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BIRD SPECIES THAT DISPERSE NATIVE SEEDS OF THE CHACO SERRANO FOREST IN A NATURE RESERVE OF CENTRAL ARGENTINA

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Abstract · Birds are capable of linking ecosystems throughout the dispersion of seeds. Such a role turns them into key elements to mitigate habitat fragmentation effects. However, it has been postulated that only legitimate dispersers may provide this service. In Vaquerías Nature Reserve, located in a fragmented landscape of the Chaco Serrano Forest, we captured birds between January and April of 2017 and 2018, retrieved whole seeds from their feces, and evaluated their germination to identify the assembly of bird species that serve as seed dispersers in the area. From feces of nine bird species, we retrieved over 100 seeds of 13 native plant species. Based on the number of whole seeds recovered from feces and their germinability, we recognized the Small-billed Elaenia (*Elaenia parvirostris*), the Creamy-bellied Thrush (*Turdus amaurochalinus*), the Black-and-chestnut Warbling Finch (*Poospiza whitti*), the Rufous-collared Sparrow (*Zonotrichia capensis*), and the Golden-billed Saltator (*Saltator aurantiirostris*) as seed dispersers of native plants in the reserve. It is worth noting that not all these species are considered frugivorous and seed dispersers. For example, the Rufous-collared Sparrow and the Golden-billed Saltator have been previously considered as granivorous, and traditionally thought of as seed predators disregarding their potential role of seed dispersers. Our results, however, indicated that they may act as legitimate dispersers of some native species. This study highlights the need to further evaluate the functional role as seed dispersers of several bird species that include fruits in their diet, considering not only fruit handling and consumption, but also information regarding seed viability and germination.

Resumen · Especies de aves que dispersan semillas nativas del bosque Chaco Serrano en una reserva natural del centro de Argentina
Las aves son capaces de vincular ecosistemas a través de la dispersión de semillas. Tal rol las convierte en elementos clave para mitigar los efectos de la fragmentación. Sin embargo, se ha postulado que solo los dispersores legítimos pueden proporcionar este servicio. En la Reserva Natural Vaquerías, ubicada en un paisaje fragmentado del bosque Chaqueño Serrano, entre enero y abril de 2017 y 2018, capturamos aves, extrajimos semillas enteras de sus heces y evaluamos su germinación para identificar el conjunto de especies de aves que sirven como dispersores de semillas en la zona. De las heces de nueve especies de aves, recuperamos más de 100 semillas e identificamos 13 especies de plantas nativas. Con base en la cantidad de semillas recolectadas de sus heces y su germinabilidad, reconocimos el fiofío pico corto (*Elaenia parvirostris*), el zorzal chalchalero (*Turdus amaurochalinus*), el sietevestidos serrano (*Poospiza whitti*), el chingolo (*Zonotrichia capensis*) y el pepitero de collar (*Saltator aurantiirostris*) como dispersores de semillas de plantas nativas de la zona. Es relevante señalar que no todas esas especies son consideradas frugívoras y dispersoras de semillas. Por ejemplo, el chingolo y el pepitero de collar han sido previamente considerados granívoros, por lo que se les asignó el papel de depredadores de semillas, despreciando su potencial rol como dispersores de semillas. Sin embargo, nuestros resultados indicaron que pueden actuar como dispersores legítimos de algunas especies nativas. Este estudio destaca la necesidad de evaluar más a fondo el rol funcional como dispersores de semillas de varias especies de aves que incluyen frutos en su dieta, considerando no solo el manejo y consumo de los mismos, sino también información sobre la viabilidad y germinación de las semillas.

Key words: Córdoba · Endozoochory · Fleshy fruits · Frugivory · Mist Net · Native Forest · Ornithocory

INTRODUCTION

The Gran Chaco Americano is the ecoregion with the highest deforestation rates in the Neotropics (Zak et al. 2008, Baumann et al. 2017). The southernmost and arid portion of the ecoregion (which is mostly represented in the Province of Córdoba, Argentina) is the one that has suffered the most intense deforestation process in recent decades (Zak et al. 2008, Barchuk et al. 2010). Remnants of that ecoregion, which act as biodiversity relicts in the area (Verga et al. 2017, 2018), currently encompass a highly fragmented mosaic of isolated forest patches, surrounded by a matrix of dense thorn scrub, product of inadequate agricultural practices; semi-natural grasslands exposed to intensive livestock grazing; and cultivated lands (Zak et al. 2008, Ren-

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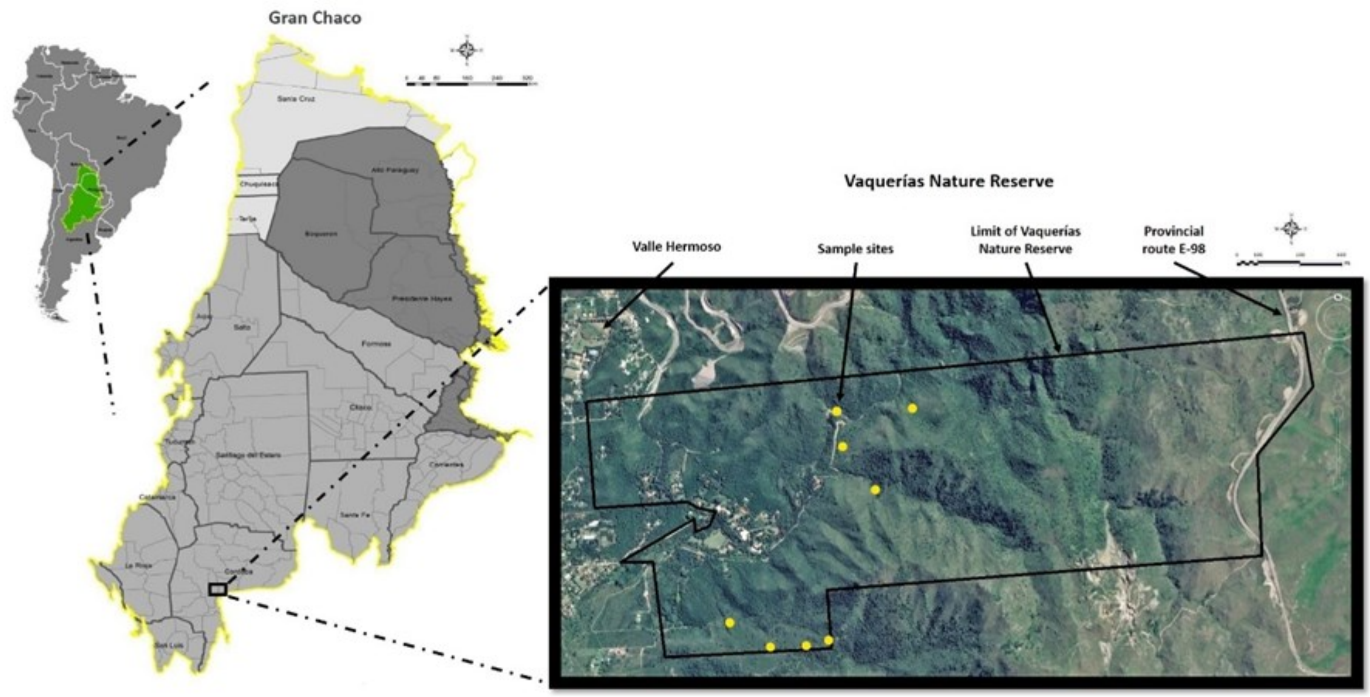

Figure 1. Location of Vaquerías Nature Reserve in the Chaco Forest of Argentina and sampling sites where the study was conducted between 2017 and 2018 (yellow dots).

ison et al. 2013, Hoyos et al. 2013).

Fragmentation of the Chaco Forest has produced negative consequences on biodiversity and its ecosystem services (e.g., Pacha et al. 2007, Grilli et al. 2017, Verga et al. 2017, 2020). Initiatives proposed to mitigate similar effects in other areas include the creation and maintenance of protected areas (Sala et al. 2000, Bruner et al. 2001, Nagendra 2008, Adeney et al. 2009, Butchart et al. 2012). The southern portion of the Chaco Forest, however, has a very low proportion of protected lands within reserves and only less than 9% of its surface is legally protected (Burkart 2005, Giraudo 2009, Nori et al. 2016). Furthermore, the few protected areas lack sufficient geographic connectivity (Morea 2014, Crespo Guerrero & Peyroti 2016). It is of great importance to maintain healthy biotic assemblies that connect protected areas, ensuring gene exchange among populations located in otherwise isolated patches, and facilitating the regeneration of disturbed areas (Gavier & Bucher 2004, Burkart 2005, Whelan et al. 2008, Moreno Velázquez 2010, Montejano 2016).

Seed dispersion may help connect fragments of native vegetation (Mackay et al. 2021). Through the dispersal of their seeds, new individuals are able to grow in places far from their parental plants, which in many cases increases the probability of their establishment and survival (Howe & Smallwood 1982, Packer & Clay 2000, Wenny 2001). Seed dispersion from a parental plant to another site can be the result of external forces, such as wind or water, or transportation by an animal (Howe & Smallwood 1982) either externally attached to fur or feathers, internally through the ingestion of fruits and the subsequent elimination of seeds with the feces, or by regurgitation (Nathan 2006, Valido et al. 2011, Rehm et al. 2019). Among all these types of dispersion, the internal transport of ingested seeds within animal guts (i.e., endozoochory) has been regarded as one of the most important for the colonization of distant ecosystems (e.g., Nogales et al. 2012, Vargas et al. 2015).

Birds stand out among seed dispersers because of their vagility, plasticity in the use of resources, and wide range of habitat occupation of some species (Whelan et al. 2008, Montejano 2016). For example, avian endozoochory has implications in the regeneration of natural communities and the maintenance of the structure and diversity of terrestrial ecosystems (Herrera & Pellmyr 2002). Moreover, birds are among the most abundant frugivores in the Chaco (e.g., Díaz Vélez et al. 2017, Vergara-Tabares et al. 2018), and therefore they may play an important role in maintaining bird-dispersed plant populations. Such role involves not only the movement of seeds away from the parent plant but also may include facilitation of seed germination (Traveset 1998, Traveset & Verdú 2002, Robertson et al. 2006, Traveset et al. 2007).

Bird species belonging to several food guilds (i.e., granivorous, frugivorous, and omnivorous) may incorporate fruit and seeds in their diet. Yet, depending on the way they handle and process the fruits they consume and the condition of the seeds after passing through their digestive tracts, birds have been classified into three functional groups (*sensu* Jordano & Schupp 2000, Jordano et al. 2007): 1) seed predators, which feed on the seed content and always damage the embryo; 2) pulp consumers, which peck the fruit to obtain the pulp, may damage the seed embryo or leave traces of pulp around the seeds, preventing germination or promoting fungal infections (Robertson et al. 2006); and 3) legitimate seed dispersers, which ingest the whole fruit and defecate or regurgitate whole seeds. Although the role of a legitimate seed disperser has traditionally been associated with species that swallow the whole fruit without mandibulating it ("gulpers"), new findings suggest that pulp consumers —also known as "mashers" (Foster 1987, Levey 1987)— may also play an important role in the seed dispersal process of some ecosystems (e.g., Ruggera et al. 2021). Moreover, pulp consumers are among the functional groups of frugivores that have been less studied, and they deserve more attention

Table 1. Average relative frequency of native plants (identified to family/species level) recorded on surveys, number of whole seeds found in feces, and germination percentage of those seeds.

Family	Species	Fleshy fruits	Average relative frequency	Number of whole seeds found in feces	Germination percentage
Solanaceae	*Salpichroa origanifolia*	Yes	0.13	5	80%
Cannabaceae	*Celtis ehrenbergiana*	Yes	0.11	7	86%
Solanaceae	*Solanum sp.*	Yes	0.09	36	58%
Anacardiaceae	*Schinus fasciculata*	Yes	0.08	1	100%
Ephedraceae	*Ephedra triandra*	Yes	0.06	2	0%
Euphorbiaceae		Yes	0.05	2	100%
Rubiaceae	*Galium latoramosum*	Yes	0.04	39	100%
Asteraceae	*Bidens pilosa*	No	0.14	2	100%
Asteraceae		No	0.11	2	0%
Poaceae (2 sp)		No	0.08	3	0%
Verbenaceae		No	0.06	1	0%
Malvaceae		No	0.04	1	100%
Unidentified species (5 sp)				6	0%

Table 2. Bird species with seeds recovered from their feces in Vaquerías Nature Reserve. References for feeding guilds: O (omnivores), G (granivores), I (insectivores), H (herbivores), F (frugivores), US (unidentified species).

Family	Species	Feeding guild	Total fecal samples collected	Samples with whole seeds	Whole seeds retrieved	Samples with broken seeds	Taxonomic identity of seeds
Columbidae	*Leptotila verreauxi*	O	1	0	0	1	US
Columbidae	*Zenaida auriculata*	G	2	1	2	2	*B. pilosa*
Columbidae	*Columbina picui*	G	2	0	0	1	US
Melanopareiidae	*Melanopareia maximiliani*	I	2	0	0	1	US
Cotingidae	*Phytotoma rutila*	H	1	1	2	0	*E. triandra*
Tyrannidae	*Elaenia parvirostris*	O	34	11	28	0	*S. fasciculata*, *C. ehrenbergiana*, Euphorbiaceae, *G. latoramosum*, US
Turdidae	*Turdus rufiventris*	O	4	0	0	1	US
Turdidae	*Turdus amaurochalinus*	O	20	3	26	0	Malvaceae, *G. latoramosum*, US
Turdidae	*Turdus chiguanco*	O	5	1	1	0	Poaceae (sp. b)
Passerellidae	*Zonotrichia capensis*	O	11	3	5	3	Asteraceae, Poaceae (sp. a), *S. origanifolia*, US
Thraupidae	*Coryphospingus cucullatus*	O	4	0	0	1	US
Thraupidae	*Sporophila caerulescens*	G	10	1	1	1	Poaceae (sp. a)
Thraupidae	*Saltator aurantiirostris*	G	15	5	37	10	*Solanum* sp., US
Thraupidae	*Poospiza whitti*	O	18	2	5	7	*S. origanifolia*, Verbenaceae
Cardinalidae	*Pheucticus aureoventris*	G	1	0	0	1	US

regarding their importance in the seed dispersion service given their abundance in some ecosystems.

Species able to effectively transport viable seeds away from the parental plant, where they experience less predation and competition (Janzen 1970), are key components in the dynamics of many terrestrial ecosystems (Terborgh 1990, Stiles 2000). Additionally, seed dispersers may have other beneficial effects on seeds, such as facilitation of seed germination by means of disinhibition or scarification (Traveset 1998, Traveset & Verdú 2002, Robertson et al. 2006, Traveset et al. 2007). As seeds pass through bird guts, the digestive process may modify seeds in ways that can increase their germination probability (Traveset et al. 2007). For example, the ingestion of the fruits implies in many cases the removal of the pulp, which usually has germination inhibitory compounds or infection-causing pathogens (Robertson et al. 2006). Besides, the passage through the digestive tract can scarify the episperm, favoring permeability to water and gases (Traveset et al. 2008), and even the fecal matter of the bird can stimulate the subsequent germination of the seed (Traveset et al. 2001). All these factors highlight the functional role of birds as effective seed dispersers (Whelan et al. 2008) and their potential to functionally connect forest fragments.

The aim of this study was to identify the bird species that comprise the assembly of legitimate seed dispersers and the assembly of plant species legitimately dispersed by birds in Vaquerías Nature Reserve, located in a fragmented landscape of the Chaco Serrano Forest on the southernmost portion of the Gran Chaco Americano. Those results allowed us to interpret the value of the reserve as a source of propagules, as well as the role and value of bird species as potential actors in the recovery and natural regeneration of areas surrounding the reserve.

METHODS

Study area. We conducted the study in the Vaquerías Nature Reserve, located in the Chaco Serrano Woodland of Córdoba, Argentina (31°7'8.33"S 64°28'4.27"W and 31°6'49.71"S 64° 25'29.83"W; Figure 1). Mean annual temperature is 17.5°C and mean annual precipitation is 750 mm, which falls mostly from October to March (Luti et al. 1979). Vaquerías is a reserve of 380 ha surrounded by a matrix that includes native forest patches, native grasslands with livestock, semi-urban areas, and small crop patches. This reserve and a few others in the area are key sites for the conservation and restoration of the Chaco Serrano Forest (Argüello et al. 2012, Toledo et al. 2012, Salazar et al. 2013, Montejano 2016). The reserve combines a variety of ecosystems in several altitudinal floors, from an open to a semi-closed forest at the lowest altitude (850 m a.s.l.), to grassland ecosystems at the highest elevation (1280 m a.s.l.; Abril 2012, Argüello et al. 2012). Approximately 389 plant species have been recorded in the reserve, of which 62 are endemic of the southern cone and 50 are exotic (Toledo et al. 2012). Forests, located mainly at low and medium altitudes of the reserve, are characterized by the greatest diversity of plant species (Argüello et al. 2012) and fructify between December and March (Demaio et al. 2015, Toledo et al. 2015). Native vegetation includes numerous

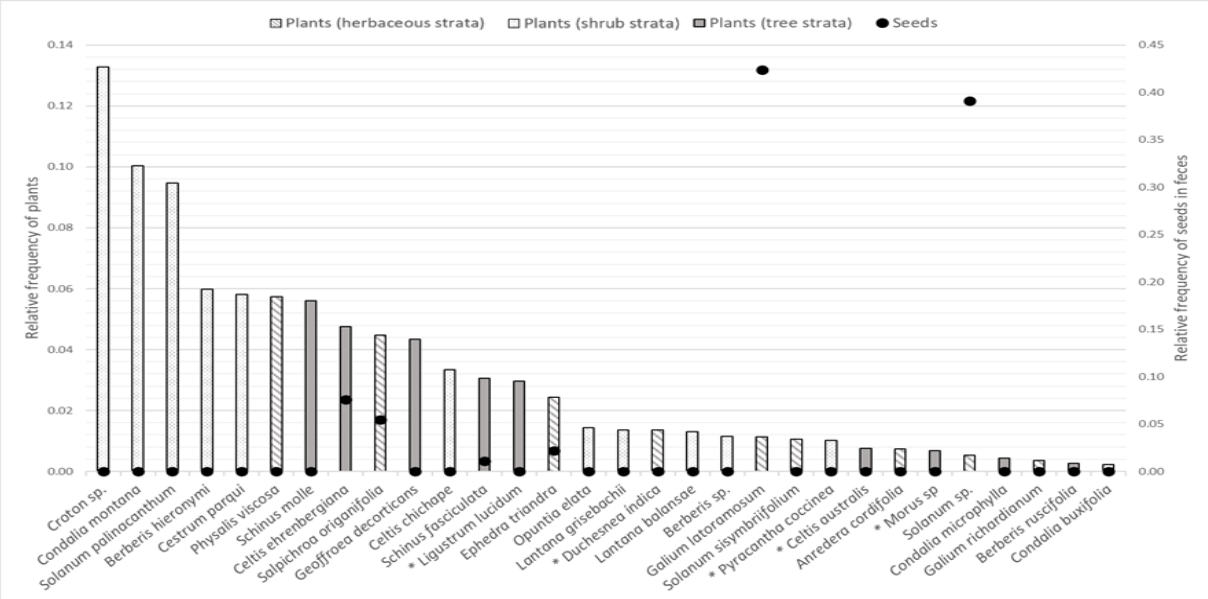

Figure 2. Average relative frequency of occurrence of native and exotic (*) plant species with fleshy fruit (Y1 axis) and relative frequency of seed species found in feces (Y2 axis).

bird-dispersed plants. Among the most abundant species are *Celtis ehrenbergiana*, *Geoffroea decorticans, Condalia buxifolia, Physalis viscosa,* and *Galium latoramosum*. A few exotic fleshy-fruited species also occur in the reserve and the most abundant, *Ligustrum lucidum* and *Pyracantha* spp., fructify in autumn and winter (Gurvich et al. 2005, Tecco et al. 2013). Fauna within the reserve is very diverse and birds represent approximately 70% of the vertebrates. The avifauna includes 189 species (Cebollada Pütz & Kufner 2012, Barri et al. 2018), of which 50 —classified as frugivorous, granivorous, herbivorous, or omnivorous— have been reported consuming fruits (Montejano 2016).

Identification of plant assembly dispersed by birds. From January to February 2017, we characterized the vegetation at the reserve to identify the fleshy-fruit plant species assembly. We randomly selected eight sites of approximately 1 ha each, located in forest areas of the reserve dominated by native vegetation and characterized by a relatively complex structure that included herbaceous, shrub, and tree strata. Previous studies in the reserve indicate that the largest proportion of bird species is concentrated in native or mixed forests with a heterogeneous vertical and horizontal structure (Montejano 2016). Selected sites were located at a minimum distance of 200 m from each other. At the center of each site, we delimited a parcel of 30 x 30 m, where we estimated the percent coverage of herbaceous, shrub, and tree strata, and measured their average height (Matteucci & Colma 1982). We also registered the frequency of occurrence of all fleshy-fruit plant species and recorded whether they were native or exotic, as well as the kind of fruit they produce (i.e., drupe, hesperidium, berry, peponoid, pome, pseudocarp, and false berry dispersed by endozoochory; Amico & Aizen 2005, Whelan et al. 2008). The frequency of occurrence was calculated as the number of individuals per species divided by the total number of individuals in all transects.

Identification of the seed disperser bird assembly. At the same sites that we described above, we captured birds between January and April of 2017 and 2018. Those months comprise the fruiting period of most of the native fleshy-fruit species in the region (Gurvich et al. 2005, Tecco et al. 2013, Demaio et al. 2015, Toledo et al. 2015, Dellafiore 2016). We captured birds with 12 x 3 m mist-nets of 15 x 15 mm mesh, during three to four consecutive days each month (Karr 1981, Ralph et al. 1996, Polanco et al. 2015). We operated four mist-nets in the morning (06:00 h–11:00 h) and evening (17:00 h–20:00 h) (Ralph et al. 1996), for a total of 377 net-hours. Upon capture, we identified individuals (Narosky & Yzurieta 2010, Remsen et al. 2021) and placed them in a cloth bag with a cardboard tray on the base for 15–20 min, where birds were expected to defecate (Ralph et al. 1996, Camargo & Vargas 2006). After releasing the birds, we collected fecal samples with clamps and stored them in glass jars at 4°C, for no longer than three weeks until processed, to avoid early seed germination and fungal growth (Funes et al. 2009). Individuals that did not defecate after 20 minutes were released without collecting a sample. We classified all bird species captured according to feeding guilds following the criteria proposed by Montejano (2016) and Barri et al. (2018) as well as the potential role as seed dispersers following Jordano (2000).

We analyzed fecal samples between February and May 2017 and 2018 at the laboratory facilities of the Centro de Ecología y Recursos Naturales Renovables of Universidad Nacional de Córdoba. The analysis consisted in extracting whole seeds (discarding broken ones) from fecal samples under a magnifying stereoscope (Optika SZM-LED2 0.7–4.5x). We then identified seed species based on external characteristics described in the literature (Demaio et al. 2015, Toledo et al. 2015), dichotomous keys, and consultations with specialists. We complemented seed identifications with the description of external characteristics of plant structures after germination. To find a relationship between the size of seeds and bird species that could disperse them (Montaldo 2005), we measured the length and width of each seed with a stereomicroscope provided with an eyepiece reticle (0.01 mm precision). We calculated a proxy of seed size upon multiplying the length and width values (hereafter seed size). We also determined seed consistency as the relative resistance of their seminal cover to the pressure of histological tweezers. Seeds with medium to high resistance were classifying

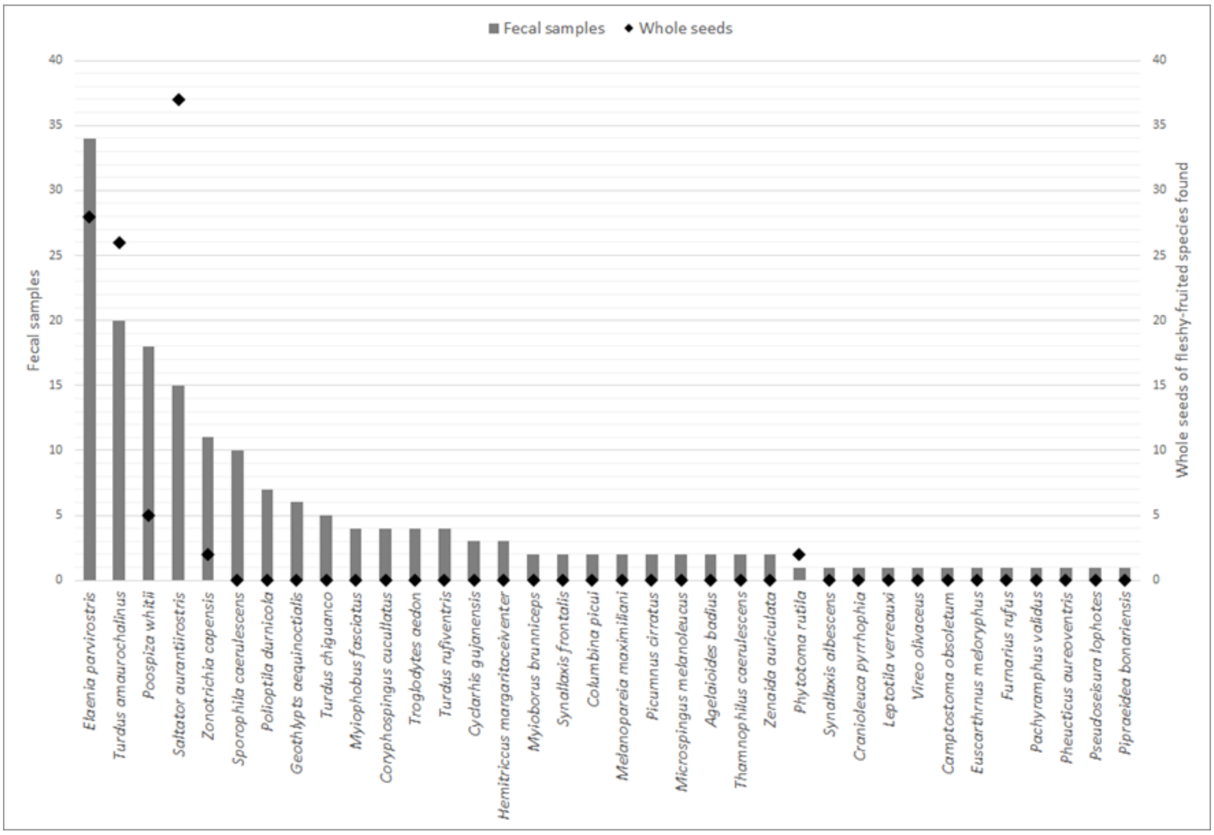

Figure 3. Number of fecal samples recovered from each bird species and whole seeds of fleshy-fruited species found in feces.

as hard, and seeds that upon pressure collapsed completely were classified as soft. All seed measurements were performed by the same person, and always following the same measurement criteria.

The dispersal of seeds by vertebrate frugivores involves the regurgitation or defecation of seeds able to germinate (Traveset 1998, Traveset et al. 2008). We assessed the germination capabilities of whole seeds after the passage through the birds' guts under controlled conditions in a greenhouse. We set to germinate all whole seeds retrieved from feces in groups of the same species, placed in Petri dishes and kept at constant humidity (60%–70%) and room temperature (20–25°C) under a natural summer photoperiod (approximately 14:10 h) for 50–60 days (Díaz Vélez et al. 2017, Vergara-Tabares et al. 2018). We considered seeds germinated when the radicle emerged from the seminal covering at least 2 mm. All germinated seeds were transferred to a pot with soil for further growth. From each plant species, we recorded the percentage of seeds germinated.

RESULTS

Identification of plant assembly dispersed by birds. At all sampling sites we found plant species of all vegetation strata (i.e., herbaceous, shrubs, and trees). We identified 115 plant species from 38 different families, of which 98 were native and 17 exotic. Only 30 of these plant species produced fleshy fruits, of which 25 were native and 5 exotic. The relative frequency of exotic fleshy-fruit species (7.04%; 26 individuals out of 369 individuals registered at the 8 transects) was lower than that of native fleshy-fruit species (92.95%; 343 individuals; Table 1, Figure 2).

Identification of the seed disperser bird assembly. We captured 237 birds and obtained fecal samples from 178 individuals belonging to 37 species and 17 avian families. The analysis of fecal contents revealed that only 28 birds belonging to 9 species (Table 2) excreted whole seeds without external damage (Figure 3). In the rest of fecal samples we found only broken seeds or no seeds at all.

Among bird species with whole seeds in their feces, the Golden-billed Saltator (*Saltator aurantiirostris*), the Small-billed Elaenia (*Elaenia parvirostris)*, the Creamy-bellied Thrush (*Turdus amaurochalinus*), the Black-and-chestnut Warbling Finch (*Poospiza whitti*), and the Rufous-collared Sparrow (*Zonotrichia capensis*) were the ones with the largest number of seeds per individual and the ones most frequently captured (Figure 3), contrasting with other bird species from which we recovered only one or two seeds per individual.

We recovered 107 whole seeds from fecal samples and identified 13 native plant species, seven of which were from fleshy fruit plants. Additionally, we found seeds of five species that we could not identify (Table 1). Dominant species in fecal samples (81.3% of the seeds) belonged to four native species with fleshy fruits, *Celtis ehrenbergiana* (a tree), *Salpichroa origanifolia*, *Solanum* sp. (both herbaceous species), and *Galium latoramosum* (a supporting climbing species). Those species were relatively abundant on vegetation surveys (Figure 2), yet the relative frequency of their seeds in feces was not the same as in the parcels: we found disproportionally more seeds of *Solanum* sp. and *G. latoramosum* in feces (χ^2 = 341.37 df = 29; p < 0.0001; Table 1, Figure 2). We found whole seeds of *G. latoramosum* in feces of the Small-billed Elaenia (15 seeds) and Creamy-bellied Thrush (24 seeds); *S. origanifolia* in feces of the Rufous-collared Sparrow (one seed) and the Black-and-chestnut Warbling Finch (4 seeds); and all seeds of *Solanum* sp. (36) were de-

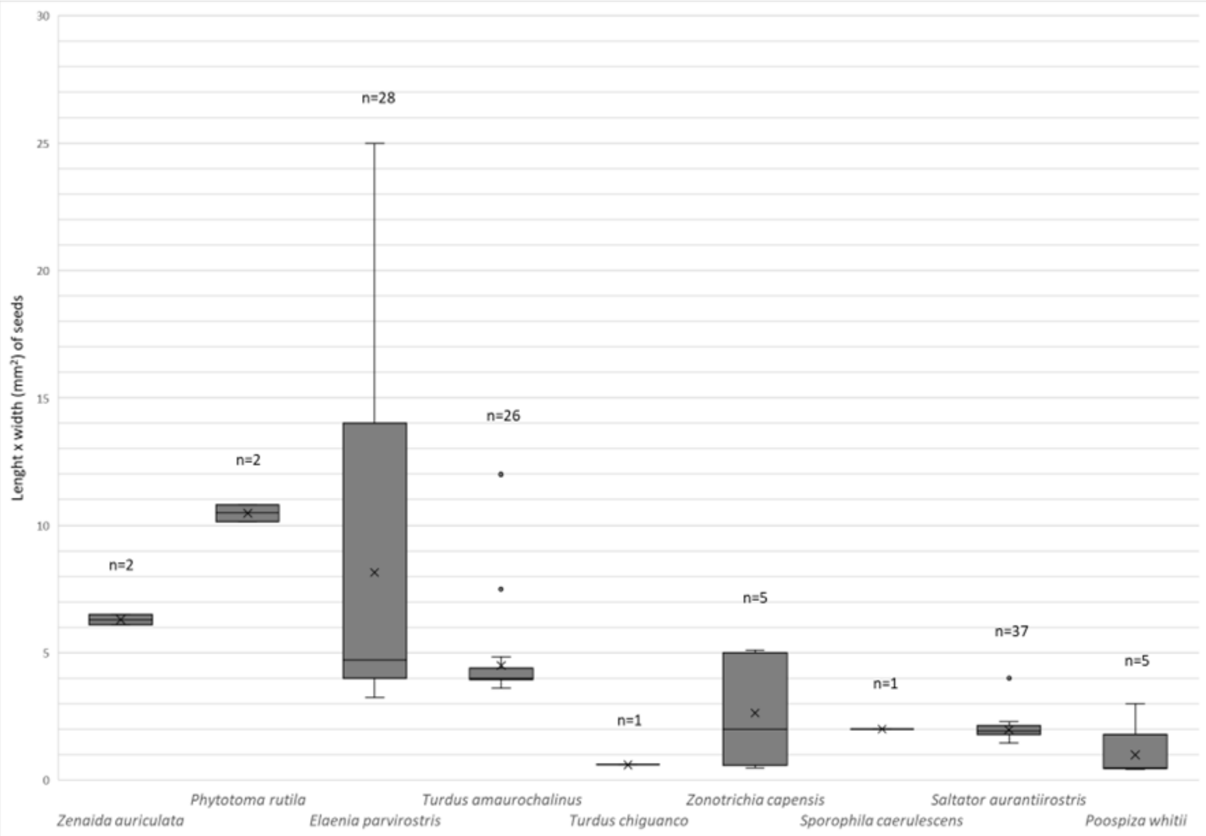

Figure 4. "Size", expressed as length x width of native seeds found in feces (N = 107) of bird species.

tected only in feces of the Golden-billed Saltator. All the *C. ehrenbergiana* (7) seeds were detected only in the feces of the Small-billed Elaenia.

The size of retrieved seeds —expressed as length by width— was highly variable, ranging from 0.42 mm^2 to 25 mm^2. Also, the ranges of seed sizes retrieved from each bird species were very different (Figure 4). For example, the Small -billed Elaenia dispersed a wide range of seeds, including the largest ones (3.24 mm to 25 mm), while the Creamy-bellied Thrush dispersed relatively large seeds (3.6 mm to 12 mm). The Golden-billed Saltator, the Black-and-chestnut Warbling Finch, and the Rufous-collared Sparrow also showed limited seed size ranges including small ones only (0.42 mm to 5.1 mm). Regarding the consistency of dispersed seeds, the Small-billed Elaenia and the Creamy-bellied Thrush dispersed only hard seeds, whereas the Golden-billed Saltator dispersed only soft seeds.

Seventy one percent of the 107 seeds retrieved from feces germinated. Germination of *C. ehrenbergiana*, *G. latoramosum*, *S. origanifolia,* and *Solanum* sp. (the most abundant species in feces samples) ranged from 58% to 100% (Table 1).

DISCUSSION

This study contributes to the current knowledge of the bird species that may act as seed dispersers of native plants and potentially serve as functional connectors between nature reserves and remnant Chaco Serrano Forest patches. Dispersal is thought to be a key process to maintain local and regional patterns of forest diversity (Wandrag et al. 2017). The identification of the vertebrates that may move seeds from healthy to degraded forests is helpful to focus conservation strategies on those species and provides further insights to understand the passive regeneration of degraded forests (Caves et al. 2013, Guidetti et al. 2016).

We retrieved whole seeds from 25% of the total birds captured. Only a small portion of the species captured were frugivores, as most were insectivorous, granivorous, or herbivorous. Yet, we did not recover feces with whole seeds exclusively from bird species that are mainly "gulpers", such as the Small-billed Elaenia and the Creamy-bellied Thrush, which swallow the whole fruit and defecate or regurgitate seeds without pulp and away from the parental plant (Ruggera et al. 2021), and which are expected to be seed dispersers (*sensu* Jordano 2000). We also found undamaged seeds in the feces of bird species that were not considered in previous studies as seed dispersers in Chaco forests. For example, the Golden-billed Saltator and the Rufous-collared Sparrow, which had been described as seed eaters or "seed predators" (Caziani 1996, Codesido & Bilenca 2004) also had viable seeds in their feces. Recently, Ruggera et al. (2021) stated that those species are functionally pulp consumers or "mashers", frequently feeding on small fleshy fruits, crushing it while handling it before swallowing. Although the mashers have been traditionally viewed as unimportant or lower quality seed dispersers due to their tendency to damage or discard seeds with pulp still attached under the maternal plant, Ruggera et al. (2016, 2021) pointed out that they are regular participants in the seed dispersal networks in the Yungas forest of Argentina. Together with those observations, our results highlight the role of the Rufous-collared Sparrow, the Golden-billed Saltator, along with the Black-and-chestnut Warbling Finch (another thraupid and also a masher) in the seed dispersal network of Chaco Serrano forests.

Among birds whose fecal samples contained seeds, the

Golden-billed Saltator, the Small-billed Elaenia, the Creamy-bellied Thrush, the Black-and-chestnut Warbling Finch, and the Rufous-collared Sparrow were the species with the greatest number of seeds per sample (individual), contrasting with the rest of the species —from which we recovered only one or two whole seeds per sample, either because there were no more seeds or they were broken. In addition, these species were the most frequently captured ones. The combination of the highest frequency of capture and number and diversity of seed content in their feces suggests that these bird species play an important role as seed dispersers in the Chaco Forest ecosystem (Jordano 2000). Regardless of the lack of comparisons with control treatments, as we did not test the germination performance for manually extracted seeds, the role of the bird species analyzed here can be considered positive given the generally high germination percentage of the seeds processed by birds. This serves as evidence for the role of these species in the seed dispersal network in the area (Jordano & Herrera 1995, Rey & Alcantara 2000).

The Golden-billed Saltator was one of the species with the highest number of individuals captured and with the greatest number of whole seeds in its feces. This was surprising because, although it is a species that feeds on fruits, its strong beak would not allow the ingested seeds to be defecated without having suffered some damage (Díaz Vélez et al. 2015, Vergara-Tabares et al. 2018). Our data, however, suggest that this species may be involved in the dispersal service of certain plants with small seeds such as *Solanum* sp.*, G. latoramosum,* or *Lantana* sp. Considering that the Golden-billed Saltator is a common resident species in the Chaco forest (Lopez De Casenave et al. 1998, Codesido & Bilenca 2004), our findings add evidence to the idea that it could be a remarkable participant in the seed dispersal process in the study area. Of 30 plant species with fleshy fruits identified in the surveys, we only recovered seeds of 9 of them from fecal samples, and only 4 plant species encompassed 80% of all seeds recovered. These predominant seeds belonged to four native species very abundant within the reserve (*C. ehrenbergiana*, *S. origanifolia*, *Solanum* sp., and *G. latoramosum*)*,* and their fleshy fruits are consumed by a diversity of bird species (Vergara-Tabares et al. 2018, pers. observ.). *C. ehrenbergiana* is a typical and common woody species of the native and mixed forests of the Chaco Serrano (Montejano 2016), yet we found its seeds only in the feces of the Small-billed Elaenia. We observed similar patterns for the rest of the predominant seed species in feces. Seeds from *G. latoramosum* were found only in the feces of the Small-billed Elaenia (15 seeds) and the Creamy-bellied Thrush (24 seeds), whereas *Solanum* sp. seeds were detected only in feces of the Golden-billed Saltator. Although this pattern could be the result of some sort of preference for certain fruits by different bird species, we did not measure preference *per se.* However, comparing the relative frequencies of plants recorded on the surveys and the relative frequencies of seed species in avian fecal samples, we could argue that birds consumed the fruits independently of their abundance in the forest. On the other hand, we also observed that several plant species recorded on the surveys were not represented among the seeds in fecal samples. Either those plant species are being dispersed by a set of bird species that we did not capture or analyze in this study (see below), or by other vertebrates that include fruit in their diets (e.g., foxes, frugivorous bats, skunks, among others; Cebollada Pütz & Kufner 2012).

Although our sampling effort was fairly high (377 net-hours during late summer and early autumn in two consecutive years), we failed to capture individuals of several frugivorous species that are known to occur in the reserve, such as the Monk Parakeet (*Myiopsitta monachus*), the Blue-crowned Parakeet (*Thectocercus acuticaudatus*), the Great Antshrike (*Taraba major*), the Great Kiskadee (*Pitangus sulphuratus*), the Streaked Flycatcher (*Myiodynastes maculatus*), the Tropical Kingbird (*Tyrannus melancholicus*), the Andean Slaty Thrush (*Turdus nigriceps*), the Chalk-browed Mockingbird (*Mimus saturninus*), the White-banded Mockingbird (*M. triurus*), and the Ultramarine Grosbeak (*Cyanoloxia brissonii*) (Montejano 2016, Barri et al. 2018). The relative low abundance of these birds in the reserve (Montejano 2016) may be related to their absence in our captures. Our sampling method, however, could also have influenced the results (Polanco et al. 2015). Unlike other methods, such as point counts, the use of mist-nets has the advantage of allowing the capture of animals and obtaining samples, as well as detecting birds with more cryptic plumage, secretive behavior, or small size (Derlindati & Caziani 2005). On the other hand, mist-nets are more affected by weather and allow sampling in only one forest layer, reducing the amount and type of bird species that can be trapped (Derlindati & Caziani 2005). Although the low tree canopy of the subtropical Chaco Forest provides an ideal system for the use of mist-nets (Derlindati & Caziani 2005), limitations to the techniques should be considered in future studies, such as operating more nets higher in the canopy and increasing the number of nets and capture sites.

The complex vertical and horizontal structure of the vegetation, along with the dominance of native plant species in the reserve, evidences the quality of this natural system as a source of propagules for surrounding forest patches. Moreover, Vaquerías Nature Reserve has been identified as a rich ecosystem that hosts a great diversity of plant (Toledo et al. 2012) and bird species (Montejano 2016), comprising a healthy remnant of forest important to help in the regeneration of surrounding, degraded forests currently in critical danger of disappearance at regional level (Barchuk et al. 2010). Further studies should be conducted at this and other reserves in the Chaco Serrano to generate additional information regarding other vertebrate species that may be involved in seed dispersion and maintenance of plant diversity in the region.

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