ORNITOLOGÍA NEOTROPICAL
(2017) 28: 43–50

ORIGINAL ARTICLE

Sociedad de Ornitología Neotropical

EARED DOVE (*ZENAIDA AURICULATA*) GRANIVORY AND ITS ROLE IN SEED DISPERSAL IN SEMIARID FORESTS OF CENTRAL ARGENTINA

Andrea Silvina Costán[1,2] · José Hernán Sarasola[1,2]

[1]Centro para el Estudio y Conservación de las Aves Rapaces en Argentina (CECARA), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Avda. Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina.

[2]Instituto de las Ciencias de la Tierra y Ambientales de La Pampa (INCITAP), Consejo Nacional de Investigaciones Científicas y Técnicas, Avda. Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina.

E-mail: Andrea Silvina Costán · andre_rita4@hotmail.com

Abstract · The Eared Dove (*Zenaida auriculata*) is one of the most abundant granivorous birds in the Neotropical region, and has been declared as a pest in several regions of southern South America. Most studies of this dove's diet have been conducted in agricultural lands in order to evaluate crop damage and dove preferences for particular crop seeds. More recently, it has been argued that Eared Doves may also play a role as seed dispersers, since often seeds contained in crops are spilled when doves are killed by predators. Here, we studied the food habits of the Eared Dove in xerophytic semiarid forests of central Argentina and the germination potential of seeds contained in crops. Based on crop contents, using an emetic formula and greenhouse germination experiments, we aimed to determine the diet of the Eared Dove and to evaluate the potential role of doves as seed predators and dispersers. Most of the birds captured (70%, n = 131) regurgitated crop contents. Crops contained almost exclusively seeds of six cultivated and 13 non-cultivated plant species, with a mean (±SD) of 207 ± 286 seeds/crop. Doves consumed seeds in asynchrony with the plant fruiting or crop-sowing cycle for both non-cultivated and cultivated species, respectively, suggesting that doves forage not only directly from plants but also from crop-seed storage facilities, spilled grain, and the seed bank. We selected some of the most representative plant species obtained from dove crops to carry out germination experiments. While all species showed some level of germination potential, seeds from cultivated plant species (n = 5) showed a higher mean germination potential (56.8%) than those from non-cultivated species (23.1%, n = 3). Our results confirm the role of the Eared Dove as seed predator but also highlight its potential role as seed disperser following predation.

Resumen · Granivoría de la Torcaza Común (*Zenaida auriculata*) y su rol en la dispersión de semillas en bosques semiáridos del centro de Argentina

La Torcaza Común (*Zenaida auriculata*) es una de las aves granívoras más abundantes de la región Neotropical, y ha sido declarada plaga en varias regiones del sur de Sudamérica. La mayoría de los estudios sobre la dieta de esta especie se han llevado a cabo en ambientes agrícolas con el fin de evaluar los daños a los cultivos y la preferencia de las palomas por las semillas de un cultivo en particular. Recientemente se ha demostrado que la Torcaza Común podría también desempañar un rol como dispersores de semillas ya que a menudo las semillas contenidas en los buches se derraman cuando las palomas son depredadas. En este trabajo estudiamos los hábitos alimenticios de la Torcaza Común en los bosques xerofítico semiáridos del centro de Argentina y el potencial germinativo de las semillas contenidas en sus buches. Basado en el contenido de buches, empleando una fórmula emética y experimentos de germinación en invernáculo, nuestro objetivo fue determinar la dieta de la Torcaza Común y evaluar su rol potencial como predadores y dispersores de semillas. La mayoría de las aves que capturamos (70%, n = 131) regurgitaron el contenido de sus buches. El contenido de los buches estuvo compuesto casi exclusivamente de semillas, correspondientes a seis especies de plantas cultivadas y 13 especies no cultivadas, con una media (± DE) de 207 ± 286 semillas/buche. Las Torcazas consumieron semillas en asincronía con la fructificación de las plantas cultivadas o ciclo de siembra de los cultivos, tanto para las especies no cultivadas como para las especies cultivadas respectivamente, lo que sugiere que las palomas forrajean no solo directamente de las plantas sino también de las plantas de almacenamiento de semillas, de semillas caídas, y del banco de semillas. Seleccionamos algunas de las especies de plantas más representativas obtenidas de los buches de las torcazas para realizar los experimentos de germinación. Sin bien todas las especies mostraron algún nivel de potencial germinación, las semillas de las especies de plantas cultivadas (n = 5) mostraron un potencial medio de germinación mayor (56,8%) que las especies no cultivadas (23,1%, n = 3 especies). Nuestros resul-

Receipt 12 August 2016 · First decision 13 October 2016 · Acceptance 12 May 2017 · Online publication 31 May 2017

Communicated by Kaspar Delhey

tados confirman el rol de la Torcaza Común como predadora de semillas pero también ponen de manifiesto su rol potencial en procesos de dispersión de semillas luego de sufrir predación.

Key words: Argentina · Eared Dove · Espinal · Granivory · Predation · Seed dispersal · *Zenaida auriculata*

INTRODUCTION

Granivory, usually also referred as seed-predation, is an important inter-specific interaction established between numerous species of birds and plants and plays a key role in shaping ecological communities (Herrera 2002). It has important effects for both seed producers and consumers: seeds are essential to sustain granivorous birds, while the avian consumption of seeds may affect plant demography and fitness by reducing recruitment of new individuals in plant populations (Vaz Ferreira et al. 2011). However, mutualistic effects for both plants and birds are also possible if seed consumers act as effective seed dispersers, allowing the establishment of seedlings far away from their mother plant, colonizing new habitats and contributing to gene flow between plant populations, especially in fragmented landscapes (Levine & Murrell 2003, Trakhtenbrot et al. 2005, Nathan et al. 2008).

Pigeons and doves (order Columbiformes) comprise ca. 303 species with a worldwide distribution (Gill 1990), and show great adaptive versatility (Lambert 1989, Pérez et al. 2001, Bucher & Bocco 2009). One of the most important ecological roles that pigeons and doves play in natural communities is related to their feeding habits. Most species in this group have almost exclusively granivorous diets (Bucher & Nores 1976, Ranvaud et al. 2001, Samamé Farfán 2005, Chacín & Calchi 2007), conferring them an important ecosystem function as seed-predators. Although the group of pigeons and doves includes a comparatively large proportion (ca. 20%) of threatened species (Walker 2007), in continental areas, and particularly in large lowland areas devoted to agricultural practices, some species of pigeons and doves may be found in high abundances and may cause extensive crop damage and economic losses and are often considered pests.

The Eared Dove (*Zenaida auriculata*) ranges from Colombia in the north to Argentina and Chile in the south (Chacín & Calchi 2007). In central Argentina, it is a resident, being common, and abundant particularly in open and savanna-like landscapes. During the last 60 years, severe Eared Dove population outbreaks have been recorded in different countries across southern South America, including Brazil, Uruguay, Colombia, and Bolivia (Bucher & Ranvaud 2006). In Argentina, Eared Dove populations have also increased markedly during that period in several provinces (Córdoba, Entre Ríos, San Luis, Chaco, and Salta), the species has been declared a pest, and management actions have been taken to reduce its population (Murton et al. 1974, Bucher 1990).

Available studies on the diet of Eared Doves in Argentina are mostly restricted to agricultural areas and conducted mainly in order to assess doves' food intake in the context of estimations of crop damages and bird population management (Bucher 1974, Bucher & Nores 1976). Most of these studies document the preference of doves for crop seeds (Bucher & Nores 1976, Ranvaud et al. 2001), with seeds of weeds and grasses serving as secondary food resources in these human-modified agricultural environments. However, dove population outbreaks are not restricted to agricultural lands. Rather, most of the locations with the highest abundances of Eared Doves are transition areas between native forest habitats and agricultural lands (Bucher & Ranvaud 2006).

In Argentina, a significant amount of natural habitat, mainly semiarid forests belonging to the Chaco and Espinal biomes persists at the borders of the agricultural frontier of the Pampas region. In natural habitats, doves may play an important ecological function as predators or dispersers of seeds of native and alien plant species. Doves may be important long-distance dispersers of seeds even when they do not defecate viable seeds, because seed dispersion by doves could take place when doves die due to predation or hunting and spill their crop contents on the ground (Bucher & Bocco 2009). In addition, recent research has also highlighted the importance of Eared Doves as part of the process of secondary seed dispersal. In semiarid forests of central Argentina, generalist predators, such as pumas (*Puma concolor*), heavily prey on abundant Eared Doves (Zanón-Martínez et al. 2016). Through the trophic interaction with their prey, pumas are able to indirectly consume large amounts of seeds contained in doves' crops, defecating and spreading thousands of viable seeds annually (Sarasola et al. 2016). Thus, independent from the final fate of seeds consumed by doves (i.e., seed predation or dispersal), dove food habits have important implications on the demography of plant species and on the dynamic of plant communities in natural environments.

In this study, we examined the food habits of the Eared Dove in the semi-arid forests of central Argentina. Using an emetic formula as a novel methodological approach, we investigated the crop contents and seed consumption of this bird species in natural habitats. We focused on the contribution of non-cultivated plants to the doves' diet as a way to provide insights into the potential ecological interactions established between doves and plants in the semi-arid forests of central Argentina through seed predation/dispersal. We also evaluated the germination potential of seeds of selected plant species found in doves' crops. We predicted that the contribution of seeds from non-cultivated plant species to the diet of Eared Doves in the semiarid forests of central Argentina would be higher than that observed in agricultural areas (Bucher & Nores 1976, Ranvaud et al. 2001) .

METHODS

Study area. The study was conducted in the Parque Luro Reserve (36°54'49"S, 64°15'41"W), La Pampa province, central Argentina. The Reserve (7604 ha) consists mainly of xerophytic open forests of caldén (*Prosopis caldenia*), which represents the characteristic landscape of the Espinal biome in the semiarid pampas of Argentina (Cabrera 1976). Grasses, such as *Stipa* spp. (Poaceae), are the main herbaceous species of the lower stratum in the Reserve, and *Condalia microphylla*, *Lycium chilense*, *L. gilliesianum* (all Solanaceae), and *Schinus fasciculatus* (Anacardiaceae) are the common shrub species where a middle stratum is present. The reserve is surrounded by agricultural lands devoted to crops such as wheat (*Triticum aestivum*, Poaceae), sunflower (*Helianthus annuus*, Asteraceae), corn (*Zea mays*, Poaceae), and soybean (*Glycine max*, Fabaceae); perennial, e.g., alfalfa (*Medicago sativa*, Fabaceae), and annual pastures, e.g., oat (*Avena sativa*, Poaceae), are also cultivated. The climate is continental semiarid and is characterized by hot summers (maximum 42°C) and cold winters (minimum -13°C) with low humidity and low annual rainfall (500–600 mm), typically concentrated in spring and summer.

Bird trapping and seed sampling. We used mist-nets to capture Eared Doves, and these were deployed near water ponds in different areas of the reserve, where we had previously observed high concentrations of doves. In Austral autumn of 2010, we visited the study area twice during March and opened mist-nets for 11 hours in each visit. In autumn of 2011, we sampled only once during March, and nets were also opened for 11 hours. During the winter season, we visited the study area in June–July 2010 and in July–August of 2011, and mist-nets were opened for 7 hours in each case. In spring season, we sampled in November 2010 and during October and November 2011; in each sampling occasion, the mist-nest were opened for 12 hours. During summer, we opened mist-nets in December 2010 and in January 2011 for 8 hours in each occasion.

Each of the birds captured was externally examined for crop load and classified into one of three categories: 1) apparently empty crops, when no evidence of seeds in the crop was perceived to the touch; 2) partially filled crops, when some seeds were noted to the touch but the crop was not full of seeds; and 3) full crops, when crops were prominent and full of seeds.

Captured birds were weighed to the nearest 0.01 g using a digital scale. To obtain samples of crop contents, we gave birds a 1.5% solution of tartrate antimony potassium, using a syringe and a tube to flush the solution directly into the crop and avoid liquid passage to the trachea. Solution was administrated at a dosage of 0.8 ml of solution per 100 g of body mass following Poulin & Lefebvre (1994). Once supplied with the emetic solution, birds were placed in individual boxes (30 x 30 x 20 cm) and kept there for a maximum of 60 min. After that time, the birds were released, and the regurgitated content of their crops was collected from the box and stored in paper envelopes prior to laboratory analysis.

Samples processing and data analysis. Identification of seeds obtained from crops was performed using a stereoscopic microscope. Seeds were identified using keys and guides relevant for the region (Marzocca 1957, Bianco et al. 2000). Seeds were counted and grouped according to sampling occasions and plant species. Chi-square tests were performed to examine independence between the response of birds to the emetic formula and their classification in each of the three crop-content groups. We also examined differences in occurrence (number of crops with seeds of a particular plant species) and number of seeds (total number of seeds in crops) of different plant groups through different sampling occasions (seasons and years), also using chi-square tests.

We assessed the germination responses of seeds for the eight-most cultivated and non-cultivated plant species found in dove crops following a similar procedure employed by Nogales et al. (2002). We selected under stereoscopic microscope 5 to 20 healthy-looking seeds from each crop for particular plant species. Each seed was placed in an individual plastic pot (5 cm diameter, 10 cm depth) containing sterilized soil from the study area. The pots were kept in a greenhouse at 25°C under the semi-controlled conditions with a night/day cycle similar to that found in the study area. Sorghum (Poaceae), sunflower, and corn were sowed in spring, wheat and oat in winter. The non-cultivated species *Chenopodium album* (Amaranthaceae), *Panicum bergii* (Poaceae), *and Lycopsis arvensis* (Boraginaceae) were sown at end of winter. Seeds were sown in the substrate at a depth 0.5–1 cm and watered every 2 days. Pots were examined for germination (i.e., cotyledon emergence) three times per week. Germination was monitored for 3 months until no new seeds germinated during a one-week period (Nogales et al. 2002, 2007). Germination values were averaged for each plant species. We used analysis of variance (ANOVA) tests to examine differences in germination responses for each plant species in these groups. Unless otherwise indicated, means (± SD) are provided (Zar 1999).

RESULTS

We captured birds during autumn and spring in each of the years but were unable to do so during winter and summer. A total of 131 doves were captured during the study period. We were able to obtain samples for crop contents for 93 doves (70%), while the remaining birds did not regurgitate. Sixty-two birds, for which crop contents were sampled using the emetic solution, were captured in 2010 and the remaining 35 doves were captured during the autumn and spring seasons of 2011. Thirty-four percent of the doves captured (44 birds) exhibited almost apparently empty crops at the moment of capture, while the remaining birds had partially filled (47%) or full crops (19%). Four doves died, three with apparently empty crops and one with a partially filled crop, while supplying the emetic solution or later in the box; however, their crop contents were also considered for diet analysis but not for the analysis of the response to the emetic solution.

Dove responses to the emetic formula. Success in obtaining samples of crop contents using the emetic formula was related to the amount of seeds in the crop (χ^2 =7.2, $P < 0.05$, df = 2). Sixty percent of the 25 doves classified as having full crops responded positively to the emetic solution. Success in getting samples from birds with partially filled (61 birds) and apparently empty crops (41 birds) was higher, with 69% and 88% of birds in these groups responding positively to the emetic formula, respectively.

Crop contents. Crop contents were composed almost exclusively of seeds, with the exception of small gastropods which were found in the diet at a very low frequency (less than 0.3% of items). A total of 20,067 seeds belonging to 19 plant species were collected from dove crops (Table 1), with a mean content of 207 (± 286) seeds/crop. Although birds were captured in natural, semiarid forest habitat, six of the plant species recorded (32%) were cultivated species: wheat, millet (*Panicum miliaceum*), sorghum, sunflower, corn, and common oat. Seeds of these cultivated species represented 30.4% (n = 6117) of the total seeds found in dove crops. The remaining thirteen species (68%) found in dove crops were non-cultivated weeds and grasses, respectively (13,950 seeds; Table 1).

The number of seeds was different between season and years, but not the frequency of occurrence. We found significant differences in the number of seeds of cultivated vs. non-cultivated plants found in crops through season and years sampled (χ^2 = 3,801, $P < 0.001$, df = 3). These differences were mainly due to annual (χ^2 = 1,590, $P < 0.001$, df = 1) and seasonal (χ^2 = 117, $P < 0.001$, df = 1) variation, the number of seeds being highest in 2010 and in autumn. However, the frequency of occurrence of seeds (defined as the percentage of dove crops that had seeds of a particular plant species) from cultivated and non-cultivated species did not vary significantly either between seasons (χ^2 = 1.6, $P > 0.20$, df = 1) or between years (χ^2 = 0.7, $P > 0.40$, df = 1).

Seeds from three out of six cultivated plant species were recorded in dove crops exclusively during the spring season, and all of the cultivated plant species were recorded during at least one of the spring seasons sampled (Table 1). However, none of these plant species was consumed exclusively in autumn. Seven out of thirteen species of non-cultivated plants were recorded in dove crops only during spring while just one plant species in this group was recorded exclusively during autumn.

The non-cultivated plant species more frequently consumed by doves during spring were white goosefoot (*Chenopodium album*, 54%), Bahía grass (*Paspalum notatum*, 6 %), Berg's panicgrass (*Panicum bergii*, 4%), Johnson grass (*Sorghum halepense*, 3%) and small bugloss (*Lycopsis arvensis*, 1%). Among cultivated species, millet (15%), wheat (8%), sunflower (6%), and common oat (*1%*) comprised the bulk of the diet of Eared Doves.

Seed germination potential. We tested the germination potential of seeds from eight of the plant species found in the crops of the Eared Doves we captured (Figure 1). The seeds included five cultivated (oat, sorghum, wheat, corn, and sunflower) and three non-cultivated plant species; the non-cultivated species included one native (Berg's panicgrass) and two alien (white goose-foot and small bugloss) plant species.

Germination potential was very variable between species. The proportion of successful germinations per species ranged from a mean of 21.3% for the small Bugloss to more than 80% for Oat seeds (Figure 1). There were no differences in the proportion of germinated seeds among the non-cultivated species ($F_{2,15}$ = 2.19, $P = 0.14$). However, we found significant differences in the germination potential among cultivated plant species ($F_{4,37}$ = 5.37, $P < 0.01$), mostly due to a lower germination proportion for corn relative to the other cultivated species (Tukey HSD test = 36.23, $P < 0.05$).

DISCUSSION

In recent decades, the conversion of native habitats to agricultural lands in Argentina has accelerated (Brown et al. 2006). One of the best-documented processes related with this conversion is the expansion of the agricultural frontier, which is with the destruction of native forests, particularly those in the semiarid regions of the Espinal and Chaco biomes (Brown et al. 2006). Over the same time period, Eared Dove population outbreaks have become frequent in several regions of Argentina, and these outbreaks were consistently marked in ecotone areas between dry-forest biomes and the agricultural plains of the Pampas region. The spatial distribution of Eared Dove population outbreaks is likely largely explained by the co-occurrence of year-round food availability from crops with suitable breeding habitat in the form of the remaining fragments of native forests (Bucher & Ranvaud 2006). The conversion of the landscape to agriculture has thus facilitated the rapid increase in Eared Dove population size and

Table 1. Seasonal variation in the average value (± SD) and frequency of occurrence in crops (%, in parentheses) of seeds of each plant species found in the crops of Eared Doves (*Zenaida auriculata*) in Parque Luro Reserve, La Pampa, Argentina during 2010 and 2011. Non-cultivated species status is indicated after names in parentheses: (1) Native and (2) Alien.

Plant species	2010		2011		Total number of seeds
	Autumn	Spring	Autumn	Spring	
Cultivated					
Panicum miliaceum	202 ± 243 (65)	5 (5)	36 ± 42 (15)	66 ± 60 (15)	2944
Triticum aestivum	11 (5)			88 ± 78 (95)	1595
Helianthus annus	78 ± 82 (68)	10 ± 7 (9)	24 ± 19 (18)	6 (5)	1227
Avena sativa				54 ± 29 (100)	216
Zea mays		8 ± 6 (100)			88
Sorghum bicolor		5 ± 3 (44)		6 ± 10 (56)	47
Cultivated subtotal	129 ± 183 (34)	7 ± 5 (21)	29 ± 28 (8)	65 ± 69 (37)	6117
Non-cultivated					
Chenopodium album (2)	172 ± 182 (53)	399 ± 545 (19)	123 ± 153 (8)	25 ± 34 (20)	10,824
Paspalum notatum (1)	66 ± 57 (77)	4 (6)		65 ± 49 (17)	1123
Panicum bergii (1)	189 ± 342 (50)	6 ± 5.6 (25)		20 ± 25 (25)	807
Sorghum halepense (2)	1 (14)	275 ± 240 (29)	13 ± 7 (43)	2 (14)	591
Lycopsis arvensis (2)				23 ± 26 (100)	278
Capsella bursa-pastoris (2)				151 (100)	151
Setaria parviflora (1)				66 (100)	66
Cucumis anguria (2)		14 ± 20 (75)		3 (25)	46
Polygonum aviculare (2)		22 (50)		1 (50)	23
Centaurea soltitialis (2)	5 ± 0.7 (100)				11
Carduus thoermeri (2)	8 (50)			7 (50)	15
Argemone subfusiforme (1)				2 (100)	2
Fumaria officinalis (2)				6.5 ± 0.7 (100)	13
Non-cultivated subtotal	134 ± 174 (45)	251 ± 443 (16)	82 ± 129 (7)	27 ± 36 (32)	13,950
Total number of seeds	**10966**	**5151**	**860**	**3081**	**20,067**

geographic range, resulting in extensive crop damage by doves in agricultural areas (Bucher 1990).

Most of the studies on Eared Dove food habits have been conducted by analyzing dead bird crop contents (see for instance Bucher & Nores 1976, Ranvaud et al. 2001, Chacín & Calchi 2007). In this study, however, we employed an emetic formula as an alternative approach, and found that Eared Doves responded effectively to this methodology. The efficiency of the emetic sampling technique was relatively high (74% of birds regurgitated) compared with previous attempts to obtain crop content samples from other Columbidae species using this methodology. Poulin et al. (1994), for example, were not able to obtain crop contents from nine individuals of three dove and pigeon species in Venezuela. However, a later experiment gained 59.5% success when sampling 37 doves in Panama (Poulin & Lefebvre 1994). In our study, doves in all three crop content categories (apparently empty, partially filled, and completely filled) reacted positively to the treatment. However, individuals with apparently empty crops showed a better response to the emetic solution in terms of proportion of birds that effectively regurgitated. Emetic formulas act as stomach irritants (Diaz 1989), and thus are expected to be more effective when they can contact greater areas of the crop wall as when the crop is partially filled or apparently empty. Mortality due to emetics may be high and may depend on the species involved, the dosage, and the effects of stressful handling (Lederer & Crane 1978). Poulin et al. (1994) reported the lowest value for mortality through the use of tartar emetic (2% and 2.6% respectively) and showed that some adjustments to the concentration of the dose of emetic formula resulted in reduced mortality. In this study, the mortality was also low (4.4%), but slightly higher than that observed in previous studies.

The diet of Eared Doves in the Parque Luro Natural Reserve included both cultivated and non-culti-

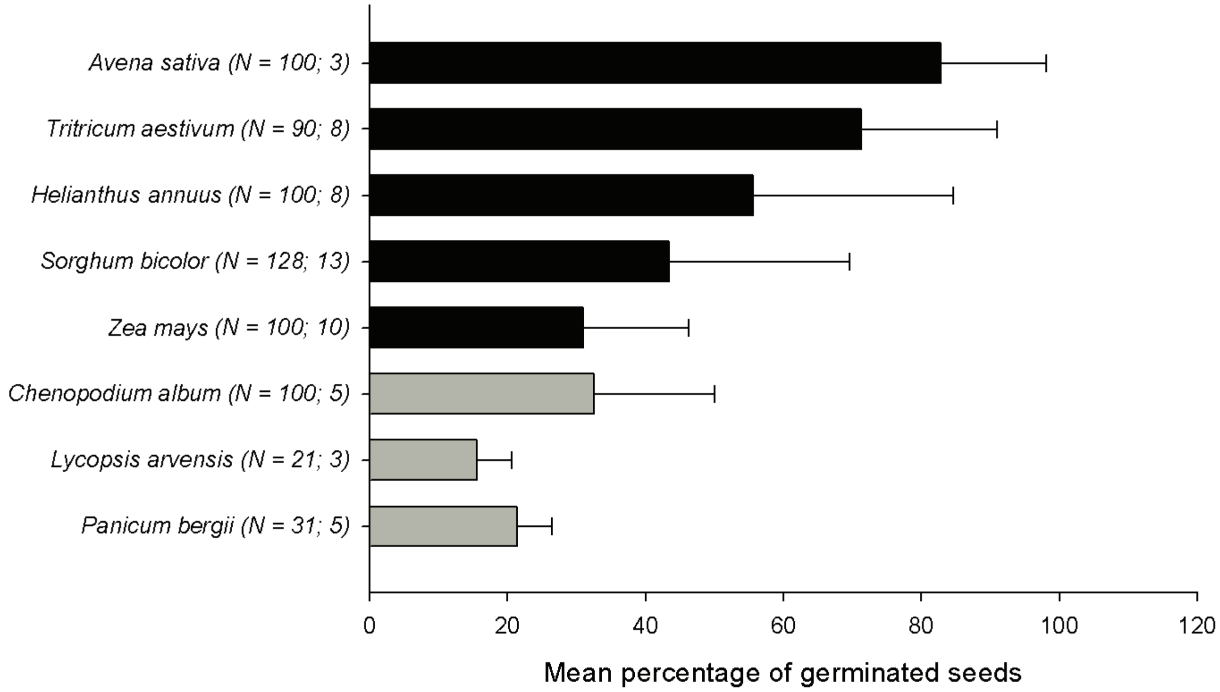

Figure 1. Germination potential of seeds of five cultivated (black columns) and three non-cultivated (grey columns) plant species found in Eared Dove (*Zenaida auriculata*) crops, captured during 2010 and 2011 in Parque Luro Reserve, La Pampa province, Argentina. Sample sizes (n = number of seeds) and number of crops from where seeds were obtained are indicated in parenthesis.

vated species. Our study area represented a large fragment of native forest where doves could find suitable sites for refuge, breeding, and foraging; growing crops and raising cattle are banned in the reserve. We thus expected to find a higher frequency of non-cultivated species in the diet of Eared Doves in our study than in previous studies conducted in agricultural habitats. Indeed, we found seeds of thirteen non-cultivated weed and grass species in Eared Dove crops, which is the highest percentage (68%) of non-cultivated plant species reported for the diet of Eared Doves. However, despite the size of the reserve and the distance from our sampling sites to the reserve borders (3–5 km), the birds whose crop contents we examined obtained a large fraction of seeds eaten from the cultivated lands surrounding the reserve. In the same way, seeds of most of the weed species found in doves crops are also common in cultivated lands, which hence preclude us to be conclusive on the origin of weed seeds consumed by doves.

Eared Doves consumed seeds of cultivated plant species during both autumn and spring, but the consumption of particular species varied between seasons and years. Such differences are probably related to differences in seed availability in the areas surrounding the reserve; these areas are largely devoted to crop and cattle production, but in a yearly rotation system. In addition, differences in frequency and occurrence of cultivated plant seeds between sampling sites may be the result of opportunistic foraging behavior by doves that forage not only on crop fields but also in rural seed storage facilities. This is supported by the fact that seeds of some of the cultivated plant species were found in dove crops outside of the seeding period (Marzocca 1957). This indicates that, in contrast to the findings of Bucher & Nores (1976), in our study area crop seed consumption by Eared Doves does not strictly follow the crop cycle. As for cultivated species, seeds of non-cultivated plant species were found in dove crops outside of plant maturation and fructification periods, indicating that doves may also forage on seeds from the seed bank. White goose-foot, for example, was the predominant species in the crops of doves in both autumn and spring, even though this plant produces seeds from summer to mid-autumn (Marzocca 1957). On the contrary, doves consumed Berg's panicgrass in large amounts but only during autumn in concordance with the fruiting season of this perennial weed species (Marzocca 1957).

In our study area, the role of Eared Doves as intermediate vectors involved in secondary seed dispersal has been recently identified through the trophic interaction established between doves and a large felid predator, the puma (Sarasola et al. 2016). However, this is just one of the multiple paths that seeds could follow throughout predator-prey relationships, and that would ultimately favor the spread of seeds contained in dove crops. Birds of prey, for example, are also effective secondary disperser of seeds of weed plants initially consumed by their prey in other regions (López-Darias & Nogales 2016), and several raptor species ranging in areas where dove populations outbreaks take place are shifting their prey preference toward this abundant prey (authors unpub. data). Thus, such mechanism of secondary seed dispersal of native and alien weed species consumed by doves could be widespread in ecotone areas between the Espinal and Pampa biomes.

Active avian seed predation may result in seed dispersal, but may also contribute to substantial seed mortality. Both processes have important implications for plant demography and community structure. Long-distance seed dispersal, for example, plays a role in large-scale ecosystems processes such as plant population spread and gene flow between populations (Nathan et al. 2008). In the case of Eared Doves, however, their function as seed predators may diminish their function as seed dispersers of native plant species. Since non-native wild species are much more common than native plant species in the diet, granivory by Eared Doves could have important ecological effects by disrupting the seed dispersal process of invasive plant species. However, extent and quantification of any ecosystem effects due to granivory of Eared Doves, either favouring or disrupting seed dispersal process, need to be determined through additional research.

ACKNOWLEDGMENTS

We are grateful to Letizia Campioni, Claudina Solaro, Soledad Liébana, Miguel Santillán and Facundo Barbar for their help in trapping and sampling doves. The Subsecretaría de Ecología of La Pampa province made this work possible by giving permission to carry out fieldwork in the Parque Luro Natural Reserve. Funding was provided by the PI R018 from the Departamento de Recursos Naturales, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa. While conducting this work, A.C. was supported by a grant from the Consejo Inter-Universitario Nacional (CIN) of Argentina. We appreciate the improvements in English usage made by Caitlin Stern through the Association of Field Ornithologists' program of editorial assistance. We also appreciate comments made two anonymous reviewers and K. Delhey that greatly improved the manuscript.

REFERENCES

Bianco, CA, CO Nuñez & TA Kraus (2000) *Identificación de frutos y semillas de las principales malezas del centro de la Argentina.* Fundación Universidad Nacional de Río Cuarto, Río Cuarto, Córdoba, Argentina.

Brown, A, U Martínez Ortíz, M Acerbi & J Corcuera (2006) *La situación ambiental Argentina 2005.* Fundación Vida Silvestre Argentina, Buenos Aires, Argentina.

Bucher, EH (1974) Bases ecológicas para el control de la paloma torcaza. *Revista de la facultad de Ciencias Exactas, Fisicas y Naturales, Univ. Nacional de Córdoba, Serie Biología* 1: 141–156.

Bucher, EH (1990) The influence of changes in regional land-use patterns on Zenaida Dove populations. Pp 291–303 *in* Pinowski, J & JD Summers-Smith (eds). Granivorous birds in the agricultural landscape. Polish Academy of Science, Warsaw, Poland.

Bucher, EH & PJ Bocco (2009) Reassessing the importance of granivorous pigeons as massive, long-distance seed dispersers. *Ecology* 90: 2321–2327.

Bucher, EH & M Nores (1976) Ecología de la alimentación de la paloma *Zenaida auriculata*. *Physis* 35: 17–32.

Bucher, EH & RD Ranvaud (2006) Eared Dove outbreaks in South America: patterns and characteristics. *Acta Zoológica Sinica* 52: 564–567.

Cabrera, AL (1976) Regiones fitogeográficas argentinas. *Enciclopedia Argentina de Agricultura y Jardinería*. Editorial Acme, Buenos Aires, Argentina.

Chacín, M & R Calchi (2007) Dieta de la paloma sabanera (*Zenaida auriculata*) en el noroeste de Venezuela durante la temporada de caza 2001. *Boletín del Centro de Investigaciones Biológicas* 41: 340–349.

Diaz, M (1989) Eficacia de un emético (apomorfina) para el estudio de las dietas de paseriformes granívoros. *Ardeola* 36: 185–191.

Gill, FB (1990) *Ornithology.* W. H. Freeman and Company, New York, New York, USA.

Herrera, CM (2002) Seed dispersal by vertebrates. Pp 185–208 *in* Herrera, CM & O Pellmyr (eds). *Plant–animal interactions: an evolutionary approach*. Blackwell Science, Oxford, UK.

Lambert, F (1989) Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis* 131: 521–527.

Lederer, RJ & R Crane (1978) The effects of emetics on wild birds. *North American Bird Bander* 3: 3–5.

Levine, JM & DJ Murrell (2003). The community-level consequences patterns. *Annual Review of Ecology, Evolution, and Systematics* 34: 549–574.

López-Darias, M & M Nogales (2016) Raptors as legitimate secondary dispersers of weed seeds. *Ibis* 158: 428–432.

Marzocca, A (1957) *Manual de malezas*. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina.

Murton, RK, EH Bucher, M Nores, E Gómez & J Reartes (1974) The ecology of the Eared Dove (*Zenaida auriculata*) in Argentina. *Condor* 76: 80–88.

Nathan, R, FM Schurr, O Spiegel, O Steinitz, A Trakhtenbrot & A Tsoar (2008) Mechanism of long-distance seed dispersal. *Trends in Ecology and Evolution* 23: 638–647.

Nogales, M, DP Padilla, C Nieves, JC Illera & A Traveset (2007) Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. *Journal of Ecology* 95: 1394–1403.

Nogales, M, V Quilis, FM Medina, JL Mora, & LS Trigo (2002) Are predatory birds effective secondary seed dispersers? *Biological Journal of the Linnean Society* 75: 345–352.

Pérez, EM, L Bulla & E Santiago (2001) Similitudes dietarias entre ocho aves granívoras en la Estación Experimental “La Iguana”, Estado Guárico, Venezuela. *Ecotropicos* 14: 49–56.

Poulin, B, & G Lefebvre (1994) Effect and efficiency of tartar emetic in determinig the diet of tropical land birds. *Condor* 96: 98–104.

Ranvaud, R, KC de Freitas, EH Bucher, HS Dias, VC Avanzo & CC Alberts (2001) Diet of Eared Doves (*Zenaida auriculata*, Aves, Columbidae) in a sugar-cane colony in south-eastern Brazil. *Brazilian Journal of Biology* 61: 651–660.

Samamé Farfán, M (2005) *Composición y variación estacional en la dieta de las palomas (Aves: Columbidae) del bosque de Zarate, Lima, y alcances sobre la dispersión de semillas*. Tesis Doctoral, Univ. Nacional Mayor de San Marcos, Lima, Perú.

Sarasola, JH, JI Zanón-Martínez, AS Costán & WJ Ripple (2016) Hypercarnivorous apex predator could provide ecosystem services by dispersing seeds. *Scientific Reports* 6: 19647.

Trakhtenbrot, A, R Nathan, G Perry & DM Richardson (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions* 11: 173–181.

Vaz Ferreira, A, EM Bruna & HL Vasconcelos (2011) Seed predators limit plant recruitment in Neotropical savannas. *Oikos* 120: 1013–1022.

Walker, JS (2007) Geographical patterns of threat among pigeons and doves (Columbidae). *Oryx* 41: 289–299.

Zanón-Martínez, JI, MÁ Santillán, JH Sarasola & A Travaini (2016) A native top predator maintained by exotic preys inside a protected area: the puma and the introduced ungulates. *Journal of Arid Environments* 134: 17–20.

Zar, J. H. (1999) Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, New Jersey, USA.