

## The avifauna of sandy coastal vegetation during migration, in the Laberinto de las Doce Leguas sub-archipelago, southern Cuba

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Las comunidades de aves han sido muy estudiadas en varias localidades costeras e interiores de Cuba durante las migraciones desde principios de 1990, aunque se les ha prestado poca atención a las regiones del sur de la isla de Cuba y cayerías aledañas. En el presente trabajo se describen algunas características de la composición y estructura de las comunidades y poblaciones de aves asociadas al complejo de vegetación costera del Laberinto de las Doce Leguas (archipiélago de los Jardines de la Reina) durante las migraciones de 2009–12. Se muestrearon los cayos Grande, Anclitas y Caguama mediante redes de niebla durante al menos dos días consecutivos en las estaciones de primavera (marzo–abril) y otoño (septiembre–octubre). Se capturaron 46 especies y 745 individuos, agrupados en seis órdenes, 12 familias y 26 géneros. Se adicionaron el Tordo de Espalda Olivada *Catharus ustulatus* y el Solibio *Icterus melanopsis* a la avifauna del archipiélago de los Jardines de la Reina con la captura y observación de dos individuos en los cayos Grande y Caguama respectivamente, el 3 y 9 de octubre de 2012. Entre los dos períodos de muestreo, no se encontraron diferencias significativas en cuanto al número de especies capturadas por día ( $12,7 \pm 3,65$  y  $12,8 \pm 4,14$ ) y a la abundancia relativa general ( $34,1 \pm 13,5$  y  $35,2 \pm 16,43$  aves / 100 horas-red). Tampoco se encontraron diferencias significativas entre las estaciones de anillamiento, con los mayores valores registrados en cayo Grande para ambas variables ( $14,7 \pm 2,81$  y  $41,6 \pm 15,06$ , respectivamente). Las hembras e inmaduros fueron los individuos numéricamente dominantes durante las migraciones otoñales en las tres localidades. Durante las migraciones primaverales, la proporción entre los sexos y las clases de edad fueron más balanceadas. No se registraron tasas anuales de retorno, y la persistencia invernal se manifestó solamente para dos Mariposas Galanas *Setophaga discolor* en cayo Grande durante los períodos invernales 2009–10.

The Jardines de la Reina archipelago (AJR), off the southern coast of Ciego de Ávila and Camagüey provinces, Cuba, comprises 661 cays and extends for 360 km forming part of the submerged plains and islets of the south-eastern platform<sup>22</sup>. Most cays form part of two groups known as the Golfo de Ana María (GAM) and Laberinto de las Doce Leguas (LDL) sub-archipelagos. The AJR's marine and terrestrial biodiversity is well protected, partly due to its geographical isolation (relatively far from the mainland), although it has been poorly studied compared to other insular and coastal regions of Cuba<sup>45</sup>. Avifaunal composition of AJR was initially described by Bond<sup>5</sup> and Garrido & García<sup>14</sup>, with subsequent contributions on species occurrence<sup>6,7</sup>, and new taxa descriptions (e.g., Cuban Pewee *Contopus caribaeus florentinoides*<sup>37</sup> and *C. c. nerleyi*)<sup>12</sup>. During the last 20 years, further broader-scale inventories have been conducted in LDL<sup>28,46</sup>. Since September 2009, we have recorded up to 119 bird species using mist-netting surveys in LDL and general counts in the least-known areas in GAM<sup>29</sup>.

Since the early 1990s, the structure and composition of avifaunal communities during migration have been extensively studied at various inland<sup>43,49,50</sup> and north-coast localities (e.g. Gibara) in Cuba, including many of the larger northern

cays<sup>41,42,49</sup>. Most of this research was conducted at 34 localities in ten regions of Cuba, with mist-nets being used to evaluate terrestrial bird communities<sup>25</sup>, in 1988–99. Except the Ciénaga de Zapata, however, little attention has been directed to southern regions of the main island and neighbouring archipelagos of Cuba<sup>17</sup>, suggesting the need for rigorous surveys of these poorly explored areas, especially using mist-nets.

Parada *et al.*<sup>30</sup> noted the relative importance of AJR as a stopover and overwintering site, based on more than 20 new Nearctic passerine migrants recorded during cursory sampling efforts. Despite increasing interest in the study of bird migration in the Caribbean Basin<sup>51</sup>, data on many aspects, e.g. location use, timing, effects of local climatic events, and volumes of movement by migratory birds, await attention<sup>19</sup>. Furthermore, studies addressing the ecology of bird assemblages during migration in LDL are important because of the convergence of many extreme environmental conditions, such as tidal waves, strong winds, high evaporation rates and intensive hydromorphism<sup>15</sup>, as well as geographical isolation on small and low-lying islands of recent geological evolution, and their high ecological fragility<sup>15</sup>. Herein, we describe the compositional and structural variables of bird

communities associated with sandy coastal scrub in LDL during spring and autumn migrations in 2009–12.

## Methods

**Study area.**—LDL is the largest insular group in AJR, 87 km south of central Cuba. The LDL stretches along the southern border of the insular platform, from the westernmost (Bretón Cay; 21°7'N 79°26'W) to the easternmost point (Cabeza del Este Cay; 20°33'N 78°21'W). We surveyed the sandy vegetation on Grande (21°00'01.7"N 79°10'53.5"W), Anclitas (20°47'59.7"N 78°56'01.9"W) and Caguama Cays (20°34'49.9"N 78°24'38.3"W) (Fig. 1). Three primary vegetation types occur on these islands: (1) mangroves of different floristic and physiognomic types, (2) xerophytic coastal scrub, and (3) rocky and sandy vegetation complexes. Cultivated Australian pine *Casuarina equisetifolia*, coconut *Cocos nucifera* and tropical almond *Terminalia catappa* are patchily distributed, probably due to past human influence<sup>46</sup>. Coastal vegetation with a mean height of 3–5 m, and scattered bushes and trees up to 7 m tall, grows on sandy soil with a patchy, thin leaf litter. Species such as black torch *Erihalis fruticosa*, Cuban silver palm *Coccothrinax*

*littoralis*, *Crossopetalum rhacoma* and *Cassia lineata* are numerically dominant, with scattered individuals of poisonwood *Metopium toxiferum* and button mangrove *Conocarpus erecta*.

**Bird surveys.**—Mist-netting protocol consisted of three four-net groups (12.0 m × 2.6 m × 30.0 mm) separated by 35–40 m and distributed across study sites, depending on the vegetation<sup>30</sup>. Net location remained constant throughout the study and nets were always operated for five hours, commencing at dawn (06h30–11h30). Each site was surveyed on at least two consecutive days under favourable conditions (clear skies and light wind) in spring (March–April) and autumn (September–October) over a four-year period (2009–12) (Table 1), for a total sampling effort (net-hours) of 890, 856 and 712 on Anclitas, Grande and Caguama Cays, respectively.

Bird identification was based on the National Geographic Society<sup>27</sup> and Garrido & Kirkconnell<sup>13</sup> field guides. We measured wing chord, tail length, tarsus and exposed culmen of each trapped bird. US Fish & Wildlife Service aluminum rings were used to mark birds, while sexing and ageing followed the criteria of Pyle<sup>32</sup> and Pyle *et al.*<sup>33</sup>. We marked small birds (e.g. Cuban Emerald *Chlorostilbon*

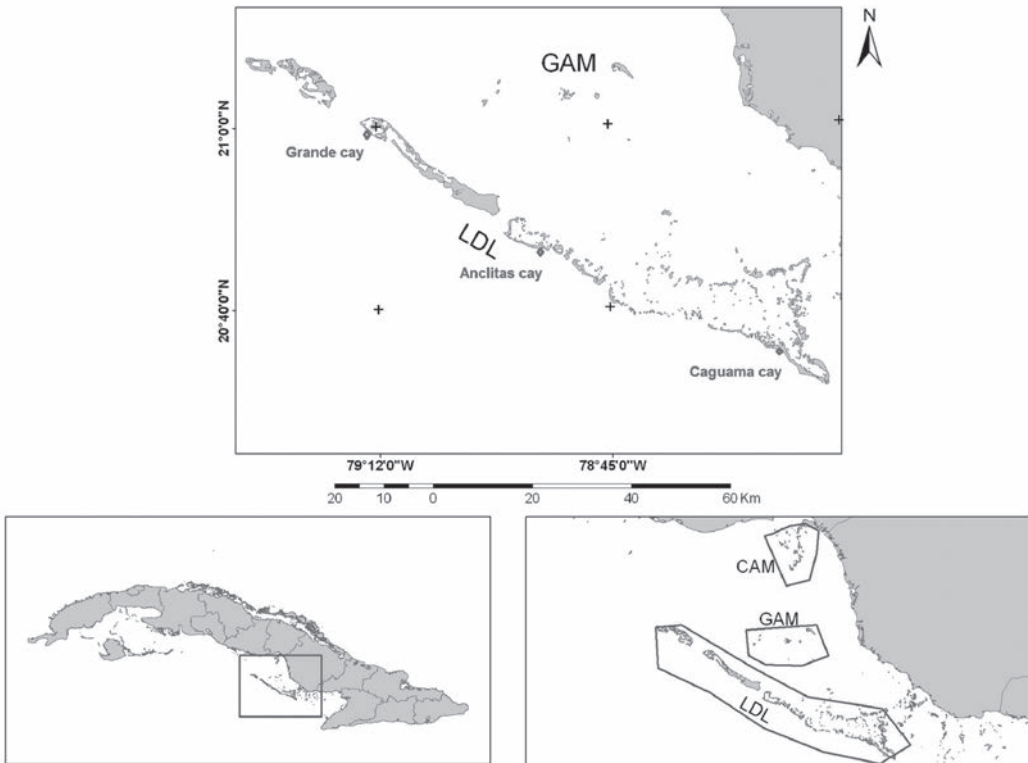


Figure 1. Geographical position of the main insular groups within the Jardines de la Reina archipelago, south-central Cuba. LDL (Laberinto de las Doce Leguas), CAM (Ana María Cays), GAM (Ana María Gulf cays).

Table 1. Mist-netting schedule (days / month) conducted during the spring and autumn migrations on Grande, Anclitas and Caguama Cays, Laberinto de las Doce Leguas sub-archipelago, southern Cuba, 2009–12. \* = Cays not surveyed due to inclement weather or logistical constraints.

Sampling season	Locality		
	Grande	Anclitas	Caguama
2009 autumn	18–20 Sep	14–16 Sep	21–22 Sep
2010 spring	12–13 Apr	20–21 Apr	*
autumn	21–22 Oct	18–19 Oct	26–27 Oct
2011 spring	8–9 Apr	12–13 Apr	4–5 Apr
autumn	10–11 Sep	17–18 Sep	14–15 Sep
2012 spring	28–29 Mar	3–4 Apr	31 Mar–1 Apr
autumn	2–3 Oct	*	8–9 Oct

*ricordii*) by clipping the right outermost rectrix. For each species, relative abundance index, expressed as birds / 100 net-hours, was calculated as well as the retrap percentage of both intra- and inter-sampling periods. All retraps were recorded and those on subsequent days were included in daily estimates of abundance and richness. As results from multiple days of ringing per study site per season were not independent, we used a site's mean per season as the experimental unit. Both intra- and inter-year site fidelity as defined by Rimmer & Darmstadt<sup>38</sup> was calculated.

**Statistical analyses.**—Overall species richness per site was calculated by rarefaction<sup>44</sup> using EcoSim 7.0<sup>18</sup>, and confidence intervals were generated by running 1,000 iterations. All statistical procedures were performed using STATISTICA v. 8.0<sup>47</sup> and Poptool v. 3.2.3<sup>20</sup>, with significance level set at  $\alpha = 0.05$  for all tests. Normality and homogeneity of variance were examined for all groups prior to statistical tests. When parametric assumptions were not met, we applied appropriate non-parametric procedures<sup>53</sup>. Means and standard deviations are reported throughout. Taxonomy and nomenclature follow AOU<sup>2</sup> and supplements published until 2013.

## Results

**Species composition.**—We mist-netted 745 individuals of 46 species, or 36% of all species reported in the archipelago<sup>29</sup>. These species represented six orders, 12 families and 26 genera (Appendix 1). The largest number of species (35) was mist-netted on Grande Cay, followed by Anclitas (30 species) and Caguama (28 species). A comparative analysis of species trapped at all three sites yielded a qualitative similarity of 46% for residents and 43% for migrants, with six and 14 species shared, respectively. During the 2012 autumn, two new additions to LDL

were documented: Swainson's Thrush *Catharus ustulatus* and Cuban Oriole *Icterus melanopsis*, with the capture and observation of singles on Grande and Caguama Cays on 3 and 9 October, respectively. These findings might constitute the first records for Cuba's southern archipelagos, raising the total number of species recorded on Grande and Caguama Cays to 72 and 75, respectively, with 121 species in AJR as a whole.

We found an endemism level in the sampled communities of 17.5% of the total species, including one genus, one species and five subspecies; three of these are distributed nationwide and two are exclusive to the study area. Concerning phenology categories, the avian community comprises 14 winter residents, 13 permanent residents and three summer residents, as well as 13 transients. Comparing localities and seasons, winter residents accounted for >50% of all mist-netted individuals at all ringing sites in autumn, as well as spring migrations, except on Anclitas, where permanent residents represented c.55% of all trapped individuals (Fig. 2). Both transients, mostly thrushes (Veery *Catharus fuscescens*, Grey-cheeked *C. minimus* and Swainson's Thrushes) and wood warblers (Bay-breasted Warbler *Setophaga castanea*, Tennessee Warbler *Oreothlypis peregrina*, Yellow-breasted Chat *Icteria virens*, Prothonotary Warbler *Protonotaria citrea*), and summer residents (Black-whiskered Vireo *Vireo altiloquus*, Grey Kingbird *Tyrannus dominicensis*) showed a similar pattern, contributing, on average, c.10% of trapped birds across ringing sites and sampling seasons, although the latter phenological category reached slightly higher percentages during autumn, especially on Anclitas Cay, when they accounted for c.30% of all trapped individuals.

Families such as Parulidae (18 species) and Tyrannidae (five) were best represented, whereas all other families consisted of  $\leq 3$  species. Regarding species' relative abundance (birds / 100 net-hours), the most commonly trapped species in spring / autumn were Yellow *Setophaga petechia* (8.65 / 4.91) and Prairie Warblers *S. discolor* (4.9 / 7.33), followed by Black-whiskered Vireo (5.48) and Palm Warbler *Setophaga palmarum* (4.38) during autumn and spring migrations.

When calculating species richness per site and sampling period, we excluded Belted Kingfisher *Megaceryle alcyon* on Grande Cay because its occurrence is considered casual given the close proximity of the mist-netting site to coastal lagoons and mangroves. No significant differences were noted between spring and autumn migrations (sampling sites pooled) for both number of species trapped per day (spring =  $12.7 \pm 3.65$  and autumn =  $12.8 \pm 4.14$ ) and overall relative abundance ( $34.1 \pm 13.50$  and  $35.2 \pm 16.43$ ) (T-test:  $t < 0.75$ ,  $df = 1$ ,  $p > 0.4570$ ). Equally, comparisons among

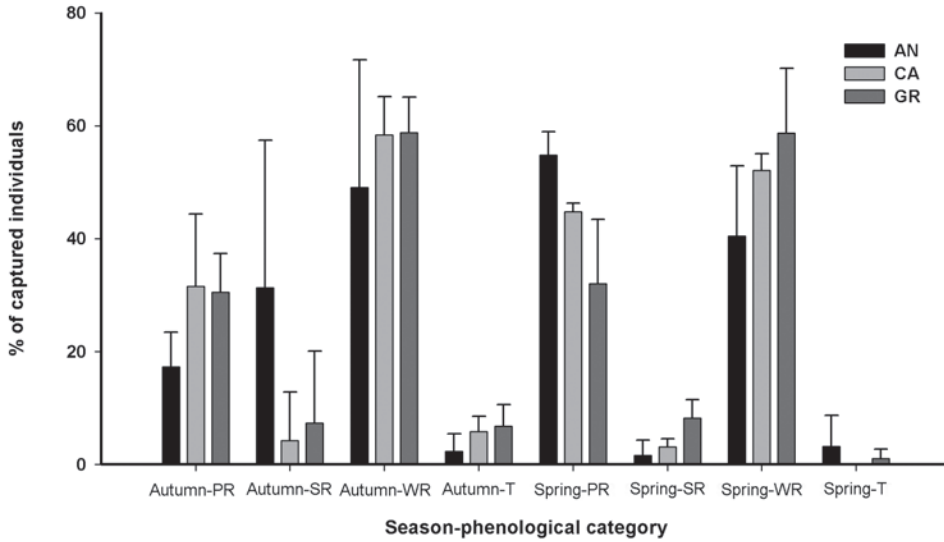


Figure 2. Trapped individuals among four main phenological categories of the sampled avian community in sandy coastal vegetation complex at three localities in the Laberinto de las Doce Leguas, Cuba, during autumn and spring migrations, 2009–12. Localities: AN (Anclitas), CA (Caguama), GR (Grande). Phenology: PR (permanent resident), SR (summer resident), WR (winter resident), and T (transient). Lines extending above the bars represent standard deviations from mean values.

ringing sites (sampling periods pooled) did not yield significant differences, with slightly higher values reported on Grande Cay for both number of species trapped ( $14.7 \pm 2.81$ ) and overall relative abundance ( $41.6 \pm 15.06$ ) compared to Caguama ( $11.8 \pm 4.07$  and  $30.1 \pm 14.05$ ) and Anclitas Cays ( $11.5 \pm 4.32$  and  $30.2 \pm 14.81$ ) (Kruskal-Wallis ANOVA test:  $H < 2.86$ ,  $P > 0.2381$ ).

We determined that, for a 217-individual standard sample in the rarefaction curve, the 95% confidence intervals overlap occurs at the point where the larger sample (Grande Cay) matches the smaller ones (Anclitas and Caguama; Fig. 3). These data demonstrate that differences in species richness among the three sampled cays were not statistically significant, with 37 species on Grande and 30 and 28 species on Anclitas and Caguama, respectively. At the three sites, the expected values of species' variance tend to decrease steadily as the number of individuals sampled increases. Similarly, no significant differences were obtained when comparing expected species richness between the two sampling periods (autumn, spring) extracted from the rarefaction curves for a 320-individuals standard sample (Fig. 4). The rate of species accumulation with increasing numbers of individuals exhibits a strikingly similar trend in both periods until reaching a 175-individuals sample. From this point, autumn tends to show, on average, slightly higher values compared to those in spring, but with a much higher variability irrespective of the number of individuals, whereas

the expected number of species variance is increasingly reduced in spring.

**Sex ratios.**—More females than males were trapped in autumn (years pooled) at the three sites, with an overall mean of 59.6% (range 50.3–69.7%) of individuals. In contrast, spring percentages were slightly biased towards males (53.4%, range 38–71%). During autumn, sex ratios did not differ significantly among sampling sites (years pooled) (all  $\chi^2_1 \leq 7.6$ ,  $P \geq 0.05$ ). However, we found significant differences in sex ratios in specific years and specific cay comparisons, e.g. Grande vs. Anclitas in 2010 ( $\chi^2_1 = 17.67$ ,  $P < 0.01$ ) and 2011 ( $\chi^2_1 = 27.52$ ,  $P < 0.01$ ) with a larger proportion of males at the former in both years. Significant differences in sex ratios were also found between Grande and Caguama ( $\chi^2_1 = 20.11$ ,  $P < 0.01$ ) in 2010 and Anclitas and Caguama ( $\chi^2_1 = 12.27$ ,  $P < 0.01$ ) in 2011. In these cases, male-biased sex composition was recorded on Grande and Caguama. In contrast, during spring skewed sex ratios were observed less frequently; i.e., only between Caguama and Anclitas (years pooled) ( $\chi^2_1 = 21.96$ ,  $P < 0.01$ ), and specifically in March–April 2012 ( $\chi^2_1 = 17.11$ ,  $P < 0.01$ ), with a lower percentage of males trapped at the former locality.

**Age classes.**—Immature (hatch-year) individuals outnumbered adults at the three sites during autumn, with 69%, 81% and 79% of samples (years pooled). Comparisons among ringing sites did not yield significant differences except between Grande and Caguama ( $\chi^2_1 = 18.58$ ,  $P < 0.01$ ) and

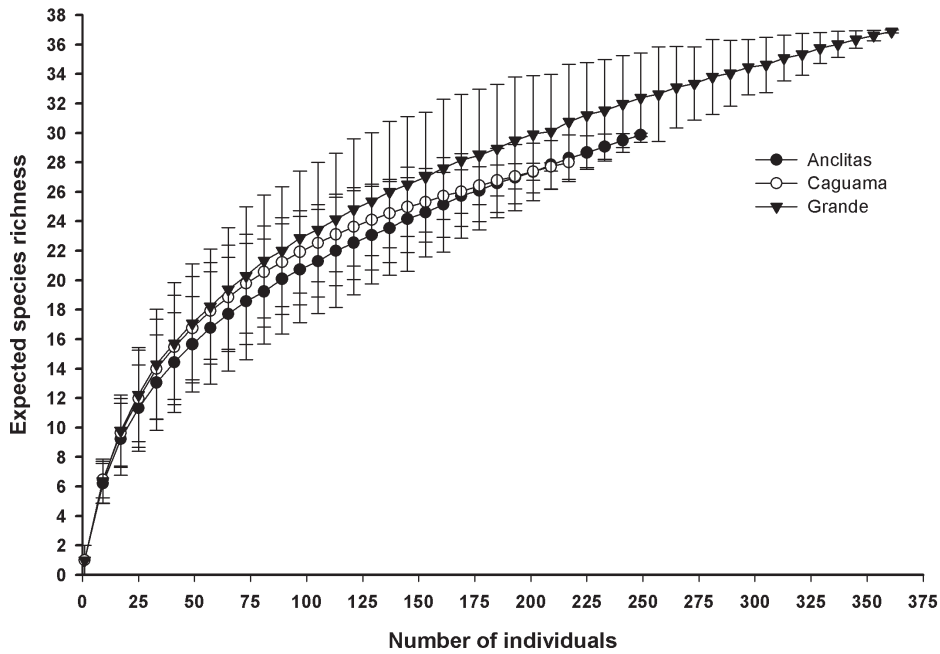


Figure 3. Rarefaction curves representing expected species richness for a standard sample of 217 individuals in three bird communities inhabiting the sandy coastal vegetation complex on Grande, Anclitas and Caguama Cays, Laberinto de las Doce Leguas, Cuba, 2009–2012.

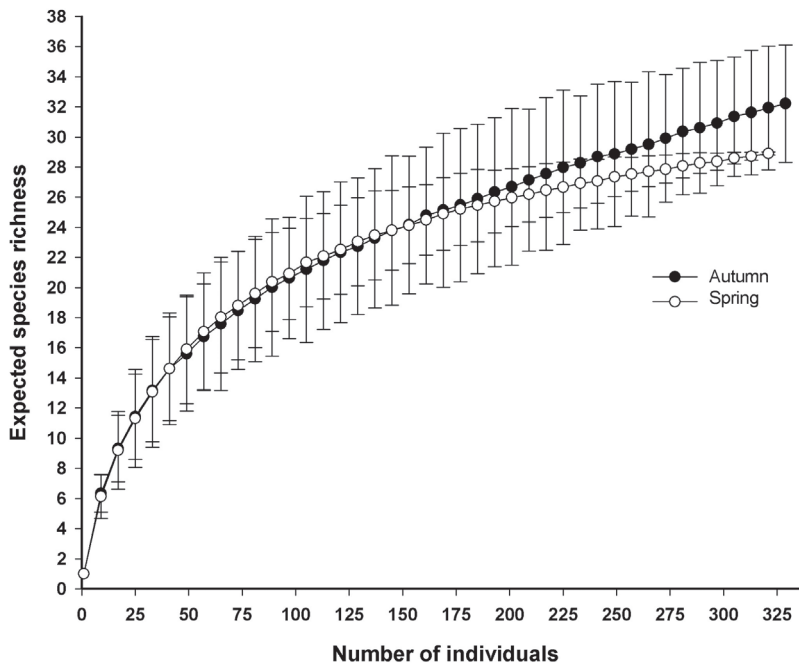


Figure 4. Rarefaction curves representing expected species richness in spring and autumn for a standard sample of 217 individuals in three bird communities inhabiting the sandy coastal vegetation complex on Grande, Anclitas and Caguama Cays, Laberinto de las Doce Leguas, Cuba, 2009–2012.



Anclitas and Caguama ( $\chi^2_1 = 22.22$ ,  $P < 0.01$ ), both in September 2009. Age ratios during spring were much less biased to a specific class, but immatures were slightly more prevalent on Caguama (55.5% of individuals) and Grande (50.3%), yet slightly under-represented on Anclitas (40%). Differences were only statistically significant when comparing Grande and Anclitas ( $\chi^2_1 = 40.83$ ,  $P < 0.01$ ), Caguama and Anclitas ( $\chi^2_1 = 35.80$ ,  $P < 0.01$ ), both in April 2011, as well as Grande and Caguama in March–April 2012 ( $\chi^2_1 = 16.62$ ,  $P < 0.01$ ).

**Retrap rates.**—During mist-netting sessions, 69 individuals of 15 species, nine of them Nearctic migrants, five permanent residents and one summer resident, were retrapped at least once. Among ringing stations, Grande and Anclitas yielded both the highest numbers of retrapped individuals (35 and 21) and overall recapture rates (11.1% and 9.6%), respectively, and on Caguama only 13 retraps or 6.7% were recorded. Among species, the highest number of individual retraps and retrap rates were recorded for Yellow Warbler, with 24 retrapped individuals and 21.4% of the overall retrap rate, followed by Prairie Warbler with 13% and 9.7% and Black-whiskered Vireo with 6% and 7.5%, respectively. Intra-year site fidelity was recorded for 20 individuals of seven species with a mean period between ringing and recapture of  $20.6 \pm 61.64$  days, range 1–206 days, but all were retrapped on consecutive days except two Prairie Warblers ringed in September 2009 and retrapped in April 2010. On the other hand, inter-year site fidelity was reported for 13 individuals of five species. Of these, seven were ringed in spring and retrapped subsequently in the same season (spring / spring return), a mean  $461 \pm 173.3$  days later, range 358–716 days, whereas four were autumn / autumn returns after a mean  $479.5 \pm 169.10$  days (range 388–733), one was a spring / autumn return (922 days) and one was an autumn / spring return (520 days). We recorded some noteworthy survival / longevity estimates. Assuming that birds hatched June–August, one Worm-eating Warbler *Helmitheros vermivorum* was at least three years and nine months old, singles of Prairie Warbler and Cape May Warbler *Setophaga tigrina* were two years and eight months old, and a Prairie Warbler was two years and two months old. Among residents, two three-year and three-month-old Yellow Warblers were trapped on Caguama, and a two-year and two-month-old individual of the same species on Anclitas. In addition, two Grey Kingbirds were retrapped on Grande; one was two years and eight months old and the other two years and two months old.

## Discussion

Current knowledge of species richness, not only on the sampled cays but for the entire LDL, relies solely

on a mist-netting protocol by which we detected 15 of the 24 additions to the avifauna of AJR. Most are uncommon or rare transients in Cuba<sup>30,31</sup>. Thus, we demonstrated the importance of mist-netting as a component of species inventories<sup>4,36</sup>, especially for recording passerines otherwise overlooked by other census techniques, and despite being time-intensive and requiring special training<sup>11</sup>. In fact, we found that the accumulation rate of newly recorded species may not have yet reached an asymptote after conducting, on average, six autumn and spring field seasons per site. Undoubtedly, increased sampling effort, both in time and space, will substantially improve knowledge of the current status of landbird migrants in the study area.

Overall, based on phenological categories, those species classed as winter residents in Cuba (mainly warblers), were remarkably dominant in both sampling periods and across the three sites, with the highest values on Grande and Anclitas Cays. Such numerical representativeness has been documented in numerous Cuban ecosystems during autumn and winter, as insectivorous warblers account for the majority of species that regularly migrate to Cuba<sup>3,13</sup>. In addition, the proportion of winter migrants within the community (30%) represents a mean value when considering that migratory species in tropical terrestrial habitats range from 4% to 51%<sup>35</sup>, although it can reach up to 58% if transients are considered. In fact, transients (28%) are as well represented as at locations in western Cuba (El Faro and Las Tumbas, Guanahacabibes), whose importance as critical stopovers for large numbers of migrants in autumn<sup>16</sup> is well known. On the other hand, permanent residents comprised the second-best represented phenological group, and were numerically dominated by the abundant *Setophaga petechia gundlachi* population in coastal mangroves, especially in March–April when the species' detectability increased at the onset of breeding. In contrast, summer residents accounted for a significant portion of the overall capture rate within bird communities, but only during autumn on Anclitas, which can be partially explained by the large numbers of hatch-year Black-whiskered Vireos present prior to migrating to the South American wintering grounds.

Most of the common species trapped during the period at the three banding sites are common winter residents and transients, with abundant populations in coastal ecosystems throughout the Cuban archipelago. To our knowledge, the mean species number trapped per day and overall relative abundance are the first such data from Cuba's sandy coastal scrub during migration. Wallace *et al.*<sup>50</sup> collected data in this habitat on Cayo Coco, but it was not analysed separately from dry coastal thorn scrub. Highest overall relative abundance (>40 birds / 100 net-hours) on Anclitas (September

2009), Grande (September 2009, October 2010 and September 2011), and Caguama (October 2012) are quite similar to those obtained in many shrub- and forest-dominated habitats on mainland Cuba by González *et al.*<sup>16</sup>; e.g., at Playa Dorada (Cayo Coco, Ciego de Ávila) in 1992, Caletones (Gibara, Holguín) in 1989, 1997, La Caridad (Mayarí, Holguín) in 1997, and El Faro (Guanahacabibes, Pinar del Río) in 1998. It should be also taken into account that in LDL, both the number of species trapped per day and overall relative abundance may have been affected, to some extent, by the under-estimated abundance of some species that exploited the study area during the sampling periods, e.g. pigeons (White-crowned Pigeon *Patagioenas leucocephala* and White-winged Dove *Zenaida asiatica*) and several mid-sized passerines (Grey Kingbird, Tawny-shouldered Blackbird *Agelaius humeralis* and Greater Antillean Grackle *Quiscalus niger*). Furthermore, field evidence suggests that many flocks could have gone undetected. These two widely known drawbacks to mist-netting protocols may have confounded estimation of the overall community's relative abundance at specific sites and seasons.

The consistency of skewed age ratios towards hatch-year birds during autumn across all years and sites supports the so-called 'coastal effect' proposed by Ralph<sup>34</sup>, by which a higher than expected percentage of juveniles occurs at coastal sites or at the peripheries of migratory routes. According to Dean *et al.*<sup>9</sup>, a proportion of hatch-year birds of  $\geq 90\%$  is common at coastal sites. This demographic pattern has been broadly confirmed by research<sup>26,52</sup> in coastal habitats of Alabama and Maine (USA), as well as on Paredón Grande and Coco Cays (north-central Cuba)<sup>42</sup> in autumn.

On the other hand, a significantly higher percentage of juveniles and lower overall relative abundance on Caguama Cay compared to the other two ringing sites in September 2009 potentially reflects temporal differences in habitat quality as a result of possible detrimental effects on foraging substrate and prey availability for insectivores following Hurricane 'Paloma' in early November 2008. Nearly one year later, we recorded the lowest relative abundance for all field seasons when extensive structural damage to coastal vegetation (defoliation, branch breakage, uprooting) was still noted on Caguama. Wallace<sup>49</sup> reported a decline in the abundance of bark-foraging (e.g., Black-and-white Warbler *Mniotilta varia*) and fly-catching insectivores (Tyrannidae) in semi-deciduous forests and coastal scrub on Cayo Coco following Hurricane 'Lili' in 1996. At our study site, sex ratios skewed towards females along with hatch-year individuals during autumn might reflect some degree of spatial segregation by Nearctic migrants displaced from optimal habitats by adults and males probably

exploiting mostly mainland ecosystems. This result supports the statement by Latta & Faaborg<sup>25</sup> that older birds and males may be disproportionately represented on Cuba and Hispaniola, and females and hatch-year birds on Puerto Rico and other islands further from the North American breeding grounds. Differences among ringing sites in specific years may be caused by the spatial variation in stopover ecology between the sexes during spring migration, e.g. habitat use, foraging behaviour, stopover length and fat storage, among others<sup>21</sup>.

Generally, both the number of recaptured individuals per species and per ringing site may be determined by the species' relative abundance and territorial behaviour, with Yellow Warbler, Prairie Warbler and Black-whiskered Vireo exhibiting the highest values, and Grande and Anclitas among sites. The currently insufficient and seasonally biased sampling effort not only may have contributed to the reduced overall recapture rate (19%), but also prevented assigning individuals unambiguously to migrants or winterers. Therefore, no overwinter site persistence and annual return rate, as defined by Latta & Faaborg<sup>24</sup>, could be determined. Our scant dataset suggests that inter-year fidelity, either as wintering or migration sites, does occur for many sampled species. Regarding the percentage of retrapped migrants within the same season during autumn, Grande and Anclitas Cays exhibited mean values compared to other coastal and inland sites in mainland Cuba. With respect to permanent residents, Grande Cay had a value slightly above the average of the aforementioned localities.

Although use of stopover sites in the Caribbean and Middle America is poorly known (but see Latta & Brown<sup>23</sup>, Deppe & Rotenberry<sup>10</sup>), the geographical location of Cuba's southern archipelagos and possibly low predation risks in the LDL may confer additional importance to the area as a stopover site for many Nearctic migrants. Any available habitat may be valuable to migratory birds for refueling<sup>39,40</sup> especially as these islands could represent almost the last land available prior to undertaking a non-stop flight across the Caribbean to northern South America. In addition, predators are characterised by low numbers and are locally distributed in the study area<sup>29</sup>, perhaps permitting uninhibited foraging relative to situations where migrants are concerned with predator avoidance<sup>8</sup>. Consequently, gaining body mass for fat-depleted birds will be favoured even in habitats with lower food availability. In this respect, many critical aspects of the wintering ecology of passerine migrants, e.g. dietary composition, mass gain rate, microhabitat usage and overwinter site fidelity, should be addressed by future studies to achieve more complete insight into the suitability of sandy coastal vegetation in LDL. This habitat, although possessing lower floristic richness compared to

similar mainland Cuban coastal habitats, and lacking marked temporal shifts in species richness, vegetation cover and individual numbers<sup>1</sup>, demands further scrutiny by expanding the sampling effort to the winter period. Likewise, coastal mangroves, which occupy a significant part of the study area's terrestrial landscape and are known to support large numbers of individuals and many species of migrants in Cuba and the Caribbean, also demand future research to better determine this habitat's suitability for both Nearctic transients and wintering residents. This may also assist clarifying species habitat usage patterns at the study site, and thus current interpretations of transients and winter residents, as well as overwinter site persistence.

Addressing the ecology of overwintering bird communities in the Caribbean should also aid a deeper understanding of species' adaptive responses to climate change, specifically the impacts of droughts and extreme weather events<sup>48</sup>. Such work will also enable the development of appropriate conservation strategies for passerines and near-passerines at regional scales within the Caribbean.

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Appendix I. Relative abundance (mean  $\pm$  SD) of 46 species reported during spring and autumn migrations (years pooled) in sandy coastal vegetation on Grande, Anclitas and Caguama Cays, Laberinto de las Doce Leguas, southern Cuba, 2009–12.

Family/Species	Locality/sampling seasons					
	Grande		Anclitas		Caguama	
	Autumn 2009–12	Spring 2010–12	Autumn 2009–12	Spring 2010–12	Autumn 2009–12	Spring 2010–12
<b>COLUMBIDAE</b>						
White-crowned Pigeon <i>Patagioenas leucocephala</i>	0.97 $\pm$ 0.198	-	-	-	-	-
White-winged Dove <i>Zenaida asiatica</i>	-	-	0.83	-	-	0.83
Zenaida Dove <i>Zenaida aurita</i>	-	-	0.56	-	-	-
<b>CUCULIDAE</b>						
Yellow-billed Cuckoo <i>Coccyzus americanus</i>	0.56	0.83	0.56	-	-	-
Mangrove Cuckoo <i>Coccyzus minor</i>	-	-	0.83	-	-	-
<b>TROCHILIDAE</b>						
Cuban Emerald <i>Chlorostilbon ricardii</i>	-	0.83	-	-	-	1.25 $\pm$ 0.594
<b>ALCEDINIDAE</b>						
Belted Kingfisher <i>Megasceryle alcyon</i>	0.56	-	-	-	-	-
<b>PICIDAE</b>						
Cuban Green Woodpecker <i>Xiphidiopicus percussus</i>	4.21 $\pm$ 5.395	1.25 $\pm$ 0.594	0.56	1.67	4.17	1.25 $\pm$ 0.594
<b>TYRANNIDAE</b>						
Cuban Pewee <i>Contopus caribaeus</i>	-	1.67	-	-	-	-
Eastern Wood Pewee <i>Contopus virens</i>	-	-	-	-	0.83	-
La Sagra's Flycatcher <i>Myiarchus sagrae</i>	0.86 $\pm$ 0.424	0.83	1.67	2.09 $\pm$ 0.587	-	1.67
Grey Kingbird <i>Tyrannus dominicensis</i>	0.83	1.67 $\pm$ 0.000	-	0.83	-	-
Loggerhead Kingbird <i>Tyrannus caudifasciatus</i>	1.85 $\pm$ 1.392	2.50 $\pm$ 0.587	1.81 $\pm$ 1.379	2.50 $\pm$ 0.000	3.75 $\pm$ 1.768	0.83
<b>VIREONIDAE</b>						
White-eyed Vireo <i>Vireo griseus</i>	1.16	-	0.83	-	-	-
Red-eyed Vireo <i>Vireo olivaceus</i>	1.03 $\pm$ 0.178	-	0.83	-	1.25 $\pm$ 0.594	-
Black-whiskered Vireo <i>Vireo altiloquus</i>	8.20 $\pm$ 10.798	1.67 $\pm$ 0.594	11.11 $\pm$ 1.181	0.83	5.83	1.25 $\pm$ 0.594
<b>TURDIDAE</b>						
Veery <i>Catharus fuscescens</i>	-	-	-	1.67	-	-
Grey-cheeked Thrush <i>Catharus minimus</i>	-	-	-	1.67	-	-
Swainson's Thrush <i>Catharus ustulatus</i>	0.83	-	-	-	-	-

**MIMIDAE**

Grey Catbird <i>Dumetella carolinensis</i>	-	0.83	0.83	-	0.83	-
Northern Mockingbird <i>Mimus polyglottos</i>	-	0.83	-	0.83	1.67	0.83

**PARULIDAE**

Ovenbird <i>Seiurus aurocapilla</i>	1.16	-	1.11	-	0.83	-
Worm-eating Warbler <i>Helmitheros vermivorum</i>	2.22 ± 1.570	0.83 ± 0.000	2.22	1.67 ± 0.000	0.83	-
Northern Waterthrush <i>Parkesia noveboracensis</i>	4.04 ± 2.802	1.67	1.94 ± 1.174	-	5.00 ± 4.130	2.50 ± 1.174
Black-and-white Warbler <i>Mniotilta varia</i>	0.70 ± 0.191	0.83	2.22	0.83 ± 0.000	1.67	0.83
Prothonotary Warbler <i>Protonotaria citrea</i>	0.56	-	-	-	-	-
Tennessee Warbler <i>Oreothlypis peregrina</i>	-	0.83	-	-	-	-
Common Yellowthroat <i>Geothlypis trichas</i>	1.50 ± 0.294	1.67	4.17 ± 1.181	0.83 ± 0.000	0.83 ± 0.000	1.67 ± 1.181
Hooded Warbler <i>Setophaga citrina</i>	0.56	-	0.56	-	-	-
American Redstart <i>Setophaga ruticilla</i>	1.61 ± 0.645	2.08 ± 1.768	1.39 ± 0.594	0.83	1.39 ± 0.000	1.67
Cape May Warbler <i>Setophaga tigrina</i>	-	2.78 ± 3.536	-	0.83	0.82	0.83
Northern Parula <i>Setophaga americana</i>	-	7.22 ± 6.484	0.83	2.50	0.83 ± 0.000	1.67
Bay-breasted Warbler <i>Setophaga castanea</i>	1.16	-	-	-	-	-
Yellow Warbler <i>Setophaga petechia</i>	6.94 ± 2.402	6.67 ± 2.355	3.98 ± 4.320	9.16 ± 7.071	4.15 ± 2.397	10.84 ± 2.355
Black-throated Blue Warbler <i>Setophaga caerulescens</i>	1.67 ± 0.000	0.83	3.75 ± 1.768	0.83	2.22 ± 1.181	-
Palm Warbler <i>Setophaga palmarum</i>	3.49	3.61 ± 0.000	4.17	1.39 ± 1.181	1.67 ± 1.181	10.0 ± 3.536
Yellow-throated Warbler <i>Setophaga dominica</i>	0.85 ± 0.300	-	-	-	1.65 ± 1.153	0.83
Prairie Warbler <i>Setophaga discolor</i>	11.01 ± 5.909	7.22 ± 0.587	5.56 ± 1.181	2.78 ± 1.768	3.74 ± 2.383	4.59 ± 0.587
Yellow-breasted Chat <i>Icteria virens</i>	-	1.67	-	-	-	-

**CARDINALIDAE**

Summer Tanager <i>Piranga rubra</i>	0.83	-	-	-	-	-
Scarlet Tanager <i>Piranga olivacea</i>	2.33	-	-	-	0.82	-
Indigo Bunting <i>Passerina cyanea</i>	0.83	-	-	-	0.83	-

**ICTERIDAE**

Tawny-shouldered Blackbird <i>Agelaius humeralis</i>	-	1.67	-	0.83	-	1.67 ± 1.181
Greater Antillean Grackle <i>Quiscalus niger</i>	2.28 ± 1.051	0.83 ± 0.000	0.70 ± 0.191	0.83	1.67 ± 1.181	1.67
Cuban Oriole <i>Icterus melanopsis</i>	0.83	-	-	-	-	0.83
Baltimore Oriole <i>Icterus galbula</i>	-	-	-	-	0.83	-