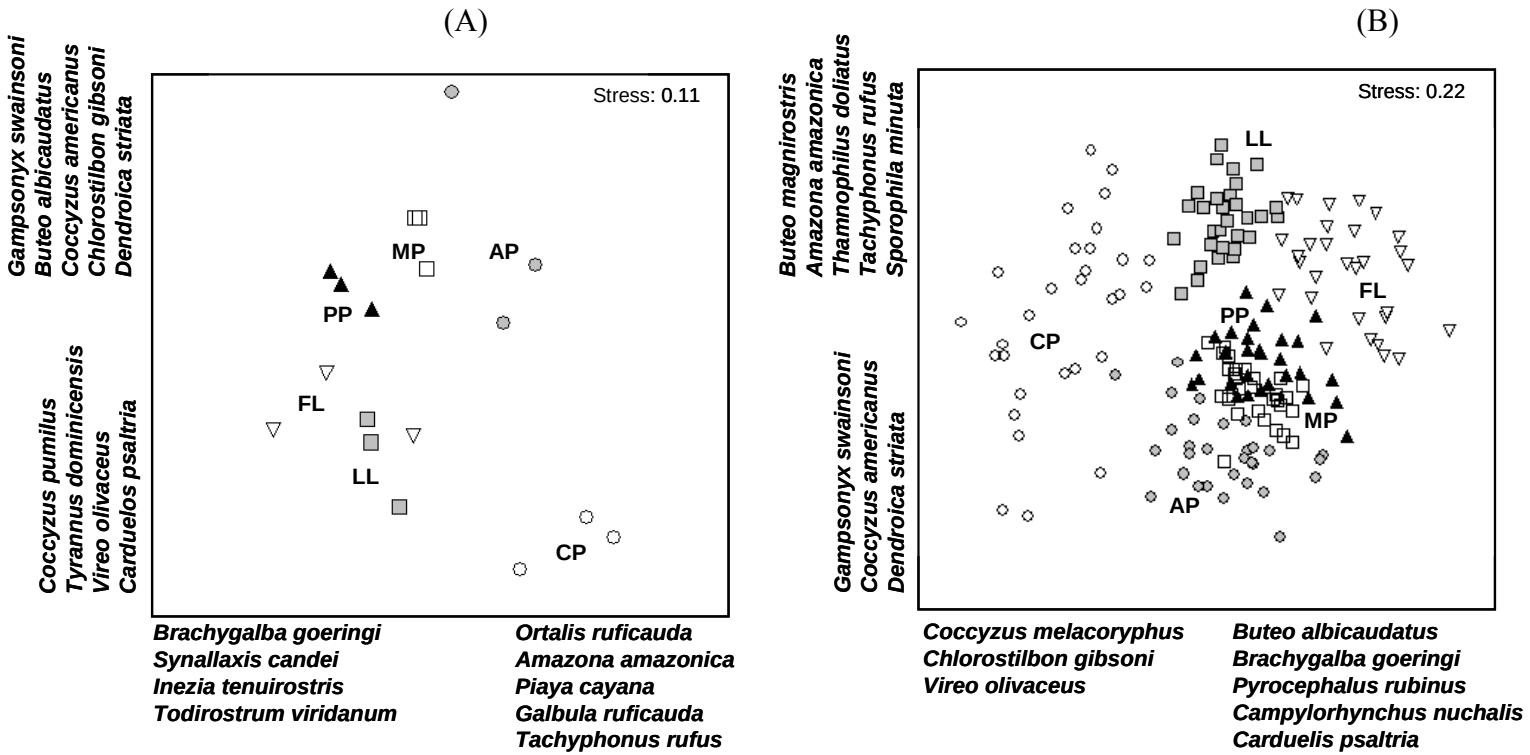
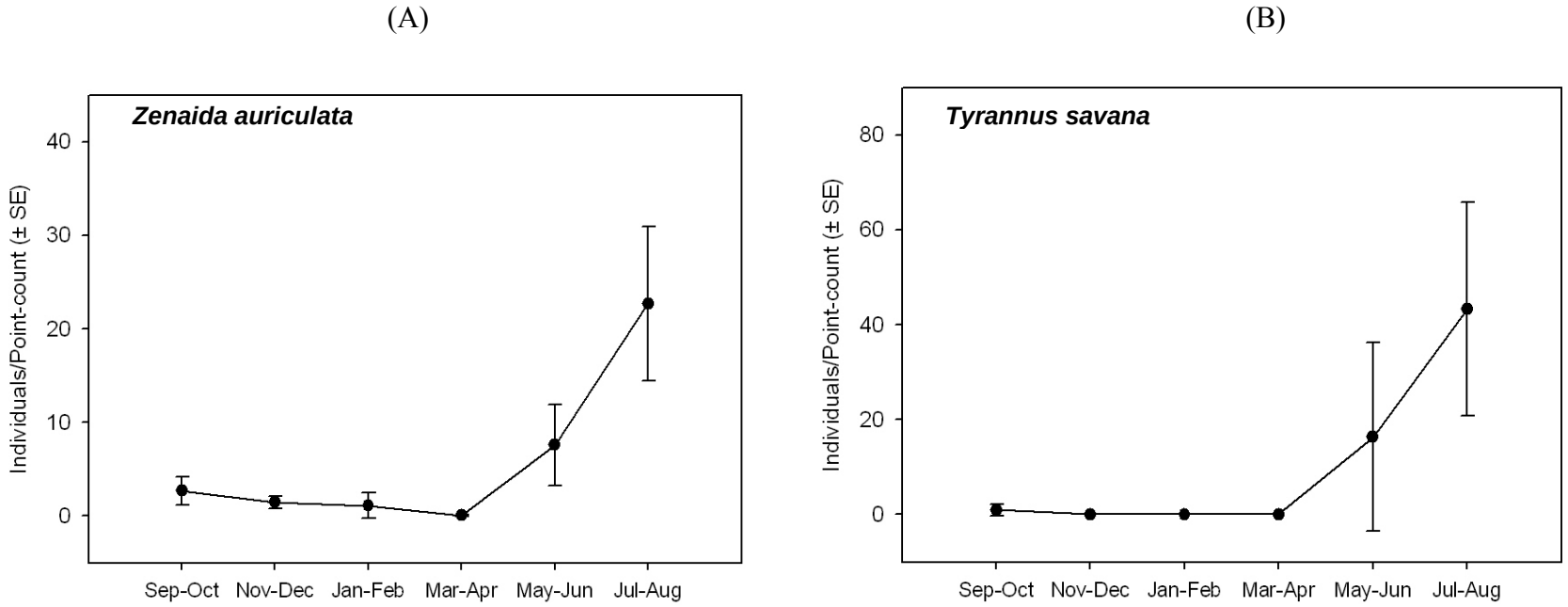


FIGURE 7. Temporal variation in the mean number of individuals per point-count for (A) *Zenaida auriculata* in Lara lowlands and (B) *Tyrannus savana* in Clarines-Píritu.



APPENDIX I. Number of individuals per species recorded during surveys in each of the six study sites during the whole study period. Study sites are the following: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu, AP = Araya peninsula, MP = Macanao peninsula.

FAMILY	COMMON NAME	SPECIES	STUDY SITE					
			PP	FL	LL	CP	AP	MP
Accipitridae	Pearl Kite	*Gampsonyx swainsonii*	0	0	0	0	2	1
	Crane Hawk	*Geranospiza caerulescens*	0	0	0	1	0	0
	Harris's Hawk	*Parabuteo unicinctus*	4	7	5	1	10	10
	Roadside Hawk	*Buteo magnirostris*	0	0	0	4	0	0
	White-tailed Hawk	*Buteo albicaudatus*	2	3	0	0	0	0
	Short-tailed hawk	*Buteo brachyurus*	0	0	0	1	0	0
Falconidae	Northern Crested-Caracara	*Caracara cheriway*	5	15	10	16	9	18
	Yellow-headed Caracara	*Milvago chimachima*	0	0	0	5	0	0
	Laughing Falcon	*Herpetotheres cachinnans*	0	0	0	0	1	0
	American Kestrel	*Falco sparverius*	0	8	3	1	7	3
Cracidae	Rufous-vented Chachalaca	*Ortalis ruficauda*	0	0	0	5	0	0
Odontophoridae	Crested Bobwhite	*Colinus cristatus*	32	13	61	48	20	25
Columbidae	Bare-eyed Pigeon	*Patagioenas corensis*	43	86	73	139	98	111
	Eared Dove	*Zenaida auriculata*	118	511	1071	149	155	254
	Scaled Dove	*Scardafella squammata*	118	165	393	297	254	322

APPENDIX I. Continued

FAMILY	COMMON NAME	SPECIES	STUDY SITE					
			PP	FL	LL	CP	AP	MP
Columbidae	Common Ground-Dove	*Columbina passerina*	136	61	191	42	116	226
	Ruddy Ground-Dove	*Columbina talpacoti*	0	0	0	2	0	0
	White-tipped Dove	*Leptotila verreauxi*	80	9	103	51	18	24
Psittacidae	Blue-crowned Parakeet	*Aratinga acuticaudata*	0	87	0	78	0	0
	Brown-throated Parakeet	*Aratinga pertinax*	2	694	538	204	0	349
	Green-rumped Parrotlet	*Forpus passerinus*	0	29	231	104	0	0
	Orange-winged Parrot	*Amazona amazonica*	0	0	0	28	0	0
	Yellow-shouldered Parrot	*Amazona barbadensis*	0	25	0	42	86	77
Cuculidae	Dwarf Cuckoo	*Coccyzus pumilus*	0	0	2	0	0	0
	Yellow-billed Cuckoo	*Coccyzus americanus*	3	0	0	0	2	0
	Dark-billed Cuckoo	*Coccyzus melacoryphus*	0	0	0	2	2	1
	Squirrel Cuckoo	*Piaya cayana*	0	0	0	1	1	0
	Groove-billed Ani	*Crotophaga sulcirostris*	23	1	48	34	0	0
	Striped Cuckoo	*Tapera naevia*	0	0	1	19	6	0
Trochilidae	Black-throated Mango	*Anthracothorax nigricollis*	0	1	0	0	0	0
	Ruby-topaz Hummingbird	*Chrysolampis mosquitus*	0	0	0	13	2	6
	Blue-tailed Emerald	*Chlorostilbon mellisugus*	6	3	0	12	3	29
	Red-billed Emerald	*Chlorostilbon gibsoni*	1	0	0	0	0	0

APPENDIX I. Continued

FAMILY	COMMON NAME	SPECIES	STUDY SITE					
			PP	FL	LL	CP	AP	MP
Trochilidae	Buffy Hummingbird	*Leucippus fallax*	81	48	57	118	115	139
Galbulidae	Pale-headed Jacamar	*Brachygalba goeringi*	0	0	2	0	0	0
	Rufous-tailed Jacamar	*Galbula ruficauda*	0	0	0	17	3	0
Bucconidae	Russet-throated Puffbird	*Hypnelus ruficollis*	30	8	19	8	35	27
Picidae	Scaled Piculet	*Picumnus squamulatus*	0	0	0	1	0	0
	Spot-breasted Woodpecker	*Chrysoptilus punctigula*	0	0	0	4	0	0
	Red-crowned Woodpecker	*Melanerpes rubricapillus*	87	183	141	72	141	42
Furnariidae	Pale-breasted Spinetail	*Synallaxis albescens*	87	46	56	29	58	8
	White-whiskered Spinetail	*Synallaxis candei*	12	37	44	0	0	0
	Plain Thornbird	*Phacellodomus inornatus*	0	0	0	30	0	0
Dendrocolaptidae	Olivaceous Woodcreeper	*Sittasomus griseicapillus*	0	0	0	3	0	0
	Straight-billed Woodcreeper	*Xiphorhynchus picus*	107	77	68	95	68	42
Thamnophilidae	Black-crested Antshrike	*Sakesphorus canadensis*	43	15	30	5	0	0
	Barred Antshrike	*Thamnophilus doliatus*	0	0	0	5	0	0
	Northern White-fringed Antwren	*Formicivora intermedia*	25	2	4	44	46	82
Tyrannidae	Southern Beardless Tyrannulet	*Camptostoma obsoletum*	0	4	3	13	1	0
	Mouse-colored Tyrannulet	*Phaeomyias murina*	0	0	8	1	0	0
	Small-billed Elaenia	*Elaenia parvirostris*	0	2	0	10	1	0

APPENDIX I. Continued

FAMILY	COMMON NAME	SPECIES	STUDY SITE					
			PP	FL	LL	CP	AP	MP
Tyrannidae	Northern Scrub-Flycatcher	*Sublegatus arenarum*	44	34	47	34	57	37
	Pale-tipped Inezia	*Inezia tenuirostris*	0	134	102	0	0	0
	Tawny-crowned Pygmy-Tyrant	*Euscarthmus meloryphus*	0	2	0	5	0	0
	Pearly-vented Tody-Tyrant	*Hemitriccus margaritaceiventer*	0	2	0	26	2	2
	Common Tody-Flycatcher	*Todirostrom cinereum*	0	0	0	4	0	0
	Maracaibo Tody-Flycatcher	*Todirostrum viridanum*	0	9	0	0	0	0
	Vermilion Flycatcher	*Pyrocephalus rubinus*	0	4	2	7	0	0
	Pied Water-Tyrant	*Fluvicola pica*	0	1	0	1	0	0
	Brown-crested Flycatcher	*Myiarchus tyrannulus*	28	33	37	40	57	65
	Great Kiskadee	*Pitangus sulphuratus*	1	4	75	84	1	0
	Social Flycatcher	*Myiozetetes similis*	0	0	3	6	0	0
	Cattle Tyrant	*Machetornis rixosus*	0	0	0	1	0	0
	Tropical Kingbird	*Tyrannus melancholicus*	2	2	3	33	4	1
	Gray Kingbird	*Tyrannus dominicensis*	4	0	0	2	0	1
	Fork-tailed Flycatcher	*Tyrannus savana*	0	5	0	1819	219	437
Vireonidae	Red-eyed Vireo	*Vireo olivaceus*	1	0	0	5	2	0
	Scrub Greenlet	*Hylophilus flavipes*	0	0	0	39	1	1
Troglodytidae	Bicolored Wren	*Campylorhynchus griseus*	0	0	212	75	5	0

APPENDIX I. Continued

FAMILY	COMMON NAME	SPECIES	STUDY SITE					
			PP	FL	LL	CP	AP	MP
Troglodytidae	Stripe-backed Wren	*Campylorhynchus nuchalis*	0	0	13	2	0	0
	House Wren	*Troglodytes aedon*	0	0	6	25	0	0
Polioptilidae	Tropical Gnatcatcher	*Polioptila plumbea*	237	253	149	103	200	149
Mimidae	Tropical Mockingbird	*Mimus gilvus*	347	339	251	195	386	414
Parulidae	Blackpoll Warbler	*Dendroica striata*	3	0	0	0	2	1
	American Redstart	*Setophaga ruticilla*	0	2	0	0	0	0
	Tropical Parula	*Parula pitiayumi*	0	0	0	1	0	0
Thraupidae	Bananaquit	*Coereba flaveola*	70	2	10	71	141	65
	White-lined Tanager	*Tachyphonus rufus*	0	0	0	25	0	0
	Glaucous Tanager	*Thraupis glaucocolpa*	0	0	0	32	0	0
	Trinidad Euphonia	*Euphonia trinitatis*	0	2	46	18	4	0
Cardinalidae	Grayish Saltator	*Saltator coerulescens*	36	13	40	63	5	0
	Orinocan Saltator	*Saltator orenocensis*	0	44	88	50	0	0
	Red-capped Cardinal	*Paroaria gularis*	0	0	0	5	0	0
	Vermilion Cardinal	*Cardinalis phoeniceus*	113	63	34	20	22	269
Emberizidae	Blue-black Grassquit	*Volatinia jacarina*	0	0	0	9	0	0
	Black-faced Grassquit	*Tiaris bicolor*	58	5	69	130	135	138
	Lesson's Seedeater	*Sporophila bouvronides*	0	0	0	2	0	0

APPENDIX I. Continued

FAMILY	COMMON NAME	SPECIES	STUDY SITE					
			PP	FL	LL	CP	AP	MP
Emberizidae	Ruddy-breasted Seedeater	*Sporophila minuta*	0	0	0	3	0	0
	Saffron Finch	*Sicalis flaveola*	0	0	3	18	0	0
	Gray Pileated-Finch	*Coryphospingus pileatus*	28	2	6	36	7	0
Icteridae	Venezuelan Troupial	*Icterus icterus*	130	183	79	4	0	163
	Yellow Oriole	*Icterus nigrogularis*	22	15	69	25	7	17
	Carib Grackle	*Quiscalus lugubris*	1	78	85	92	80	2
	Shiny Cowbird	*Molothrus bonariensis*	0	0	64	7	0	0
	Oriole Blackbird	*Gymnomystax mexicanus*	0	0	0	6	0	0
Fringillidae	Lesser Goldfinch	*Carduelis psaltria*	0	0	1	0	0	0

APPENDIX II. Sampling effort and model selection of detection functions based on visual records of arid zone birds detected in the six study sites (n = total number of observations used to generate the model, m = number of estimated parameters in detection function, AIC = Akaike's Information Criterion).

Species	n	Model Selected (Key function + adjustment term)	m	AIC
Patagioenas corensis	281	Uniform + Simple Polynomials	5	2910.07
Zenaida auriculata	751	Uniform + Cosines	3	7100.74
Scardafella squammata	257	Uniform + Cosines	3	2206.22
Columbina passerina	475	Uniform + Cosines	3	3979.53
Aratinga pertinax	407	Uniform + Cosines	3	4244.75
Aratinga acuticaudata	72	Uniform + Simple Polynomials	3	794.29
Forpus passerinus	127	Uniform + Cosines	3	1158.74
Amazona barbadensis	76	Uniform + Cosines	3	879.92
Leucippus fallax	405	Uniform + Cosines	5	3919.88
Melanerpes rubricapillus	218	Uniform + Simple Polynomials	5	2010.07
Xiphorhynchus picus	90	Half Normal + Hermite Polynomials	4	835.55
Sublegatus arenarum	176	Uniform + Cosines	3	1349.95
Myiarchus tyrannulus	129	Hazard Rate + Cosines	2	1100.70

APPENDIX II. Continued

Species	n	Model Selected (Key function + adjustment term)	m	AIC
Tyrannus savana	199	Uniform + Simple Polynomials	4	1932.79
Polioptila plumbea	461	Half Normal + Hermite Polynomials	4	3545.86
Mimus gilvus	1122	Half Normal + Cosines	2	4793.58
Coereba flaveola	225	Uniform + Simple Polynomials	4	1676.29
Cardinalis phoeniceus	272	Uniform + Cosines	4	2372.05
Tiaris bicolor	367	Uniform + Cosines	3	2915.97
Icterus icterus	121	Uniform + Simple Polynomials	5	1106.82
Icterus nigrogularis	92	Half Normal + Cosines	3	343.65

APPENDIX III. Sampling effort and model selection of detection functions based on auditory records of arid zone birds detected in the six study sites (n = total number of observations used to generate the model, m = number of estimated parameters in detection function, AIC = Akaike's Information Criterion, * = model included left truncation of data at 20 m of the point count).

Species	n	Model Selected (Key function + adjustment term)	m	AIC
Colinus cristatus	155	Hazard Rate + Cosines*	3	1312.32
Leptotila verreauxi	213	Half Normal + Cosines*	2	1578.77
Scardafella squammata	1147	Hazard Rate + Simple Polynomials*	4	3953.63
Columbina passerina	109	Uniform + Cosines*	3	841.92
Leucippus fallax	95	Half Normal + Cosines	1	226.37
Hypnellus rufucollis	107	Uniform + Cosines	2	387.96
Melanerpes rubricapillus	398	Uniform + Cosines	2	3282.74
Synallaxis albescens	243	Half Normal + Cosines	1	2178.66
Synallaxis candei	69	Half Normal + Cosines	1	573.00
Xiphorhynchus picus	359	Hazard Rate + Simple Polynomials	4	3175.86
Sakesphorus canadensis	72	Half Normal + Cosines*	1	235.97
Formicivora intermedia	145	Hazard Rate + Cosines	2	450.02
Inezia tenuirostris	210	Half Normal + Cosines	1	522.82

APPENDIX III. Continued

Species	n	Model Selected (Key function + adjustment term)	m	AIC
Myiarchus tyrannulus	119	Hazard Rate + Simple Polynomials	2	915.71
Pitangus sulphuratus	109	Uniform + Cosines*	1	473.05
Campylorhynchus griseus	188	Hazard Rate + Cosines*	2	748.79
Polioptila plumbea	499	Hazard Rate + Simple Polynomials*	2	3722.47
Mimus gilvus	571	Hazard Rate + Cosines*	3	1887.10
Coereba flaveola	114	Hazard Rate + Cosines	2	429.78
Saltator coerulescens	114	Uniform + Cosines*	3	444.91
Saltator orenocensis	113	Hazard Rate + Cosines*	2	960.06
Cardinalis phoeniceus	203	Hazard Rate + Cosines	2	720.15
Tiaris bicolor	79	Hazard Rate + Cosines	2	230.68
Icterus icterus	382	Hazard Rate + Simple Polynomials*	2	3463.40

CHAPTER II

BIRD-HABITAT RELATIONSHIPS IN ARID SCRUBLANDS OF NORTHERN VENEZUELA

INTRODUCTION

Bird species often respond to specific attributes of the habitats, so a better understanding of bird-habitat relationships can help identify environmental conditions that influence the distribution and abundance of bird species (Young and Hutto 2002). Previous studies on bird-habitat associations typically have used physical structure of the vegetation, floristic composition, or both as surrogates of habitat characteristics (Block and Brennan 1993). These components of the vegetation provide important elements of a bird's habitat (i.e., food resources, nesting sites, cover from predators) (Morrison et al. 1998). Given that changes in vegetation can alter habitat quality, knowledge of bird-habitat relationships can be important for conservation (e.g., to predict susceptibilities of species to habitat modification; Sedgwick 1987, Fielding and Haworth 1995, Derrickson et al. 1998). Better predictive capabilities may be particularly relevant for species with specialized habitat requirements (i.e., habitat specialists) because extinction risk via habitat loss is positively correlated with the degree of habitat specialization (Owens and Bennett 2000, Norris and Harper 2004).

Detailed bird-habitat associations remain unknown for most Neotropical birds and, further, information on habitat requirements needed to make even simple conservation decisions is lacking for most species, whether threatened or common. Arid

scrublands in northern Venezuela constitute an interesting model system to investigate bird-vegetation associations relevant to conservation applications. This is, in part, because of the relatively large number of habitat specialists in these areas (e.g., *Amazona barbadensis, Leucippus fallax, Chlorostilbon gibsoni, Picumnus cinnamomeus, Synallaxis candei, Inezia tenuirostris, Todirostrum viridanum, Cardinalis phoeniceus, Arremonops tocuyensis*). These species are restricted to arid lands of northern Venezuela and northeastern Colombia (Stotz et al. 1996, Stattersfield et al. 1998) and their long-term survival is threatened by ongoing changes in vegetation structure and composition brought about by overgrazing by goats, mining, wood collection, and high-impact tourist developments (Stattersfield et al. 1998, pers. observ.). Identification of specific attributes of the vegetation that are associated with such habitat specialists is needed to develop predictive models that will allow an assessment of the possible effects of those land-use changes on population persistence and risk of extinction in Venezuelan arid scrubs.

Both floristic and structural characteristics of vegetation have long been recognized as factors that can influence bird species richness, abundance, and habitat use (Wiens and Rotenberry 1981, Cody 1985, Rotenberry 1985, Block and Brennan 1993) but the relative importance of different variables in shaping bird communities varies considerably from habitat to habitat. Identification of a general pattern that describes the effect of vegetation structure on bird diversity and abundance in deserts and arid zones has been difficult. Foliage-height diversity (MacArthur and MacArthur 1961) was neither a good predictor of bird diversity in the Sonoran desert scrub (Tomoff 1974) nor in Venezuelan arid scrubs (Bosque 1984). Structural complexity of vegetation and vegetation volume, however, were positively correlated to both bird species diversity and

density in different scrub habitats of North and South America (Tomoff 1974, Wiens and Rotenberry 1981, Mills et al. 1989, 1991, Marone 1991). Several studies have indicated that floristic composition of the vegetation might have an even greater influence on bird species richness and abundance in these habitats. Sites dominated by columnar cacti in arid scrublands of northwestern Venezuela had higher bird diversity and densities than sites dominated by other plant species (Bosque 1984), possibly because these cacti provide sufficient resources to allow coexistence of more species and individuals (Silvius 1995). In addition, birds found in arid scrub habitats are highly selective in their choice of plants for nesting and foraging (Tomoff 1974, Bosque 1984, Parker 1986, Bosque and Lentino 1987, Kozma and Mathews 1997, Sanz 2004).

The objectives of this study were to compare structural and floristic features of the vegetation in six Venezuelan arid zones and to identify how such variables influence bird abundances. I addressed the latter question from two perspectives. First, I examined the relative importance of physical structure and floristic composition of the vegetation on the abundance of all bird species in the community. Because of strong associations of some arid scrub birds to particular plants for foraging and breeding (Tomoff 1974, Bosque 1984, Parker 1986, Bosque and Lentino 1987, Sanz 2004), I expected floristics to play a major role in explaining patterns of bird distribution and abundance. Second, I tested whether the whole set of vegetation variables affected the abundances of habitat specialists and generalists in different ways. It has been suggested that the influence of habitat features on bird distribution and abundance depends on the degree of habitat specialization of the bird species in question. Wiens and Rotenberry (1981), for example, found that patterns in bird-habitat relationships were more apparent for local specialists

than for generalists in North American shrub steppes. Thus, I expected that abundances of habitat specialists in Venezuelan arid scrublands would be more strongly associated with vegetation variables than would abundances of habitat generalists.

METHODS

Study Areas. Fieldwork was conducted from September 2004 to August 2005 in six isolated arid regions in northern Venezuela (Fig. 1), regions which differed in area and geological origin. Three of these were located in the eastern part of the country: Clarines-Píritu (CP), Araya Peninsula (AP), and Macanao Peninsula (MP) on Margarita Island; three were in the west: Paraguaná Peninsula (PP), Falcón lowlands (FL), and Lara Lowlands (LL). All regions were characterized by a mean annual temperature of 28°C, an annual rainfall between 300 and 700 mm, and xerophytic vegetation (Huber 1997).

Vegetation Sampling. Three 50-ha plots, located at least 3 km apart, were established in thorn scrub vegetation in each of the six study areas (N = 18 plots). On each plot, 10 points were selected for bird surveys (see below). The first point was randomly established with the subsequent nine points systematically located at least 250 m apart and at least 100 m from vegetation borders and roads. Vegetation was sampled in square plots (25 m x 25 m) around each of these points. I measured vegetation variables that included both floristic and structural attributes. The selection of variables was based on a modification of the variables suggested by Bibby et al. (2000) for studies in dry areas. I also included measurements of cacti because of the importance of Cactaceae in my study areas.

I counted and identified all trees, shrubs, and cacti within each square plot. Diameter at breast height (dbh, approximately at 1.2 m) of all trees ≥ 10 cm was measured with a diameter tape. A measuring rod was used to determine the height of 10 individual shrubs per species and 10 individual cacti per species that made contact with line intercepts oriented in the four cardinal directions in each plot. The percentage of ground cover and the percentage of canopy cover were determined using a GRS densitometer (Geographic Resource Solutions, Arcata, California) at the center, corners, and at 20 random points within the plot. Percentage of either canopy or ground cover for a given sampling plot was derived from the number of points with canopy or ground coverage, divided by the total number of points sampled. Canopy height was determined, using a laser rangefinder, at the same points where canopy and ground cover were recorded.

Bird Sampling. Bird surveys were conducted bimonthly in each plot, from September 2004 to August 2005, from 6:00 to 10:00 am during three consecutive days (one day per plot). The sequence in which point counts in each plot were visited was alternated among sampling periods to compensate for the effects of hourly variation in bird activity. At each of the 10 point-counts in a plot, the number of individuals for all the bird species detected, both visually and aurally, was recorded during 10 min. Species flying over a point that did not use thorn scrub vegetation, such as vultures (Cathartidae), herons and egrets (Ardeidae), and swallows (Hirundinidae), as well as nocturnal species, such as owls (Strigidae) and nightjars (Caprimulgidae), were not included in the surveys.

Analyses. Prior to statistical analyses, all vegetation data were tested for assumptions of normality using the Shapiro-Wilk test. As most of the vegetation variables did not meet

the normality assumption of parametric tests, even after transformations, non-parametric methods were used throughout. Several variables were highly correlated ($r \geq 0.80$), so within each correlated group some variables (tree density, total cacti species, and total tree species) were excluded from all subsequent analyses.

I tested for differences in floristics and vegetation structure to determine if vegetation was similar among the six study areas. First, I conducted two nested permutational multivariate analyses of variance (PERMANOVA, Anderson 2001) to determine whether vegetation structure and floristic variables varied among areas. I used study areas and plots nested within study areas as factors and five floristic and 11 structural vegetation variables, respectively, as response variables. Comparisons were based on Euclidean distances and significance was estimated based on 9999 permutations of residuals under a reduced model (Anderson and ter Braak 2003). These tests were followed by *a posteriori* pairwise comparisons. Next, I used analyses of similarity (ANOSIM, Clark and Warwick 2001) to compare vegetation composition among the six regions. ANOSIM is a non-parametric analysis, which tests whether differences among samples within pre-defined groups (30 points within each study area) were less than expected when compared to differences among samples across the six study areas. I conducted four ANOSIMs, one for each plant group (trees, shrubs, and cacti) and one for all groups combined. ANOSIM estimates a similarity value (R) among all groups as well as separate pairwise comparisons and provides R values that are a relative measure of separation of the a priori-defined groups. An R = 0 indicates that similarities between and within plots are the same on average, while an R = 1 indicates that all plots within each study area are more similar to each other than any plots from different arid zones. Four

Non-metric Multidimensional Scaling ordinations (NMS, Clarke and Warwick 2001) were also conducted to graphically represent the results of each ANOSIM.

I conducted a Detrended Correspondance Analysis (DCA) to determine whether to use Redundancy Analysis (RDA) or Canonical Correspondence Analysis (CCA), following Lepš and Šmilauer (2003). This determination is based on the length of the gradient (the extent of species turnover along ordination axes), which is used to decide between linear (RDA) or unimodal (CCA) ordination methods for the analysis of bird-habitat relationships. Linear methods are more appropriate when the length of the longest gradient is shorter than 3 SD, whereas unimodal methods should be used when that value is larger than 4 SD. For my data, the length of the longest gradient was < 3 for all the analyses mentioned above and, thus, the linear RDA was preferred over the unimodal CCA. Redundancy analysis is an ordination technique that consists of a canonical form of a Principal Components Analysis (PCA) (Jongman et al. 1995). It allows the estimation of the amount of variance in the bird distribution matrix that is explained by a canonical variate from the vegetation matrix based on a multiple regression of all species simultaneously with linear constraints on the regression coefficients (ter Braak and Šmilauer 2002). The results of the analysis consist of principal axis scores and eigenvalues plus the canonical coefficients derived from the multiple regression (Shaw 2003), interpretation of the results can be easily derived from ordination diagrams (i.e. biplot or triplot). The latter display scores for sites (represented by symbols), bird species (represented by arrows), and vegetation variables (represented by arrows).

I conducted two independent RDA analyses to examine the relationship between features of the vegetation and bird abundance; explanatory variables included five floristic attributes in the first analysis, and 11 structural variables in the second. To determine whether habitat relationships of specialist birds differed from those of generalists, I conducted two additional RDA, one for each group of birds, including both floristic and vegetation structure attributes (16 in total) as explanatory variables. The bird matrix for the habitat specialists included seven species and the one for generalists included the 14 most common species recorded in the sampling areas. In all the analyses, bird data consisted of mean abundance per species, calculated as the total number of individuals of each species per point divided by the total number of visits (six) to that point.

Descriptive statistics represent averages ± SE. Shapiro-Wilk test was conducted on SPSS 15.0 (SPSS 2006). The non-parametric multivariate analysis of variance and the *a posteriori* comparisons were run on program PERMANOVA (Anderson 2005). ANOSIM and NMS analyses were run on PRIMER v5.2.9 (Clark and Gorley 2003). All PCA, DCA, and RDA were conducted using CANOCO 4.5 (ter Braak and Šmilauer 2002).

RESULTS

Vegetation characteristics. A total of 56 plant species was recorded across the six study areas including 9 cacti, 19 shrubs (including terrestrial bromeliads, agaves, and aloe), and 28 trees (see Appendix). The mean number of species per sampling plot (0.0625 ha) was 4.0 ± 0.10 cacti (range: 1.0 – 8.0, $N = 180$), 3.2 ± 0.13 shrubs (range: 0.0 – 9.0, $N = 180$),

and 4.2 ± 0.14 trees (range: 1.0 – 11.0, $N = 180$). The most common cacti in all six areas were *Opuntia wentiana, Stenocereus griseus*, and *Melocactus* sp. The most abundant shrubs were *Croton* sp., *Castella erecta*, and *Cnidoscolus urens*. Common trees in all areas belong mainly to Fabaceae (*Prosopis juliflora, Cercidium praecox, Pithecellobium ungis-cati, Caesalpinia coriaria*) and Capparidaceae (*Capparis odoratissima*) (Table 1).

Mean numbers of species within each plant category (Table 2) varied significantly among areas (PERMANOVA, $F_{5,162} = 12.35$, $P = 0.0001$) and among plots (PERMANOVA, $F_{12,162} = 4.36$, $P = 0.0001$). *A posteriori* pairwise comparisons indicated that Paraguaná peninsula, Falcón lowlands, and Macanao peninsula differed from all other areas ($P < 0.05$ in all cases), but Araya peninsula showed no differences in terms of floristics when compared to Lara lowlands ($t_{58} = 1.17$, $P = 0.223$) or Clarines-Píritu region ($t_{58} = 0.94$, $P = 0.393$). Differences in composition among areas were minor (but significant) when only cacti were considered (ANOSIM Global R = 0.237, $P = 0.001$, Fig. 2A), but were more pronounced when comparisons were based on shrubs (ANOSIM Global R = 0.401, $P = 0.001$, Fig. 2B) or tree species (ANOSIM Global R = 0.627, $P = 0.001$, Fig. 2C). These latter two groups thus likely drove floristic differences among the study areas when all species were included in the analysis (ANOSIM Global R = 0.444, $P = 0.001$, Fig. 2D). Points in Clarines-Píritu region were separated from those of other study areas, indicating that this area was the most distinct in terms of plant composition (Fig. 2C and 2D). R values of pairwise comparisons involving this area were the highest of all (range: 0.473 – 0.669, $P = 0.001$ for all cases).

Vegetation in the study areas had a low and open canopy, and an intermediate percentage of ground cover (Table 3). These scrublands also had a high density of non-

columnar cacti, medium densities of columnar cacti and shrubs, and a low tree density. When tree density was separated into tree size classes, it was clear that the total was mainly accounted by the contribution of small trees (dbh ≤ 10 cm).

Multivariate comparisons indicated that the 11 structural variables varied among the six areas (PERMANOVA, $F_{5,162} = 7.25$, $P = 0.0001$) and among plots (PERMANOVA, $F_{12,162} = 3.49$, $P = 0.0001$) within study areas. Pairwise comparisons, however, indicated that Falcón lowlands, Lara lowlands, and Araya peninsula did not differ from each other (Falcón-Lara, $t_{58} = 1.30$, $P = 0.133$; Falcón-Araya, $t_{58} = 1.51$, $P = 0.066$; Lara-Araya, $t_{58} = 1.01$, $P = 0.362$). Obvious differences among study areas included higher density of shrubs in the Clarines-Píritu region and higher density of non-columnar cacti in Lara lowlands, as well as greater percentage of ground cover in both Clarines-Píritu and Paraguaná peninsula (Table 3).

Bird diversity. A total of 96 bird species representing 26 families was recorded throughout the study areas. Seventy-three species that were widely distributed, and known to occupy more than two habitat types (i.e., arid scrublands, dry forests, humid forests) in the Neotropics, were referred to as habitat generalists. The 14 most common generalist species were included in the analysis of bird-vegetation associations: *Zenaida auriculata*, *Scardafella squammata, Columbina passerina, Leptotila verreauxi, Synallaxis albescens, Xiphorhynchus picus, Sublegatus arenarum, Myiarchus tyrannulus, Campylorhynchus griseus, Polioptila plumbea, Mimus gilvus, Coereba flaveola, Saltator coerulescens,* and *Icterus nigrogularis*. Only 7 species (7.3%) were considered habitat specialists with relatively limited distribution in northern Venezuela, Colombia and the Caribbean islands. These included *Amazona barbadensis, Leucippus fallax, Synallaxis*

candei, Inezia tenuirostris, Todirostrum viridanum, Cardinalis phoeniceus, and *Tiaris bicolor*.

Bird-vegetation relationships. Species recorded only once or twice ($N = 22$) were excluded from the original bird matrix before conducting the RDA. Vegetation variables explained small but significant amounts of variation in bird distribution when all bird species were included in the analysis (Table 4). Eigenvalues for the first axis of RDAs based on structural variables and on floristic variables were less than 10%, indicating a very weak gradient along this axis. Floristic variables explained a total of 12% (F-ratio = 4.91, $P = 0.002$) of the variation in bird distribution patterns, whereas structural variables explained 18% (F-ratio = 3.33, $P = 0.002$).

Sample-vegetation variable biplots (Fig. 3) showed that sample plots largely did not segregate by study areas. Samples from Clarines-Píritu did, however, show a clear separation from other areas when the analysis was based on vegetation structural variables (Fig. 3B). Percentage of ground cover and density of shrubs were the most important variables separating this area from the other five. Both species-vegetation biplots (Figs. 4 and 5) showed associations between the abundance of bird species and different vegetation variables. In the species-floristic biplot (Fig. 4), there was a clear separation between species that were more abundant in plots dominated by non-columnar cacti, such as *Campylorhynchus griseus*, and species, such as *Tiaris bicolor,* whose abundances were higher in plots with more shrubs and small trees. All floristic variables had significant ($P < 0.005$) conditional effects on the variation explained, but in all cases the amount of variance in species data accounted for was very low (< 4% for each variable). In the case of the species-vegetation structure biplot (Fig. 5), the percentage of

ground cover accounted for most variation, but its contribution to the amount of variance in species data was also low (5.5%). Other variables with significant ($P < 0.005$), but even lower conditional effects, included density of non-columnar cacti, shrub density, and shrub height.

When separate RDAs were conducted for specialists and generalists using all vegetation variables, there was a stronger gradient along the first axis for specialists than for generalists (Table 5). Vegetation variables explained a total of 30% (F-ratio = 4.36, P = 0.002) of the variation in the distribution of specialists, and 26% (F-ratio = 3.49, P = 0.002) of the variation in the distribution of generalists. Both the species-vegetation correlations and the percentage of variance in the species-vegetation relation explained by the first two axes were greater for the analysis based on habitat specialists. This suggests vegetation variables measured in this study on had more influence on the distribution of habitat specialists than of habitat generalists. Three sub-groups of habitat specialists were associated with different vegetation variables (Fig. 6). The first group, composed of *Amazona barbadensis*, *Leucippus fallax*, and *Tiaris bicolor*, included species whose abundance was positively associated with the percentage of ground cover and the number of small tree species. The second was composed of *Synallaxis candei*, *Inezia tenuirostris*, and *Todirostrum viridanum*, species that were all restricted to the western areas and which apparently responded positively to the density of non-columnar cacti and percentage of canopy cover. Finally, the third group was represented only by *Cardinalis phoeniceus,* whose abundance was correlated with the height of shrubs and cacti (both columnar and non-columnar). In the species (generalists)-vegetation biplot (Fig. 7), density of non-columnar cacti accounted for the most variation, and abundances

of species such as *Icterus nigrogularis* and *Campylorhynchus griseus* were strongly associated with this variable. In contrast, density of non-columnar cacti had no apparent effect in the analysis that included habitat specialist birds ($P = 0.118$). Percentage of ground cover also had an important effect in the analysis that included the generalist birds (e.g., *Coereba flaveola*).

DISCUSSION

Arid scrublands in northern South America are typically characterized as low and sparse plant formations dominated by species belonging to Cactaceae, Capparidaceae, and Fabaceae, and with considerable areas of bare ground (Sarmiento 1972, 1976). Study areas in the present study fit this characterization both in floristic and structural attributes of vegetation. Although there were significant differences in mean values of both floristic and structural variables among the six study regions, the lack of separation of the sampling points into groups corresponding to each area indicated that, overall, the six areas had relatively similar vegetation. In some of the analyses, however, sampling points in Clarines-Píritu segregated as a unit different from all other study areas, mainly because this area had more ground cover and shrubs than all other areas. Annual rainfall, the most important climatic variable affecting plant life in arid scrubs (Sarmiento 1976), varies slightly among areas (between 400 and 700 mm in the case of Clarines-Píritu region and Lara lowlands, and below 600 mm for all other areas). This variation may explain the distinct nature of Clarines-Píritu relative to the other five areas, where there were more individuals of the same species (e.g., shrubs) per unit of area. Differences in floristics among the study areas may be partly explained by factors such as regional effects or the

presence of exotic plants. Regional effects may drive differences among areas because some plant species are restricted to some of the study areas because of historical and biogeographical reasons. Non-columnar cacti of the genus *Mammillaria* were only recorded in two of the western areas (Falcón and Lara lowlands) even though some species of the genus have been reported for eastern Venezuela (Hoyos 1985). Finally, introduction of exotic species in some of the study areas further increased floristic differences. *Stapelia gigantea* is an invasive (I. Herrera pers. comm.) only present in Lara lowlands, whereas *Calotropis procera* has been reported in several of the study areas (Hoyos 1985, pers. observ.), but in this study it was recorded only in plots within Falcón lowlands.

Abundances of most bird species were not well explained by variation in either floristic or structural vegetation variables. This lack of close association suggests that other environmental factors not considered in this study (e.g., abiotic factors) likely influence bird distribution and abundance and that most of the measured variables could be only indirect reflections of what birds are responding to. Spatial scale may represent another important influence not considered in this study. Bird distribution and abundance patterns related to habitat characteristics are known to be scale-dependent (Wiens et al. 1987, Michaels and Cully 1998, Karl et al. 2000). There is evidence that birds respond to landscape-scale habitat features, such as topography or habitat heterogeneity (Cunningham and Johnson 2006, Mitchell et al. 2006).

Structural variables explained a slightly higher percentage of the variation in bird distribution than did floristic ones, but because of the small magnitude of the difference, it was not possible to evaluate the relative importance of each group of variables. Thus, I

can only conclude that both types of variables do have some influence on bird distribution in the Venezuelan arid scrublands. The complementary effects of vegetation structure and floristics on bird distribution and abundance have also been found in other habitats, such as grasslands (Rotenberry 1985) and forests (Arnold 1988, Estades 1997). The relevance of floristic composition to bird communities in arid scrublands highlighted in some studies (Tomoff 1974, Bosque 1984) was not evident in the present study. The association between floristics and birds seems to be linked to microhabitat selection, specifically related to nesting (Tomoff 1974, Bosque and Lentino 1987, Kozma and Mathews 1997, Sanz 2004), a factor that was not evaluated in this study. Direct measurements of resources (e.g., nesting sites and materials, food) are needed to elucidate how bird communities in arid scrublands respond to floristic composition of the vegetation.

Vegetation variables explained more variation in distributions of habitat specialists and generalists when groups were considered separately than when they were combined in one analysis. Further, aspects of the vegetation explained similar amounts of variation (25-30%) in the distribution of both groups of birds, suggesting that habitat specialists of arid scrublands are not more strongly associated to the vegetation variables measured in this study than are generalists. These results are opposite to what was found for habitat specialists in open and forested habitats of North America (Wiens and Rotenberry 1981, Dettmers et al. 2002). The distribution of the habitat specialists in Venezuelan arid scrublands seems, instead, to be more related to historical and biogeographical factors than to any particular habitat or vegetation feature, as has been

suggested for restricted-range birds in other tropical dry forests that showed no or little association with vegetation variables (Gillespie et al. 2001).

Habitat specialists differed in their responses to vegetation variables. This may be related to differences in foraging strategies, since birds belonging to different guilds tend to respond differentially to the same vegetation variables (Tomoff 1974, López de Casenave et al. 1998). *Cardinalis phoeniceus,* an opportunistic species (Poulin et al. 1994a) that feeds on fruits, seeds, and insects (Poulin et al. 1994b), was associated to cacti and shrub height, presumably because it moves through different vegetation strata looking for food and because it usually sings from tops of columnar cacti (Hilty 2003). The three species restricted to the western areas, *Synallaxis candei*, *Todirostrum viridanum*, and *Inezia tenuirostris*, are insectivores that take insects under vegetation cover (Bosque 1984, Hilty 2003) and were associated with the same variables related to vegetation cover (canopy cover, density of non-columnar cacti, and ito a lesser degree, density of large trees). This association between surface or short-flight insectivores and tree and shrub cover seems to be a pervasive one, since it has been previously reported for different habitats, including scrublands (Marone 1991) and forests (Yahner 1986, Chettri et al. 2005). Although they belong to different feeding guilds, *Amazona barbadensis*, *Leucippus fallax*, and *Tiaris bicolor* appeared close together in the ordination diagram, probably as a response to the density of columnar cacti. The columnar cactus *Stenocereus griseus* is an important food resource for the three species, providing fruits for *Amazona barbadensis*, fruits and seeds for *Tiaris bicolor*, as well as nectar and juices for *Leucippus fallax* (Poulin et al. 1994b, Silvius 1995). The association between these three species and the percentage of ground cover is hard to explain.

Even though habitat-specialist birds did not respond strongly to vegetation variables, this study suggests that some structural attributes are important for the survival of this particular group of species. Thus, management and conservation programs devoted to protecting these birds should focus on the maintenance of the structural integrity of the habitat. Concerning future studies, two topics deserve further investigation. First, a multiscale approach, with the consideration of landscape-level variables, may complement the findings of this study. Second, in-depth studies that determine the influence of environmental features on habitat use (e.g., foraging, nesting performance) of habitat-specialists will provide a connection between the observed distribution patterns and the processes underlying them.

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TABLE 1. Mean number of individuals (± SE) per sampling plot (0.0625 ha) for the five most common species of cacti, shrubs, and trees in the six sampling areas in northern Venezuela: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu region, AP = Araya peninsula, MP = Macanao peninsula.

SPECIES	PP	FL	LL	CP	AP	MP
CACTI						
Stenocereus griseus	37.3 ± 7.27	81.1 ± 16.47	59.3 ± 10.48	31.6 ± 5.47	80.5 ± 14.16	145.2 ± 20.71
Cereus repandus	0.4 ± 0.27	1.1 ± 0.53	11.5 ± 2.49	16.3 ± 3.60	5.4 ± 1.04	2.3 ± 0.55
Opuntia caribea	0.00	22.5 ± 6.05	19.1 ± 8.52	0.00	16.7 ± 8.66	0.00
Opuntia wentiana	309.2 ± 33.10	455.9 ± 59.31	913.6 ± 123.29	306.1 ± 56.40	583.2 ± 65.14	318.6 ± 40.51
Melocactus sp.	0.7 ± 0.51	25.0 ± 9.05	36.7 ± 14.76	14.8 ± 3.51	22.1 ± 4.04	57.3 ± 19.30
SHRUBS						
Bromelia humilis	0.00	0.00	0.00	239.1 ± 72.32	14.9 ± 5.65	0.00
Cnidoscolus urens	9.9 ± 5.25	1.1 ± 0.64	4.4 ± 1.23	11.7 ± 3.41	10.1 ± 2.50	9.0 ± 1.96
Croton sp.	28.3 ± 8.38	0.3 ± 0.30	105.5 ± 24.98	11.1 ± 3.59	7.2 ± 2.81	37.7 ± 14.02
Gossypium sp.	0.2 ± 0.16	0.00	0.00	19.7 ± 9.67	0.00	19.7 ± 9.01
Castella erecta	9.8 ± 3.54	42.6 ± 10.81	4.2 ± 3.20	2.4 ± 1.06	36.5 ± 4.05	4.8 ± 1.55
TREES						
Capparis odoratissima	0.9 ± 0.27	0.2 ± 0.12	0.00	18.6 ± 4.32	3.2 ± 0.52	3.4 ± 0.52
Pithecellobium ungis-cati	0.9 ± 0.38	0.4 ± 0.16	0.9 ± 0.24	2.5 ± 0.55	7.5 ± 0.84	5.5 ± 0.72
Prosopis juliflora	11.5 ± 1.38	19.1 ± 3.75	14.8 ± 2.53	11.8 ± 1.96	2.2 ± 0.77	0.5 ± 0.19
Caesalpinea coriaria	0.2 ± 0.09	24.1 ± 8.10	0.2 ± 0.17	0.3 ± 0.20	9.3 ± 2.52	3.9 ± 1.09
Cercidium praecox	0.4 ± 0.34	3.9 ± 1.44	8.3 ± 1.93	0.00	8.5 ± 2.11	3.1 ± 0.76

TABLE 2. Floristic attributes (Mean ± SE) of the six Venezuelan arid zones. Sampling areas are the following: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu region, AP = Araya peninsula, MP = Macanao peninsula.

VARIABLE	PP	FL	LL	CP	AP	MP
# cacti species	2.7 ± 0.20	3.6 ± 0.23	5.2 ± 0.23	4.2 ± 0.18	5.0 ± 0.21	3.5 ± 0.15
# columnar cacti species	1.2 ± 0.11	1.2 ± 0.14	2.3 ± 0.13	1.9 ± 0.07	2.3 ± 0.15	1.6 ± 0.10
# non-columnar cacti species	1.6 ± 0.12	2.4 ± 0.15	2.9 ± 0.16	2.2 ± 0.15	2.7 ± 0.11	1.8 ± 0.08
# shrub species	2.7 ± 0.30	1.6 ± 0.16	3.3 ± 0.28	4.0 ± 0.37	3.6 ± 0.29	4.1 ± 0.25
# tree species	3.2 ± 0.34	3.1 ± 0.24	3.9 ± 0.28	5.0 ± 0.26	5.3 ± 0.43	4.9 ± 0.29
# large tree (dbh ≥ 10cm) species	2.0 ± 0.17	1.2 ± 0.14	1.7 ± 0.19	1.8 ± 0.21	2.0 ± 0.28	1.0 ± 0.18
# small tree (dbh ≤ 10cm) species	2.3 ± 0.32	2.9 ± 0.23	3.3 ± 0.25	4.8 ± 0.27	4.8 ± 0.40	4.7 ± 0.28

TABLE 3. Structural features (Mean ± SE) of the six Venezuelan arid zones. Sampling areas are the following: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu region, AP = Araya peninsula, MP = Macanao peninsula.

VARIABLE	PP	FL	LL	CP	AP	MP
Tree density (ind/m^2)	0.7 ± 0.06	2.2 ± 0.34	1.2 ± 0.14	2.1 ± 0.32	1.3 ± 0.13	1.0 ± 0.13
Large tree (dbh ≥ 10cm) density (ind/m^2)	0.2 ± 0.02	0.1 ± 0.02	0.1 ± 0.03	0.1 ± 0.02	0.1 ± 0.02	0.1 ± 0.01
Small tree (dbh ≤ 10cm) density (ind/m^2)	0.5 ± 0.06	2.0 ± 0.34	1.0 ± 0.13	1.9 ± 0.32	1.2 ± 0.13	1.0 ± 0.13
Columnar cacti density (ind/m^2)	1.5 ± 0.29	3.3 ± 0.66	2.9 ± 0.40	1.9 ± 0.23	4.3 ± 0.61	5.9 ± 0.83
Non-columnar cacti density (ind/m^2)	13.2 ± 1.45	20.2 ± 2.41	39.6 ± 5.37	13.1 ± 2.33	25.6 ± 2.50	15.2 ± 1.50
Shrub density (ind/m^2)	2.4 ± 0.40	3.3 ± 0.65	6.2 ± 1.11	15.3 ± 3.05	3.2 ± 0.38	4.0 ± 0.60
% ground cover	68.7 ± 2.13	37.4 ± 3.80	33.4 ± 3.51	76.6 ± 2.82	45.1 ± 2.59	50.9 ± 2.15
% canopy cover	38.2 ± 2.53	30.2 ± 2.62	26.9 ± 2.42	33.2 ± 2.92	24.9 ± 1.84	17.5 ± 1.16
Canopy height (m)	2.3 ± 0.19	1.7 ± 0.15	1.4 ± 0.12	2.1 ± 0.15	1.5 ± 0.15	1.0 ± 0.06
Shrub height (m)	1.2 ± 0.07	1.1 ± 0.09	0.8 ± 0.06	0.8 ± 0.06	1.0 ± 0.05	0.9 ± 0.06
Columnar cacti height (m)	3.6 ± 0.58	1.7 ± 0.19	1.7 ± 0.13	2.0 ± 0.14	1.6 ± 0.08	1.7 ± 0.06
Non-columnar cacti height (m)	0.7 ± 0.05	0.5 ± 0.04	0.4 ± 0.03	0.5 ± 0.02	0.5 ± 0.03	0.5 ± 0.04

TABLE 4. Results of RDAs for 73 bird species and five floristic and 11 structural vegetation variables in six aridlands of northern Venezuela.

Analysis – variables	**Axes**			
	I	**II**	**III**	**IV**
RDA – 5 floristic variables				
Eigenvalues	0.066	0.029	0.016	0.009
Correlations: bird species – floristics	0.645	0.514	0.524	0.448
Cumulative percentage of variance:				
of bird species	6.6	9.5	11.1	12.0
of bird species – floristics relation	53.4	77.0	90.1	97.3
RDA – 11 structural variables				
Eigenvalues	0.072	0.035	0.028	0.015
Correlations: bird species – vegetation structure	0.652	0.570	0.637	0.568
Cumulative percentage of variance:				
of bird species	7.2	10.8	13.6	15.1
of bird species – vegetation structure relation	40.4	60.1	75.9	84.2

TABLE 5. Results of RDAs including groups of birds that vary in the level of habitat specialization (7 specialists and 14 common generalists) and 16 vegetation attributes (both structural and floristic variables) in six arid scrublands of northern Venezuela.

Analysis – variables	**Axes**			
	I	**II**	**III**	**IV**
RDA Habitat specialist birds – 16 vegetation variables				
Eigenvalues	0.198	0.051	0.027	0.017
Correlations: bird species – vegetation attributes	0.731	0.491	0.457	0.351
Cumulative percentage of variance:				
of habitat-specialist species	19.8	24.9	27.6	29.3
of habitat-specialist birds – vegetation relation	66.0	83.0	92.0	97.7
RDA Habitat generalist birds – 16 vegetation variables				
Eigenvalues	0.093	0.061	0.041	0.024
Correlations: bird species – vegetation attributes	0.629	0.657	0.640	0.524
Cumulative percentage of variance:				
of habitat-generalist species	9.3	15.3	19.4	21.8
of habitat-generalist birds – vegetation relation	36.3	60.2	76.1	85.5

FIGURE 1. Location of study areas in northern Venezuela. Study areas are the following: PP = Paraguaná peninsula, FL = Falcón lowlands, LL = Lara lowlands, CP = Clarines-Píritu region, AP = Araya peninsula, MP = Macanao peninsula.

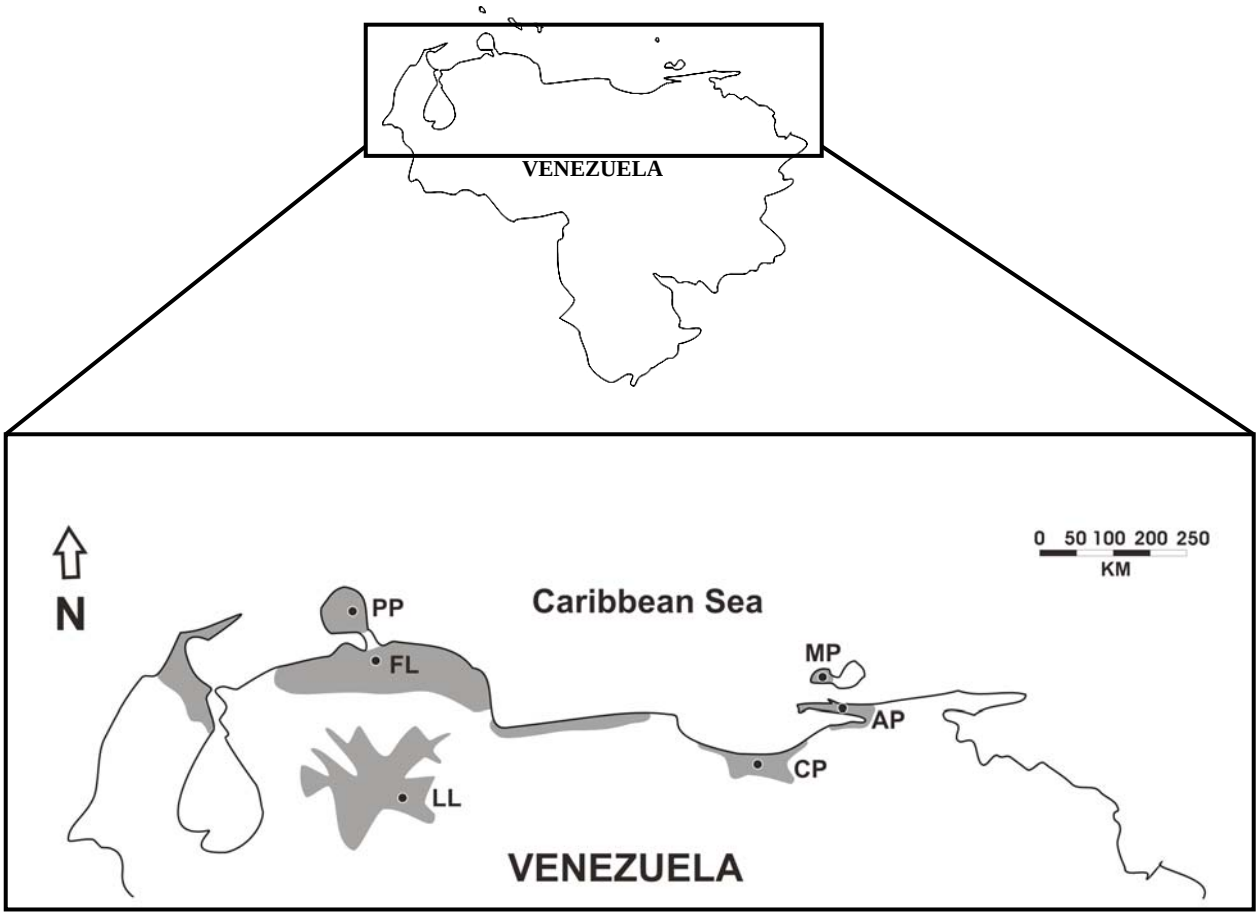


FIGURE 2. NMS ordination of plant composition among study areas. (A) Cacti only; (B) Shrubs only; (C) Trees only; (D) All plant categories combined. Species showing high correlations with the two axes are indicated. Study areas are the following: Paraguaná peninsula (filled up-triangles), Falcón lowlands (open down-triangles), Lara lowlands (filled squares), Clarines-Píritu region (open squares), Araya peninsula (filled circles), Macanao peninsula (open circles).

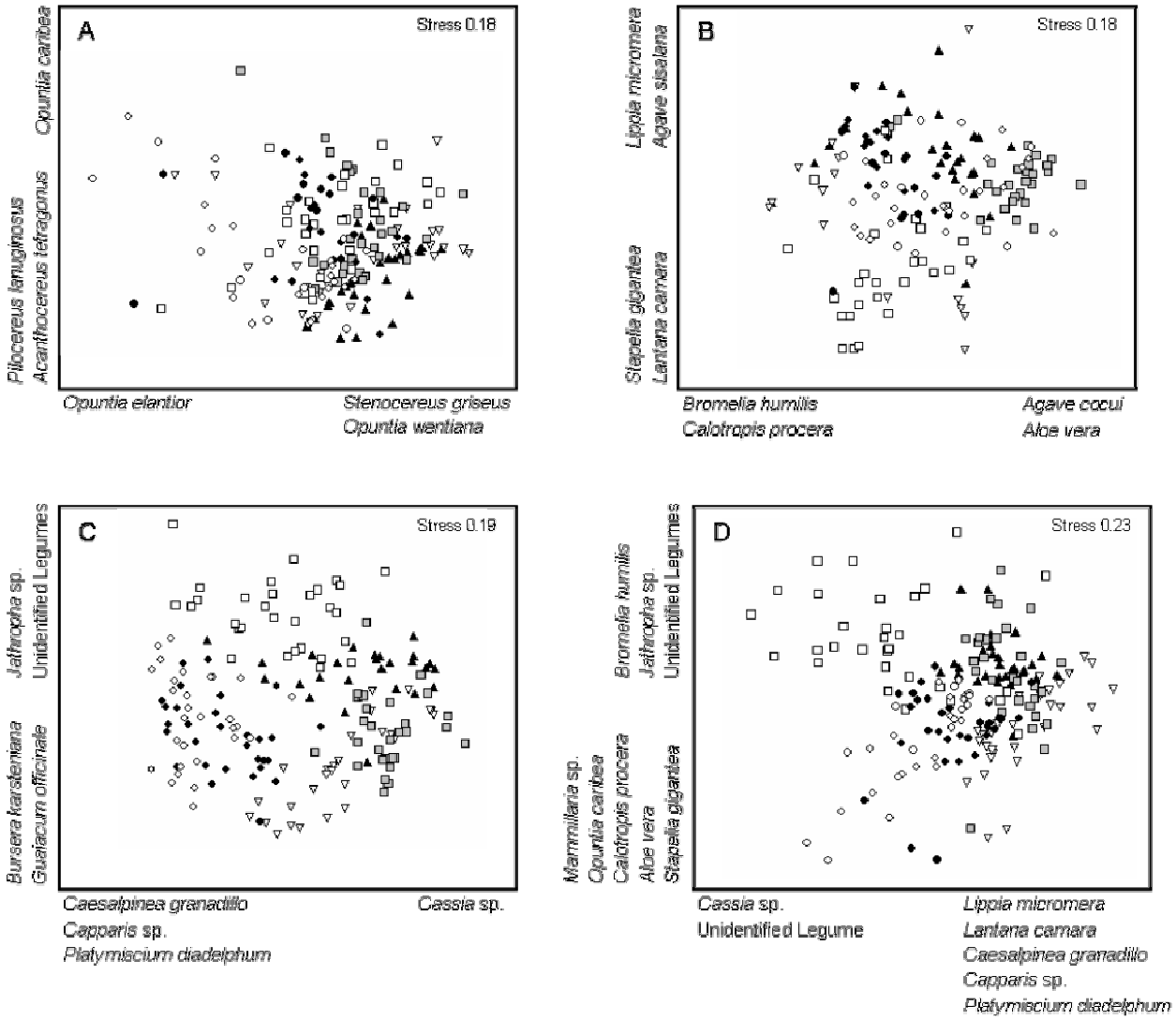


FIGURE 3. Bi-plot from redundancy analyses of sampling plots and (A) floristic and (B) structural vegetation variables. Dashed arrows indicate variables; symbols indicate study areas: Paraguaná peninsula (filled up-triangles), Falcón lowlands (open down-triangles), Lara lowlands (filled squares), Clarines-Píritu region (open squares), Araya peninsula (filled circles), Macanao peninsula (open circles). Floristic variables represent the mean number of species for each plant category indicated in the diagram. Structural variables are: DST = mean density of small (dbh ≤ 10 cm) trees; DLT = mean density of large (dbh ≥ 10 cm) trees; DS = mean density of shrubs; DCC = mean density of columnar cacti; DNCC = mean density of non-columnar cacti; GC: percentage of ground cover; CC: percentage of canopy cover; HC = mean canopy height; HS = mean shrub height; HCC = mean height of columnar cacti; HNCC = mean height of non-columnar cacti.

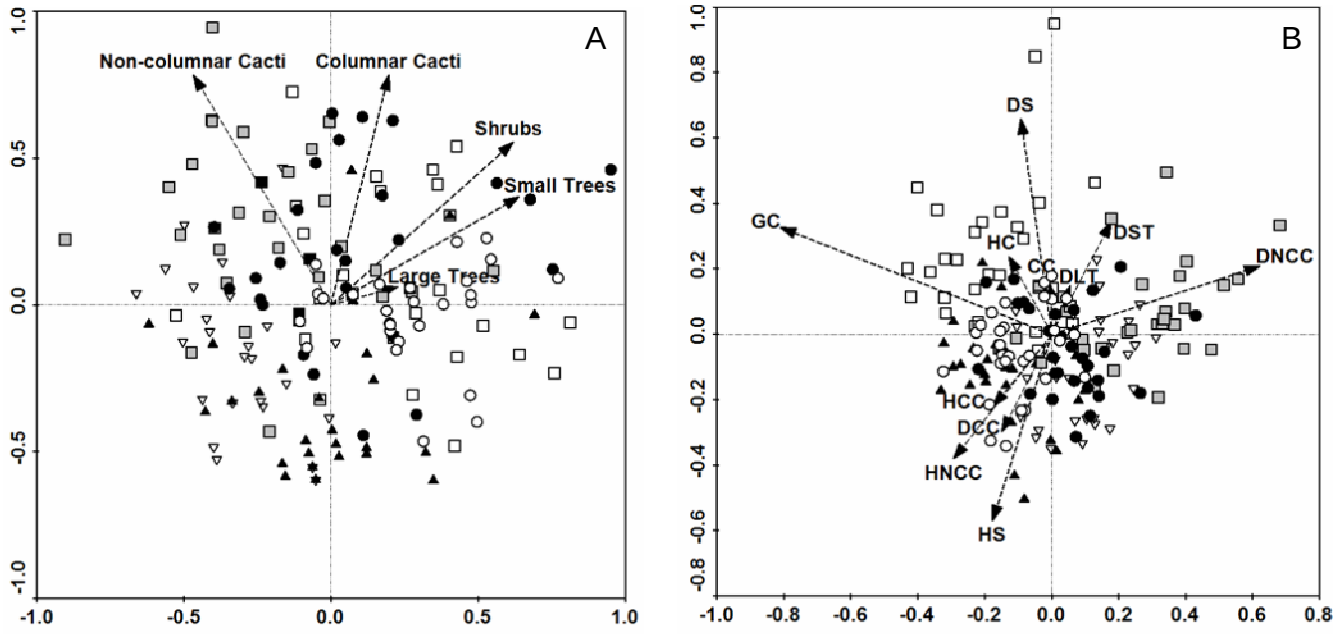


FIGURE 4. Bi-plot from a redundancy analysis of bird species and floristic variables. Floristic variables represent the mean number of species for each plant category indicated in the diagram. Only correlation for bird species with a fit range > 10% (N = 14) are shown. Dashed arrows indicate floristic variables; solid arrows indicate bird species.

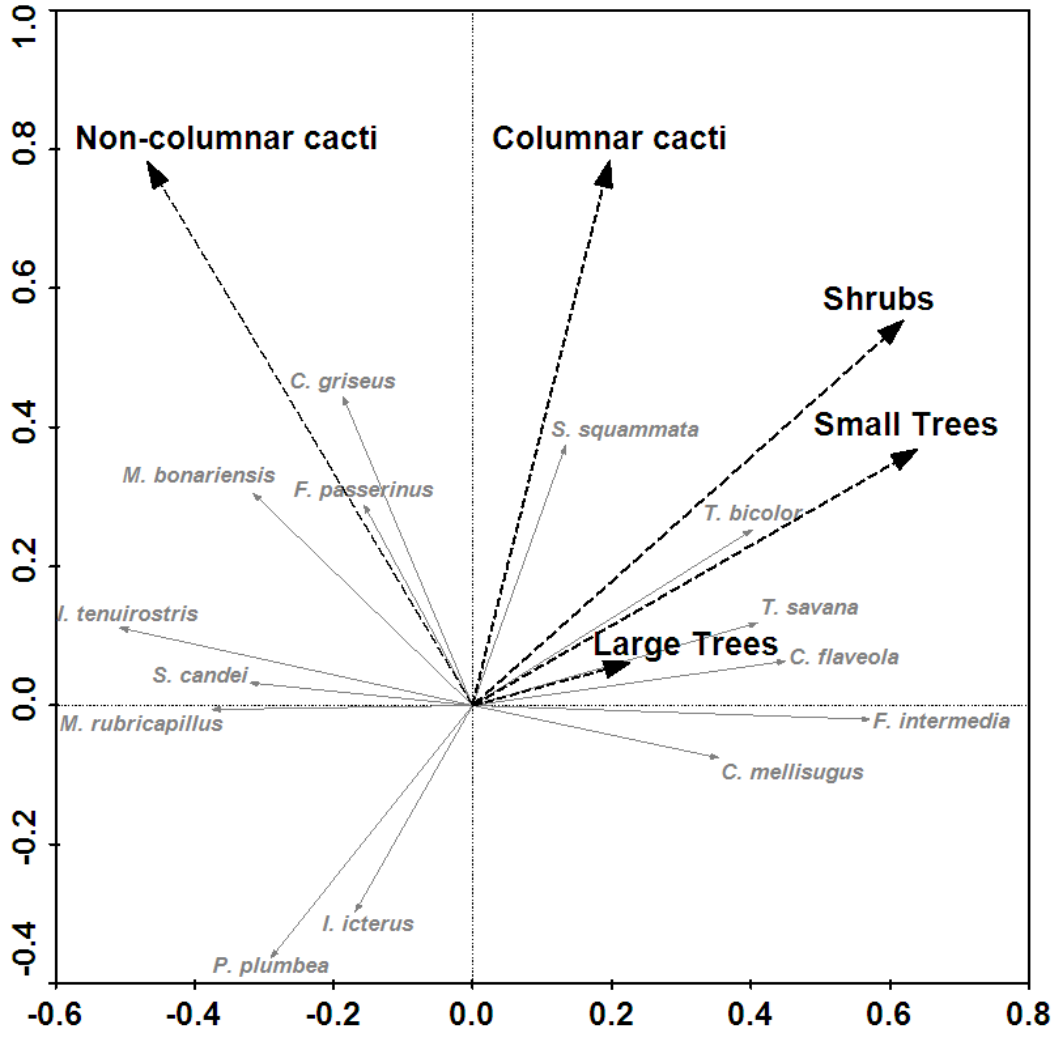


FIGURE 5. Bi-plot from a redundancy analysis of bird species and vegetation structural variables. Only correlation for bird species with a fit range > 10% ($N = 25$) are shown. Dashed arrows indicate floristic variables; solid arrows indicate bird species. Structural variables are: DST = mean density of small (dbh ≤ 10 cm) trees; DLT = mean density of large (dbh ≥ 10 cm) trees; DS = mean density of shrubs; DCC = mean density of columnar cacti; DNCC = mean density of non-columnar cacti; GC: percentage of ground cover; CC: percentage of canopy cover; HC = mean canopy height; HS = mean shrub height; HCC = mean height of columnar cacti; HNCC = mean height of non-columnar cacti.

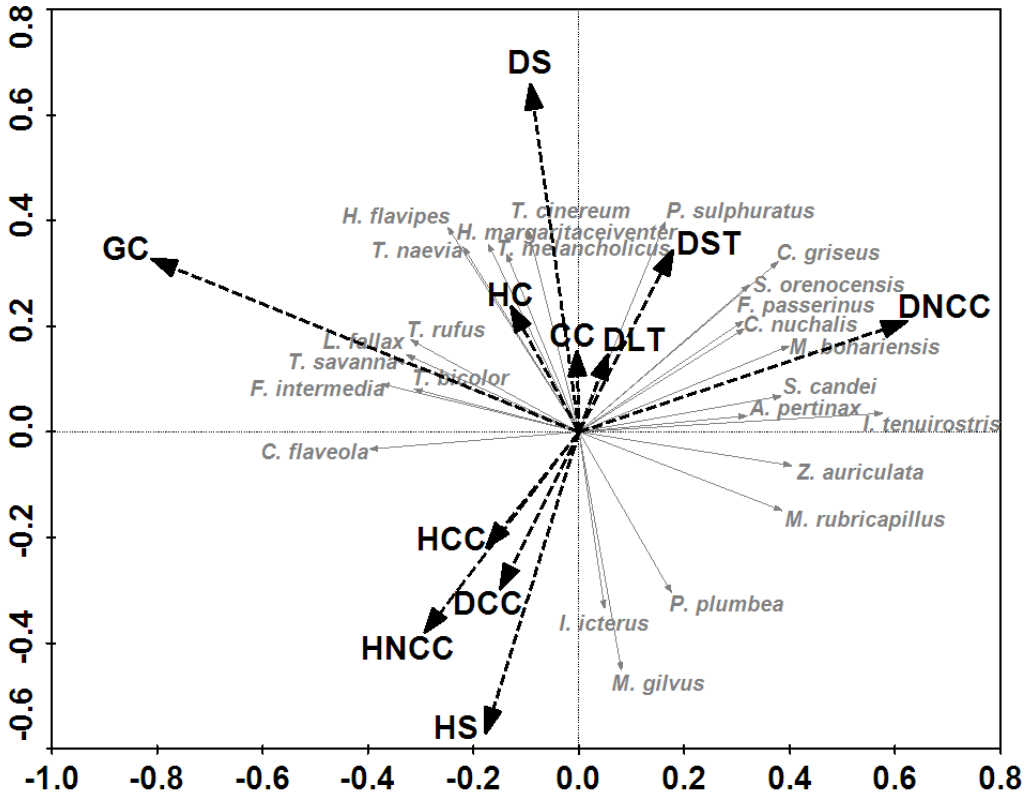


FIGURE 6. Bi-plot from a redundancy analysis of habitat-specialist birds and vegetation variables (both floristics and structural). Dashed arrows indicate variables; solid arrows indicate bird species. Floristic variables represent the mean number of species for each plant category indicated in the diagram. Structural variables are: DST = mean density of small (dbh ≤ 10 cm) trees; DLT = mean density of large (dbh ≥ 10 cm) trees; DS = mean density of shrubs; DCC = mean density of columnar cacti; DNCC = mean density of non-columnar cacti; GC: percentage of ground cover; CC: percentage of canopy cover; HC = mean canopy height; HS = mean shrub height; HCC = mean height of columnar cacti; HNCC = mean height of non-columnar cacti.

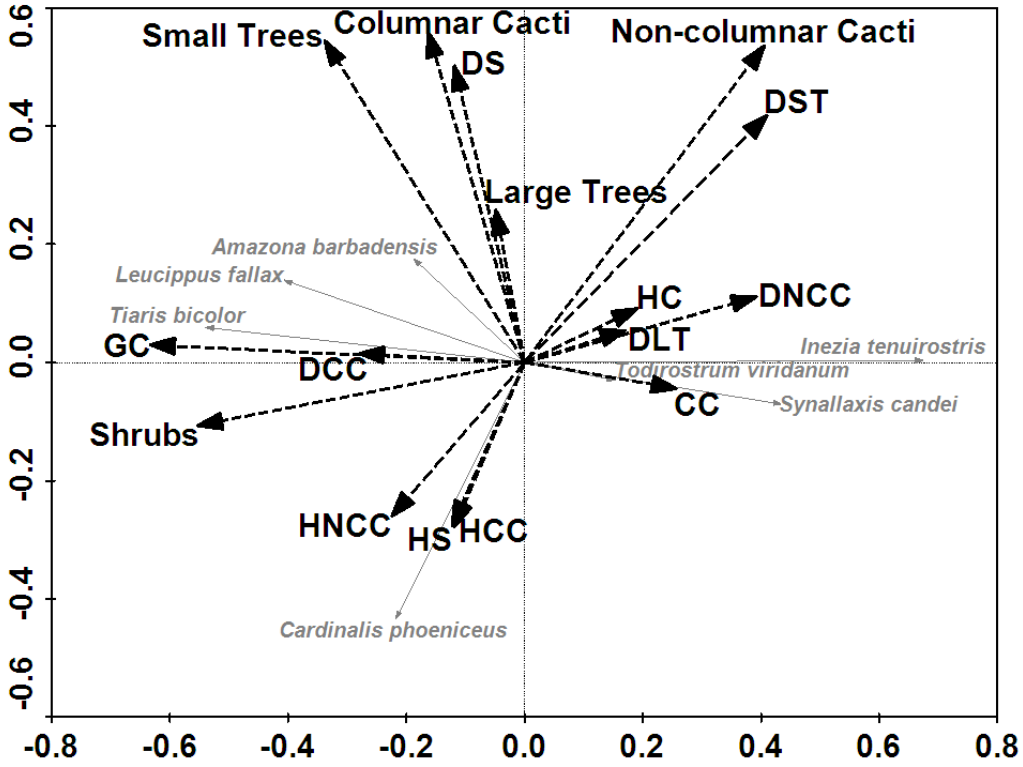
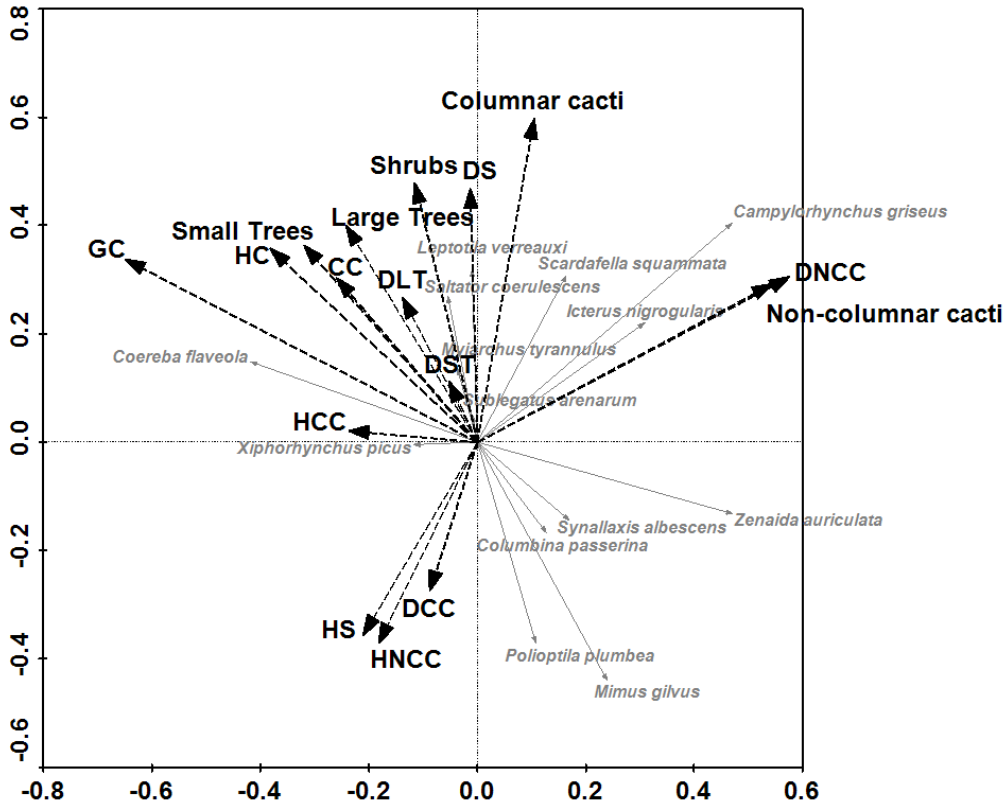


FIGURE 7. Bi-plot from a redundancy analysis of 16 common habitat-generalists birds and vegetation variables (both floristics and structural). Dashed arrows indicate variables; solid arrows indicate bird species. Floristic variables represent the mean number of species for each plant category indicated in the diagram. Structural variables are: DST = mean density of small (dbh ≤ 10 cm) trees; DLT = mean density of large (dbh ≥ 10 cm) trees; DS = mean density of shrubs; DCC = mean density of columnar cacti; DNCC = mean density of non-columnar cacti; GC: percentage of ground cover; CC: percentage of canopy cover; HC = mean canopy height; HS = mean shrub height; HCC = mean height of columnar cacti; HNCC = mean height of non-columnar cacti.



APPENDIX. Family, species, and floristic category of plants in Venezuelan arid zones.

FAMILY	SPECIES	CATEGORY
Agavaceae	*Agave cocui*	Shrub
	Agave sisalana	Shrub
Asclepiadaceae	*Calotropis procera*	Shrub (exotic)
	Stapelia gigantea	Shrub (exotic)
Boraginaceae	*Bourreria cumanensis*	Tree
Bromeliaceae	*Bromelia chrysantha*	Shrub
	Bromelia humilis	Shrub
Burseraceae	*Bursera karsteniana*	Tree
Cactaceae	*Acanthocereus tetragonus*	Non-columnar cactus
	Mammillaria sp.	Non-columnar cactus
	Melocactus sp.	Non-columnar cactus
	Opuntia caribaea	Non-columnar cactus
	Opuntia elatior	Non-columnar cactus
	Opuntia wentiana	Non-columnar cactus
	Pereskia guamacho	Tree
	Pilosocereus lanuginosus	Columnar cactus
	Stenocereus griseus	Columnar cactus
	Cereus repandus	Columnar cactus
Capparidaceae	*Capparis hastata*	Tree
	Capparis pachaca	Tree
	Capparis odoratissima	Tree
Convolvulaceae	*Ipomoea* sp.	Shrub
Euphorbiaceae	*Cnidoscolus urens*	Shrub
	Croton sp.	Shrub
	Jathropha gossypiifolia	Shrub
	Jathropha sp.	Tree
Fabaceae-Mimosoideae	*Acacia flexuosa*	Tree
	Pithecellobium ungis-cati	Tree
	Prosopis juliflora	Tree

APPENDIX. Continued.

FAMILY	SPECIES	CATEGORY
Fabaceae-Caesalpinioideae	*Caesalpinia coriaria*	Tree
	Caesalpinia granadillo	Tree
	Cassia sp.	Tree
	Cercidium praecox	Tree
Fabaceae-Papilionoideae	*Platymiscium diadelphum*	Tree
Fabaceae-Unknown	Unidentified 1	Tree
	Unidentified 2	Tree
	Unidentified 3	Tree
	Unidentified 4	Tree
	Unidentified 5	Tree
	Unidentified 6	Tree
Liliaceae	*Aloe vera*	Shrub
Malpighiaceae	*Malpighia emarginata*	Tree
Malvaceae	*Gossypium* sp.	Shrub
Sapotaceae	*Bumelia* sp.	Tree
Simaroubaceae	*Castela erecta*	Shrub
Solanaceae	*Lycium nodosum*	Shrub
Sterculiaceae	*Melochia tomentosa*	Shrub
Theophrastaceae	*Jacquinia aristata*	Tree
	Jacquinia revoluta	Tree
Verbenaceae	*Lantana camara*	Shrub
	Lippia micromera	Shrub
	Lippia origanoides	Shrub
Zygophyllaceae	*Bulnesia arborea*	Tree
	Guaiacum officinale	Tree
Unknown	Unidentified 8	Tree
	Unidentified 19	Shrub

CHAPTER III

COMPARATIVE PHYLOGEOGRAPHY OF THREE BIRD SPECIES RESTRICTED TO ARID ZONES OF NORTHERN SOUTH AMERICA

INTRODUCTION

Comparative phylogeography, "the geographical comparison of evolutionary subdivision across co-distributed species" (Arbogast and Kenagy 2001), is a relatively new approach to the study of community composition that allows determination of the long-term stability of a current species assemblage (Zink et al. 2001). Patterns of phylogeographic congruence imply that taxa under study have had a geographic association across time and have shared a common history. Thus, if common patterns of geographic subdivision are observed, the assumption is that those patterns have emerged as a result of the same historical or geological events (i.e., vicariance) (Arbogast and Kenagy 2001).

Comparative phylogeography is also relevant to conservation. Congruent phylogeographic patterns may provide evidence that particular areas are geographic centers of genetic diversity (Avise 1992) and, when combined with ecological data (i.e., endemism, species richness), can be used to identify areas that must be targeted by conservation efforts (Moritz and Faith 1998, Crandall et al. 2000). Such efforts are needed to preserve the genetic integrity of regional faunas. Additionally, information derived from phylogeographic analyses may yield guidelines useful to managers

interested in translocations or reintroductions of individuals from one population into another (Avise 1992).

Arid zones of northernmost South America are of special biogeographic interest because xeric conditions have existed since at least the last glacial maximum (13,000-18,000 BP) (Ochsenius 1983) and because these zones currently represent remnants of a much broader expanse of arid lands that was covered by xerophytic vegetation during past glacial times (Nassar et al. 2002). Additionally, these aridlands of northern South America harbor several restricted-range and habitat-specialist bird species (Stotz et al. 1996, Stattersfield et al. 1998, Hilty 2003), and because of that have been designated as an Endemic Bird Area (Stattersfield et al. 1998).

Recent studies in Venezuelan arid zones have described genetic variation of different taxa, such as bats and cacti. Results show interesting patterns of genetic structure that are explained by differences in dispersal strategies and the extent of gene flow between populations of the study species (for cacti see Nassar et al. 2001, 2002, 2003; for bats see Newton et al. 2003). Here, I present the results of a study centered on three bird species, which are specialists of arid scrublands and are restricted to these same areas. Results of this study complement the findings from other taxa, and provide a better understanding of the evolution of arid zone biotas in northern South America. The target species are the Yellow-shouldered Parrot (*Amazona barbadensis*), the Buffy Hummingbird (*Leucippus fallax*), and the Vermilion Cardinal (*Cardinalis phoeniceus*). Selection of species for studies of comparative phylogeography is of extreme importance because the generality and strength of the results will be greater if the group of species is more diverse in terms of taxonomy and ecology (Zink 1996). I chose these three target

species because they are co-distributed across arid zones in northern South America and because they belong to distantly related families of birds and show differences in population sizes and dispersal abilities. For example, the Yellow-shouldered Parrot is a threatened species that became rare in some of the areas during the last decades (Rodríguez and Rojas-Suárez 1995), whereas the Buffy Hummingbird is the most common of the habitat specialists restricted to these arid zones (see Chapter 1).

The general objective of this study was to examine patterns of genetic diversity of three co-distributed habitat specialists across their entire distributional range. I used mtDNA sequence data to i) investigate patterns of genetic diversity within and among populations of three bird species, ii) determine if a correlation exists between the genetic distance and the geographic distance among populations, and iii) examine if genealogical congruence exists among the three co-distributed species. I expected that if the three target species shared a common history and if the same isolating barriers separated their populations, then geographically congruent patterns should be recognized (Zink 2002). Congruent phylogeographic patterns would suggest that the presence of these species in the same bird assemblages has been stable across time. Incongruent patterns are evidence of species' differences in response to barriers or selective gradients, levels of gene flow, effective population size, or lack of long-term sympatry in the ancestral species assemblage (Zink 1997, Crisci et al. 2003). Finally, I discuss how the phylogeographic patterns found in the present study may be used to help set priorities for conservation of birds restricted to arid zones of northern South America.

METHODS

Sample collection and storage. Samples of the three target species (Yellow-shouldered Parrot, Buffy Hummingbird, and Vermilion Cardinal) were collected during various trips between September 2004 and June 2007 to aridlands in northern Venezuela and some Caribbean islands, throughout the distributional range of each species (Fig. 1, Table 1). Hummingbirds and cardinals were captured using mist nets, whereas samples from parrots were collected from chicks taken manually from nests or from captive adults with known localities of origin. I collected blood, tissues, or/and feathers from individuals of the three species; additional samples (toepads) of parrots and cardinals were obtained from museum collections (Table 1, Appendix). Blood was collected from parrots and cardinals using heparinized microcapillary tubes following venipuncture of the brachial vein with a sterile syringe needle (Gaunt and Oring 1997) and stored in lysis buffer. Small portions of pectoral muscle were taken from hummingbirds, and from a few parrots and cardinals that were found dead, and preserved in 100% ethanol. Two symmetrical tail feathers were plucked from individuals of the three species (Smith et al. 2003) and preserved in 100% ethanol.

DNA extraction, amplification, and sequencing. DNA extractions from blood samples were performed using standard phenol-chloroform procedures followed by ethanol precipitation (Sambrook and Russell 2001). DNA extractions from muscle tissues, feathers, and toepads were performed using the DNeasy Tissue Kit (Qiagen, Valencia, California) following the manufacturer's protocol. For feather samples, I added 30 µl of 10% (100 mg/ml) 1,4-Dithiothreitol (DTT; US Biological, Swampscott, Massachusetts) solution to the digestion buffer before adding the proteinase K.

Three mitochondrial genes were amplified using polymerase chain reaction (PCR): the complete ATP-synthase 8 and ATP-synthase 6 (ATPase8 and ATPase6; 842 bp) regions; the entire subunit 2 of the NADH dehydrogenase (ND2; 1041 bp), and part of the 12S rRNA (12S; 436 bp). I amplified the ND2 gene using combinations of primers L5216, H5766, L5758, and H6313 (Table 2; Sorenson et al. 1999). Whenever possible, the whole gene (1041 bp) was amplified as a single fragment to reduce the likelihood of amplifying nuclear pseudogenes, but this was not always feasible due to degradation of some of the samples. For the ATP8 and ATP6 genes, amplification reactions employed the external primers CO2GQL and CO3HMH, and the internal primer A8PWL (Table 2; Bermingham 2003). The 12S gene was amplified using the primer pair developed by T. Burke (Table 2; Miyaki et al. 1998). PCR amplifications typically consisted of an initial denaturation at 94°C for 2 min, followed by 35 cycles of 94°C denaturation for 45 s, 52°C annealing for 30 s and 72°C extension for 60 s. Samples were then extended at 72°C for 10 min. Each reaction contained 2.0 µl of 10 pM solution of each primer, 5.0 µl of 10X reaction buffer with 20 mM magnesium chloride, 4.0 µl dNTP mix (0.2 mM for each nucleotide), 0.25 µl of Takara® Ex Taq polymerase (Takara Bio, Madison, Wisconsin), and 1-2 µl of DNA template in a total volume of 50 µl. All PCR amplifications were conducted in a MJ Research PTC-200 Thermal Cycler (Bio-Rad, Hercules, California). Amplification products were confirmed visually on agarose gels stained with Ethidium Bromide and were cleaned using the QIAquick PCR Purification Kit (Qiagen, Valencia, California) following manufacturer's protocol or treated with 2 µl ExoSAP-IT® (USB Corporation, Cleveland, Ohio) at 37°C for 27 min and at 80°C for an additional 15 min. Sequencing reactions were conducted using the amplification primers

via dye-terminator cycle sequencing. Sequences were then obtained in an ABI Prism 3100 Genetic Analyzer (Applied Biosystems, Foster City, California).

Analyses. Sequence assembling and editing were conducted using GENEIOUS PRO 3.5.6. (Biomatters Ltd., Auckland, New Zealand), and multiple alignments were done using CLUSTALW2 (Larkin et al. 2007), and posteriorly verified and edited by eye using JALVIEW (Clamp et al. 2004). Data from the three mtDNA regions were combined for subsequent analyses. I used ARLEQUIN 3.11 (Excoffier et al. 2005) to calculate average number of pairwise differences (k), haplotype (h) and nucleotide (π) diversity of the three target species. Haplotype diversity is the probability that two randomly chosen haplotypes in a sample are different, whereas nucleotide diversity is a measure of pairwise nucleotide differences per site among haplotypes in a sample (Nei 1987).

To investigate geographic genetic structure, unrooted haplotype networks with 95% parsimoniously plausible connections were constructed for each species using statistical parsimony run in the program TCS v1.21 (Clement et al. 2000). Loops due to homoplastic ambiguities in the networks were resolved following the criteria suggested by Crandall and Templeton (1993). ARLEQUIN 3.11 was also used to measure the amount of variance distributed among populations (F_{ST}) and to conduct an Analysis of Molecular Variance (AMOVA, Excoffier et al. 1992). The AMOVA is a testing procedure based on permutational analysis, which allowed me to examine the overall genetic structure of populations of each of the species being studied. By using an AMOVA, information on DNA haplotype divergence can be incorporated into an analysis of variance format, derived from a matrix of squared-distances among all pairs of haplotypes. This analysis produces estimates that reflect the correlation of haplotypic

diversity at different levels of hierarchical subdivision: among individuals within a population, among populations, and among groups of populations (east vs. west, island vs. mainland) (Excoffier et al. 1992).

The demographic history of each species was examined by constructing mismatch distributions. A mismatch distribution reflects the frequency distribution of pairwise genetic differences among individual haplotypes and its shape is an indicator of population expansion (Rogers and Harpending 1992, Rogers 1995). Unimodal distributions suggest rapid population expansion, whereas more ragged distributions suggest that the size of the population has changed little over time. I used ARLEQUIN 3.11 (Excoffier et al. 2005) to obtain the observed and expected values of the mismatch distribution, to calculate the raggedness index (*r*, Harpending 1994), which measures the smoothness of observed mismatch distributions and has larger values for more stable populations, and to estimate the sum of squared deviations (SSD), which test the fit of the observed data to the expected population growth model.

For each of the target species, sequence data were used to establish phylogenetic relationships among mtDNA haplotypes using the maximum likelihood criterion (ML) for tree selection in PAUP v4.0b10 (Swofford 2002). Closely related species of the same genus or family were used as outgroups. The Blue-fronted Parrot (*Amazona aestiva*) and the Yellow-headed Parrot (*Amazona ochrocephala*) were outgroups for the Yellow-shouldered Parrot; the Speckled Hummingbird (*Adelomyia melanogenys*) and the Collared Inca (*Coeligena torquata*) were used as outgroups for the Buffy Hummingbird; and the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) was the outgroup for the Vermilion Cardinal. Support for these analyses was assessed using 100 bootstrap

replications. To select the model of nucleotide substitution that best fitted the data, I used a hierarchical likelihood ratio test as implemented in MODELTEST 3.6.6 (Posada and Crandall 1998). The model selected was the General Time Reversible + Gamma rate correction (GTR + Γ). Estimated values of Ti:Tv ratio and gamma-distribution shape parameter (α) were 1.0081 and 0.2081, respectively, for the Yellow-shouldered Parrot, 1.0433 and 0.0400 for the Buffy Hummingbird, and 1.7202 and 0.0400 for the Vermilion Cardinal.

I used a Mantel test (Mantel 1967) to examine whether genetic distance (F_{ST}) and geographical distance (measured as the most plausible colonization route between each population pair) were correlated between all pairs of sampling areas for each target species. This test measures the association between elements in two matrices (i.e., a genetic distances matrix and a geographical distances matrix), and then assesses the significance of this association by comparing the correlation coefficient (R_0) calculated for the original matrices to a large number of correlation coefficients calculated after permutation of rows and columns in one of the matrices. Significance was estimated by the number of permutated coefficients that exceeded the value of the original R_0. The Mantel test was run in ARLEQUIN 3.11.

RESULTS

Genetic variation. The Buffy Hummingbird showed the highest degree of sequence variation of the three species, with 3.4% of variable sites. The Yellow-shouldered Parrot and the Vermilion Cardinal had similar levels of sequence variation, with 0.8% and 1.3% of variable sites, respectively. These variable sites defined 54 haplotypes in the Yellow-

shouldered Parrot, 88 in the Buffy Hummingbird, and 66 in the Vermilion Cardinal. Haplotype diversity (*h*) was above 75% for all populations of the Vermilion Cardinal and above 90% for all populations of the Buffy Hummingbird (Table 3). For the Yellow-shouldered Parrot, however, haplotype diversity was above 90% in most of the populations but one (MP), where haplotype diversity was 60% (Table 3). Nucleotide diversity (π) varied within and among species (Table 3), with the Buffy Hummingbird having the highest levels of nucleotide diversity.

Geographic structure. All three species showed some differentiation among populations as indicated by significant pairwise values of F_{ST} (Table 4). No significant correlations were detected between pairwise F_{ST} and geographic distance in the Yellow-shouldered Parrot (R_0 = 0.108, P = 0.279) or in the Vermilion Cardinal (R_0 = -0.059, P = 0.752). Conversely, the correlation was significant in the Buffy Hummingbird (R_0 = 0.548, P = 0.024).

Overall geographic structure among populations was supported by AMOVA´s for the Yellow-shouldered Parrot. For this species, most of the molecular variation (60%) was represented by genetic diversity among populations, both in the analyses without groups and in the analyses in which populations were categorized into groups (Table 5A). In the latter analyses, it was evident that geographic structure was not explained by variation between either western and eastern populations or between populations located on islands vs. populations on the mainland. In the AMOVA's for the Buffy Hummingbird and the Vermilion Cardinal, some geographic structure was indicated with 27% and 26%, respectively, of the molecular variation partitioned among populations (Tables 5B, 5C). In the analyses in which populations were classified into groups, most of the variance

(65% for the Buffy Hummingbird and 67% for the Vermilion Cardinal) was explained by variation among individuals within populations, and there was no support for the distinction of groups of populations located in western and eastern Venezuela.

In the unrooted haplotype networks of the three species, some geographic structure among populations was also evident as indicated by the clustering of haplotypes from different populations (Figs. 2, 3, 4). In all three species, most haplotypes were often restricted to a single population and only a few haplotypes were shared among populations. In the case of the Buffy Hummingbird (Fig. 3) and the Vermilion Cardinal (Fig. 4), haplotypes were shared only between neighboring localities, whereas haplotypes of the Yellow-shouldered Parrot were shared among populations located in the east (AP, MP) and in the west (FL, BO) (Fig. 2). The haplotype network of the Buffy Hummingbird indicates a separation between haplotypes of western and eastern populations. Two haplotypes, however, from western populations (LL and PP) were more closely related to haplotypes of the eastern populations and one haplotype from an eastern population (MP) was more related to a haplotype belonging to a western population (PP).

Historical demography. The mismatch distributions of the populations of the Yellow-shouldered Parrot supported a recent demographic expansion in these species on BO (Fig. 5). The mismatch distributions of all populations of the Buffy Hummingbird (Fig. 6) were ragged, indicating that the size of all of them has been stable across time. Finally, in the case of the Vermilion Cardinal, the unimodal shape of the mismatch distributions of three populations (AP, CP, and FL) was an indication of demographic expansions (Fig. 7). The other three populations of the Vermilion Cardinal (MP, LL, and PP) showed

ragged mismatch distributions (Fig. 7) were indicative of stable population size over time. Although the value of raggedness index (*r*) was low for all populations of each of the species, an indication of demographic expansion, none of them were significant (Table 6).

Intraspecific phylogenetics. Heuristic maximum likelihood tree searches found the most likely trees for each of the three species (Figs. 8, 9, 10). The monophyly of each of the species with respect to outgroups was highly supported in each of the haplotype trees. Separation of clades in the phylogenetic trees resembled the patterns of haplotype networks and reciprocally monophyletic groups did not correspond to unique populations or regions (e.g., western vs. eastern, island vs. mainlands). Haplotype trees for both the Buffy Hummingbird and the Vermilion Cardinal illustrate that most haplotypes from the western populations (PP, FL, LL) form a clade. In both species, however, there was no clear geographic structuring within this clade, as haplotypes of the same population are distributed throughout the clade. Haplotypes of the eastern populations were polyphyletic in both species. Most haplotypes of the Yellow-shouldered Parrot are part of a large clade, and within this large clade some population structure can be identified.

DISCUSSION

Genetic diversity and geographic structure. Levels of genetic diversity in the three target species are comparable to those found in other bird species in the Neotropics (e.g., Bates et al. 2003, González et al. 2003). Geographic patterns of genetic diversity varied among the three species; areas with higher and lower values were not the same for the three birds. Haplotype and nucleotide diversity for the Yellow-shouldered Parrot were lower on

Margarita Island (MP) than in populations on the adjacent mainland (AP) and other islands (BO and LB). This geographic pattern of diversity, however, was not observed in the other two species. Genetic diversity of the Buffy Hummingbird was similar among all populations. In contrast, nucleotide diversity of the Vermilion Cardinal was lower in the two mainland populations (CP, AP) in eastern Venezuela than in all other populations, including the Margarita Island population, which is also located in the eastern part of the country. Larger and more continuous habitats are thought to facilitate maintenance of high levels of genetic diversity (Frankham et al. 2004). Thus, one might expect that lands in northwestern Venezuela, the most extensive arid zone in the country (Sarmiento 1976), an area that has remained dry for at least 14,000 years (Ochsenius 1983), would harbor higher levels of genetic diversity in organisms adapted to this habitat. Recent studies of genetic diversity of cacti (*Melocactus curvispinus*, *Pereskia guamacho*, *Stenocereus griseus*, *Cereus repandus*, *Pilosocereus lanuginosus*) conducted in the same aridlands as the present study, did in fact, indicate an area of high genetic diversity in northwestern Venezuela, corresponding to LL and FL (Nassar et al. 2002, 2003). The only species in the present study, however, with high nucleotide diversity in two of the three western populations (LL and PP) was the Buffy Hummingbird, but that value was similar to the nucleotide diversity in an eastern population (MP). The highest levels of nucleotide diversity of the parrot and the cardinal, however, were found in eastern populations, contrary to expectations given that aridlands in this part of the country are relatively narrow and more subdivided than in the western part. However, it has been proposed that during the last Glacial Maximum (18,000 years BP), the climate in Venezuela was drier than at present (Shubert 1988). Thus, aridlands in the eastern region, likely were more

extensive and may have allowed the maintenance of larger, and more genetically diverse, populations (Nassar et al. 2001).

Haplotype networks, F_{ST} values, and results of AMOVA´s all indicated geographic structure in the three target species. Geographic structure was expected in these species because these birds are specialists of aridlands which, in northern South America, form a disjunct habitat; intervening habitats are known to be able to isolate taxa among deserts or aridlands (Zink 1997). Evidence of genetic structure among populations in arid habitats had been detected in several bird species in North American deserts (Zink et al. 2001, Zink 2002, Scariglia and Burns 2003), as well as in cacti (Nassar et al. 2001) and bats (Newton et al. 2003) in aridlands of northern Venezuela. The extent of geographic structure, however, varied among the three target birds and did not show congruent patterns, indicating that diverse factors influenced geographic patterns of genetic diversity. All the analyses suggested some large-scale geographical structure in the Yellow-shouldered Parrot and, to a lesser degree in the hummingbird and the cardinal. These differences may be a result of differences in levels of gene flow, effective population sizes and/or levels of philopatry and dispersal capabilities of the target species. Gene flow decreases genetic distinctiveness between populations and increases genetic variability within a local population (Templeton 2006). Thus, the high levels of within-population genetic variation and lack of differentiation between populations found in both the Buffy Hummingbird and the Vermilion Cardinal indicate some gene flow among populations of these species. In the case of the Buffy Hummingbird, the extent of such gene flow seems to be limited by geographic distance among populations (isolation by distance). Differences in the level of philopatry were also evident among the target

species, and these differences may help explain the observed patterns of geographic structure. Available information suggests that the Yellow-shouldered Parrot is characterized by high philopatry (maximum home range about 20 km^2; Sanz and Grajal 1998), whereas high dispersal capabilities (even migratory behavior) have been suggested for the Buffy Hummingbird (McNeil and Rodriguez 1985). Even during the Pleistocene, when the climate in northern Venezuela was drier than at present (Shubert 1988, Rull 1996) and aridlands had a broader distribution throughout the region, behavioral constraints (i.e., philopatry) may have limited gene flow among populations of the parrot.

Genetic structuring among populations, however, was not absolute. In all three species, haplotypes of individuals in eastern populations were closely related to haplotypes of individuals in western populations (and vice versa), which indicates some level of gene flow between these two regions or insufficient time for lineage sorting. In all three species, however, a congruent pattern involved shared haplotypes between two adjacent areas (AP, MP), indicating a history of recent contact between populations of Margarita Island and Araya Peninsula. There is evidence that changes in sea level connected the island and mainland repeatedly during the late Pleistocene (Ochsenius 1983), but the estimates of time periods when the sea receded and connected the island with the mainland are not clear.

Historical demography. Mismatch distributions indicated that some populations of the Yellow-shouldered Parrot and the Vermilion Cardinal have experienced demographic expansions in recent times within the aridlands of northern South America, whereas the size of populations of the Buffy Hummingbird apparently has changed little. The discrepancy between the mismatch distribution and the raggedness index, observed in the

Yellow-shouldered Parrot, has been reported in other bird species (e.g., *Piranga rubra*, Shepherd and Burns 2007) as well, such discrepancies can be attributable to different factors and imply that the data do not correspond with the specific expectations of either the demographic expansion or the stable-equilibrium models. Additionally, it has been demonstrated that the raggedness index usually performs poorly to detect demographic expansions, because it is a very conservative test with low power to reject the null hypothesis (constant population size) when the alternative hypothesis (demographic expansion) is true (Ramos-Osins and Rozas 2002).

Nucleotide diversity values have also been used to infer the direction of the demographic expansion (Merila et al. 1997, Zink 2002). When nucleotide diversity in one population is particularly low in comparison with other populations, this could be an indication that populations are expanding into that area. Using nucleotide diversity to infer the direction of the population expansion in the three target species of this study also highlighted different patterns among species. Based on nucleotide diversity values, it seems that the Yellow-shouldered Parrot had recently expanded from mainland populations into the islands of Margarita and Bonaire, whereas the Vermilion Cardinal showed an opposite pattern of expansion, from Margarita Island to adjacent mainland areas in eastern Venezuela, which matched the results of the mismatch distributions. The population of the Buffy Hummingbird apparently expanded into the Araya Peninsula on the eastern coast of Venezuela.

Phylogeographic congruence. Even though the three target species are currently co-distributed and restricted to the same aridlands, different analyses evidenced a lack of congruence in phylogeographic patterns. Unrooted haplotype networks and intraspecific

maximum likelihood trees of the three species showed incongruent topologies, an indication that the current distribution of these species is the result of species-specific histories. Additionally, analyses of demographic history of the target species indicated that all three species have experienced recent population expansions but in different directions. Thus, the ancestors of the study species were probably geographically restricted and were not part of the same species assemblage (see Zink et al. 2001).

Intraspecific phylogenetics. There are no recognized subspecies in the Vermilion Cardinal, and both the haplotype network and the maximum likelihood tree of this species indicated no clear discrete evolutionary entities. A previous mtDNA study conducted with a small number of samples from the Yellow-shouldered Parrot failed to support the subspecies *barbadensis* (mainland populations) and *rothschildi* (island populations) (Amato 1995). Both the phylogeny and the AMOVA conducted in this study indicated that there is no genetic separation among mainland and island populations. In the Buffy Hummingbird, three subspecies have been recognized: *fallax* (north-central region of Venezuela including Lara in the western part of the country), *cervina* (northeastern Colombia and northwestern Venezuela), and *richmondi* (northeastern Venezuela) (Hilty 2003). Haplotypes belonging to the *richmondi* subspecies formed a clade but individuals belonging to the neighboring subspecies *fallax* and *cervina* appeared together both in the haplotype network and in the phylogenetic tree. Further revision of the validity of these two subspecies seems necessary, because the designation of subspecies that do not represent independent entities may misdirect conservation efforts (see Zink 2004).

Conservation implications. Population-level results indicated different patterns of geographic genetic structuring among populations of the three target species. In the Yellow-shouldered Parrot, the remaining largest populations that were well sampled (AP, MP, FL, and BO) showed differentiation with respect to haplotype frequency and sequence divergence. The degree of geographic structure observed across the current distributional range of this species suggests that individual populations may be demographically isolated. As this species has experienced population declines across its distributional range in the last century, with some populations (i.e., Aruba, Netherland Antilles) having been extirpated (Juniper and Parr 1998, Hilty 2003), the information derived from this study is particularly relevant for the conservation and management plans of the species. Data presented here can be used as a basis for a preliminary designation of management units (*sensu* Moritz 1994) for the Yellow-shouldered Parrot; however, the incorporation of information derived from further analyses of other molecular markers will provide more support to identify populations of this parrot as evolutionarily-significant units for conservation. Meanwhile, the data compiled in this study may be used as baseline information to guide management efforts focused on this species. Any initiative to manage the species should strive to maintain genetic diversity of each population.

In the case of the Buffy Hummingbird and the Vermilion Cardinal, most of the total genetic variation was found within populations. Thus, from a conservation perspective, it is not possible to assign conservation priorities to any specific population. As the main objective in conservation genetics is to preserve the genetic identity of a species, based on the results of this study, the preservation of all the populations of the

Buffy Hummingbird and the Vermilion Cardinal is not required, because the risk of negatively affecting the species' gene pools by local population extinctions should be relatively low (Nassar et al. 2003).

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Table 1. Sampling location (Fig. 1), and sample size for the three species used in the analyses. (*) includes museum samples.

Sampling location	Yellow-shouldered Parrot	Buffy Hummingbird	Vermilion Cardinal
FL: surroundings of Coro city, Falcón State, Venezuela	14	13	15
PP: Paraguaná peninsula, Falcón State, Venezuela	1	17	14
LL: Lara lowlands, Lara State, Venezuela	2*	19	11
CP: Anzoátegui State, Venezuela	2*	15	8
AP: Araya peninsula, Sucre State, Venezuela	15	19	11
MP: Margarita Island, Venezuela	22	22	32
LB: La Blanquilla Island, Venezuela	1*	--	--
BO: Bonaire, Netherland Antilles	20	--	--
TOTAL	**77**	**106**	**91**

Table 2. Primers used in this study.

Primer	Gene	Sequence	Reference
L5216	ND2	5'-GGCCCATACCCCGRAATTG-3'	Sorenson et al. 1999
H5766	ND2	5'-RGAKGAGAARGCYAGGATYTT KCG-3'	Sorenson et al. 1999
L5758	ND2	5'-GGNGGNTGAATRGGNYTNAAYCARAC-3'	Sorenson et al. 1999
H6313	ND2	5'-ACTCTTRTTTAAGGCTTTGAAGGC-3'	Sorenson et al. 1999
CO2GQL	ATP8/6	5'-GGACAATGCTCAGAAATCT GCGG-3'	Bermingham 2003
CO3HMH	ATP8/6	5'-CATGGGCTGGGGTC RACTATGTG-3'	Bermingham 2003
A8PWL	ATP8/6	5'-CCTGAACCTGACCATGAAC-3'	Bermingham 2003
12S L	12S rRNA	5'-GGATTAGATACCCCACTATGC-3'	Miyaki et al. 1998
12S H	12S rRNA	5'-AGGGTGACGGGCGGTATGTACG-3'	Miyaki et al. 1998

Table 3. Variation in number of haplotypes for each population of the three target species, and estimates of haplotype diversity (*h*), per site nucleotide diversity (π), and average pairwise number of nucleotide differences (*k*).

Species Population	***n***	**Number of haplotypes**	***h***	**π**	***k***
Yellow-shouldered Parrot					
AP	15	13	0.9810	0.0025	5.50
LB	1	1	1.0000	0.0000	0.00
MP	22	8	0.6017	0.0014	3.18
CP	2	2	1.0000	0.0089	8.00
LL	2	2	1.0000	0.0044	4.00
FL	14	13	0.9890	0.0053	12.35
PP	1	1	1.0000	0.0000	0.00
BO	20	18	0.9842	0.0022	5.15
TOTAL	77	54	0.9498	0.0063	13.90
Buffy Hummingbird					
AP	19	13	0.9240	0.0035	7.87
MP	23	17	0.9368	0.0079	17.13
CP	15	13	0.9714	0.0059	13.17
LL	19	18	0.9942	0.0080	14.26
FL	13	13	1.0000	0.0047	9.95
PP	17	16	0.9926	0.0078	14.79
TOTAL	106	88	0.9881	0.0085	18.45
Vermilion Cardinal					
AP	11	8	0.8909	0.0008	1.09
MP	32	21	0.9456	0.0054	12.39
CP	8	5	0.7857	0.0004	1.00
LL	11	7	0.8182	0.0010	2.29
FL	15	13	0.9714	0.0016	3.60
PP	14	14	1.0000	0.0030	6.90
TOTAL	91	66	0.9851	0.0039	8.91

Table 4. Pairwise F_{ST} values between populations of the three target species. Values given in bold are significant after Bonferroni correction.

A) Yellow-shouldered Parrot

Population	AP	CP	LB	MP	LL	FL	BO	PP
AP	0.0000							
CP	0.1321	0.0000						
LB	-0.4784	-0.7778	0.0000					
MP	**0.1198**	0.3968	-0.2711	0.0000				
LL	0.3512	0.1111	0.1111	0.6541	0.0000			
FL	**0.2463**	-0.1291	-2.5712	**0.2797**	0.2057	0.0000		
BO	**0.1955**	0.2401	-1.1220	**0.1641**	**0.5230**	**0.3056**	0.0000	
PP	0.9658	0.9637	1.0000	0.9886	0.9819	0.9526	0.9812	0.0000

B) Buffy Hummingbird

Population	AP	CP	MP	LL	FL	PP
AP	0.0000					
CP	0.0528	0.0000				
MP	0.0010	**0.0409**	0.0000			
LL	**0.0409**	0.0170	**0.0349**	0.0000		
FL	0.0392	0.0145	0.0330	0.0030	0.0000	
PP	0.0420	0.0179	0.0359	0.0066	0.0038	0.0000

C) Vermilion Cardinal

Population	AP	CP	MP	LL	FL	PP
AP	0.0000					
CP	0.1586	0.0000				
MP	**0.0687**	**0.1047**	0.0000			
LL	0.1455	0.1970	**0.1110**	0.0000		
FL	**0.0674**	**0.1129**	**0.0422**	0.1022	0.0000	
PP	0.0531	0.0985	**0.0286**	**0.0882**	0.0144	0.0000

Table 5. Results of the Analysis of Molecular Variance of the three target species. Populations were divided into two groups: west (PP, FL, LL, and BO) and east (CP, AP, MP, and LB), for the comparison among groups.

A) Yellow-shouldered Parrot

Groups	Source of variation	df	Percent variation	Φ-statistic	*P*
None specified	Among populations	7	60.5	0.60	< 0.0001
	Within populations	69	39.5		
East vs. west	Among groups	1	-35.0	-0.35	0.7185
	Among populations within groups	6	90.6	0.67	< 0.0001
	Within populations	69	44.4	0.56	< 0.0001
Islands vs. mainland	Among groups	1	-28.2	-0.28	0.2727
	Among populations within groups	6	84.6	0.66	< 0.0001
	Within populations	69	43.6	0.56	< 0.0001

B) Buffy Hummingbird

Groups	Source of variation	df	Percent variation	Φ-statistic	*P*
None specified	Among populations	5	26.9	0.27	< 0.0001
	Within populations	100	73.1		
East vs. west	Among groups	1	27.1	0.27	0.0987
	Among populations within groups	4	7.7	0.11	< 0.0001
	Within populations	100	65.2	0.35	< 0.0001

C) Vermilion Cardinal

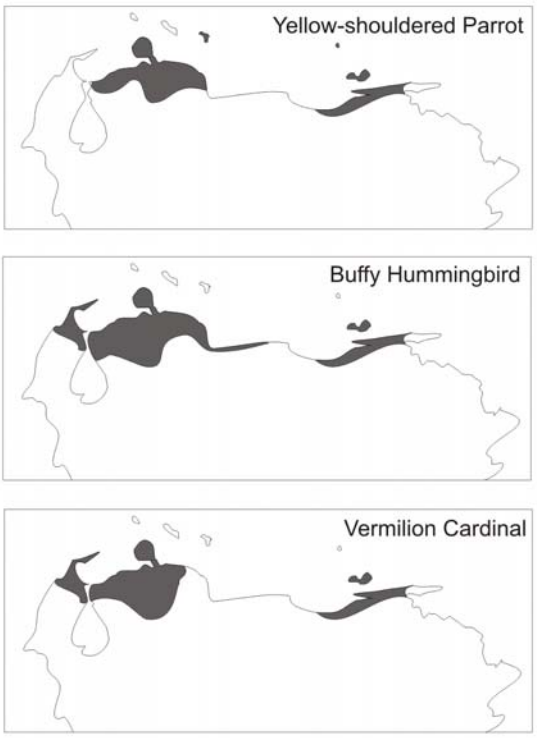
Groups	Source of variation	df	Percent variation	Φ-statistic	*P*
None specified	Among populations	5	26.1	0.26	< 0.0001
	Within populations	85	73.9		
East vs. west	Among groups	1	25.7	0.26	0.1124
	Among populations within groups	4	7.6	0.10	< 0.0001
	Within populations	85	66.7	0.33	< 0.0001

Table 6. Estimates raggedness index (*r*) and their respective *P* values for each population of the three target species.

	Yellow-shouldered Parrot		Buffy Hummingbird		Vermilion Cardinal	
Population	***r***	***P***	***r***	***P***	***r***	***P***
AP	0.012	0.95	0.025	0.69	0.059	0.94
CP	---	---	0.014	0.88	0.301	0.19
LB	---	---	---	---	---	---
MP	0.099	1.00	0.018	0.83	0.023	0.44
LL	---	---	0.006	1.00	0.072	0.61
FL	0.041	0.45	0.024	0.74	0.031	0.70
BO	0.017	0.80	---	---	---	---
PP	---	---	0.024	0.37	0.026	0.69

Figure 1. A) Distributional range of the three target species and B) map of the arid zones of northern South America indicating localities where samples were collected.

A) Distributional ranges of the target species



B) Map of sampling localities

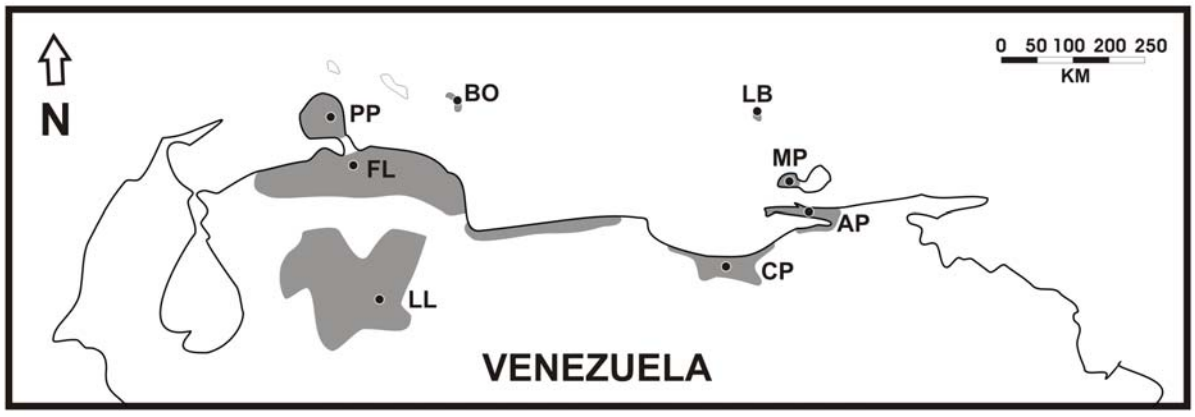


Figure 2. Unrooted parsimony network of mtDNA haplotypes of the Yellow-shouldered Parrot. Circles represent each haplotype and the size of the circle indicates the frequency of the haplotype (the largest haplotype in the diagram was shared by 17 individuals). Black dots and numbers correspond to mutational steps between haplotypes. Each color represents a different population: AP (gray), MP (yellow), CP (blue), LB (white), LL (red), FL (green), and BO (brown).

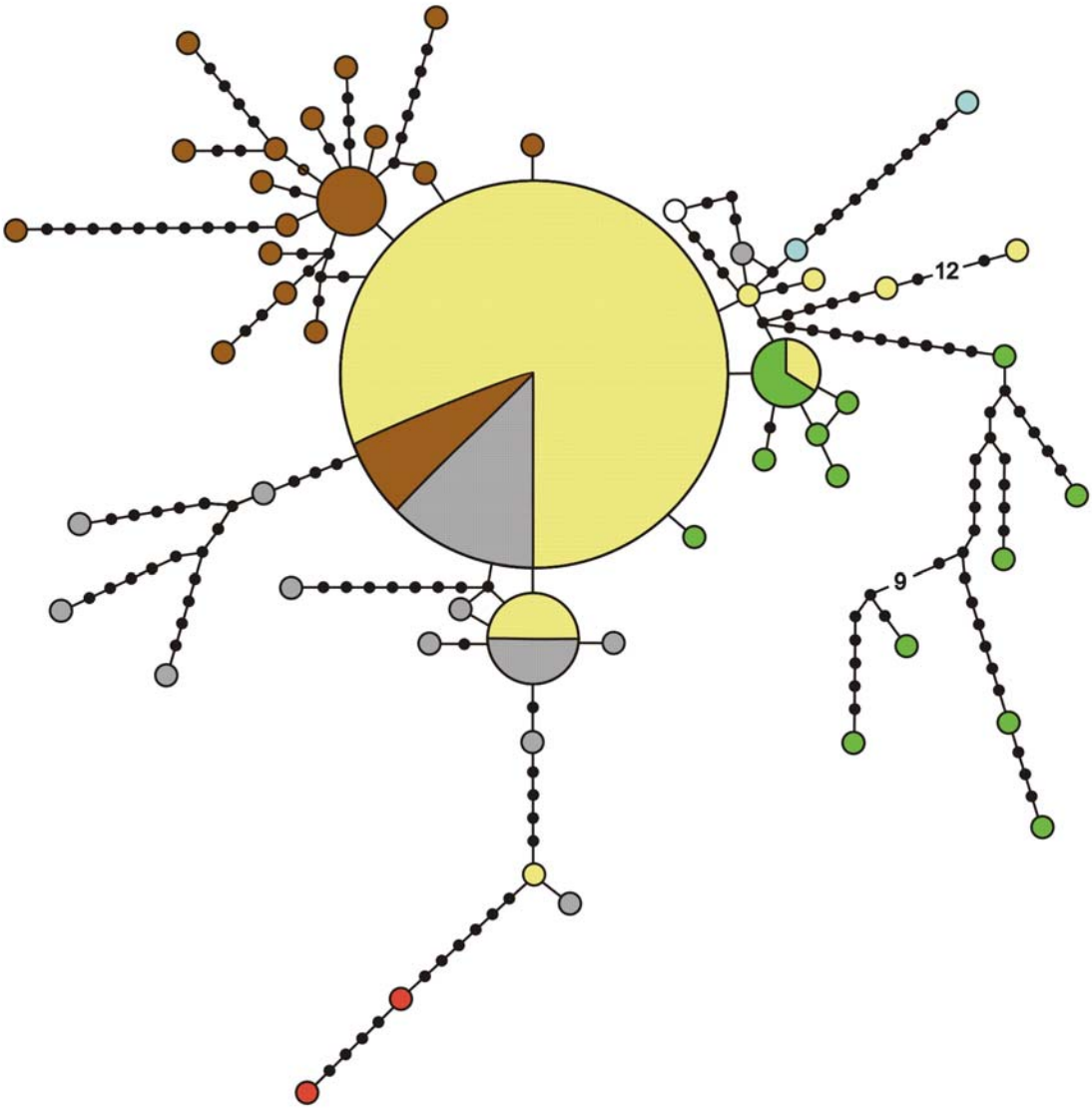


Figure 3. Unrooted parsimony network of mtDNA haplotypes of the Buffy Hummingbird. Circles represent each haplotype and the size of the circle indicates the frequency of the haplotype. Black dots and numbers correspond to mutational steps between haplotypes. Each color represents a different population: AP (gray), MP (yellow), CP (blue), LL (red), FL (green), and PP (purple).

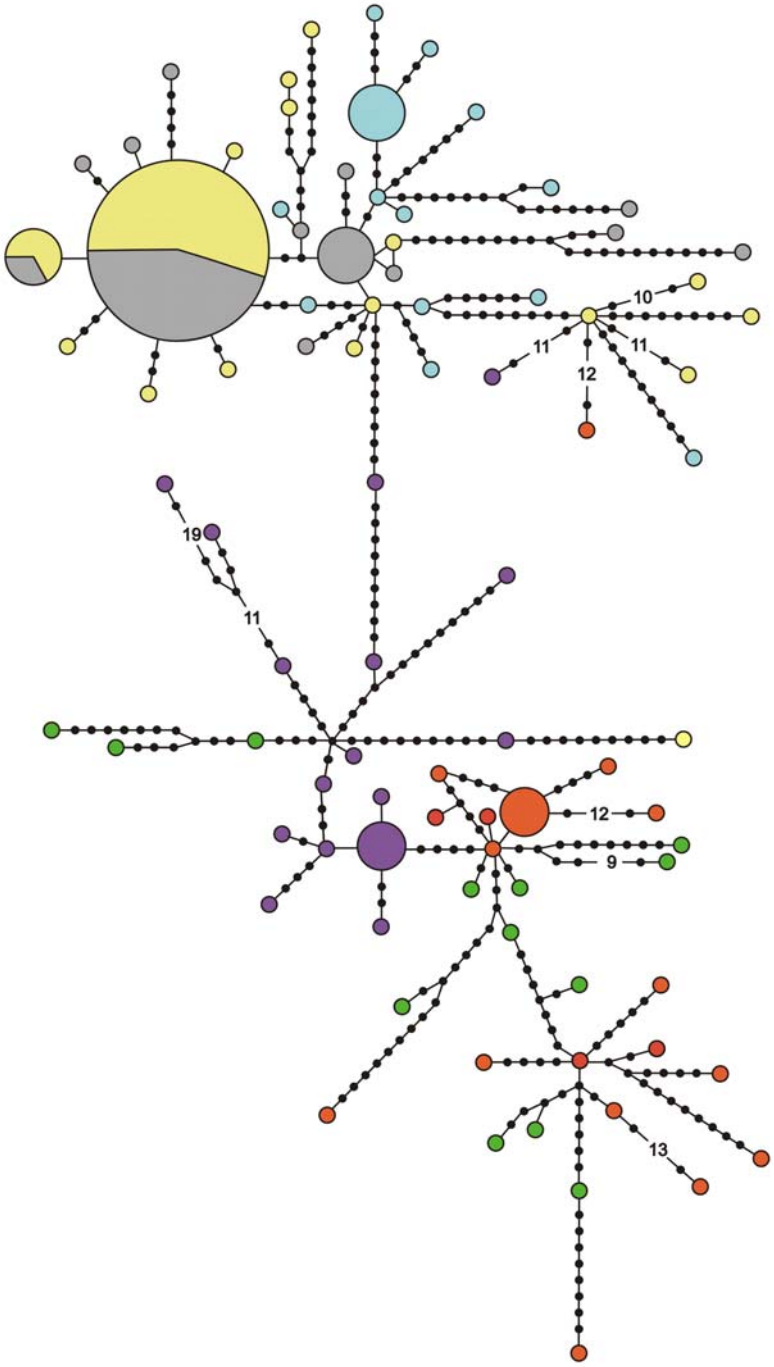


Figure 4. Unrooted parsimony network of mtDNA haplotypes of the Vermilion Cardinal. Circles represent each haplotype and the size of the circle indicates the frequency of the haplotype. Black dots and numbers correspond to mutational steps between haplotypes. Each color represents a different population: AP (gray), MP (yellow), CP (blue), LL (red), FL (green), and PP (purple).

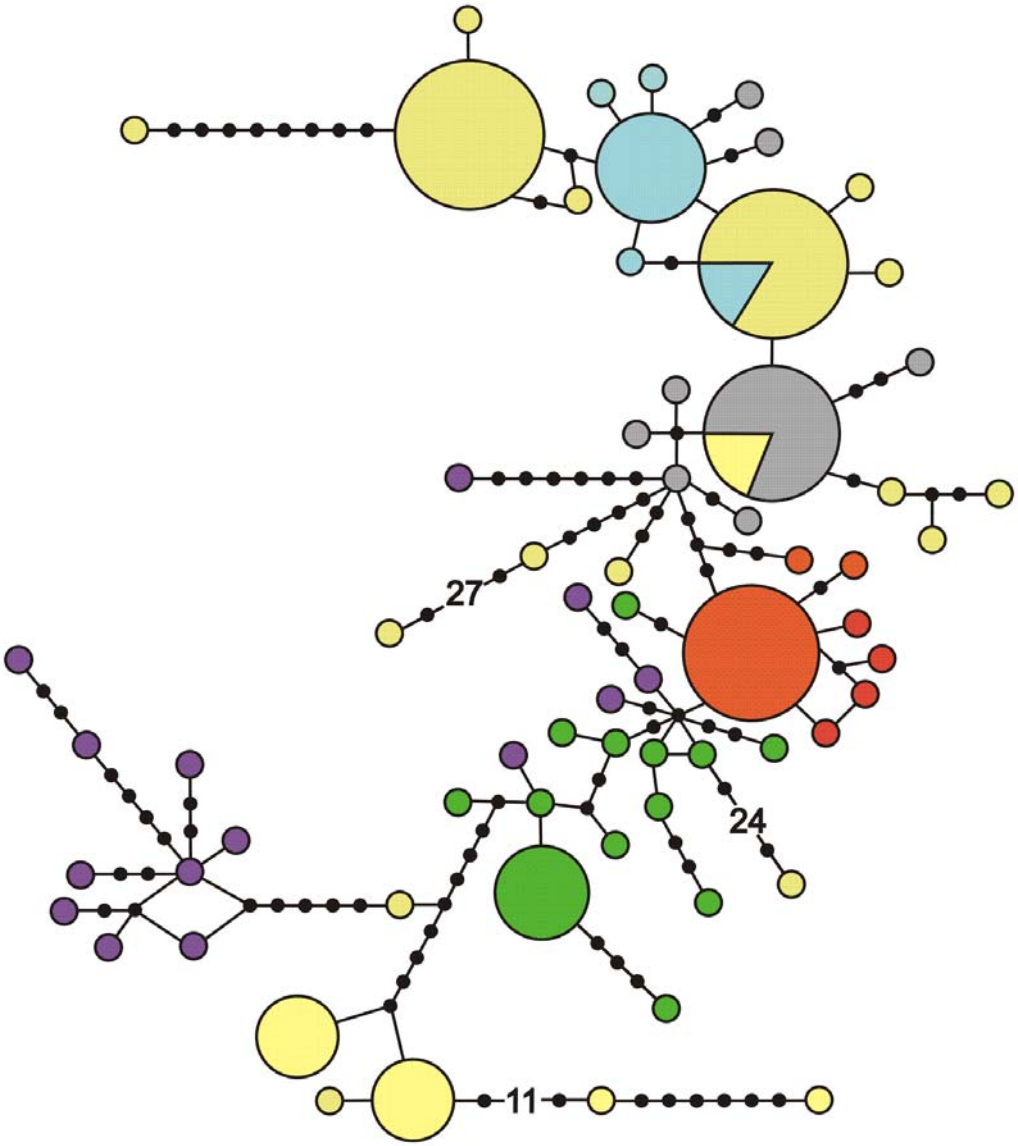


Figure 5. Mismatch distributions of all haplotypes for four populations of the Yellow-shouldered Parrot. Solid lines indicate the observed distribution of pairwise differences and dashed lines show the expected distributions under a model of sudden population expansion.

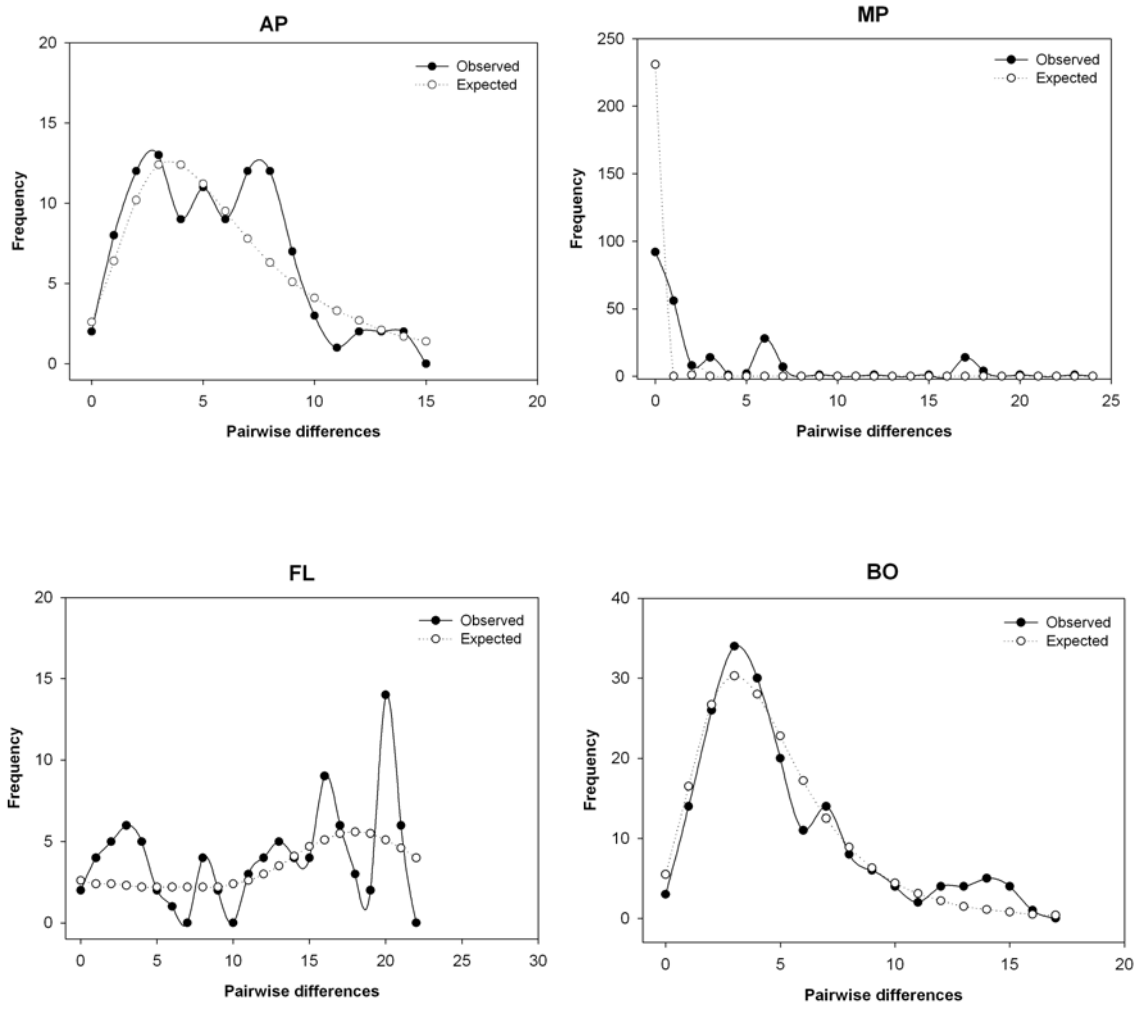


Figure 6. Mismatch distributions of all haplotypes for six populations of the Buffy Hummingbird. Solid lines indicate the observed distribution of pairwise differences and dashed lines show the expected distributions under a model of sudden population expansion.

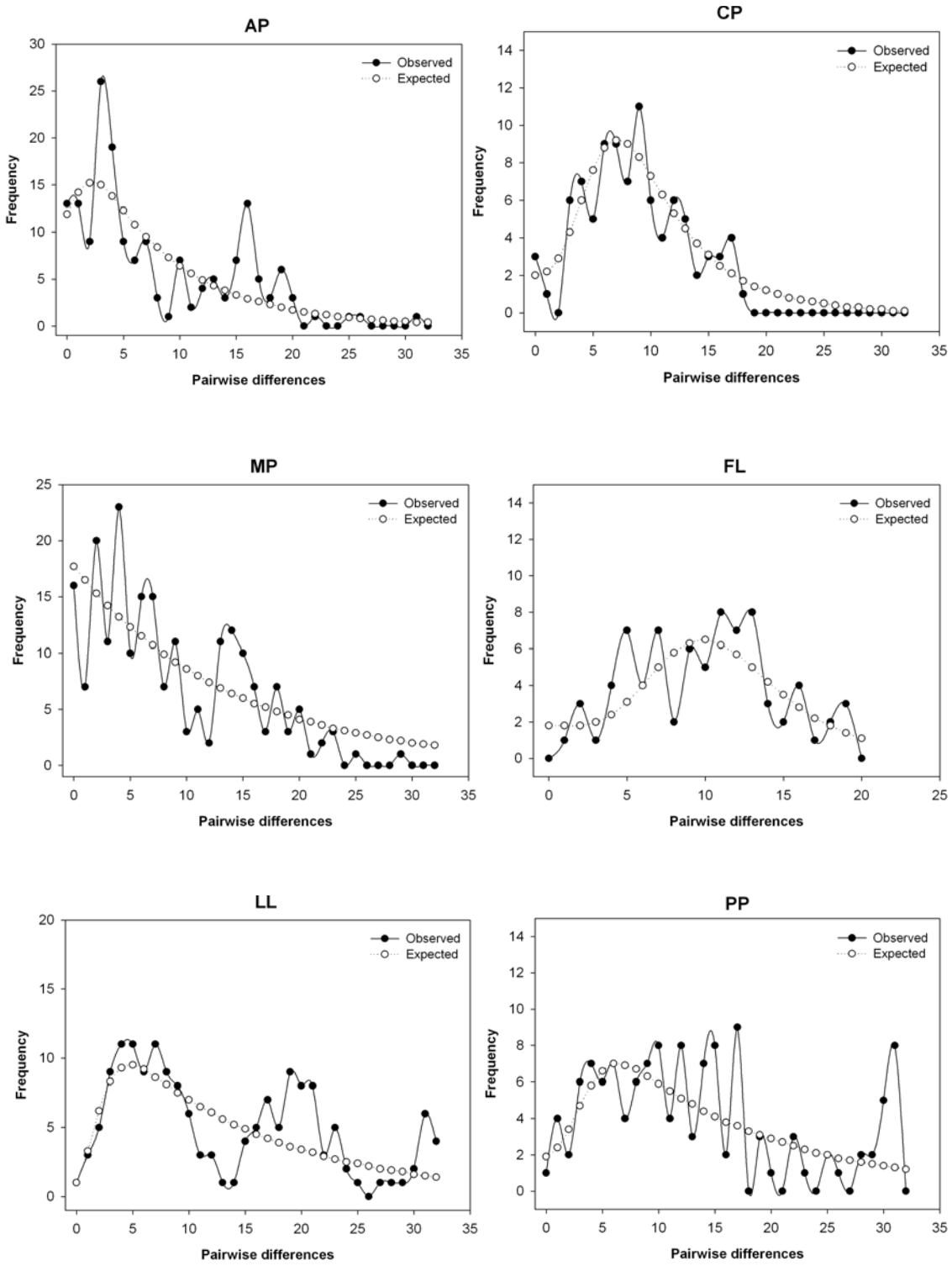


Figure 7. Mismatch distributions of all haplotypes for six populations of the Vermilion Cardinal. Solid lines indicate the observed distribution of pairwise differences and dashed lines show the expected distributions under a model of sudden population expansion.

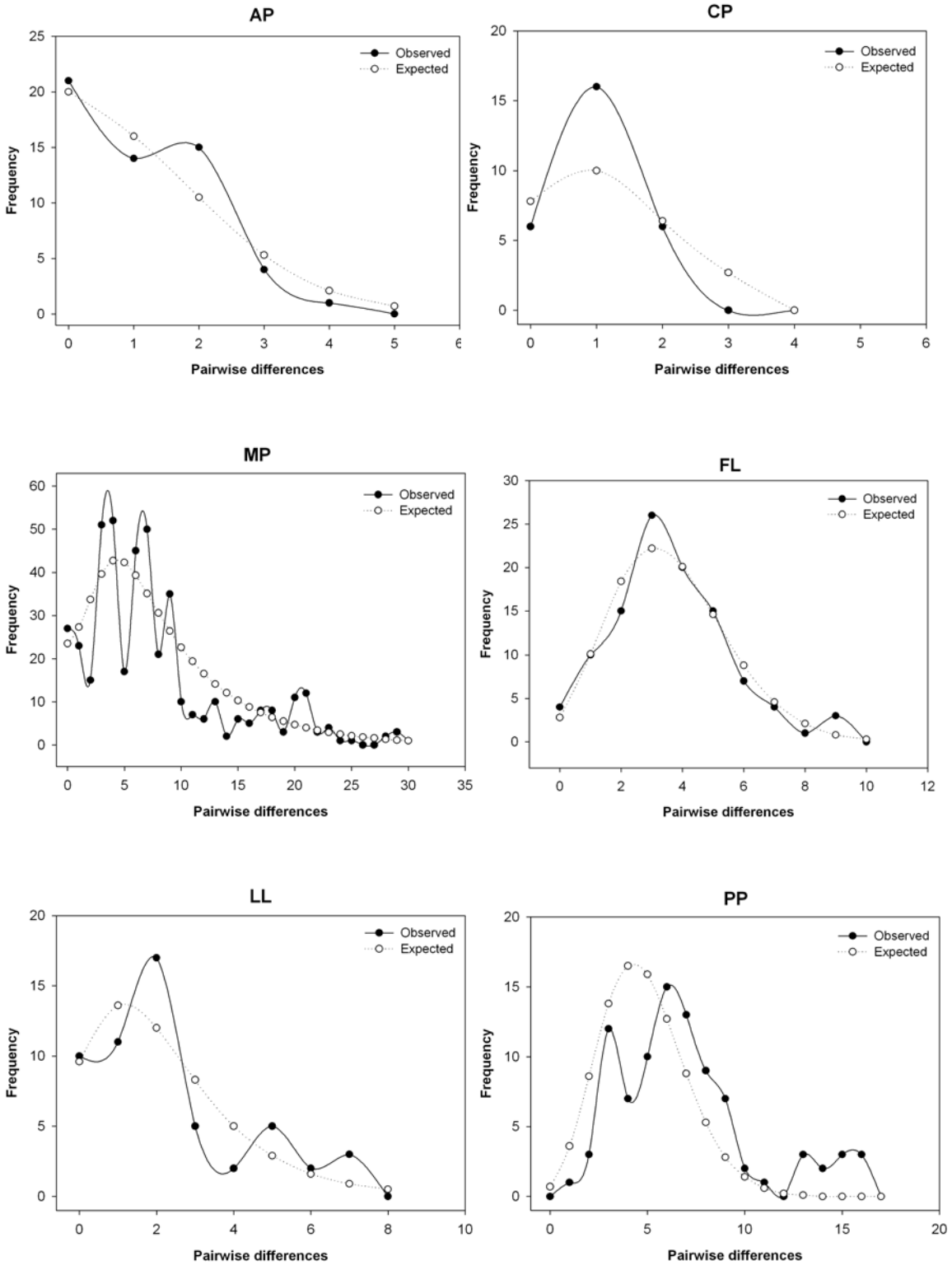


Figure 8. Intraspecific maximum likelihood phylogeny of the Yellow-shouldered Parrot. Individuals are identified by its population acronym: AP = Araya peninsula, BO = Bonaire, CP = Anzoátegui, FL = falcón lowlands, LB = La Blanquilla Island, LL = Lara lowlands, MP = Margarita Island, PP = Paraguaná peninsula. Branch lenghts are drawn in proportion to genetic diversity as indicated by the scale bar. Asterisks (*) indicate nodes with bootstrap values > 75%.

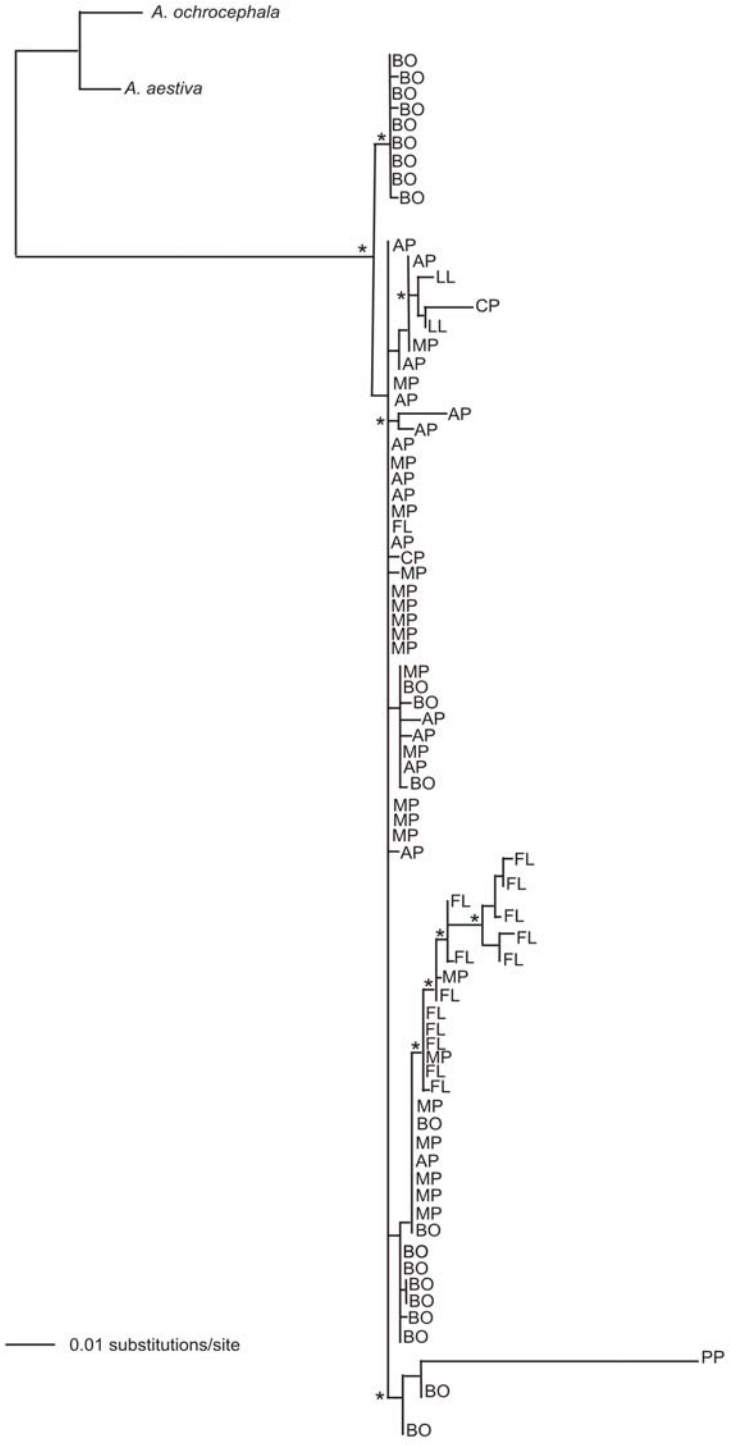


Figure 9. Intraspecific maximum likelihood phylogeny of the Buffy Hummingbird. Individuals are identified by its population acronym: AP = Araya peninsula, CP = Anzoátegui, FL = falcón lowlands, LL = Lara lowlands, MP = Margarita Island, PP = Paraguaná peninsula. Branch lenghts are drawn in proportion to genetic diversity as indicated by the scale bar. Asterisks (*) indicate nodes with bootstrap values > 75%.

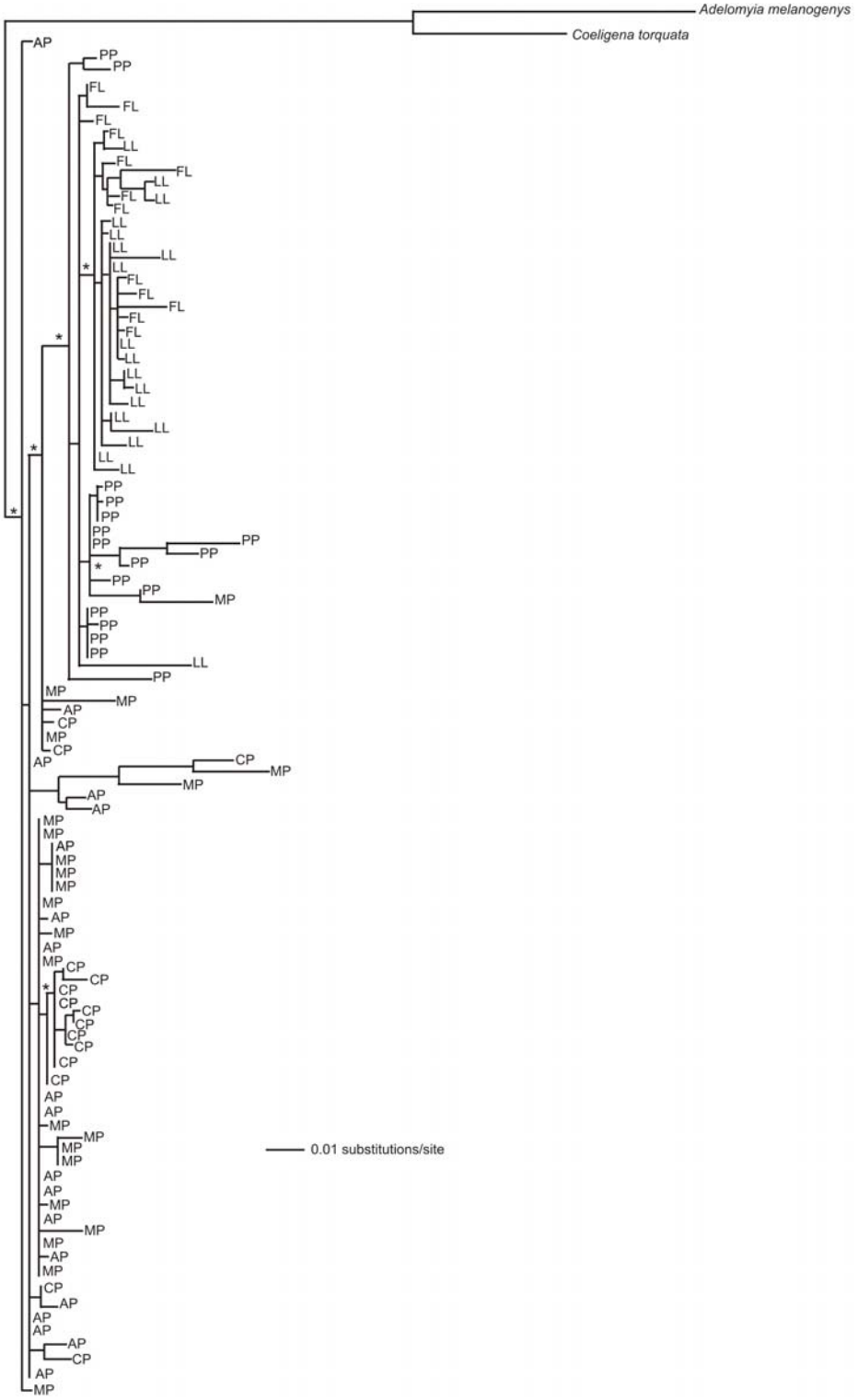
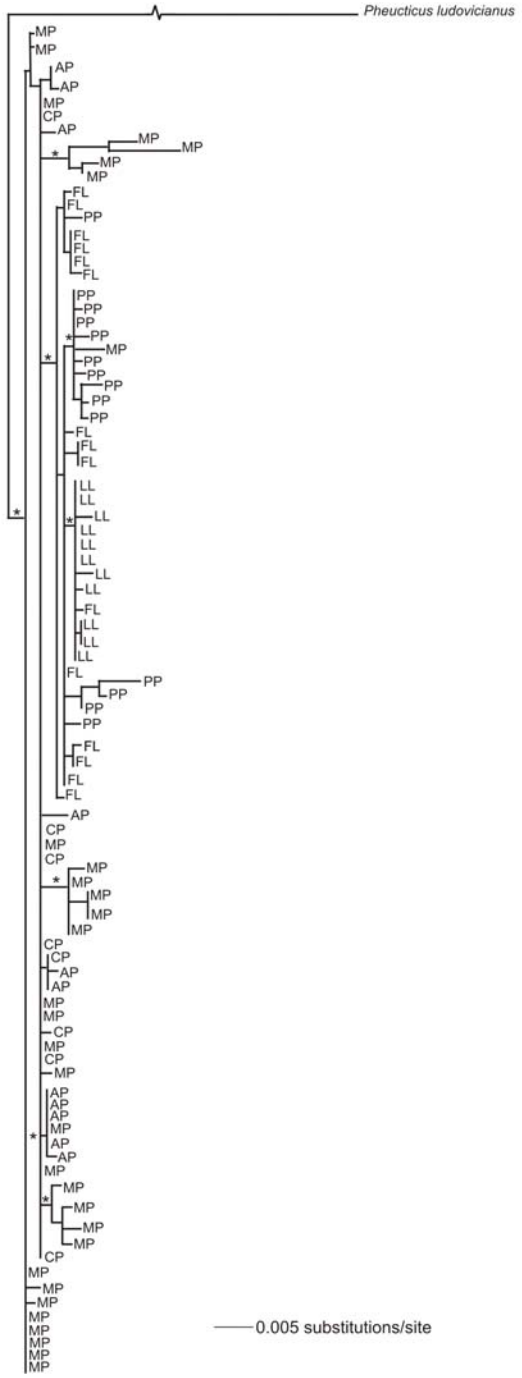


Figure 10. Intraspecific maximum likelihood phylogeny of the Vermilion Cardinal. Individuals are identified by its population acronym: AP = Araya peninsula, CP = Anzoátegui, FL = falcón lowlands, LL = Lara lowlands, MP = Margarita Island, PP = Paraguaná peninsula. Branch lenghts are drawn in proportion to genetic diversity as indicated by the scale bar. Asterisks (*) indicate nodes with bootstrap values > 75%.



Appendix. Localities and specimen information for samples used in this study.

Species	Collection	Population	Locality
Amazona barbadensis	This study	AP	Venezuela: Sucre, Taguapire, 10° 37' N, 64° 00' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Taguapire, 10° 37' N, 64° 00' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Taguapire, 10° 37' N, 64° 00' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Taguapire, 10° 37' N, 64° 00' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Taguapire, 10° 37' N, 64° 00' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Caimancito, 10° 37' N, 63° 49' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Caimancito, 10° 37' N, 63° 49' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Caimancito, 10° 37' N, 63° 49' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Cerezal, 10° 39' N, 63° 47' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Cerezal, 10° 39' N, 63° 47' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Cachicato, 10° 33' N, 63° 49' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Cachicato, 10° 33' N, 63° 49' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Guayacán, 10° 38' N, 63° 49' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Guayacán, 10° 38' N, 63° 49' W
Amazona barbadensis	This study	AP	Venezuela: Sucre, Guayacán, 10° 38' N, 63° 49' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W

Appendix. Continued

Species	Collection	Population	Locality
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	BO	Netherland Antilles: Bonaire, Gotomeer, 12° 14' N, 68° 22' W
Amazona barbadensis	This study	CP	Venezuela: Anzoátegui, Jose, 10° 05' N, 64° 55' W
Amazona barbadensis	COP14783	CP	Venezuela: Anzoátegui, Barcelona, 10° 13' N, 64° 68' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, Pedregal, 11° 05' N, 70° 10' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, La Negrita, 11° 31' N, 69° 55' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, La Negrita, 11° 31' N, 69° 55' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, La Negrita, 11° 31' N, 69° 55' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, La Negrita, 11° 31' N, 69° 55' W
Amazona barbadensis	This study	FL	Venezuela: Falcón, La Negrita, 11° 31' N, 69° 55' W
Amazona barbadensis	COP34037	LB	Venezuela: La Blanquilla Island, 11° 51' N, 64° 36' W
Amazona barbadensis	COP77484	LL	Venezuela: Lara, Sierra de Tamayare, 10° 53' N, 70° 13' W
Amazona barbadensis	COP77793	LL	Venezuela: Lara, Carora, 10° 16' N, 70° 06' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W

Appendix. Continued

Species	Collection	Population	Locality
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Amazona barbadensis	This study	PP	Venezuela: Falcón, Cerro Santa Ana, 11° 42' N, 69° 56' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 40' N, 63° 47' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 40' N, 63° 47' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 39' N, 63° 47' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 39' N, 63° 47' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Sector La Alegría, 10° 38' N, 63° 47' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Sector La Alegría, 10° 38' N, 63° 47' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Sector La Alegría, 10° 38' N, 63° 47' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Sector Cerezal, 10° 39' N, 63° 47' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Sector Guamachal, 10° 39' N, 63° 46' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Sector Guamachal, 10° 39' N, 63° 46' W
Cardinalis phoeniceus	This study	AP	Venezuela: Sucre, Sector Guamachal, 10° 39' N, 63° 46' W

Appendix. Continued

Species	Collection	Population	Locality
Cardinalis phoeniceus	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Cardinalis phoeniceus	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Cardinalis phoeniceus	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Cardinalis phoeniceus	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Cardinalis phoeniceus	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Cardinalis phoeniceus	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Cardinalis phoeniceus	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Cardinalis phoeniceus	This study	CP	Venezuela: Anzoátegui, Nuevo Unare, 10° 04' N, 65° 12' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 19' N, 69° 38' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 19' N, 69° 38' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 19' N, 69° 39' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 19' N, 69° 39' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 17' N, 69° 36' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 17' N, 69° 36' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Médanos de Coro N. P., 11° 26' N, 69° 40' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Médanos de Coro N. P., 11° 26' N, 69° 40' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, Médanos de Coro N. P., 11° 26' N, 69° 40' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, 20 Km west of Coro, 11° 21' N, 69° 49' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, 20 Km west of Coro, 11° 21' N, 69° 49' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, 25 Km west of Coro, 11° 19' N, 69° 52' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, El Carrizal, 11° 23' N, 69° 33' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, El Carrizal, 11° 23' N, 69° 33' W
Cardinalis phoeniceus	This study	FL	Venezuela: Falcón, El Carrizal, 11° 23' N, 69° 33' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W

Appendix. Continued

Species	Collection	Population	Locality
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Tapa de Piedra, 10° 06' N, 69° 32' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Tapa de Piedra, 10° 06' N, 69° 32' W
Cardinalis phoeniceus	This study	LL	Venezuela: Lara, Sector Tapa de Piedra, 10° 06' N, 69° 32' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Sector El Indio, 10° 58' N, 64° 09' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Sector El Indio, 10° 58' N, 64° 09' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Guacuco, 11° 05' N, 63° 58' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Guacuco, 11° 05' N, 63° 58' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Las Marvales, 10° 58' N, 64° 05' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Las Marvales, 10° 58' N, 64° 05' W

Appendix. Continued

Species	Collection	Population	Locality
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W
Cardinalis phoeniceus	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, 8 Km south of Adícora, 11° 49' N, 69° 50' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, 8 Km south of Adícora, 11° 49' N, 69° 50' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, Cerro Santa Ana, 11° 49' N, 69° 58' W
Cardinalis phoeniceus	This study	PP	Venezuela: Falcón, Moruy, 11° 42' N, 69° 56' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 40' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 40' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 40' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 40' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 40' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 39' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 39' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 39' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Surroundings of Guayacán, 10° 39' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Sector La Alegría, 10° 38' N, 63° 47' W

Appendix. Continued

Species	Collection	Population	Locality
Leucippus fallax	This study	AP	Venezuela: Sucre, Sector La Alegría, 10° 38' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Sector La Alegría, 10° 38' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Sector La Alegría, 10° 38' N, 63° 47' W
Leucippus fallax	This study	AP	Venezuela: Sucre, 3 Km south of Caimancito, 10° 36' N, 63° 55' W
Leucippus fallax	This study	AP	Venezuela: Sucre, 3 Km south of Caimancito, 10° 36' N, 63° 55' W
Leucippus fallax	This study	AP	Venezuela: Sucre, 3 Km south of Caimancito, 10° 36' N, 63° 55' W
Leucippus fallax	This study	AP	Venezuela: Sucre, 5 Km east of Araya, 10° 34' N, 64° 13' W
Leucippus fallax	This study	AP	Venezuela: Sucre, 5 Km east of Araya, 10° 34' N, 64° 13' W
Leucippus fallax	This study	AP	Venezuela: Sucre, Sector Guamachal, 10° 39' N, 63° 46' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Nuevo Unare, 10° 04' N, 65° 12' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Nuevo Unare, 10° 04' N, 65° 12' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Nuevo Unare, 10° 04' N, 65° 12' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Nuevo Unare, 10° 04' N, 65° 12' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, 15 Km south of Clarines, 10° 01' N, 65° 11' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, 15 Km south of Clarines, 10° 01' N, 65° 11' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	CP	Venezuela: Anzoátegui, Jose, 10° 04' N, 64° 55' W
Leucippus fallax	This study	FL	Venezuela: Falcón, Médanos de Coro N. P., 11° 26' N, 69° 40' W
Leucippus fallax	This study	FL	Venezuela: Falcón, Médanos de Coro N. P., 11° 26' N, 69° 40' W
Leucippus fallax	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 17' N, 69° 36' W
Leucippus fallax	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 17' N, 69° 36' W
Leucippus fallax	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 17' N, 69° 36' W
Leucippus fallax	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 17' N, 69° 36' W

Appendix. Continued

Species	Collection	Population	Locality
Leucippus fallax	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 17' N, 69° 36' W
Leucippus fallax	This study	FL	Venezuela: Falcón, Surroundings of La Negrita, 11° 17' N, 69° 36' W
Leucippus fallax	This study	FL	Venezuela: Falcón, 20 Km west of Coro, 11° 21' N, 69° 49' W
Leucippus fallax	This study	FL	Venezuela: Falcón, 20 Km west of Coro, 11° 21' N, 69° 49' W
Leucippus fallax	This study	FL	Venezuela: Falcón, 20 Km west of Coro, 11° 21' N, 69° 49' W
Leucippus fallax	This study	FL	Venezuela: Falcón, 20 Km west of Coro, 11° 21' N, 69° 49' W
Leucippus fallax	This study	FL	Venezuela: Falcón, Sector La Zábila west of Coro, 11° 19' N, 69° 52' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Padre Diego, 10° 09' N, 69° 31' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Banco de Baragua, 10° 08' N, 69° 35' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Tapa de Piedra, 10° 06' N, 69° 32' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Tapa de Piedra, 10° 06' N, 69° 32' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Tapa de Piedra, 10° 06' N, 69° 32' W
Leucippus fallax	This study	LL	Venezuela: Lara, Sector Tapa de Piedra, 10° 06' N, 69° 32' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, La Chica Creek, 11° 06' N, 64° 25' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W

Appendix. Continued

Species	Collection	Population	Locality
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Sector Comején, 11° 03' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Murrión, 11° 00' N, 64° 12' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Chacaracual, 10° 57' N, 64° 17' W
Leucippus fallax	This study	MP	Venezuela: Nueva Esparta, Guacuco, 11° 05' N, 63° 58' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 8 Km south of Adícora, 11° 49' N, 69° 50' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 8 Km south of Adícora, 11° 49' N, 69° 50' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 8 Km south of Adícora, 11° 49' N, 69° 50' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Leucippus fallax	This study	PP	Venezuela: Falcón, 20 Km west of Pueblo Nuevo, 11° 58' N, 70° 01' W
Leucippus fallax	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Leucippus fallax	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Leucippus fallax	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W

Appendix. Continued

Species	Collection	Population	Locality
Leucippus fallax	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Leucippus fallax	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Leucippus fallax	This study	PP	Venezuela: Falcón, Laguna Boca de Caño, 12° 01' N, 69° 51' W
Leucippus fallax	This study	PP	Venezuela: Falcón, Cerro Santa Ana, 11° 49' N, 69° 58' W
Leucippus fallax	This study	PP	Venezuela: Falcón, Cerro Santa Ana, 11° 49' N, 69° 58' W