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Guillermo Blanco, Carolina Bravo, Erica C Pacifico, Daniel Chamorro, Karina Lilian Speziale, Sergio A Lambertucci, Fernando Hiraldo, José L Tella

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Internal seed dispersal by parrots: an overview of a neglected mutualism

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ABSTRACT

Despite the fact that parrots (Psitacifformes) are generalist apex frugivores and present in high densities and biomass in many forest ecosystems, they have largely been considered plant antagonists and thus neglected as seed dispersers of their food plants. Endozoochorous dispersal was investigated by searching for seeds in faeces opportunistically collected at communal roosts, foraging sites and nests of eleven parrot species in different habitats and biomes in the Neotropics. Multiple intact seeds of seven plant species of five families were found in 9-49% of faeces from four parrot species. The mean number of seeds of each plant species per dropping ranged between 1 and 59, with a maximum of 481 seeds from the cacti *Pilosocereus pachycladus* in a single dropping of Lear's Macaw (*Anodorhynchus leari*). All seeds retrieved were small (<3mm) and corresponded to herbs and relatively large, multiple-seeded fleshy berries and infrutescences from shrubs, trees and columnar cacti, often also dispersed by stomatochory. A preliminary overview of the potential constraints driving seed dispersal suggest that, despite the obvious size difference between seeds dispersed by endozoochory and stomatochory, there is no clear difference in fruit size depending on the dispersal mode. Regardless of the enhanced or limited germination capability after gut transit, a relatively large proportion of cacti seeds frequently found in the faeces of two parrot species were viable according to the tetrazolium test and germination experiments. The conservative results of our preliminary sampling and a literature review clearly indicate that the importance of parrots as endozoochorous dispersers has been largely under-appreciated due to the lack of research systematically searching for seeds in their faeces. We encourage the urgent evaluation of seed dispersal and other mutualistic interactions mediated by parrots before their generalized population declines contribute to the collapse of key ecosystem processes.

Key-words: endozoochorous seed dispersal, fruit size, mutualistic interactions, Psittaciformes, stomatochory, vertebrate frugivores

INTRODUCTION

How organisms mould the environment in which they live by influencing the demography and population dynamics of other organisms is a central issue in ecology (Hooper *et al.*, 2005; Rietkerk & Van de Koppel, 2008). Factors underlying these processes are being increasingly addressed through the identification of the interacting organisms and the recognition and comprehensive understanding of the nature of their interactions (Wilson, 1992). As a consequence, a detailed natural history and the synthesis of the overwhelming patterns of interaction among species are continuously feeding back and merging under the growing consideration of previously unknown and overlooked ecological linkages and processes of variable complexity, and the probability of being observed in nature (Thompson, 2005; Stang *et al.*, 2007; Loreau, 2010; Bascompte & Jordano, 2014).

Vertebrate frugivores have been repeatedly highlighted as key 'mobile linkers' with a pervasive influence in ecosystem integrity by promoting the interchange of genetic information through seed flow (Fleming & Kress, 2013; Jordano, 2014). By enhancing the demography of their food plants, frugivores can influence the composition and abundance of plant communities, thus playing a major role in ecosystem structure and functioning (Wisz *et al.*, 2013). The importance of frugivores as plant mutualists has traditionally focused on internal dispersal (endozoochory) requiring the ingestion and subsequent defecation or regurgitation of viable seeds to be efficiently dispersed (Fleming & Kress, 2013; Jordano, 2014). Crucially, the identification of the major among the potential dispersers is essential to fully understand dispersal mutualisms and the influence of each disperser species or group of species on the conservation of ecosystem integrity.

Among birds, effective endozoochory has been primarily attributed to fruit gulpers swallowing entire fruits and, to a lesser extent, to fruit mashers feeding on fruit pulp where small seeds can be embedded and then inadvertently swallowed (Fleming & Kress, 2013; Jordano, 2014). While the size of seeds dispersed by gulpers is constrained by gape-size, it has been argued that dispersal by fruit mashers is restricted only to minute seeds (generally smaller than 2mm), because these frugivores discard larger seeds while biting and mandibulating fruit pulp (Wheelwright, 1985; Fleming & Kress, 2013; Jordano, 2014). Fruit mashers often also act as seed predators, leading to a wide range of interactions across an antagonism-mutualism gradient (Wheelwright & Orians, 1982; Hulme, 2002).

In particular, parrots (Psitacifformes) can alternatively feed on pulp, discarding seeds, or can actively search for large seeds that are often crushed with the bill to promote digestion, thus acting as seed predators (Janzen, 1981). However, despite the fact that most seed predators have been shown to eventually act as facultative primary dispersers (Norconk, Grafton & Conklin-Brittain, 1998; Vander Wall, Kuhn & Beck, 2005), parrots have been largely neglected as endozoochorous dispersers. This is striking because, although parrots undoubtedly destroy the seeds of many plant species, they can also inadvertently or actively ingest tiny ~~seed~~ embedded in pulp and disperse them in viable condition (Fleming *et al.*, 1985; Oliveira, Nunes & Farias, 2012). Indeed, a parrot species has recently been shown to be the major endozoochorous disperser of alpine flora in New Zealand (Young, Kelly & Nelson, 2012). This suggests that the overlooked potential of parrots in long-distance endozoochory may have precluded the proper evaluation of bird-plant mutualistic networks, and the comprehensive understanding of evolution and coevolution of vertebrate frugivores and their food plants, especially in the tropics. If endozoochory by parrots could be probed ~~widespread~~, their variable but comparatively large size, high mobility and abundance in frugivorous assemblages (Blanco *et al.*, 2015; Marsden & Royle, 2015; Renton *et al*,. 2015) could be presumed crucial in plant life cycles and ecosystem functioning.

In this study, we evaluated whether a random sample of Neotropical parrot species can defecate intact seeds of their food plants. This sampling was conceived as an exploratory study aimed to preliminary assess the potential role of parrots as endozoochorous dispersers, rather than to comprehensively evaluate internal dispersal by the sampled species or its consequences for their food plant populations, which requires specific research. Therefore, we did not systematically or seasonally search for faeces, but collected them opportunistically at communal roosts, foraging sites and nests in different habitats and biomes. We also evaluated the viability of the dispersed seeds regardless of their enhanced or limited germination capability due to the transit across the gut. Finally, we conducted a preliminary overview of the thus far largely neglected dispersal interactions between parrots and plants, in order to call attention on their potential implications in plant-frugivore mutualistic networks and forest conservation.

MATERIAL AND METHODS

Fieldwork

Fresh faeces were collected at communal roosts, foraging sites and nests of several parrot species inhabiting different biomes, including austral and tropical dry, montane and humid forests in variable states of conservation, and urban and agro-pastoral areas, in Ecuador, Peru, Brazil, Chile and Argentina (Table 1).

Faeces found beneath the trees used by communally roosting parrots were sampled early in the morning just after parrots left the roosts, which were used by single species thus precluding confusing their faeces with those of other species. Non-adjacent faeces found beneath the roosting trees were collected in order to avoid duplication of samples corresponding to the same individual. We also collected several faeces during observations of parrot foraging activity and during the handling of developing nestlings. Every faecal sample was collected in a paper bag, dried rapidly with a forced-air heater to prevent fungal growth and stored at room temperature until arrival at the laboratory.

On the same dates, we recorded the main foraging activities and the consumed part of each plant species exploited by parrots within the sampling site surroundings. These observations often corresponded to the flocks attending the communal roosts and breeding areas where faeces were collected. Foraging flocks were recorded during roadside surveys at low speed, making stops to record what they were eating (Blanco *et al.*, 2015). We recorded whether foraging parrots were feeding on pulp of ripe or unripe fruits and their mature or immature seeds, and specifically whether the consumed fruits correspond to plants with tiny seeds that could be swallowed and pass through the gut into the faeces. The size, measured with callipers, of a sample of ripe fruits of each species consumed by parrots, as well as the number of seeds per fruit, was recorded in the field or extracted from the literature.

Laboratory work

Faeces were disaggregated on petri dishes and intact seeds were separated with the aid of binocular microscopes (20x). The seeds were immediately washed with deionized water, gently dried with laboratory blotting paper and stored in paper bags in dark conditions and at room temperature. Seeds were identified and samples of seeds of each species measured for the diameter of the smallest and largest axis to the nearest 0.1mm with a digital calliper.

The viability of defecated seeds was determined by means of the tetrazolium test (Moore, 1985). This was aimed as an exploratory approach to assess the possibility that defecated seeds retain viability, rather than to precisely determine viability rate. Briefly, the seeds were cut and incubated in a 1% solution of 2,3,5-triphenyl tetrazolium chloride for 48h; tetrazolium reacts with respiring radicles to produce a red stain indicating viable seeds, while non-stained white radicles indicate non-viable seeds (Moore, 1985). We further assessed the reliability of the tetrazolium test to reflect the potential germination capacity of seeds after parrot gut passage by means of a simple germination experiment. After being washed, 160 seeds of *Pilosocereus pachycladus* from faecal samples of *Anodorhynchus leari* were set to germinate in petri dishes (5.5 cm in diameter) over two sheets of filter paper (Filter-Lab 1300). We used eight petri dishes, with 20 seeds each. Petri dishes were incubated in a chamber at 20 ºC and a photoperiod of 12 h. The petri dishes were regularly watered and sealed with parafilm to prevent them from desiccating. Germination success was scored after 60 days.

Overview of seed dispersal by parrots

We attempted to find all studies evaluating the presence of intact seeds in parrot faeces in the wild, and those experimentally testing endozoochory in captivity, by using key word searching in ISI Web of Science and Google Scholar. In addition, we surveyed dietary studies and consulted previous literature reviews on diet of parrots (e.g. Matuzak, Bezy & Brightsmith, 2008; Juniper & Parr, 2010; Renton *et al.*, 2015) to assess the exploitation of plants with tiny seeds that could be potentially dispersed by endozoochory.

The size of seeds actually dispersed by endozoochory recorded in the present study was compared with those potentially dispersed by endozoochory and with those dispersed by stomatochory, using the data reported by Blanco *et al.* (2015). The size of fruits whose seeds were actually or potentially dispersed by endozoochory was also compared with those dispersed by stomatochory. This overview thus focused on preliminarily exploring the potential role of parrots as seed dispersers of their food plants by different but complementary and redundant mechanisms, and its potential implications in the evolution of fruit traits.

RESULTS

We searched for seeds in 578 fresh faeces of 11 parrot species on different dates, and in different contexts and habitats in the Neotropics. Overall, we found 1787 seeds of seven plant species of five families in 65 faeces from four parrot species, while the remaining seven parrot species showed no seeds in their faeces (Table 1). The proportion of faeces with seeds ranged between ~9% and ~49% depending on species and context (Table 1). Most faeces with seeds contained seeds from a single species (92%, *n* = 65), while the remaining faeces showed seeds of two species of the Cactaceae family (Table 1). The mean number of seeds of each plant species per faecal sample of each parrot species in each context ranged between 1 and 59, with a maximum of 481 seeds of *P. pachycladus* (Cactaceae) in a single faecal sample of *A. leari* (Table 1, Fig. 1).

Parrot species showing no seeds in their faeces were mostly foraging on multiple plant parts other than fruit, especially flower buds, nectar, bark and sprouts of native and exotic trees and shrubs, leaves, flowers, bulbs and seeds of grasses, cereal grain from agricultural and grazing areas, and wood parasitic fungi. They were also observed feeding on pulp of large-seeded fruits, both of native and exotic trees and shrubs, and predating on their seeds (Table 1). The results showing few or no seeds in faeces are clearly conservative when the sampling was conducted in seasonal periods with very low abundance of fruit/seeds or lacking fruiting plants (e.g. both *Enicognathus* species and *Cyanoliseus patagonus* sampled in late austral winter).

The mean dimensions of a sample of seeds present in the faeces is shown in Table 2 for each plant species, pooling those found in faeces of different parrot species. These seeds usually correspond to relatively large, multiple-seeded fleshy berries and aggregates of drupes with juicy pulp from plants of variable growth forms (Table 2). Several of the plant species dispersed by endozoochory were also observed being dispersed by stomatochory (e.g. entire fruits of *Rubus* sp. dispersed by *Psittacara hockingi*, and fruits of *P. pachycladus* transported with the feet in flight by *A. leari*).

Results of the tetrazolium test indicated that a proportion of seeds of *P. pachycladus* and *Cereus jamacaru* retrieved from faeces of two different parrot species and sampling contexts were viable (Table 2). The germination success of a sample of *P. pachycladus* seeds (35.6%, n =160) was slightly less but not statistically different (Fisher's exact test $P = 0.199$) than the proportion of viable seeds as assessed by the tetrazolium test (Table 2), which indicates that this test reliably reflected the potential of seeds to germinate after passing through the parrots' gut. The seeds of the remaining species, which were found much less frequently in faeces, were inviable according to the tetrazolium test (Table 2).

Seeds dispersed by endozoochory (actual or potential) were smaller than those dispersed by stomatochory ($\log_{10}$ seed length, two-way ANOVA, $F_{2,26} = 23.88$, $P < 0.0001$, $\log_{10}$ seed width, $F_{2,26} = 20.68$, $P < 0.0001$; post-hoc tests indicated no size difference between seeds actually and potentially dispersed by endozoochory, both $P > 0.05$, Fig. 2). The size of fruits whose seeds were actually or potentially dispersed by endozoochory was similar for fruit length ($\log_{10}$ transformed, t-test, $t = 0.304$, P = 0.76) and slightly larger for fruit width ($\log_{10}$ transformed, t-test, $t = 2.07$, $P = 0.049$, $n_1 = 13$, $n_2 = 15$) than those dispersed by stomatochory (Fig. 3).

DISCUSSION

Despite the fact that parrots have traditionally been neglected as internal seed dispersers, we found seeds of several plant species in a small sample of parrot faeces collected in a variety of habitats and biomes in the Neotropics. The sampled parrot species and populations were not selected for their known frugivorous habits or local and seasonal use of fruits from particular plant species. Instead, faecal collection opportunities during the course of other studies were occasionally encountered and used to assess endozoochory, even when there were no fruiting plants on the sampling dates. As a consequence, we did not find seeds in the faeces of several of the sampled parrot species because they were not foraging on fruits during the study period, but rather on a variety of other resources. However, as trophic generalists exploiting all seasonally available feeding opportunities (e.g. Ragusa-Netto & Fecchio, 2006; Gilardi & Toft, 2012; Lee *et al.*, 2014; Blanco *et al.*, 2015; Renton *et al.*, 2015), these and many other parrot species have been occasionally or frequently recorded exploiting all major neotropical plant families with tiny-seeded fruits (see diet reviews by Matuzak, Bezy & Brightsmith, 2008; Juniper & Parr, 2010; Renton *et al*, 2015). Therefore, the conservative results of our preliminary sampling and the literature review clearly indicate that the importance of parrots as endozoochorous dispersers has been largely under-appreciated due to the lack of research systematically searching for seeds in their faeces.

As expected from our random sampling contexts, dates and habitats, the proportion of faeces with seeds greatly differed between plant and parrot species. Both the occurrence and number of seeds in faeces were especially high for cacti from the Caatinga, dispersed by a medium-size parakeet (*T. acuticaudata*) and a large macaw (*A. leari*); two other parrot species were recorded foraging on the same cacti species but seeds were not retrieved from their faeces, probably due to the small number of faeces analysed. The recorded figures were similar and even higher regarding the number of seeds per dropping than those reported in the literature for recognized avian frugivores (Fleming & Kress, 2013; Jordano, 2014), as also reported for the New Zealand kea, *Nestor notabilis* (Young, Kelly & Nelson, 2012). Besides Cactaceae, we found seeds from Moraceae, Rosaceae, Asteraceae and Plantaginaceae families. Our review of the literature showed that intact seeds of other plant families have been retrieved from parrot faeces, including Mutingiaceae, Dilleniaceae, Myrtaceae, Araliaceae, Coriariaceae, Elaeocarpaceae, Ericaceae, Podocarpaceae, Polygonaceae, Rubiaceae and Lauraceae (Fleming *et al*,. 1985; Oliveira, Nunes & Farias, 2012; Young, Kelly & Nelson, 2012; Thabethe *et al.*, 2015). Internal dispersal of tiny seeds of these and other plant families were suspected in other studies not searching for seeds in faeces (e.g. Eitniear, Mcghee & Waddell, 1994; Norconk, Grafton & Conklin-Brittain, 1998; Contreras-González *et al.*, 2009; Blanco *et al.*, 2015). The variety of habits, growth forms and seed and fruit types of plants dispersed by endozoochory strengthens the key mutualist role of parrots on plant assemblages by complementing previously recorded interactions, including pollination, stomatochorous seed dispersal, seed facilitation for secondary dispersers and plant healing (Douglas, Winkel & Sherry, 2013; Blanco *et al.*, 2015; Tella *et al.*, 2015).

All seeds found in the faeces were small (<3mm) and corresponded to herbs and relatively large, multiple-seeded fleshy berries and infrutescences with juicy pulp from columnar cacti, shrubs and trees (see also Fleming *et al.*, 1985; Oliveira, Nunes & Farias, 2012, Young, Kelly & Nelson, 2012). Importantly, parrots are singular dispersers owing to their unique ability to simultaneously or alternatively move minute seeds from fleshy fruits by endozoochory, stomatochory and probably epizoochory (see Fig. 1c). Parrots are apparently not limited by gape size to disperse tiny seeds, although the smallest species could crush the smallest seeds, but this requires further testing. Conversely, the smallest species can be limited by body-size to disperse large seeds by stomatochory, but they can still disperse by this method seeds much larger than those dispersed by endozoochory (Boehning-Gaese, Gaese & Rabemanantsoa, 1999; Sazima, 2008; Blanco *et al.*, 2015; Tella *et al.*, 2015). Our exploratory analysis of these constraints suggests that, despite the obvious size difference between seeds dispersed by endozoochory and stomatochory, no clear differences arise for fruit size depending on the dispersal mode. This appears to be primarily due to the widespread range of size and shape of fruits dispersed by stomatochory, including those much longer than wide, e.g. multi-seeded pods corresponding to legumes (Fabaceae) and other large fruits (Blanco *et al.*, 2015; Tella *et al.*, 2015). Seed dispersal mutualisms mediated by parrots can thus have multiple potential implications for the understanding of bird-fruit interactions, especially because only internal seed dispersal constrained by gape size has been generally considered as an evolutionary force selecting for avian-dispersed seed size (Wheelwright, 1985; Fleming & Kress, 2013; Galetti *et al*,. 2013; Jordano, 2014).

A relatively large proportion of the cacti seeds frequently found in the faeces of two parrot species were viable according to the tetrazolium test. The maximum germination success in laboratory conditions of seeds extracted from mature fruits of *C. jamacaru* (94.0%: Meiado *et al.*, 2010, 89.0%: Abud *et al.*, 2013, both at 25 ºC and 12h photoperiod) was similar to the proportion of viable seeds of the same cacti retrieved from *A. leari* faeces (92.7%). Germination success recorded by Abud *et al.* (2010) for *P. pachycladus* seeds in the same conditions was, however, higher than the proportion of viable seeds and germination success of seeds from parrot faeces recorded in this study. Sample size of the species whose seeds were inviable (≤ 20 seeds in all cases) was insufficient to adequately determine this trait, given the variable natural viability of seeds (Long *et al.*, 2015) and the low germinability of several of the recorded species (e.g < 35% in *Tacinga inamoema*, Nascimento *et al.*, 2015). Seed viability, especially of those seeds from the plant species less frequently found in faeces, could also be affected by the seed drying conditions carried out in the field, and the subsequent storage after analysis, or they may actually be affected by passage through the parrots' gut. Alternatively, these seeds could correspond to immature fruits often exploited by parrots (Norconk, Grafton & Conklin-Brittain, 1998; Blanco *et al.*, 2015). In any case, our exploratory experiments and findings add to those of previous studies suggesting that parrots can be endozoochorous dispersers enhancing or limiting seed germinability to variable extents depending on plant and parrot species (Fleming *et al.*, 1985; Oliveira, Nunes & Farias, 2012, Thabethe *et al.* 2015), as stated for recognized avian seed dispersers (Traveset *et al.*, 2007).

In conclusion, despite the fact that parrots constitute an evolutionarily ancient, highly diversified and widely distributed group of generalist apex frugivores (Toft & Wright, 2015), they have been largely overlooked as genetic linkers of their food plants, and thus excluded from animal-plant interaction networks (Fleming & Kress, 2013; Bascompte & Jordano, 2014). This exclusion has likely been promoted by the relatively large size, canopy use and high mobility of parrots, hindering detailed observations of stomatochory (Blanco *et al*,. 2015; Tella *et al.*, 2015) and, especially due to the difficulty of mist-netting them to collect faeces to evaluate endozoochory. Importantly, this knowledge gap implies a markedly biased view of frugivore-plant mutualistic interactions towards fruit gulpers, despite the fact that parrots constitute rich species guilds showing a greater range of size, morphology and foraging behaviours, and accounting for a higher density and biomass than other recognized frugivores in many tropical and temperate ecosystems (Blanco *et al.*, 2015; Marsden & Royle, 2015; Renton *et al.*, 2015; Toft & Wright, 2015). This supports the emerging view showing that many species traditionally assumed only as seed predators can also act as pervasive seed dispersers owing to their comparatively high abundance (Heleno *et al.*, 2011; Orłowski *et al.*, 2015). Worryingly, in addition to the loss of frugivore-plant interactions (so far mostly focused on fruit gulpers) due to forest destruction and fragmentation (Markl *et al.*, 2012; Sebastián-González *et al*., 2015), the intensive persecution and capture of parrots for the pet trade may be decimating populations of once common species (Tella & Hiraldo, 2014; Annorbah, Collar & Marsden, 2015; Toft & Wright, 2015), thus disrupting largely unknown mutualistic interactions between parrots and their food plants. We encourage an urgent comprehensive evaluation of seed dispersal and other mutualistic interactions mediated by parrots before their generalized population declines contribute to the collapse of key ecosystem processes.

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Table 1. Presence of intact seeds found in parrot faeces collected in several contexts and Neotropical habitats and biomes, and number of seeds per dropping. Collection data and main food of parrot species without seeds in the sampled faeces are also shown.

Parrot species (context[a])	Habitat, locality, date	% faeces with seeds, n	Plant species (Family)	Faeces with seeds (%)[b]	Mean ± SD seeds/ faeces (range)
With seeds in sampled faeces					
Psittacara hockingi (CR)	Montane forest, Leymebamba, Perú, Dec. 2014	24.1, $n = 29$	*Rubus* sp. (Rosaceae)	6 (20.7)	3.3 ± 4.1 (1- 11)
			Maclura tinctoria (Moraceae)	1 (3.4)	1
Thectocercus acuticaudatus (CR, FA)	Caatinga, Canudos, Brazil, Jan.-April 2015	30.2, $n = 43$	*Pilosocereus pachycladus* (Cactaceae)	13 (30.2)	25.3 ± 37.8 (1-107)
			Tacinga inamoema (Cactaceae)	1 (2.3)	2
Anodorhynchus leari (CR, FA)	Caatinga, Canudos, Brazil, Jan.-April 2015	49.3, $n = 75$	*Pilosocereus pachycladus* (Cactaceae)	37 (49.3)	40.9 ± 90.8 (1-481)
			Tacinga inamoema (Cactaceae)	3 (4.0)	1.0 ± 0.0 (1)
Anodorhynchus leari (N)	Caatinga, Canudos, Brazil, April 2015	22.2, $n = 18$	*Pilosocereus pachycladus* (Cactaceae)	2 (11.1)	8.5 ± 6.4 (4-13)
			Cereus jamacaru (Cactaceae)	3 (16.7)	58.7 ± 80.8 (1-151)
Myiopsitta monachus (BC)	Urban, Buenos Aires, Argentina, May 2015	8.6, $n = 35$	Unindentified (Asteraceae)	2 (5.7)	2.0 ± 0.0 (2)
			Plantago major (Plantaginaceae)	1 (2.9)	4
Without seeds in sampled faeces					
		n	Foraging observations		
Forpus coelestis (CR)	Coastal-urban, Santa Elena, Ecuador, Dec. 2014	250	fruit pulp (*Ficus* sp.), nectar, bark		
Eupsittula cactorum (N)	Caatinga, Canudos, Brazil, Jan. Feb. 2015	10	fruit pulp (Cactaceae), flowers, nectar, bark		
Amazona lilacina (CR)	Tumbesian forest, Santa Elena, Ecuador, Dec.2014	32	fruit pulp (mostly *Spondias purpurea*, *Cordia lutea*)		
Amazona aestiva (CR)	Caatinga, Canudos, Brazil, Jan.-April 2015	9	fruit pulp (Cactaceae), flowers, bark		
Enicognathus ferrugineus (FA)	Urban, Bariloche, Argentina, June-Sept. 2015	42	fruit pulp (*Malus*), large seeds (*Prunus*, *Quercus*), flower buds, nectar, fungi, grasses		
Enicognathus leptorhynchus (CR)	Agro-grazing, Osorno, Chile, Sept. 2015	20	cereal grain, grasses, flower buds, fungi		
Cyanoliseus patagonus (CR)	Steppe, Junín de los Andes, Argentina, Sept. 2015	15	cereal grain, flower buds, bark		

[a] CR: communal roost, FA: foraging areas, N: nestling, BC: breeding colony.

[b] note that several faeces showed the simultaneous presence of seeds of several plant species.

Table 2. Features of plants and fruits whose seeds were found in parrot faeces, and seed viability according to the tetrazolium test.

Plant species	Growth form	seed size, mm (*n*)	Fruit type	Fruit size, mm[b]	No. of seeds[b]	tested/viable seeds (%viable)
Rubus sp.	shrub	2.56 x 1.51 (6)	berry	15.0 x 15.0	48	20/0 (0.0)
Maclura tinctoria	tree	2.15 x 1.32 (1)	multiple drupe	20.0 x 12.0	50	1/0 (0.0)
Pilosocereus pachycladus	columnar tree-like cacti	1.89 x 1.35 (154)[a]	berry	50.5 x 38.1[1]	3800[1]	1194/490 (41.0)
Tacinga inamoema	opuntiad cacti	1.98 x 1.21 (6)[a]	berry	35.0 x 30.0[2]	tens[3]	4/0 (0.0)
Cereus jamacaru	columnar tree-like cacti	2.62 x 1.73 (20)	berry	82.3 x 62.6[4]	1400[4]	124/115 (92.7)
Unindentified Asteraceae	probably herb	2.09 x 0.81 (4)	**?**	**?**	**?**	4/0 (0.0)
Plantago major	herb	1.77 x 1.09 (2)	capsule	5.0 x 3.5	10	4/0 (0.0)

[a] Seeds from faeces of *T. acuticaudatus* and *A. leari*.

[b] Approximate mean fruit size and number of seeds per fruit or infrutescence, measured in the field or extracted from the literature (1= Abud *et al.* 2010, 2 = Souza *et al.* 2007, 3= Menezes *et al.* 2013, 4= Abud *et al.* 2013).

Figure 1. (A) Partially eaten *Pilosocereus pachycladus* (Cactaceae) fruit, and (B) detail of its red pulp showing multiple tiny seeds. (C) Adult Lear's Macaw *Anodorhynchus leari* defecating in flight on a conspecific (probably its mate); note the red colour of the faecal material corresponding to feeding on *P. pachycladus* fruits, which illustrates potential endozoochory and epizoochory. Seeds of *Cereus jamacaru* (D) and *P. pachycladus* (E) retrieved from parrot faeces. Photographs by E. Pacifico (A, B), J. Marcos Rosa (C) and C. Bravo (D, E).

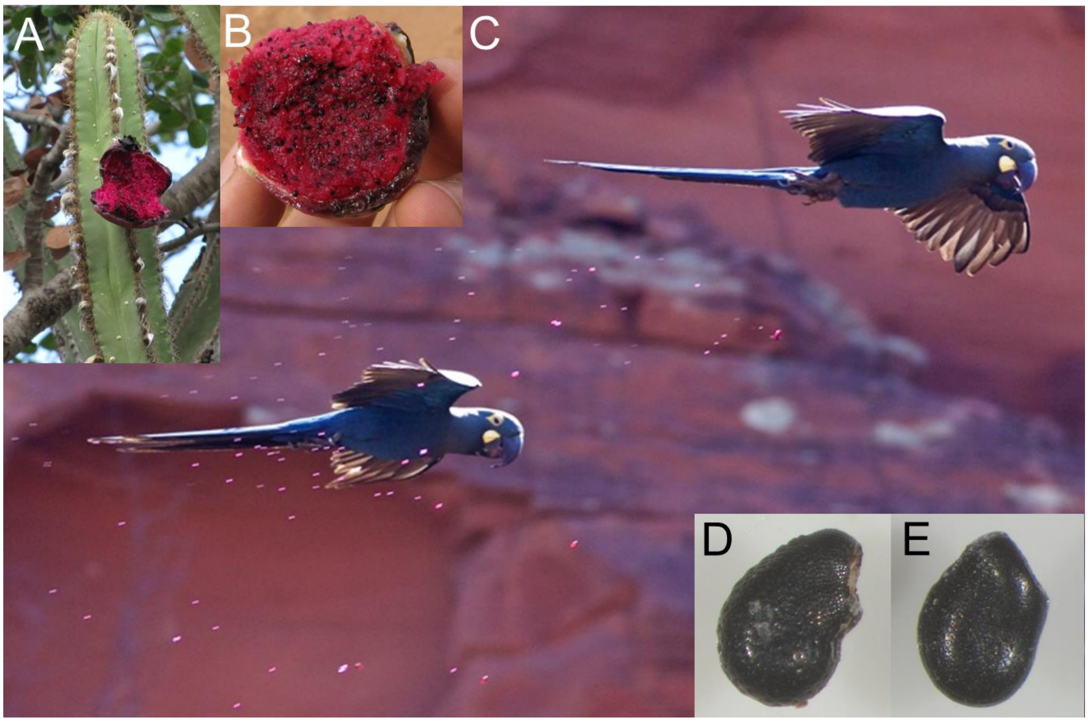

Figure 2. Length and width of seeds dispersed by endozoochory and stomatochory by parrots. Data from seeds dispersed by stomatochory and potential endozoochory were extracted from Blanco *et al.* (2015).

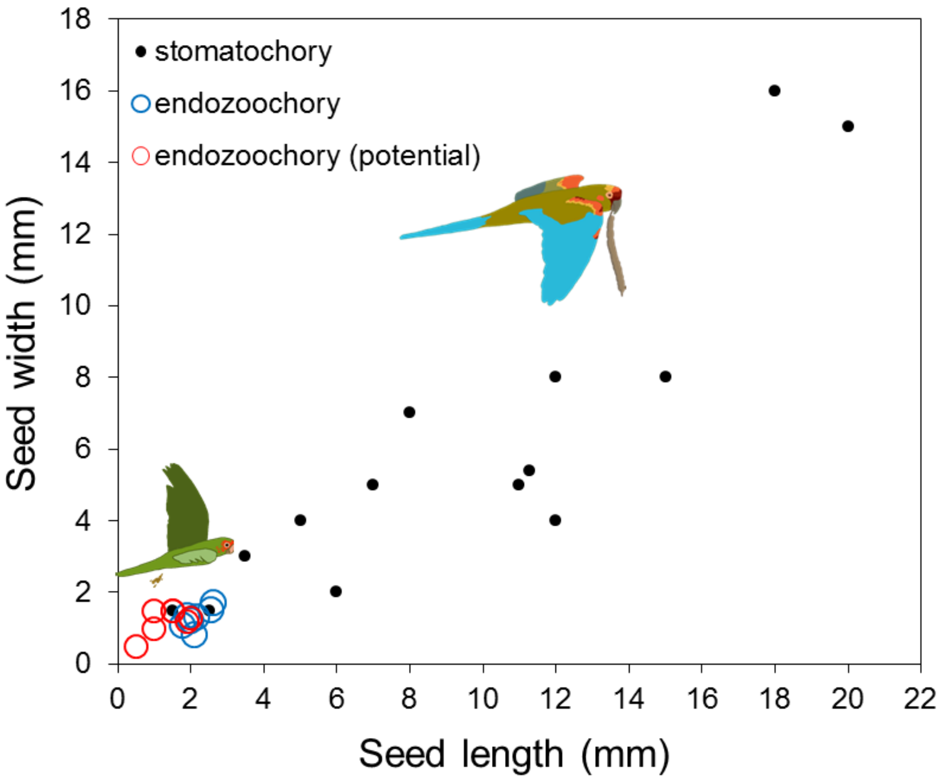

Figure 3. Size (length and width) of fruits whose seeds were dispersed by endozoochory and stomatochory by parrots. Data were pooled for fruits whose seeds were actually or potentially dispersed internally by parrots; data for fruits dispersed by stomatochory and potential endozoochory was extracted from Blanco *et al.* (2015). The boxes depict the interquartile ranges (25th to 75th percentiles), the horizontal thick lines represent the medians, the black squares show the means, the whiskers extend to 1.5 times the interquartile range, and the asterisks denote the extreme cases.