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ARTICLE

The abundance of Red-bellied Macaws (*Orthopsittaca manilata*) and Orange-winged Parrots (*Amazona amazonica*) in relation to fruiting Moriche Palms (*Mauritia flexuosa*) at the Aripo Savannas, Trinidad

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ABSTRACT: The largest remaining savanna ecosystem on the island of Trinidad is the Aripo Savannas Environmentally Sensitive Area (ASESA). It has been historically fragmented due to a number of anthropogenic activities. This study focused on the densities of the Red-bellied Macaw (*Orthopsittaca manilata*) and Orange-winged Parrot (*Amazona amazonica*), which are known to rely on palms for roosting, nesting and feeding at the ASESA, in relation to the distribution of the fruiting Moriche Palms (*Mauritia flexuosa*) at the ASESA. There was a significant correlation between the total number of birds and number of fruiting Moriche Palms on transects for macaws (r_s = 0.708, P = 0.022) but not for parrots (r_s = 0.421, P = 0.225). Average group size increased significantly from the late rainy to the early dry season in macaws, but not in parrots. Point count surveys estimated higher densities than line transects for both macaws (129 *vs.* 87/km^2) and parrots (193 *vs.* 103/km^2). The use of peripheral areas showed that fragmentation had no effect on the foraging behavior of macaws or parrots. Nevertheless, if the savannas become increasingly modified, human-parrot conflicts may increase and so food resources should be integrated into management plans for this protected area.

KEY-WORDS: feeding ecology, fragmentation, population density, Psittacidae, seed dispersal.

INTRODUCTION

Thirty percent of Neotropical psittacid species face some threat of extinction and 70% have decreasing population sizes (Collar 2000). The two main drivers of psittacid population decline are habitat loss and the wildlife trade (Juniper & Parr, 1998, Snyder *et al.* 2000, Wiley *et al.* 2004, Deem *et al.* 2008). Bennett & Owens (1997) attribute the high vulnerability of psittacids to their frugivorous diet, large body sizes and small clutch sizes.

Psittacids usually make substantial foraging movements between roosting and feeding sites, exploiting a variety of vegetation types (Ragusa-Netto 2004). Some species switch their diets in response to resource scarcity (Renton 2001, Moegenburg & Levey 2003). Other species move across patchy habitats in relation to the seasonal availability of food resources (Ortiz-Maciel *et al.* 2010). These studies have primarily focused on the feeding behavior of psittacids in forests. Nevertheless, psittacids inhabit a wide range of habitats from semi-open country to savannas (Ragusa-Netto 2004), and avian resource use within Neotropical savannas remains poorly understood (Maruyama *et al.* 2013). Furthermore, little is known about the interaction between frugivores such as psittacids and the Moriche Palm (*Mauritia flexuosa*) (Villalobos & Bagno 2012), a characteristic species of Neotropical savanna ecosystems including those in Trinidad. Knowledge of how populations respond to the variation in distribution of resources is essential for understanding how species function in their environments (Matuzak *et al.* 2008) and identifying key resources, habitats and areas to be conserved (Renton 2001).

The Aripo Savannas Environmentally Sensitive Area (ASESA) is one of only two remaining natural savanna ecosystems in Trinidad. It supports highly diverse floral and faunal communities. A total of 132 species of birds have been recorded of which three; Lilac-tailed Parrotlet (*Touit batavicus*), Orange-winged Parrot (*Amazona amazonica*), and Red-bellied Macaw (*Orthopsittaca manilata*) are psittacids. Some of these birds are highly associated with the Moriche Palm, such as the rare Moriche Oriole (*Icterus cayanensis chrysocephalus*), the

Sulphury Flycatcher (*Tyrannopsis sulphurea*) and the Fork-tailed Palm-swift (*Tachornis squamata*) (EMA 2007). During World War II the United States Army used the ASESA as a base during which time roads and bunkers were built. The roads divided the savannas subsequently facilitating quarrying, illegal logging and hunting, which continue today. After the army abandoned the base in 1956 settlements were established around the ASESA (EMA 2007). Historic fragmentation may have had an impact on the Moriche Palms and consequently its seed dispersers such as the Red-bellied Macaw (Federman *et al.* 2013). Moriche Palms are long lived diploid dioecious plants, and are the dominant palm species bordering the seasonally inundated savannas, in bands 3–20 m wide (Federman *et al.* 2013). In these areas where monodominant stands exist, the presence of other fruiting species is minimal, allowing researchers to directly explore the relationship between avian frugivores and fruit availability (Moegenburg & Levey 2003).

Red-bellied Macaws usually form flocks of up to 100 individuals, as they are highly social and have been reported to be fairly common in the ASESA (Forshaw 2010). Orange-winged Parrots also form flocks of up to 100 individuals, but are mostly seen flying in pairs (Forshaw 2010). These psittacids are non-threatened but are dependent upon palm swamp for roosting, feeding and nesting, which makes them vulnerable to threats against this habitat (Bonadie & Bacon 2000, Renton 2004, Brightsmith 2005). The objective of this study is to describe the feeding ecology of the Red-bellied Macaws and Orange-winged Parrots at the ASESA with particular interest in the relationship between the distribution of fruiting Moriche Palms and psittacid abundance and feeding behavior.

METHODS

Study area

The ASESA (10°35'N; 61°12'W) is a triangular area located south of the Northern Range on the island of Trinidad of the Republic of Trinidad and Tobago (Fig. 1). Its borders are the Valencia River (west); the Aripo River and the Eastern Main Road (east); and the abandoned Trinidad Government Railway Reserve (TGR, south). The ASESA covers 18.8 km^2 of land surface (EMA 2007).

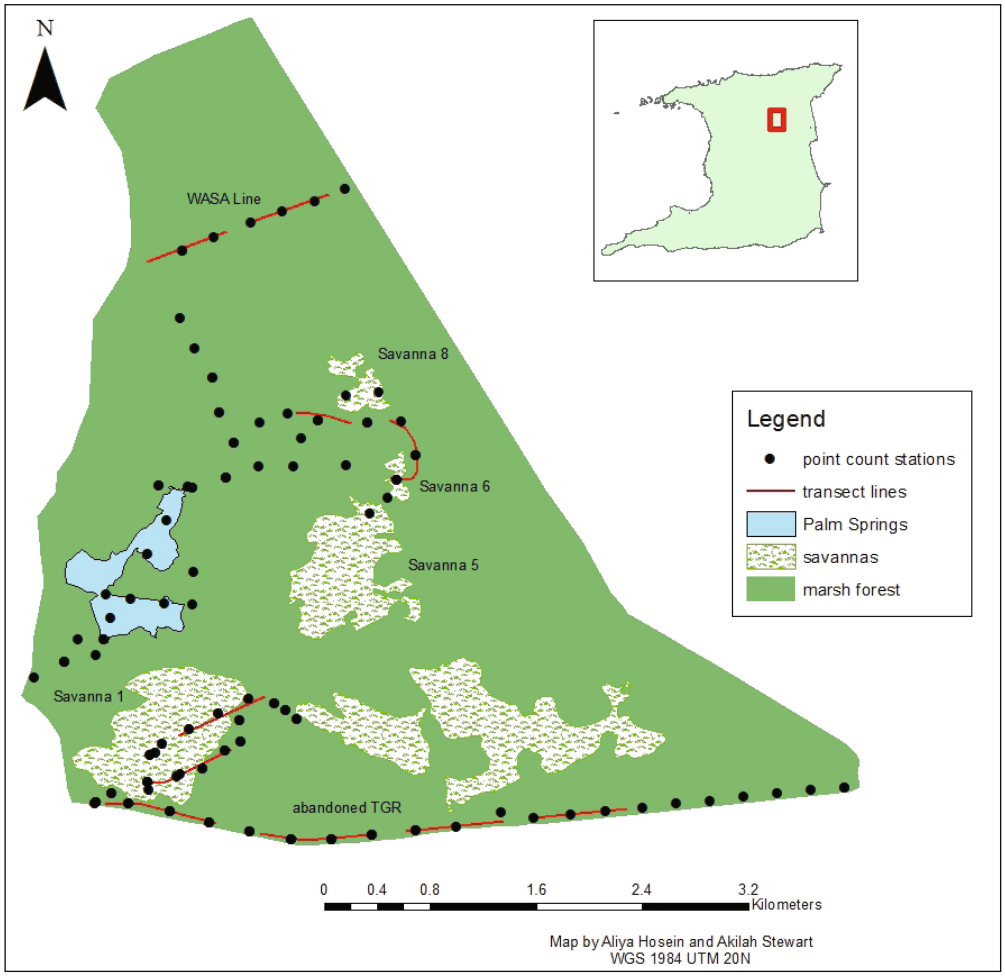

Figure 1. Location of transect lines and point count stations in the Aripo Savannas Environmentally Sensitive Area (ASESA). The ASESA's location in Trinidad is indicated by the red box in the inset map of the island (top right hand corner).

Beard (1946) described the Aripo Savannas as an edaphic marsh savanna formation comprising three vegetative communities: marsh forest, savanna and palm marsh. The land area is mostly marsh forest dominated by the palms; Palma Real (*Oenocarpus bataua*), Manac (*Euterpe precatoria* and *E. oleracea*), Timite (*Manicaria saccifera*), Royal Palm (*Roystonea oleracea*) and Cocorite (*Attalea maripa*) and associated plants. Wild Calabash (*Tabebuia stenocalyx*), Agalie (*Ficus* sp.), Matapal (*Clusia palmicida*), Biscuit Wood (*Ilex arimensis*), and Bois Charbon (*Diospyros ierensis*), are found in the lower stratum. Galba (*Calophyllum lucidum*), Wild Kaimit (*Pouteria* sp.), Yellow Mangue (*Symphonia globulifera*), Bois Bande (*Parinari campestris*), Cajuca (*Virola surinamensis*) and Wild Pine (*Podocarpus coriaceus*) comprise the upper stratum (Young 2006).

The savannas occur as 10 open areas of grass-sedge vegetation amidst the marsh forest (Richardson 1963). Trinidad and Tobago experiences a rainy season which lasts from May to December and a dry season from January to April. In the rainy season the hardpan layer in the savannas prevents percolation of water and the soil becomes waterlogged. In the dry season precipitation is low and the soil becomes extremely hard. These conditions prevent woody plants from colonizing savannas. Savannas are dominated by sedges and grasses such as the endemic *Rhynchospora aripoensis* and *Xyris grisebachii* (Beard 1946). The sedge *Lagenocarpus rigidus* is the most widespread species found throughout the savannas (Cooper *et al.* unpub. data). Among the grasses and sedges there are also bladderworts, ground orchids (*Cyrtopodium parviflorum*), carnivorous sundews (*Drosera capillaris*), Savanna Roseau (*Bactris campestris*) and the occasional tangle of parasitic vine (*Cassytha americana*) (Young 2006).

The palm marsh forms an intermediate between the savannas and marsh forest. It is found either fringing the savannas or in isolated islands (palm islands) within the savannas (Beard 1946) with Fat Pork (*Chrysobalanus icaco*) and Savanna Serrette (*Byrsonima crassifolia*) in the lower stratum and Moriche Palms (*Maurita flexuosa*) in the upper stratum (Young 2006).

Abundance

To sample macaw and parrot abundance the variable distance line transect survey method was used (Casagrande & Beissinger 1997, Buckland 2006, Thomas *et al.* 2010) from October 2014 to March 2015, and point counts from January to November 2014 and in January, July and November 2015. A total of 10 transects on existing access trails (Buckland *et al.* 2010), each 1 km long, were dispersed at least 300 m apart (Matuzak *et al.* 2008) throughout the study area to get a representative sample of resource availability (Renton 2001). The transect lines traversed a variety of habitat types: pine/palm marsh ecotone (TGR1 and 2); palm marsh (TGR3); palm marsh/marsh forest (TGR4, BT, S82); savanna (HR); palm marsh/savanna ecotone (S81); and marsh forest/savanna ecotone (WASA1 and 2). Each transect was sampled once in both the late rainy season (October to December) and the early dry season (January to March) from 06:00 to 09:00 h (EST). Sunrise varied from 05:45 to 06:30 h in this period.

Existing trails were used because the area is inundated during the rainy season, which would make some of the area inaccessible, and the ASESA is protected and new trails cannot be cleared. Point count stations, about 250 m apart, were randomly positioned along and within the general area of the designated trails (Fig. 1).

Point counts were conducted from 06:00 to 11:00 h and at each station observation lasted for 10 min. When one or more macaws or parrots were encountered, date, time, location, vegetation type, number of individuals, if perched, and initial perpendicular distances from the observer were recorded. When a macaw was heard but not seen it was recorded as one individual (Pizo *et al.* 1995, Galetti 1997). Care was taken to avoid multiple counts of the same bird, and birds flying over the area were recorded separately from perched birds. A Nikon Forestry Pro laser rangefinder was used to measure distances, and Eagle Optics Ranger 8 × 42 Roof Prism Binoculars RGR-4208 to correctly locate and count psittacids. Species identification was confirmed using Forshaw (2010).

Diet

The feeding behavior of the psittacids were recorded simultaneously during line transect surveys. One feeding bout was recorded whenever one or more macaws or parrots were found feeding on a plant species. If the bird(s) moved to another plant to feed during the same observation period, a new feeding bout was recorded (Galetti 1993, Galetti & Pizo 1996). For each feeding bout the date, time, location, number of birds foraging, the plant species consumed and part eaten (flowers, pulp or seeds), and vegetation type, were recorded (Galetti 1997, Renton 2001). Specific attention was paid to the location of birds so that groups could be separated and length of visit could be calculated (Moegenburg & Levey 2003, Ragusa-Netto 2004). A feeding bout ended when macaws or parrots finished foraging and moved away (Contreras-González *et al.* 2009).

Fruiting Moriche Palms

The numbers of female Moriche Palms already bearing immature (exocarp green-brown with green flesh) and ripe (exocarp red-brown with yellow flesh) fruits on both

sides of each transect were counted (Bonadie & Bacon 2000) in the late rainy season. This number did not change during the early dry season.

Data analysis

Spearman's rank correlation analysis was used to examine the relationship between the number of fruiting palm trees and total numbers of parrots and macaws detected in each transect in the two sampling periods combined (Galetti 1997, Bonadie & Bacon 2000, Ragusa-Netto 2004). The Mann Whitney *U*-test was used for pairwise comparisons, such as group sizes of species and their distribution in relation to seasons, since data followed a non-normal distribution. Statistical analyses were performed using the R software, v. 3.1.2 (R Core Team 2014), for statistical computing and graphing. All statistical tests used $\alpha = 0.05$.

All distances for parrots and macaws were pooled across survey months to increase the number of detections for calculating density estimates from point count and line transect surveys using the conventional distance sampling (CDS) engine in Distance 6.2 (Buckland *et al.* 2001, Thomas *et al.* 2010). The outermost distances at which detections were low were excluded from the analysis to get a better fit of detection models. Additionally, all detections of parrots and macaws were treated as clusters. All detection functions were considered and model selection was based on minimum difference in Akaike's Information Criterion AIC_c (values < 2 considered similarly parsimonious; Rivera-Milán *et al.* 2005).

RESULTS

Red-bellied Macaw and Orange-winged Parrot density

Red-bellied Macaws and Orange-winged Parrots were seen on each visit to the ASESA. Mean ± 1 standard deviation of macaw group size in the late rainy season was 3.47 ± 4.53 individuals (range = 1–15, $n = 34$), whereas group size was 5.87 ± 9.18 individuals (range = 2–50, $n = 39$) in the early dry season. Red-bellied Macaw group sizes were significantly different between the two study periods ($U = 420$, $P = 0.006$). The Red-bellied Macaws were mostly observed in the southwestern half of the ASESA along the abandoned TGR, in Savanna 1 and Palm Springs. They were least abundant at the northern and north western end in the marsh forest and palm marsh, and were mostly flight records in these areas (Hosein 2015).

Regarding the Orange-winged Parrot, mean ± 1 standard deviation of group size in the late rainy season was 2.69 ± 3.65 individuals (range = 1–25, $n = 91$) individuals compared to 2.14 ± 1.89 individuals (range 1–18, $n = 137$) in the early dry season. Orange-winged Parrot group sizes did not differ significantly between the two study periods ($U = 6218.5$, $P = 0.970$). Parrots were observed along all transect lines and at all point count stations. They were consistently found perched in the palm fringes of savannas 1 and 8, as well as in the marsh forest at the northern end of the ASESA.

Macaws were detected at a maximum distance of 155.4 m from the line transect. The uniform key function with cosine adjustment term ($\chi_1 = 3.82$, $P = 0.05$; $AIC_C = 1.62$) provided the best fit to the data. Parrots were detected at a maximum distance of 170 m, but in order to remove outliers, perpendicular distances were truncated at 150 m. The uniform key function with cosine adjustment term ($\chi_1 = 5.07$, $P = 0.02$; $AIC_C = 0.49$) provided the best fit to the data.

Point count surveys produced higher density estimates for both species (Table 1). Maximum detection distance for the macaws and parrots were 220 and 200 m, respectively. The half-normal key function with cosine adjustment term provided the best fit to the data for both macaws ($\chi_2 = 11.02$, $P < 0.05$; $AIC_C = 0.21$) and parrots ($\chi_4 = 8.57$, $P < 0.05$; $AIC_C = 0.49$).

Fruiting Moriche Palms

A total of 1946 mature canopy-sized Moriche Palms were recorded, of which 110 were fruiting. Transect TGR3 had the highest total number of Moriche Palms per km (333), and transect TGR2 had the highest number of fruiting palms (29). There were no Moriche Palms in WASA2. Neither male nor female palms were flowering during the transect study period.

Table 1. Mean ± 1 standard deviation (SD) of the density (Number/km^2) and coefficient of variation (CV) of Red-bellied Macaws and Orange-winged Parrots from line transect (October 2014 to March 2015) and point count (2014 to 2015 in consecutive months) surveys in the ASESA, Trinidad. *n* = Number of observations.

	Red-bellied Macaw			Orange-winged Parrot		
	n	**Mean ± SD Number/km^2**	**CV (%)**	***n***	**Mean ± SD Number/km^2**	**CV (%)**
Line transect	31	87.4 ± 47.7	54.6	90	102.9 ± 24.4	23.7
Point count	39	129.2 ± 40.5	31.3	157	192.5 ± 37. 3	19. 5

Red-bellied Macaw and Orange-winged Parrot diet

Orange-winged Parrots were not observed feeding on the palm fruits or fruits of any other available plant species, such as Manac (*Calyptroma rivalis*), Gri Gri (*Acrocomia aculeate*), Pois Doux (*Inga ingoides*) or Cajuca during survey periods. However, they were seen with a feeding flock of macaws on two occasions along the abandoned TGR. The Red-bellied Macaws were observed feeding on Moriche Palm fruits. Out of 11 feeding observations, eight were made along TGR2 during both survey periods. Single feeding observations were made in Hedgerow, Bunker Trail and WASA 1 during the late rainy season. A positive correlation was found between the total number of birds in the two sampling periods and number of fruiting Moriche Palms on the 10 transects for macaws (r_s = 0.708, P = 0.022) but not for parrots (r_s = 0.421, P = 0.225). The feeding macaw flock sizes ranged from 15 to 30 individuals. They generally divided into smaller groups of 2 to 5 around the feeding palm tree. Macaws vocalized during feeding and occasionally switched between individual fruiting Moriche Palms. Feeding took place between 7:00 h and 8:30 h, and lasted between 10 and 30 min. At the end of the feeding bout about half of the flock would circle around the feeding area and return to the feeding palm, at which point the other half of the flock would join before flying off together. They only fed on ripe palm fruits with the exception of one pair that were seen feeding on immature fruits. Some macaws perched on the bunch and used their beaks to remove the scales of the exocarp, after which they would eat the exposed pulp. The fruits were partially eaten and left attached to the bunch with the pulp exposed. Other macaws removed the fruit from the bunch and perched on the palm frond of the same tree, or flew to the nearest palm with the fruit in their beaks. They would then manipulate the fruit with their feet by rolling the fruit while removing the scales of the exocarp. Macaws usually ate all the pulp from fruits that were removed from the bunch. They then dropped the clean endocarp to the base of the palm on which they were perched. Neither intraspecies antagonistic nor sentinel behaviors were observed during feeding.

DISCUSSION

Macaws and parrots are still abundant in the ASESA, although widespread fragmentation and human encroachment has occurred in the area (EMA 2007). Density estimates from point count surveys exceeded line transect counts, similar to findings reported for Green-rumped Parrotlets (*Forpus passerines*) in the Llanos of Venezuela (Casagrande & Beissinger 1997). Orange-winged Parrot density was higher than Red-bellied Macaw, but in other studies Red-bellied Macaw density was higher than other psittacid species at sites containing *Mauritia*-dominated palm swamps (Karubian *et al.* 2005, Rodrigues *et al.* 2012). Both behaviors and the different habitat types surveyed in this study could explain the higher density of Orange-winged Parrot reported. Our results indicate that the ASESA at present is able to sustain large psittacid populations because of its palm species which supply fruits throughout the year with peak ripe fruit availability during the driest months (Villalobos & Bagno 2012) and other flowering and fruiting tree species. However, due to their low reproductive output, sustained fragmentation of reserves can also cause low psittacid species diversity and densities, as seen in Brazil and Argentina (Marsden *et al.* 2000, Marsden & Pilgrim 2003, Rivera-Milán *et al.* 2005).

Despite their conspicuous vocalizations and size, lower number of sightings and smaller average group sizes were recorded for the macaws in the late rainy season compared to the early dry season. The increase in Red-bellied Macaw flock size from rainy to dry season was also recorded at the palm swamps of the Brazilian Cerrado. Sightings become difficult during the mating period when pairs are formed and they are less vocal. They also cover a larger area when searching for suitable nesting sites, thereby resulting in a decrease in density of individuals (Rodrigues *et al.* 2012). Weather is also known to bring about significant changes in psittacid behavior: rain and lower temperatures reduce song, flying and communal roosting (Brightsmith 2004).

The Red-bellied Macaw prefers palm marsh habitats (Bonadie & Bacon 2000, Oehler *et al.* 2001, Renton 2004, Brightsmith 2005, Rodrigues *et al*. 2012) whereas Orange-winged Parrots can be found in a variety of habitats, such as mangroves, gallery forests and also drier woodlands (Forshaw 2010). The diets of both species contain mostly palm fruits (Bonadie & Bacon 2000) but according to Roth (1984) Red-bellied Macaw is specialized on the Moriche Palm fruit and, therefore, remains close to these palms. This would explain its high abundance in the palm marshes at the ASESA. The distributions of fruiting Moriche Palms and Red-bellied Macaws were correlated in the ASESA, and a close association with the Moriche Palm has also been observed in the palm swamps of the Nariva Swamp and Brazilian cerrados (Bonadie & Bacon 2000, Villalobos & Bagnos 2012, Rodrigues *et al.* 2012).

Interestingly, most macaw sightings and feeding observations were made along the abandoned TGR, at the edge of the ASESA adjoining a residential area, and in the palm marsh fringing Savanna 1, where fruiting Moriche Palms were most abundant, suggesting that their behavior may not be affected thus far by habitat fragmentation. Savanna 1 is located near Cumuto village and Forestry Division buildings and is the designated

tourism and education zone. Psittacids demonstrate the ability to track food resources thereby changing habitat use on both spatial and temporal scales (Renton 2001). It is possible that psittacids compare suitable foraging sites. Moegenburg and Levey (2003) have shown that relative abundance of fruits and not absolute abundance affects foraging choices in frugivores. The high number of macaws present in the south western end of the ASESA may be in relation to the availability of the Moriche Palm fruits. This implies the need to study its fruit tracking behavior across the entire landscape (Moegenburg & Levey 2003) including the nearby villages and palm swamp in the Arena Forest.

Macaws and parrots foraging in developed areas can result in increased conflicts between humans and psittacids as savannas become increasingly modified (Matuzak *et al.* 2008). Oehler *et al.* (2001) predict that a decrease in palm fruit availability may intensify the use of substitute food resources such as cacao and other cultivated crops by psittacids, thereby creating competition for food resources between local farmers and psittacids. This particularly applies to the Orange-winged Parrot that already exhibits this behavior and is classified as vermin under the Conservation of Wild Life Act of Trinidad and Tobago. Its depredation of crops can be lethally controlled on privately owned land, but could be prevented by augmenting food species in protected areas.

It is known that Red-bellied Macaws function as seed dispersers since they can transport and eat the Moriche Palm fruits without damaging seeds. On a small spatial scale this is critical for gene flow for the Moriche Palm population. Federman *et al.* (2013) reported high levels of nearest-neighbour mating in a collection area of 10 km^2 at the ASESA. They suggest this may be related to fragmentation and uncontrolled hunting of other seed dispersers such as the Red Brocket Deer (*Mazama americana*). The macaws sometimes left the fruit attached to the bunch while feeding. Other studies from central Brazil have shown that, as a result, the exposed pulp was made available in the canopy layer to other bird species including Palm Tanager (*Thraupis palmarum*), Sayaca Tanager (*Thraupis sayaca*), Black-faced Tanager (*Schisthochlamis melanopis*), Chopi Blackbird (*Gnorimopsar chopi*) and Curl-crested Jay (*Cyanocorax cristatellus*) (Tubelis 2009, Villalobos & Bagno 2012). In a study by Tubelis (2009) an Ash-throated Crake's (*Porzana albicollis*) stomach was found to contain solely Moriche Palm pulp, indicating that fruits opened by psittacids were also eaten by other bird species while on the ground. Both Palm Tanager and Ash-throated Crake can be found at the Aripo Savannas.

Results from this study highlight the importance of palm marshes within the ASESA to Red-bellied Macaw and Orange-winged Parrot populations as habitats in which food resources are obtained. It is also a site in which the public can see large numbers of free-living parrots and macaws to foster a culture of responsibility for protecting the environment.

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