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DOES AVIAN GUT PASSAGE FAVOUR SEED GERMINATION OF WOODY SPECIES OF THE CHACO SERRANO WOODLAND IN ARGENTINA?

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Abstract

Frugivorous birds are key dispersal agents of many plant species and also may facilitate seed germination after gut-passage. However, the general effects of gut-passage on seed germination are still not clear, with positive, negative and neutral effects reported on seed germination. We evaluated seed germination of seven bird-dispersed plant species of the Chaco Serrano Woodland in Córdoba, Argentina: *Celtis ehrenbergiana*, *Condalia* spp., *Lantana camara*, *Lithraea molleoides*, *Lycium cestroides*, *Schinus fasciculatus* and *Zanthoxylum coco*. We compared germination percentages and germination speed among seeds ingested by birds, manually extracted seeds, and seeds from intact fruits in order to understand which mechanisms are acting on bird gut-passed seeds. For six plant species, the action of frugivorous birds increased seed germination percentages and provides faster germination, either through scarification, deinhibition, or through combined mechanisms. Our results contribute to better understand the mechanisms acting on bird gut-passed seeds. Also, we show the pivotal role that frugivorous birds exert on the seed germination of native woody plant species in the threatened ecosystem of Chaco Serrano Woodland.

Keywords: avian gut passage, deinhibition, germination, scarification, native woody species

Introduction

The consequences of avian fruit consumption on seed germination are important for assessing the effectiveness of frugivores in plant establishment and regeneration (Traveset 1998; Traveset et al. 2007; Schupp et al. 2010). The overall effects of gut-passage on seed germination are not consistent, with positive, negative and neutral effects on seed germination all reported (Traveset 1998; Traveset et al. 2007). The results of the interaction seems to be highly dependent on the plant and bird species interacting and on the methodology used in the testing (Robertson et al. 2006).

In bird-dispersed species, facilitation of seed germination may occur through different mechanisms; among those, two of the most important are deinhibition and scarification (Traveset 1998; Traveset and Verdú 2002; Robertson et al. 2006; Traveset et al. 2007). The deinhibition effect implies that through avian fruit ingestion, germination is increased only by separating seeds from the fruit pulp. This effect could occur even if seeds are regurgitated. The fruit pulp may contain germination inhibitors such as lipids, glycoalkaloids, coumarin, and various light-blocking pigments (Cipollini and Levey 1997; Samuels and Levey 2005; Traveset et al. 2007). In addition, high sugar content in fruit pulp may provoke high osmotic pressure (Traveset 1998; Samuels and Levey 2005), or it can be a source of infections by fungi or other pathogens affecting seed viability and germination (Traveset 1998; Samuels and Levey 2005). The scarification effect (chemical or mechanical) on germination involves modifications of the seed coat (Traveset 1998; Traveset and Verdú 2002; Samuels and Levey 2005; Robertson et al. 2006; Traveset et al. 2007; Traveset et al. 2008). The magnitude of the scarification effect depends on the characteristics of the frugivore species (length of the digestive tract, presence of a gizzard, seed retention time) as well as fruit and seed traits of each plant species (pulp composition, seed age, seed size, coat thickness and texture) (Traveset et al. 2007).

Most studies that evaluated effects of avian fruit consumption on seed germination tested the combined effects of scarification and the deinhibition effects without separating the two effects (Traveset and Verdú 2002; Samuels and Levey 2005). Samuels and Levey (2005) reviewed the literature and found that only 18% of the studies evaluating the effect of gut-

passage on germination included comparisons that allowed the distinction between the scarification and the deinhibition effects to be made (this requires a comparison of seeds from intact fruits, manually extracted seeds, and gut-passed seeds). The recognition of the two components of germination stimulation has clarified greatly what is required to improve our knowledge on the role of frugivorous birds as seed dispersers in natural environments. Several of the previous studies suggested that pulp removal alone by frugivorous birds would be sufficient to increase seed germination, without evidence of a scarification effect (Izhaki and Safriel 1990; Barnea et al. 1991; Reid and Armesto 2010; Lehouck et al. 2011). On the other hand, a review from Traveset and Verdú (2002) showed that avian gut-passed seeds increase their germination percentages compared with manually extracted seeds, suggesting a high importance of the scarification effect. Moreover, Robertson et al. (2006) showed that deinhibition studies are prone to artefacts of the testing environment where whole fruits are tested in Petri dishes which prevent the washing away of inhibitors that would happen naturally in field conditions on soil. Thus the importance of the deinhibition effect may have been overestimated as a result of using an inappropriate method.

The Chaco subtropical forest of Argentina became a priority for biodiversity conservation because it is a threatened ecosystem that has suffered a strong increase in the rate of deforestation and habitat fragmentation due to the expansion of agriculture and urbanization (Gavier and Bucher 2004; Zak et al. 2004; Galetto et al. 2007; Aide et al. 2012), and suffered the proliferation of invasive exotic plant species (Giorgis *et al.* 2011). There are many species of woody plants, shrubs, grasses and vines in this ecosystem that are consumed and dispersed by frugivorous birds (Ponce et al. 2012; Díaz Vélez 2013). Birds are the only volant frugivores (no frugivorous bats exist in the area), and they may play an important role in maintaining bird-dispersed plant populations, not only by promoting seed movement, but also by increasing the likelihood or speed of seed germination. However, only a few studies have examined seed germination of Chaco bird-dispersed species (Funes et al. 2009; Grilli et al. 2009; Ashworth and Martí 2011), and even fewer studies have evaluated the different mechanisms that could facilitate seed germination (Renison et al. 2010). In this work, we want to answer two main questions: Does avian gut passage have a positive, a negative or a

neutral effect on seed germination of native woody plant species? If it has a positive effect: Is this facilitation occurring through deinhibition, scarification or both?

Methods

Study site

The study was performed in the Chaco Serrano Woodland of Córdoba, Argentina. Mean annual temperature is 17.5°C. Most precipitation falls from October to March (on average 750 mm per season, Luti et al. 1979; Moglia and Gimenez 1998) coinciding with the fruiting peak of bird-dispersed plants. The dry season extends from April to September (on average 116 mm per season), which coincides with the period of low temperatures (Capitanelli 1979).

The Chaco vegetation at the study site is highly fragmented due to recent agricultural and urban expansion (Zak et al. 2004). Fruits were collected from eight fragments (31°09'S to 31°13'S and 64°13'W to 64°17'W) which are composed of secondary forest with a canopy that usually reaches 7-9 m high. Native vegetation includes numerous bird-dispersed species, the majority of which are trees and shrubs, with some climbers (such as *Passiflora morifolia*, *P. suberosa*) and many herbs (such as *Salpichroa origanifolia*, *Solanum chenopodioides*, *Rivina humilis*, *Lantana grisebachii*) (Cagnolo et al. 2006; Ponce et al. 2012; Díaz Vélez 2013).

Species studied

We collected fruits of seven native bird-dispersed woody species that are commonly eaten by birds and that were the most abundant in a bird-dispersed seed rain experiment performed within the study area (Díaz Vélez 2013). The characteristics of the plant and frugivorous bird species that consume their fruits are listed in Table 1.

Seed treatments and germination experiments

In order to understand which mechanisms are acting on bird gut-passed seeds, the scheme proposed by Samuels and Levey (2005) was used to compare germination percentages among seeds ingested by birds, manually extracted seeds, and seeds from intact fruits (Fig. 1). The three seed treatments were:

- a) Gut-passed seeds (G): seeds that were defecated and/or regurgitated by birds. If this treatment determines an increase of the percentage of seed germination, the mechanisms inferred are deinhibition and scarification.
- b) Intact fruits (F): mature fruits collected from at least 10 individuals of each plant species and stored in paper bags until the beginning of the germination experiment. The dehydration process that fruits suffer inside the paper bags simulates what would happen with those non-dispersed fruits, i.e., fruits that fall on the ground. Since *L. cestroides* is the only species with more than one seed per fruit, the percentage of seed germination was calculated by adding the germinated seeds plus the number of un-germinated seeds within intact fruits opened at the end of the experiment to get a total seed count per fruit.
- c) Manually extracted seeds (M): seeds were manually removed from mature fruits, and any pulp remaining on the seed coat was washed off. This condition allows knowing whether the seeds are subject to an inhibitory mechanism produced by the pulp. For *Z. coco*, the seeds were left in water for one day to facilitate the extraction of the oily blackish mesocarp that is firmly attached to the seed. The great majority of the oily mesocarp was extracted using tweezers.

Each replicate, for each treatment, consisted of a group of seeds or fruits from only one species placed in a transparent plastic container of 5 cm height, 8 cm diameter (250 cm³) (Table 2). For the “intact fruit” and “manually extracted seeds” treatments, we used mature fruits collected from the same individual plant or seed trap. The number of seeds per replicate and replicates per treatment varied among plant species and were determined according to the average number of seeds found in the faecal or regurgitated samples (Table 2). Seed sources and replicates for the three germination treatments are shown in Table 2.

Germination experiments were carried out in a germination chamber. Each replicate was placed in a transparent plastic container, covered with holes for ventilation, containing 1 centimetre of sterilized soil mixed with sand. The plastic containers were kept in a germination chamber at 25°C with 14 hours of light. Seeds or fruits were sown in the substrate and watered regularly. The groups of seeds or fruits were examined for germination (radicle emergence) twice a week. Germinated seeds were counted and removed to reduce interaction with un-germinated seeds and to avoid re-counting. Germination was monitored

for one year in *L. cestroides* and *Condalia* spp. (from August 2009 to August 2010) and for eight months in the remaining plant species (from June 2011 to February 2012). We decided to reduce the time of the second germination experiment because we did not record seed germination after eight months in the first experiment.

Statistical analyses

We calculated the number and percentage of germinated seeds for each treatment at the end of the experiment for the seven plant species selected. The percentage of seed germination was analyzed with a generalized linear model with a binomial error structure and logit link function, using the seed treatments as fixed factor (three levels: gut-passed seeds, manually extracted seeds and intact fruits). A quasi-binomial error structure was used due to over-dispersion in the response variables in many species (see Table 3). When differences among treatments were significant, “*Di Rienzo, Guzmán and Casanoves*” (DCG) a posteriori test was performed. The GLMs were performed in Infostat (Di Rienzo et al. 2013) and its interface to R (R 2.15.0, R development core team 2012). As an estimate of germination speed, we used the Survival Analysis module of Kaplan-Meier available in SPSS 10 to compare cumulative germination percentages among treatments. We used log-rank tests (Mantel-Cox), a non-parametric test recommended for evaluating the effect of categorical predictive variables. In all cases, $p \leq 0.05$ was considered to assess significant differences among treatments (Traveset et al. 2008).

Results

Germinability

There were significant treatment effects on germination percentage for all species (Table 3, Fig 2). In general, there was a reduced likelihood of seed germination in intact fruits, ranging from 4 to 22%, however *C. ehrenbergiana* presented an average germination percentage higher than 50%. Germination of gut-passed seeds varied from 17 to 74 % and from 8 to 73% for manually extracted seeds.

Gut-passed seeds showed significantly higher germination percentages than intact fruits in all the species with the exception of *S. fasciculatus* (Fig. 2F). In *S. fasciculatus*, the

germination of manually extracted seeds was significantly higher than gut-passed seeds and intact fruits. *C. ehrenbergiana*, *L. camara*, *L. molleoides*, *Z. coco* gut passed seeds showed significantly higher values than manually extracted seeds (Fig. 2 A,C,D,G). From these four species only in *L. camara* manually extracted seeds also differed from intact fruits (Fig. 2C). In *L. cestroides* and *Condalia spp.* manually extracted seeds differed from intact fruits, but not with gut passed seeds (Fig. 2 B, E).

Germination speed

There were large treatment effects on the speed at which seeds germinated (Table 4, Fig. 3). Overall, the cumulative germination of gut-passed seeds differed significantly from manually extracted ones, being faster in *C. ehrenbergiana*, *L. camara*, *L. molleoides* and *Z. coco* (Fig. 3A, C, D and G) and slower in *Condalia spp.*, *L. cestroides* and *S. fasciculatus* (Fig. 3B, E and F). Gut-passed seeds also germinated significantly faster than those of intact fruits, but in *Condalia spp.* and *S. fasciculatus* the differences were not significant (Fig. 3B and 3F). Manually extracted seeds germinated significantly faster than those of intact fruits for all species, excepted for *Z. coco*, in which the difference was not significant (Fig. 3G).

Discussion

Frugivorous birds are key agents for the maintenance and expansion of many plant species, because they disperse the plant's seeds and may facilitate their germination. In this study we analyzed germination percentage and speed of germination in seven species of the Chaco Serrano Forest of Córdoba, Argentina, in order to disentangle if birds are having a positive, a negative or a neutral effect on seed germination. In addition, as proposed by Samuels and Levey (2005) we aimed to understand through which mechanisms this interaction is occurring. For most of the plant species in this study (six out of seven), the action of frugivorous birds facilitated seed germination, either through scarification (*C. ehrenbergiana*, *L. molleoides* and *Z. coco*), deinhibition (*Condalia spp.* and *L. cestroides*) or through combined mechanisms (*L. camara*).

In *C. ehrenbergiana*, *L. molleoides* and *Z. coco* there were significantly higher percentage of seed germination and speed of germination in gut-passed seeds compared to manually extracted seeds, which is indicative of a scarification effect. Therefore, these species must have a double dependency on birds –i.e., for dispersal and germination. It is possible that in *C. ehrenbergiana* and *L. molleoides* also a deinhibition effect exists which was only detected in their speed of germination. It is important to highlight that the seeds of *C. ehrenbergiana* germinated successfully more than 50% even in intact fruits. In addition, Renison et al. (2011) found that seeds of this species when ingested by *Rhea americana* had lower germination than those of intact fruits and suggested that *C. ehrenbergiana* seeds could be adapted to dispersal by small bird species with shorter gut retention times, which is supported by our results. In *Z. coco* since pulp removal of this species is difficult (probably not fully removed in our manually extracted treatment), we cannot discard a deinhibition effect. However, in another congeneric species, *Z. dissitum*, Ying-Zi et al. (2009) observed higher germination after seeds were scarified with sulfuric acid. Therefore, our results and those in *Z. dissitum* suggested that scarification is the main mechanisms in this genus.

In *Condalia spp.* and *L. cestroides* higher germination percentages in manually extracted seeds and gut passage seeds than those from intact fruits were observed suggesting that the seeds increased their germinability by a deinhibition effect (Traveset 1998; Traveset and Verdú 2002; Robertson et al. 2006; Traveset et al. 2007). The speed of germination also suggested this pattern even though it does not fully support it, in both species the speed of seed germination of extracted seeds was significantly greater than for that from seeds residing in intact fruit, but germination speed of extracted seeds was also faster than that for gut passed seeds.

Therefore, in *L. cestroides* the speed results suggested that birds, even though they provide a deinhibition, they are not capable of promoting the greatest germination velocity possible for the species. In *Condalia spp.*, gut passed seeds showed similar speed than intact fruits, thus birds seem not to exert any benefit in the speed of germination, deinhibition may be acting only in the germinability of this species. For *Condalia spp.* Renison et al. (2010) also found that seed germination was higher in manually extracted seeds of *Condalia*

microphylla in relation to intact fruits, but seeds ingested by *R. americana* showed lower germination percentages. Altogether, the comparison of our results and the previous work of Renison et al. (2010) for *C. ehrenbergiana* and *Condalia spp.* suggest that different bird species may exert different effects on seed germination and that the different plant species also respond differently to gut passage. In addition, performing experiments that will consider the different *Condalia* species coexisting in the study area (*C. buxifolia*, *C. microphylla* and *C. montana*) would be important for assessing the array of interactions between these plant species and their seed dispersers.

Only in *L. camara* do birds seem to exert both mechanisms, because statistically significant differences were observed between gut passage seeds and manually extracted seeds and between the latter and seeds from intact fruits in both of the variables analyzed. Thus, birds are highly important for seed germination of this species which is considered a native invasive species because it is originally from other phytogeographic regions of the country (Giorgis and Tecco 2014). Therefore, these results are important if they are intended to develop some management strategy in this species.

Finally, in *S. fasciculatus*, the fruit pulp is firmly attached to the seed, making pulp removal by abrasion in bird guts possibly difficult, which might explain the higher germination and speed in manually extracted seeds in relation to gut-passed ones. The low values obtained in gut passed seeds suggested that in this species birds might be exerting a negative effect on seed germination. It is possible that other bird species or other terrestrial dispersers, may be involved in pulp removal of *S. fasciculatus* fruits producing different results. A deinhibition mechanism was observed in other congeneric species (*S. Terebinthifolius*) from Argentina, Paraguay and Brazil (Panetta and Mckee 1997; D'Avila et al. 2010).

Our detailed sampling effort to obtain defecated seeds contributes to better understand the role that the community of frugivorous birds exerts on the seed germination of native plant species in the Chaco Serrano Woodland. In addition, except for *S. fasciculatus* most species of the Chaco Serrano region depend on birds for their dispersal and germination, therefore birds facilitated the maintenance of their populations in this region. However, it

would be ideal to repeat these experiments in field conditions because it is possible that even though we did not use Petri dishes, the relatively small volume of soil used in each container within the experimental chambers may have been insufficient to allow inhibitors to leach away and may have altered the micro-organisms available for decomposition, modifying the pulp breakdown as it would occur naturally in the soil (Robertson et al. 2006). These alterations may have exacerbated the inhibitors effects observed here in intact fruits.

Finally it is important to clarify that a faster germination could have either negative or positive consequences for plant populations, depending on climatic conditions of the area at the time when seeds germinate. The environmental conditions in the Chaco Serrano Woodland are very different in the wet and dry seasons (Torres and Galetto 2011). The species reported here are dispersed during the wet season (Díaz Vélez 2013). Therefore, a faster germination may be advantageous for these species, because it would ensure seedling establishment during the wet period, as also occurs in other regions with pronounced seasonality, such as some temperate and desert areas (Traveset 1998). However, the exact consequences of different germination speeds for Chaco Serrano Woodland species requires further study. Germination speed is a complex variable and the advantages or disadvantages for each plant species may be influenced by the action of granivores and herbivores, as well as fluctuations in resource availability during seedling establishment (Daws et al. 2002; Yirdaw and Leinonen 2002). Also, it has been suggested that variability in germination speed add temporal heterogeneity to seed germination responses, which may favour species establishment and regeneration (Izhaki and Safriel 1990; Reid and Armesto 2010).

Concluding remarks

Despite the effects of frugivorous birds on seed germination, it is essential to establish the regeneration possibilities for the bird-dispersed plant species (Baskin and Baskin 1998), which remain unknown for many ecosystems from Argentina and South America (Reid and Armesto 2011). Since our study considers seed dispersal of common plant species by the most abundant bird dispersers of the area (Ponce et al. 2012; Díaz Vélez 2013), we provide a broad view of the impact of bird species on these woody species. Frugivorous birds not only move seeds to different microsites, but also provide different treatments to the seeds,

enhancing the chances of seed germination and plant establishment in the Chaco Serrano Woodland (Díaz Vélez 2013).

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Table 1. List of species studied in the Chaco Serrano Woodland in Córdoba, Argentina. Family, common name, growth forms, fruiting periods, fruit traits and frugivorous bird species that consume the fruits.

	Plant species						
	<i>Celtis ehrenbergiana</i>	<i>Condalia spp.^a</i>	<i>Lantana camara</i>	<i>Lithraea molleoides</i>	<i>Lycium cestroides</i>	<i>Schinus fasciculatus</i>	<i>Zanthoxylum coco</i>
Family	Celtidaceae	Rhamnaceae	Verbenaceae	Anacardiaceae	Solanaceae	Anacardiaceae	Rutaceae
Common name	Tala	Piquillín	Bandera española	Molle de Beber	Tumiñico	Moradillo	Coco
Growth form	Tree	Shrub-small tree	Shrub	Tree	Shrub-small tree	Shrub	Tree
Fruiting period ^b	Jan-Aug	Jan-Feb	Jan-May	Jan-Oct	Jan-May	Jan-Aug	Jan-Aug
Fruit type ^c	drupe	drupe	drupe	drupe	berry	drupe	dehiscent follicle
Fruit diameter (mm)	6-9	8	4-7	6-8	5-6	4-5	5-7
Fruit colour	yellow-orange	dark purple-dark red	blue-black	translucent with black pulp	dark red-purple	violet-purple	shiny black
Bird species ^d	Elasp, Pitsul, Salaur, Thrbon, Turama	Elasp, Pitsul, Salaur, Thrbon, Turama	Elasp, Turama	Colmel	Elasp, Pitsul, Poonig, Salaur, Thrbon, Turama	Elasp, Salaur, Thrbon, Turama	Elasp, Pitsul, Salaur,

^aThis Includes three species (*Condalia montana*, *C. buxifolia* and *C. microphylla*) difficult to tell apart because their seeds are very similar.

^bData obtained from seed traps located in the forest fragments (Díaz Vélez 2013).

^cOne seed per fruit in all, except for *L. cestroides* (29 seeds per fruit in average).

^dData obtained from personal observations in the study area and literature (Ponce et al. 2012, De la Peña 2012, Díaz Vélez 2013); Abbreviations: Colmel: *Colaptes melanochloros*; Elasp: *Elaenia parvirostris* and *E. albicep*; Pitsul: *Pitangus sulphuratus*; Poonig: *Poospiza nigrorufa*; Salaur: *Saltator aurantirostris*; Thrbon: *Thraupis bonariensis*; Turama: *Turdus amaurochalinus*.

Table 2. Seed sources of bird-dispersed seeds, number of seeds per replicate and number of replicates per treatment.

	Plant species						
	<i>C. ehrenbergiana</i>	<i>Condalia spp.</i>	<i>L. camara</i>	<i>L. molleoides</i>	<i>L. cestroides</i>	<i>S. fasciculatus</i>	<i>Z. coco</i>
Source of	traps ^a	mist nets ^b	traps	traps	mist nets	traps	traps
bird-dispersed seeds							
Number of seeds per replicate	16	7	20	10	28	20	16
Number of replicates per treatment	13	4	5	6	17	7	5

^aSeed traps: a total of 240 50 x 50 cm nylon traps were placed below tree species in eight forest fragments of the Chaco Serrano Woodland during 6 months (January to June, 2011).

^bMist nets: Nets (12 m x 2.6 m, 36 mm mesh size) were placed in different locations in eight forest fragments (total 1023 net hours) during the fruit peak of bird-dispersed plants (January to April, 2009). We placed a plastic sheet beneath each deployed net in order to collect the faecal samples as birds upon being caught might drop them. Also, we held captured birds in cloth bags for no more than 20 minutes to collect faecal samples.

Table 3. Degrees of freedom (df) and p values for the GLM performed for each plant species comparing intact fruit, manually extract seeds and gut-passed seeds.

Plant species	df	P value
<i>C. ehrenbergiana</i> *	2	0.05
<i>Condalia spp.</i> *	2	0.03
<i>L. camara</i> *	2	<0.0001
<i>L. molleoides</i>	2	<0.0001
<i>L. cestroides</i> *	2	<0.0001
<i>S. fasciculatus</i> *	2	<0.0001
<i>Z. coco</i>	2	<0.0001

* Species that were analysed with a quasi-binomial error structure due to over-dispersion

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Table 4. Chi squared values (χ^2) and p values for the Log-rank tests (Mantel-Cox) performed for each plant species comparing intact fruit (F), manually extract seeds (M) and gut-passed seeds (G).

Plant species	Pairwise comparisons					
	F vs G		F vs M		G vs M	
	χ^2	P value	χ^2	P value	χ^2	P value
<i>C. ehrenbergiana</i>	56.243	<0.0001	5.106	0.024	33.703	<0.0001
<i>Condalia spp.</i>	3.451	0.063	12.07	0.001	4.003	0.045
<i>L. camara</i>	50.469	<0.0001	16.950	<0.0001	11.955	0.001
<i>L. molleoides</i>	24.007	<0.0001	4.27	0.039	5.757	0.016
<i>L. cestroides</i>	130.102	<0.0001	168.646	<0.0001	3.944	0.047
<i>S. fasciculatus</i>	0.181	0.67	85.855	<0.0001	76.59	<0.0001
<i>Z. coco</i>	34.956	<0.0001	1.684	0.194	26.341	<0.0001

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Fig. 1. Experimental identification of mechanisms related to the increase of seed germination and acting (or not) on bird gut-passed seeds following the scheme proposed by Samuels and Levey (2005). G: "Gut-passed seeds", F: "Intact fruits", M: "Manually extracted seeds"

Fig. 2. Proportion of germination for each seed treatment: G: "Gut-passed seeds", F: "Intact fruits", M: "Manually extracted seeds"; for (A) *C. erenbergiana*, (B) *Condalia* spp., (C) *L. camara*, (D) *L. molleoides*, (E) *L. cestroides*, (F) *S. fasciculatus*, and (G) *Z. coco*. Different letters indicate significant differences, $P \leq 0.05$.

Fig. 3. Cumulative seed germination percentages for each seed treatment: G: "Gut-passed seeds", F: "Intact fruits", M: "Manually extracted seeds"; for (A) *C. ehrenbergiana*, (B) *Condalia* spp., (C) *L. camara*, (D) *L. molleoides*, (E) *L. cestroides*, (F) *S. fasciculatus*, and (G) *Z. coco*. Different letters indicate significant differences, $P \leq 0.05$.

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$G > M > F$	Scarification + Deinhibition effect
$G = M > F$	Deinhibition effect
$G > M = F$	Scarification effect
$G = M = F$	Neutral effect

Fig. 1. Experimental identification of mechanisms related to the increase of seed germination and acting (or not) on bird gut-passed seeds following the scheme proposed by Samuels and Levey (2005). G: "Gut-passed seeds", F: "Intact fruits", M: "Manually extracted seeds"

Fig. 1

Fig. 2. Proportion of germination for each seed treatment: G: "Gut-passed seeds", F: "Intact fruits", M: "Manually extracted seeds"; for (A) *C. ehrenbergiana*, (B) *Condalia spp.*, (C) *L. camara*, (D) *L. molleoides*, (E) *L. cestroides*, (F) *S. fasciculatus*, and (G) *Z. coco*. Different letters indicate significant differences, $P \leq 0.05$.

Fig. 2

224x238mm (300 x 300 DPI)

Fig. 3. Cumulative seed germination percentages for each seed treatment: G: "Gut-passed seeds", F: "Intact fruits", M: "Manually extracted seeds"; for (A) *C. ehrenbergiana*, (B) *Condalia spp.*, (C) *L. camara*, (D) *L. molleoides*, (E) *L. cestroides*, (F) *S. fasciculatus*, and (G) *Z. coco*. Different letters indicate significant differences, $P \leq 0.05$.

Fig. 3

292x413mm (300 x 300 DPI)