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# SURVIVAL AND EMERGENCE OF ADULT SEED BEETLES (COLEOPTERA: CHRYSOMELIDAE: BRUCHINAE) FROM LEGUME SEEDS EGESTED BY VERTEBRATES

Osvaldo R. Di Iorio

Entomología, Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, 4º Piso, Pabellón II, (CP 1428) Ciudad Universitaria, Buenos Aires, Argentina. — megacyllene@yahoo.com.ar

**Abstract:** Adults of *Amblycerus*, *Scutobruchus*, *Rhipibruchus*, *Pseudopachymerina*, and *Stator* (Coleoptera: Chrysomelidae: Bruchinae) emerged from seeds of their respective host plants deposited with fecal matter of the grey fox (*Lycalopex griseus*), cattle (*Bos taurus*), and ñandú (*Rhea americana*) in arid areas of western-central Argentina. Thus, these vertebrates may help in the dispersal of the seed beetles. This goes against the general statement that passage of seeds through the vertebrate gut kills the bruchid larvae contained inside the seeds as an effect of stomach acids. The droppings with seeds need to be stored for some time, because the seed beetles emerge several months later, particularly when they hibernate inside the seeds. Pre- and post-dispersal predation of legume seeds are discussed in the light of the proposed guilds of oviposition preferences in seed beetles.
**Key words:** Coleoptera, Chrysomelidae, seed beetles, vertebrates, interactions, Argentina.

**Supervivencia y emergencia de brúquidos adultos (Coleoptera: Chrysomelidae: Bruchinae) en semillas de leguminosas excretadas por vertebrados**
**Resumen:** Adultos de *Amblycerus*, *Scutobruchus*, *Rhipibruchus*, *Pseudopachymerina* y de *Stator* (Coleoptera: Chrysomelidae: Bruchinae) emergieron de las semillas de sus respectivas plantas hospedadoras depositadas en la material fecal del zorro gris (*Lycalopex griseus*), ganado bovino (*Bos taurus*), y ñandú (*Rhea americana*) en areas áridas del oeste y centro de la Argentina. En consecuencia, estos vertebrados podrían ayudar en la dispersión de los escarabajos de las semillas. Esto es opuesto a la afirmación de que el pasaje de las semillas a través del tubo digestivo de los vertebrados mata a las larvas de estos escarabajos por la acción de los ácidos estomacales. Las deposiciones con semillas necesitan ser guardadas por un tiempo, ya que los brúquidos emergen varios meses después, particularmente cuando hibernan dentro de las semillas. Se discute acerca de la predación antes y después de la dispersión de las semillas a la luz de los gremios de preferencias en la oviposición de los escarabajos de las semillas.
**Palabras clave:** Coleoptera, Chrysomelidae, escarabajos de las semillas, vertebrados, interacciones, Argentina.

## Introduction

### Interactions among vertebrates, insects and seeds

Animal-dispersed plants, insects seed predators and seed dispersers may be considered to constitute a complex evolutionary triad in which each component simultaneously interacts with the other two. The relationships between plants and the insects that feed on their fruits (especially those that eat the seeds) has received much attention in the literature, as well as the mutualistic interaction between plants and vertebrate seeds dispersers. In contrast, the third side of the conceptual triangle, namely the interaction between seed dispersers and insects seed predators, remain poorly known (Traveset, 1992).

According to Miller (1994), the "passage of bruchid infested *Acacia* seeds through the ungulate gut may decrease the bruchid infestion of egested seeds through the action of the gut acids upon the bruchid larvae (Pellew & Southgate, 1984; Coe & Coe, 1987; Miller & Coe, 1993). This three-way relationship was first proposed by Halevy (1974) and Lamprey *et al.* (1974) for *Bruchidius* sp. infesting seeds of indehiscent *Acacia tortilis* (Forsskal) Hayne seeds. For example, Coe & Coe (1987) found that seeds obtained from the dung of eland (5%) and greater kudu (11%) had a lower bruchid infestation than seeds from the tree (24%), and Jarman (1976) found that 13% of *A. tortilis* seeds fed to impala were infested whereas no seeds retrieved from the dung were infested". Miller (1994) also found that infested *A. tortilis* seeds egested by wild giraffe and impala exhibited a significantly lower bruchid infestation (3.0 and 2.0 % respectively) than uningested infested seeds (68.0% and 68.0% respectively). While uningested infested seeds of three *Acacia* species have infestation rates of 36.5 to 68.0%, infested seeds ingested by kudu, steenbok, duiker (ungulates) and ostriches showed any bruchid infestation after they were egested. Therefore, Miller (1994) concluded that his study agrees wirh the previous statements of Halevy (1974), Lamprey *et al.* (1974) and Coe & Coe (1987).

In the last years, indirect evidences of insect seed predators killed by mammal ingestion of fruits were presented using experimental designs that excluded vertebrate fruit predators, thus the predation of seeds by bruchid beetles in areas without cattle was significantly higher than in the areas with cattle (Herrera, 1989; Peguero & Espelta, 2013). These last authors also cited that frugivores may indirectly control the size of seed predator populations by killing insect larvae or pupae still in the seeds when fruits are consumed, based on Hauser (1994), Gómez & González-Megías (2002), and Bonal & Muñoz (2007).

### Consumption of legume pods by vertebrates in Argentina

*Acacia* and *Prosopis* trees (Mimosaceae) are some of the main floristic components in the flora of the arid and semiarid Monte and Chaco biogeographical provinces in Argentina (Burkart, 1976; Cialdella, 1984). These trees may produce high numbers of pods that are consumed by caprine, equine

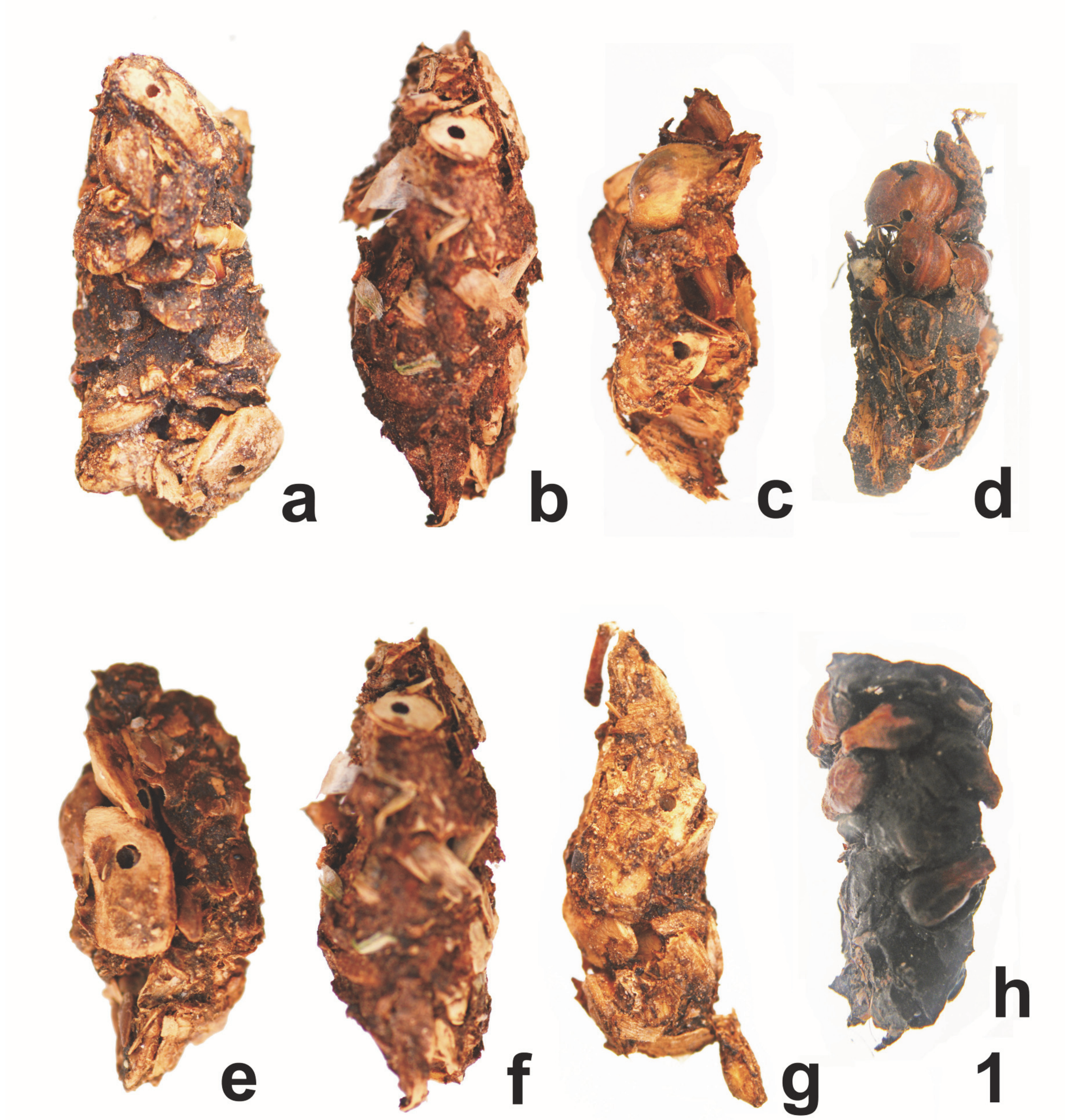


**Figure 1.** Fecal matter of *Lycalopex griseus* (gray fox) (Argentina: La Rioja) with emergence holes of bruchid beetles: a-c, e-g, *Prosopis flexuosa* and/or *P. chilensis*; d, *Prosopis torquata*; h, exclusively with skins and seeds of *Vitis vinifera*.

and bovine cattle, foxes, rodents and birds (Mares *et al*., 1977; Campos & Ojeda, 1997; Aibar & Ortega-Baes, 2001; Jausoro *et al*., 2004).

The gray fox, *Lycalopex griseus* (Gray, 1837) (Mammalia: Canidae) "*has a broad diet which includes Prosopis pods and seeds, as well as insects and vertebrates*" (Mares *et al*., 1977). *Prosopis* seeds were found in the droppings of foxes in the Andalgalá area in Catamarca (Kingsolver *et al*., 1977). Following Campos & Ojeda (1997), the gray fox maintains viability without increasing germination of the ingested seeds of *Prosopis flexuosa* DC. [Mimosaceae] in Mendoza. In Sierra de las Quijadas (San Luis), pods of *Prosopis torquata* (Cav. ex Lag.) DC. [Mimosaceae] was consumed by the gray fox in a 70 % during the dry season (autumn and winter), and 10 % in the wet season (spring and summer) (Mangione & Nuñez, 2004). In change, the diet of the gray fox in Mendoza (Ñacuñán and Telteca Reserves) in winter includes mammals (80 and 86 % in each locality respectively), Coleoptera (70 and 90 %), Orthoptera (30 and 45 %), Scorpionida: Bothriuridae (10 and 70 %), and fruits of *Prosopis flexuosa* (20 and 45 %), *Prosopanche americana* (R. Br.) Baill. [Hydnoraceae] (0 and 60 %), and *Lycium* sp. [Solanaceae] (10 and 20 %) (Asencio *et al*., 2004).

The diet of another fox, *Lycalopex gymnocercus* (Fischer, 1814) (Mammalia: Canidae), included pods of *Geoffroea decorticans* (Gill. ex Hook. & Arn.) Burkart (Caesalpinaceae), and *Prosopis caldenia* Burkart (Mimosaceae) among other seeds of non legume plants in La Pampa (Crespo, 1971). Similarly, the fox *Cerdocyon thous* Linnaeus, 1766 (Mammalia: Canidae) consumed mainly fruits (95 % of 120 collected droppings), containing over 20,000 seeds of 11 woody and 1 herbaceous plants, while that the more consumed plant was *Acacia aroma* Gill. (Mimosaceae) (mentioned as *Acacia macracantha*). Viability of the seeds was not decreased after

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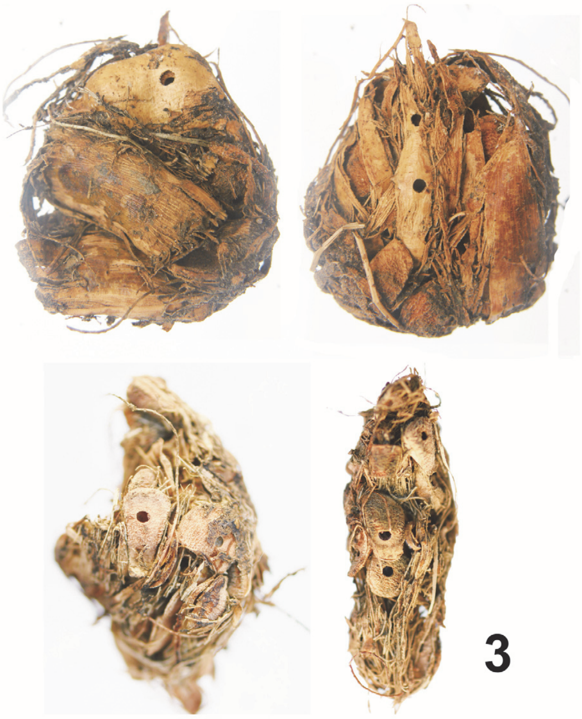

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**Figure 2.** Uniseminate endocarps of *Prosopis flexuosa* with emergence holes of bruchid beetles from fecal matter of *Lycalopex griseus* (gray fox) (San Juan: La Laja).

**Figure 3.** Fecal matter of *Rhea americana* (ñandú) with seeds and pod fragments of *Prosopis caldenia* (Argentina: La Pampa) with emergence holes of bruchid beetles.

the pass through the digestive tract of the fox, but germination rate was not increased (Varela & Ortiz, 2001). Also the bird *Rhea americana* Linnaeus, 1758 (Aves: Rheidae), locally known as "ñandú", consumed pods of *Prosopis nigra* DC. (Mimosaceae), decreasing the germinative power of the seeds, but these seeds reached their maximal germinative percentage with an higher velocity (Pratolongo, 2000).

There are no mention of emergences of adult bruchid beetles after the ingested fruits and seeds of *Acacia*, *Geoffroea* and *Prosopis* passed through the digestive tract of foxes (Crespo, 1971; Mares *et al*., 1977; Kingsolver *et al*., 1977; Campos & Ojeda, 1997; Varela & Ortiz, 2001; Asencio *et al*., 2004; Mangione & Nuñez, 2004), goats (Páez *et al*., 2004), cows and horses (Eilberg, 1973; Aibar & Ortega-Baes, 2001; Varela & Ortiz, 2001; Jausoro *et al*., 2004), and ñandú (Pratolongo, 2000).

Therefore, the main goals of this work are: 1) to provide new data about the interaction between vertebrate seed dispersers and insect seed predators, showing that some seed beetles can survive and emerge from legume seeds after they were deposited in droppings by vertebrates from Argentina; 2) to postulate that these seed dispersers also help in the dispersal of the seed beetles; 3) to discuss if the seed predation by the beetles is pre- or post-dispersal by the vertebrates according to the oviposition guilds proposed for seed beetles.

## Materials and methods

Droppings of gray foxes (Fig. 1-2) were collected at La Rioja (Anillaco, Los Molinos, Pampa Grande), San Juan (La Laja), and San Luis (Sierra de las Quijadas) provinces in western-central Argentina. As the gray foxes also consumed terrestrial insects, the initial purpose of these collections was to investigate the presence of remains of Cerambycidae (Insecta: Coleoptera), particularly some rare species of Anoplodermatinae and Prioninae with terrestrial habits in desertic areas. As the gray fox droppings were keeped and not inmediately analized for its initial purpose, seed beetle emergences were produced. Additional evidences were later also obtained from droppings of herbivore vertebrates: a cow dung from La Rioja, and a fecal matter of ñandú from La Pampa (Fig. 3).

Except in the genus *Scutobruchus*, that are not restricted to any species of *Prosopis* (Kingsolver & Muruaga de L'Argentier, 2004), the remaining seed beetles were identified to species by the author following Kingsolver (1982), Johnson *et al*. (1983), and Terán (1962). Specimens of seed beetles are deposited in the collection of the author (ODIC), together with samples of fox and ñandú droppings mounted on small hardboards and pinned with the specimens. All plant species were identified by the author, except *Cucurbitella asperata* (Gill. ex Hook. & Arn.) Walp. (Cucurbitaceae) by Raúl Pozner (Instituto Darwinion, Buenos Aires, Argentina).

In general the droppings contained a single plant species. The similar seeds of some *Acacia* species in the droppings were distinguished by the color of epicarp fragments: light reddish brown in *A. aroma*, and dark brown in *A. caven*. In the case of the very similar endocarps of *P. chilensis* and *P. flexuosa*, these plants were distinguished only when fragments of the epicarps were examined (inmaculate in *P. chilensis*, violet maculate in *P. flexuosa*). Some previous references were not seen, cited in the text in base to posterior references, and mentioned in the reference list as "cited by".

## Results

• **Gray fox (*Lycalopex griseus*)**

The diet of the gray fox in La Rioja includes 20 % of some arthropods: Insecta: Coleoptera: Curculionidae; Scarabaeidae: Dynastinae; Tenebrionidae; Arachnida: Scorpionida. The remaining 80 % comprises vegetable matter of diverse origins: 1) pods of *Acacia aroma*, *Prosopis chilensis* (Mol.) Stuntz, *Prosopis flexuosa* (Fig. 1 a-c, e-g) and *Prosopis tor-*

*quata* (Cav. ex. Lag.) DC. (Mimosaceae) (Fig. 1 d), all from Anillaco, this last plant was the most consumed species; 2) pods of *Geoffroea decorticans* in Pampa Grande; 3) fruits of *Cucurbitella asperata* in Anillaco and Los Molinos, locally known as "sandía del zorro" ("fox watermelon"); 4) rippen fruits of the olive tree, *Olea europaea* L. (Oleaceae) in Los Molinos, and 5) rippen grapes, *Vitis vinifera* L. (Vitaceae), in Anillaco (Fig. 1 h). Except by the species of *Acacia* and *Prosopis*, that may be mixed in different depositions, the remaining plants were found in single depositions of one or more droppings found together.

The epicarp and mesocarp of *G. decorticans* are digested by the gray fox, while in *Prosopis*, the epicarp is fragmented or not (fig. 1 d), and the mesocarp is completely digested. Thus the uniseminated endocarps remain intact (Figs.1-2). In contrast, the pods of *A. aroma* are completely disassembled, and the naked seeds are mixed with the remaining materials. The droppings of the gray fox can remain by several months dried on the ground thanks to the arid climate, but no germination of seeds were observed.

The species of Bruchinae emerged from the seeds contained in the droppings can be discriminated by the ingested plant species and localities as follows:

***Acacia aroma***
La Rioja: Anillaco, 22-XI-1998, *Pseudopachymerina grata* Terán, 1962; Anillaco, without date, *Stator* sp. near *tigrensis* Pic, 1938.

The specimens of *Stator* are slightly different from *S. tigrensis* by the black color of the abdomen and the pygidium, this last with only with two latero-basal spots of yellowish pubescence.

***Geoffroea decorticans***
La Rioja: Pampa Grande, without date: *Amblycerus caryoboriformis* (Pic, 1910).

***Prosopis torquata*** (Fig. 1 d)
La Rioja: Anillaco, 10-XI-1998: *Scutobruchus* sp. 1. / Anillaco, 21-XI-1998: *Scutobruchus* sp. 1; *Scutobruchus* sp. 2; *Rhipibruchus atratus* Kingsolver, 1982. / Anillaco, 22-XI-1998: *Scutobruchus* sp. 1.
San Luis: Sierra de las Quijadas, 10-X-1998: *Scutobruchus* sp. 1.

***Prosopis flexuosa***
San Juan: La Laja, 8-VIII-1998: *Scutobruchus* sp. 1; *Scutobruchus* sp. 2; *Rhipibruchus atratus*.

***Prosopis flexuosa / chilensis*** (Fig. 1 a-c, e-g)
La Rioja: Anillaco, 22-XI-1998: *Scutobruchus* sp. 3; *Rhipibruchus atratus*. / Anillaco, 27-III-2000: *Scutobruchus* sp. 2.

***Prosopis flexuosa / chilensis / torquata***
La Rioja: Anillaco, 27-III-2000: *Scutobruchus* sp. 1; *Scutobruchus* sp. 2; *Rhipibruchus atratus*.

• **Bovine cattle (*Bos taurus*)**
Pods consumed by bovine cattle in the area of Anillaco-Los Molinos-Anjullón (La Rioja) belong mainly to *A. aroma*, *P. chilensis*, *P. flexuosa*, and more rarely to *Acacia caven*. In all cases, the endocarps appear disaggregated, and the free seeds are mixed with the rest of the fecal matter. As the cow dung can remain humid for several days after deposition, all viable seeds were germinated down, inside, and over the surface of the dung cow.

Only one species of Bruchinae emerged from the seeds contained in one cow dung as follows:

***Prosopis chilensis***
La Rioja: Anjullón, II-2002: *Scutobruchus* sp. 1.

• **Ñandú (*Rhea americana*)**
The fecal matter of this bird (Fig. 3) was obtained in a pure forest of *Prosopis caldenia*. The epicarps and mesocarps of the pods are digested, and the endocarps with the seeds are mixed with the rest of the undigested materials, including some pod fragments (Fig. 3).

The following bruchid species emerged from the endocarps and pod fragments contained in the fecal matter:

***Prosopis caldenia***
La Pampa: Paraje La Araña: *Scutobruchus* sp. 1.

## Discussion

The results presented here cannot be discussed without attention to the guilds of Bruchinae by its oviposition preferences as proposed by Johnson & Romero (2004). The studied species of bruchid beetles were divided in three guilds: 1) Guild A ("mature fruit guild"): species that oviposit only on the surface of the fruits; 2) Guild B ("mature seed guild"), in which ovipositions were made on mature seeds still in fruits on the plant (or perhaps also in fruits fallen to the ground ?); and 3) Guild C ("scattered seed guild"), species that oviposits only on mature seeds after they have fallen to the ground [i.e., the seeds exposed by dehiscent pods, or by other different situations in indehiscent pods]. A total of 88 species of bruchids were given for guild A, 11 for guild B, and 15 for guild C (Table I). The genera in the guild that oviposits on legume fruits in guilds A or B are usually different from the genera that oviposit on seeds in the guild C (Johnson & Romero, 2004).

These authors also stated that, depending on the structure of the fruits, one plant species may be oviposited upon by all three guilds, some only by two guilds and some by only one guild. This may be due because several different instances are involved: 1) the maturity of the seeds inside the pods on the plant needs to be determined for each plant species in particular (making difficult a distinction of the bruchid species between guilds A and B); 2) some dehiscent pods are first indehiscent, not exposing the seeds, and subject by infestation by species in the guilds A or B, depending on the maturity degree of the seeds; 3) even in the pods with explosive dehiscence, the seeds are enclosed in the pods for a certain time (guilds A and B), until dry conditions obligate the pods to the expulsion of the seeds (guilds C). Regretably, a table of legume species and associated bruchid guilds was not given (Johnson & Romero, 2004).

Therefore, there are two possible scenarios and more than one case in which seed predation by bruchid beetles can occurr as follows:

**1. Before the seeds are exposed**

**a**) When the pods are on the plant in the cases of indehiscent fruits (pre-dispersal predation by seed beetles in guilds A and B).

**b**) When indehiscent pods finally fall to the ground, and remain entire for a time, before exposing their seeds by

**Table I.** Guilds of seed beetles (Coleoptera: Chrysomelidae: Bruchinae) according to their oviposition preferences (modified from Johnson & Romero 2004). Species remarked in color are present in Argentina. **(1)** According to Janzen *et al.* (2010); **(2)** According to Forget *et al.* (1999); **(3)** According to the present author (pers. obs.).

| Guild A | Guild A (continuation) | Guild B | Guild C |
|---|---|---|---|
| *Acanthoscelides alboscutellatus* | *Merobruchus insolitus* | *Acanthoscelides guazumae* | *Caryoborus gracilis* |
| *Acanthoscelides baboquivari* | *Merobruchus julianus* | *Bruchidius natalensis* | *Caryoborus serripes* |
| *Acanthoscelides chiricahuae* | *Merobruchus knulli* | *Bruchidius schoutedeni* | *Caryobruchus gleditsiae* |
| *Acanthoscelides compressicornis* | *Merobruchus major* | *Sennius fallax* | *Pachymerus cardo* |
| *Acanthoscelides fraterculus* | *Merobruchus paquetae* | *Sennius bondari* | *Speciomerus giganteus* |
| *Acanthoscelides kingsolveri* | *Merobruchus placidus* | *Specularius impressithorax* | *Stator chihuahua* |
| *Acanthoscelides lobatus* | *Merobruchus porphyreus* | *Stator beali* | *Stator generalis* |
| *Acanthoscelides longescutus* | *Merobruchus santarosae* | *Stator championi* | *Stator mexicanus* |
| *Acanthoscelides mundulus* | *Merobruchus solitarius* | *Stator limbatus* | *Stator pygidialis* |
| *Acanthoscelides oblongoguttatus* | *Merobruchus sonorensis* | *Stator pruininus* | *Stator sordidus* |
| *Acanthoscelides pallidipennis* | *Merobruchus terani* | *Zabrotes interstitialis* | *Stator subaeneus* |
| *Acanthoscelides prosopoides* | *Merobruchus triacanthus* | *Zabrotes subfasciatus* | *Stator testudinarius* |
| *Acanthoscelides siemensi* | *Merobruchus vacillator* | | *Stator vachelliae* |
| *Acanthoscelides submuticus* | *Merobruchus xanthopygus* | | |
| *Algarobius johnsoni* | *Mimosestes acaciestes* | | |
| *Algarobius prosopis* | *Mimosestes amicus* | | |
| *Algarobius riochama* | *Mimosestes janzeni* | | |
| *Amblycerus dispar* | *Mimosestes mimosae* | | |
| *Amblycerus cistelinus* | *Mimosestes nubigens* | | |
| *Amblycerus crassipunctatus* | *Neltumius arizonensis* | | |
| *Amblycerus hoffmanseggi* | *Neltumius gibbithorax* | | |
| *Amblycerus nigromarginatus* | *Neltumius texanus* | | |
| *Amblycerus piurae* | *Pachymerus bactris* **(1)** | | |
| *Amblycerus submaculatus* | *Penthobruchus germaini* | | |
| *Amblycerus tachigaliae* **(2)** | *Pseudopachymerina grata* **(3)** | | |
| *Amblycerus testaceus* | *Pseudopachymerina spinipes* | | |
| *Amblycerus vitis* | *Pygiopachymerus lineola* | | |
| *Bruchidius strangulatus* | *Rhipibruchus atratus* | | |
| *Bruchus brachialis* | *Rhipibruchus jujuyensis* | | |
| *Bruchus pisorum* | *Rhipibruchus oedipygus* | | |
| *Caryedes brasiliensis* | *Rhipibruchus picturatus* | | |
| *Caryedes grammicus* | *Rhipibruchus prosopis* | | |
| *Caryedon fasciatus* | *Rhipibruchus psephenopygus* | | |
| *Caryedon germari* | *Rhipibruchus rugicollis* | | |
| *Ctenocolum janzeni* | *Scutobruchus ceratioborus* | | |
| *Eubaptus rufithorax* | *Sennius abbreviatus* | | |
| *Megabruchidius tonkineus* **(3)** | *Sennius laminifer* | | |
| *Megacerus baeri* | *Sennius leptophyllicola* | | |
| *Megacerus discoidus* | *Sennius medialis* | | |
| *Megacerus schaefferianus* | *Sennius morosus* | | |
| *Merobruchus bicoloripes* | *Sennius simulans* | | |
| *Merobruchus boucheri* | *Stator monachus* | | |
| *Merobruchus chetumalae* | *Stator trisignatus* | | |
| *Merobruchus columbinus* | *Stator vittatithorax* | | |

deterioration due to environmental conditions (pre-dispersal predation by guilds A and B).

**c**) When the pods are still on the plant in the cases of explosive dehiscent fruits, that remain closed for a time until favorable conditions (pre-dispersal predation by seed beetles in guilds A and B) [e.g. *Caesalpinia gilliesii* (Wall. ex Hook.) Dietr. in the Caesalpiniaceae].

**2. After the seeds are exposed**

**a**) In indehiscent pods fallen to the ground sufficiently deteriorated, and the seeds are exposed (pre-dispersal predation by guild C).

**b**) The seeds are exposed by a short time in dehiscent fruits even on the plants (pre-dispersal predation by guild C).

**c**) The seeds from dehiscent fruits naturally fall to the ground (pre-dispersal predation by guild C).

**d**) The seeds are transported and accumulated for a posterior consumption (post-dispersal predation by guild C).

**e**) The seeds are exposed in vertebrate droppings after the consumption of the fruits (palms) and pods (legumes) (post-dispersal predation in guild C).

**f**) The seeds are exposed after edible parts (pulpose mesocarp) of the fruits were consumed and/or transported by vertebrate fruit consumers (post-dispersal predation by guild C), i.e., some monkeys and rodents with the fruits of some palms (Silvius & Fragoso, 2002).

Bruchids are capable to oviposit in seeds exposed in vertebrate excrements. The bruchid *Stator vachelliae* Bottimer, 1973 finds the seeds of *Acacia farnesiana* (L.) Wild. (Mimosaceae) in the feces of horses, deer, and ctenosaur lizards, the current major dispersers, attacking only those seeds located on the surface (Traveset, 1990). In San Carlos, Panama, the poisonous seeds of *Enterolobium cyclocarpum* (Jacq.) Griseb. (Mimosaceae) are dispersed by cattle that eat the thick, sweet fruit valves that contain viable seeds that pass intact through the guts of these vertebrates. *Stator generalis* Johnson & Kingsolver, 1976 eggs were glued to these seeds and adult bruchids emerged from them (Johnson & Romero, 2004). Also one undetermined species of *Stator* emerged from the droppings of the grey fox with seeds of *Acacia aroma* (indehiscent pods). The seeds of *A. aroma* were exposed in the excrements, but the eight species of *Stator* in the guild C are not present in Argentina (Table I), and some of them are absent in South America (Johnson *et al.*, 1989).

In the guild A were located *S. bisbimaculatus* (Pic, 1930) [a synonym of the following species, according to Johnson *et al.*, 1989], *S. monachus* (Sharp, 1885), and *S. vittatithorax* (Pic, 1930) (Table I), all present in Argentina. Both species of *Stator* has several species of *Acacia* as hosts (Kingsolver & Muruaga de L'Argentier, 2004), but all of these *Acacia* has dehiscent pods (Di Iorio, pers. obs.).

All plants considered here as consumed by vertebrates in Argentina has indehiscent pods that remain for a time on the trees, thus subject to bruchid infestation by the species in the guild A. In this guild were also included several species of *Amblycerus* (but not *A. caryoboriformis*), *Pseudopachymerina spinipes* (Erichson, 1834) (the sibling species of *P. grata*), all species of *Rhipibruchus*, and one *Scutobruchus* (Table I). Also in a palm, bruchid beetles can be pre-dispersal rather than post-dispersal seed predators (Table I).

As the bruchids emerged from seeds in droppings belong to the guild A (with the probable exception of the undetermined *Stator*), this is an indication that the fruits eated by the gray fox, the bovine cattle and the ñandú were infested before they were eated, and the predation of the seeds by the corresponding seed beetles are cases of pre-dispersal predation. These vertebrates are signaled here for the first time as helpers in the dispersal of the respective bruchid beetles. The number of emergences from different localities, sampling data and host plants shows also that this is not an isolated, and/or an accidental phenomenon, and by the contrary, this is habitual for the species of vertebrates, seeds and beetles considered here.

Eilberg (1973) found "weevils" (= bruchid beetles) inside the seeds of *Prosopis ruscifolia* Griseb. (Mimosaceae) removed from horse dung. She interpreted that the seeds were infested by the insects after the dung was deposited (post-dispersal predation by guild C), but this may be another case of pre-dispersal predation. This tree produces indehiscent pods that are infested by two species of *Rhipibruchus* (guild A) and one *Scutobruchus* (Kingsolver & Muruaga de L'Argentier, 2004), the same species included in guild A by Johnson & Romero (2004) (Table I).

One of the most cited works about bruchid beetles killed by the digestive fluids of vertebrate guts (Lamprey *et al.*, 1974) is not conclusive about this matter. Lamprey *et al.* (1974) reached this conclussion after a comparison of bruchid predation in seeds[1] stored for over a year (ranging from 95.6-99.6 % to 72.0-99.0%) with predation in seeds collected from mammal faeces (22.0-31.0 %). Probably the store of the seeds for over a year increased its predation by the bruchid beetles, especially if they belonged to the guild C, as happen with the beans stored as food by humans, that are reinfested until they are completely destroyed (Di Iorio, pers. obs.). The seed beetles considered by Lamprey *et al.* (1974) were two species of *Bruchidius*, not considered in the list of Johnson & Romero (2004).

Furthermore, Lamprey *et al.* (1974) mentioned that "in 184 fecal pellets of dorcas gazelles, six *Acacia rutkhiu* seeds were found, of which four contained well-grown bruchids" (larvae and/or adults?). Probably bruchid emergences would have been obtained if the fecal pellets and/or the seeds were keeped intact by a time.

Only Traveset *et al.* (1995) established that some vertebrates may even act as mutualists of insects, transporting viable larvae inside the seeds within their guts to different places (no names were given). Also in southeastern Brazil, frugivorous birds and mammals frequently ingest fruits infested by larvae of Curculionidae (Coleoptera), which resist the passage through the digestive tract, and are regurgitated or defecated alive (Guix, 2006). Nevertheless, the larvae of the weevil genus *Heilipus* (Coleoptera: Curculionidae) in fruits of *Ocotea puberula* L. (Lauraceae) were killed when the fruits were consumed by the black howler monkey, *Alouatta caraya* (Humboldt, 1812) (Mammalia: Primates) (Bravo & Zunino, 1998).

## Final remarks

Each interaction between seed beetles and vertebrate seed dispersers needs to be studied in particular. The fact that no emergences of adult bruchids from seeds in droppings were recorded in literature was probably due that the droppings with the seeds need to be keeped for a time after they were collected. The seed beetles can emerge several months later, particularly when they hibernate in diapause inside the seeds.

Also further studies in interactions between seed dispersers, seed predators and plants will can include simple experimental designs (entire fruits vs. naked seeds) for to establish if each seed predator corresponds to a case of pre- (guilds A and B) and/or post-dispersal predation (guild C) (see Jansen *et al.*, 2010). This also will increases the list of the known seed beetles in each guild (Table I) from complementary studies of bruchid natural history. A list of bruchid guilds per plant species is also an expected issue highly desirable.

**Note**:

[1] Apparently not entire fruits, but "fruits" and "seeds" were used indistinctly in several works, making the lecture of the results and conclussions very confusious, in view that these two terms implicate a completely different ovipositing behaviour of bruchid beetles.

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