

Toward reliable estimates of seed removal by small mammals and birds in the Neotropics

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Received February 21, 2005 – Accepted July 25, 2005 – Distributed May 31, 2007

(With 1 figure)

Abstract

Birds are often considered seed predators of less importance when compared to rodents or granivorous ants in studies of seed predation using selective exclosures. However, it is possible that the role of granivorous birds interacting with seeds on the floor of Neotropical forests is being underestimated, if the selective exclosures designed to allow exclusive access to small rodents do not work properly in the Neotropics. We used an experimental approach to evaluate whether birds could remove seeds from selective exclosures designed to allow exclusive access to rodents. We compared seed removal from two paired treatments in the field: an open treatment (control) allowing the access to all vertebrates, and a selective exclosure treatment, where seeds were placed under a cage staked to the ground and covered on top and on the laterals by wire mesh of varying sizes. Treatments were placed in the center of a sand quadrat in order to record the visit of vertebrates from their footprints. Although the selective exclosures are used to tell apart the small mammal seed removal from that of other animals, birds could persistently remove seeds from selective exclosures. Thus, the role of birds interacting with seeds on the floor of tropical forests may be underestimated for some plant species, due to an artifact of the exclosure method employed. Exclosures of 40 x 40 x 40 cm should be efficient to deter the removal of seeds by birds, allowing the consumption of the seeds by small mammals at the same time.

Keywords: Columbidae, experimental bias, granivory, seed predation, Tinamidae.

Rumo a estimativas confiáveis de remoção de sementes por pequenos mamíferos e aves no Neotrópico

Resumo

Aves são freqüentemente consideradas predadores de sementes de pouca importância, quando comparadas a roedores e formigas granívoras em estudos sobre predação de sementes que utilizam exclusões seletivas. Contudo, é possível que o papel de aves granívoras que interagem com sementes no solo de florestas Neotropicals vem sendo subestimado, se as exclusões seletivas usadas para permitir o acesso exclusivo a pequenos roedores não funcionam de forma apropriada no Neotrópico. Foi usada uma abordagem experimental para avaliar se aves poderiam remover sementes do interior de exclusões seletivas desenhadas para permitir acesso exclusivo a roedores. Comparou-se a remoção de sementes em dois tratamentos no campo: um tratamento aberto (controle) que permite o acesso a todos os vertebrados, e um tratamento de exclusão seletiva, no qual as sementes eram dispostas sob uma gaiola metálica fixada ao solo e recoberta por tela metálica de tamanhos variados. Os tratamentos foram dispostos no centro de uma parcela de areia de forma a registrar a visita de vertebrados por meio de pegadas. Embora as exclusões seletivas sejam usadas para estimar separadamente a remoção de sementes por pequenos mamíferos daquela praticada por outros animais, aves puderam remover sementes das exclusões seletivas. Assim, o papel de aves interagindo com sementes no solo de florestas tropicais pode estar sendo subestimado para algumas espécies de plantas, devido a um artefato do método de exclusão empregado. Exclusões de 40 x 40 x 40 cm devem ser eficientes para deter a remoção de sementes por aves, permitindo o consumo de sementes por pequenos mamíferos ao mesmo tempo.

Palavras-chave: Columbidae, viés experimental, granivoria, predação de sementes, Tinamidae.

1. Introduction

The role of birds as seed predators is being increasingly recognized, especially in arid and semiarid ecosystems (Thompson et al., 1991; Marone et al., 2000; Kelt et al., 2004). In more mesic habitats however, and in the Neotropics in particular, birds are often considered seed predators of less importance when compared to rodents or granivorous ants (Hulme, 1998). But the ubiquitous richness, abundance and biomass of terrestrial seed-eating birds, like tinamous, pigeons, doves and finches from Neotropical forests (Willis and Oniki, 1981; Terborgh et al., 1990) pointed to a possible role of these birds in seed predation after the seeds fall to the ground or are dispersed from the mother trees. Some studies have already suggested that seed-eating birds can influence the dynamics of several plant species in the Neotropics (Érard and Sabatier, 1986; Santamaría and Franco, 2000), but the experimental evidence of the role of birds as seed predators is still scarce (but see Pizo and Vieira, 2004). A simple, cost-effective method to study post-dispersal seed predation is based on the use of selective exclosures.

Selective exclosures, an inexpensive and logistically effective method, have been widely used in temperate areas to assess seed removal, giving insights about patterns of resource use by different guilds of animals and their role in seed predation (Hulme, 1998). This method operates with open and semi-open treatments, allowing a selected subset within an animal community to have exclusive access to the seeds. Controls (open treatments) may be compared to semi-open treatments (selective exclosures), leading to estimates of the relative contribution of each animal or set of species to the seed removal of a given plant. However, selective exclosures have less often been used in tropical forests (Horvitz and Schemske, 1986; Gryj and Dominguez, 1996; Holl and Lulow, 1997; Sánchez-Cordero and Martínez-Gallardo, 1998; Notman and Gorchoy, 2001; Pizo and Vieira, 2004), where rodents have been regarded as the principal seed removers (Hulme, 1998). It is possible that the role of granivorous birds interacting with the seeds on the floor of tropical forests is being underestimated, if the selective exclosures designed to allow exclusive access to small rodents do not work properly in the Neotropics. Indeed, it is hard to develop an efficient device to independently measure the proportions of seeds removed by Neotropical birds and small mammals, because they can overlap in their time schedules, diet, and body size. For instance, squirrels (*Sciurus* spp.) and White-tipped doves (*Leptotila verreauxi*) are sympatric seed predators found over a large range in the Neotropics (Becker and Dalponte, 1991, Sánchez-Cordero and Martínez-Gallardo, 1998, Terborgh et al., 1990, Willis and Oniki, 1981). Both are active during the day, consume seeds collected on the floor, and have similar size. Thus, caution is required in the application of the guidelines used for selective exclosures in temperate areas. In spite of the increasing number of papers dealing with seed removal in tropical

forests, there is no published assessment of the effectiveness of selective exclosures in these areas, and if they can be used to measure the seed removal by birds.

In this study we used an experimental approach to evaluate the effectiveness of selective exclosures designed to allow exclusive access to small mammals (rodents) in two forest patches of southeastern Brazil. Our objectives were to evaluate whether birds could remove seeds from selective exclosures designed for rodents, and whether seed removal estimates using selective exclosures follow those generated by small mammals under natural conditions.

2. Material and Methods

We tested the reliability of selective exclosures in two semideciduous forest patches in southeastern Brazil, the 300 ha São José forest, Rio Claro, São Paulo (22° 25' S and 47° 33' W) and the 2178 ha Caetetus Ecological Station (Caetetus), Gália, São Paulo (22° 24' S and 49° 42' W). Both forests have a floristic composition characterized by *Meliaceae*, *Rutaceae*, *Mimosaceae*, and *Fabaceae* (Pagano et al., 1987; Durigan et al., 2000). At least 13 species of terrestrial granivorous birds occur at the forest edge or within the study sites including three species of tinamous (*Crypturellus* spp.) (Tinamidae), two pigeons (*Columba* sp.) and seven species of doves (among the genera *Leptotila*, *Geotrygon*, *Zenaida*, *Columbina* and *Claravis*) (Columbidae) and one quail (*Odontophorus capueira*) (*Phasianidae*) (Willis and Oniki, 1981, 2002), as well as several small rodents in the genera *Akodon*, *Oligoryzomys*, *Holochilus*, and *Sciurus* (P. Rubim and M. Galetti unpubl. data).

In this study we employ the term "seed" to the unit of dispersal. We used popcorn seeds (*Zea mays* - Poaceae) (mean \pm SD in mm: diameter 5.89 ± 0.46 ; weight 0.14 ± 0.02 g; $n = 10$) as baits to test the efficiency of selective exclosures. Popcorn seeds were ideal for testing the exclosures because they were not toxic and were readily consumed by vertebrates at our study sites (A. V. Christianini pers. obs.). Commercial seeds have also been employed in other studies of seed removal worldwide (Thompson et al., 1991; Kelt et al., 2004).

By varying the size of cages and the combined mesh used to selectively exclude animals we build up four models of selective exclosures used in the experiments (Table 1). The size of the cages was similar to those used in exclosure treatments of many previous studies (references above). We tested the exclosures using cafeteria experiments where each experimental unit (seed station) included two or three paired treatments placed within 30 cm of each other. Each treatment contained a Petri dish (nine cm diameter) fixed by a central nail three cm above the ground surface. Ten popcorn seeds were placed in each dish. We spread Tanglefoot® on the nail in order to prevent the access of ground invertebrates like ants to the seeds. Treatments in a single seed station differed from each other in that different subsets of the animal community were excluded from the dishes:

Table 1. Cage models used in the experiments on selective exclusion effectiveness. All measurements are in cm.

Cage	Model I	Model II	Model III	Total exclusion
Size above ground (length, width, height)	Small (16 x 16 x 9)	Large (20 x 20 x 9)	Large (20 x 20 x 9)	Small (16 x 16 x 9)
Wire mesh laterals	2.7 x 3.5	2.7 x 3.5	2.7 x 3.5	1.5 x 2.0
Wire mesh top	2.7 x 3.5	2.7 x 3.5	1.5 x 2.0	1.5 x 2.0
Designed to provide exclusive access to: ¹	Small mammals	Small mammals	Small mammals	None

¹Ground invertebrate access was prevented spreading Tanglefoot® on the nail to which the petri dish containing the seeds was fixed.

- Open treatment (control): no exclusion methods for vertebrates were used; seeds were available to birds and mammals;
- Selective exclusion treatment: the Petri dish was placed within a small or large sized cage (see Table 1) staked to the ground, the top and sides covered by narrow (1.5 x 2.0 cm) or wide (2.7 x 3.5 cm) wire mesh. Seeds were therefore available to any vertebrate that could pass the wire mesh and remove the seeds (e.g. rodents); and
- Total exclusion (second control): the Petri dish was placed within a small cage (Table 1) staked to the ground, the top and sides covered with narrow (1.5 x 2.0) mesh.

Treatments were placed in the center of a sand quadrat of 65 x 65 cm in order to record the visit of vertebrates from their footprints. Vertebrates were assigned to one of the following categories according to their size: small mammals (e.g. rodents ≤ 300 g), larger mammals (> 300 g), and birds. We followed Becker and Dalponte (1991) to identify mammalian footprints. Feces and seed fragments were also used to identify the vertebrate visitors.

Each seed station was replicated 10 times in five transects in the study areas. To avoid the influence of the edge on seed removal, all seed stations were at a minimum distance of 100 m from the nearest edge of the fragment. Thus, seed predation by granivorous birds associated with edges or open areas (e.g. *Columba picazuro*, *Zenaida auriculata*) was not assessed. Minimal distance between seed stations was 10 m and between transects 100 m. Seed stations operated for a short time interval (one to six days at a time), in order to minimize potential cues to visually oriented granivores. We checked the seed stations daily and when seed removal occurred, we recorded the type of animal and number of seeds removed per treatment, removing the seed station afterwards. Seeds preyed upon or removed were pooled and arbitrarily assigned as removed, since their fate was not relevant for the test of the method. Stations that had their seeds removed and received the visit of animals from two or more categories between consecutive daily inspections, were not considered in the analysis. On these occasions, we ignored the visit and refilled the seeds in the dishes, starting to record the visits on the following day. Experiments were not carried out during rainy days.

Tests of selective exclusions were conducted during January and May-July 2000, and February-March

2001. Total sampling effort was 436 seed stations.d¹. We also set up a camera-trap with a passive infrared trigger mechanism and automatic, weather proof, 35 mm Yashica cameras with auto flash (Wildlife Pro Camera System, Forest Suppliers Inc.) at each of five seed stations in Caetetus, to record animals visiting the seed stations. Cameras recorded visits for a combined total sampling of 600 hours. The treatment of total exclusion was used together just with the tests of cage Model III (Table 1; N = 142 seed stations.d¹).

3. Statistical Analysis

We analysed data on seed removal using two approaches. First, we compared seed removal levels between the selective exclusion treatments and open treatments separately for a given model of cage and type of animal that removed the seeds (small mammal or bird). Since data was not normally distributed even after transformations, we used the Wilcoxon-paired sample test. The result of this test can indicate if the selective exclusions are biasing the foraging of small mammals, in which case seed removal from selective exclusions would differ from controls. If the exclusions can provide estimates of seed removal by small mammals similar to those found under natural conditions, seed removal from selective exclusions would not differ from controls. Ideally, the selective exclusions should allow the consumption of seeds by small mammals at the same levels of the controls, while deterring seed removal by birds. Spearman rank correlation was applied to the number of seeds removed from the selective exclusions and the controls at the same seed stations for a given model of cage and type of animal that removed seeds. If the selective exclusions work properly, high positive correlation between treatments would be obtained for seed removal by small mammals, while low correlation coefficients between treatments are expected for seed removal by birds. The comparison of seed removal between selective exclusions, total exclusions and controls was made with Friedman's ANOVA. All tests followed Zar (1999).

4. Results and Discussion

We recorded a total of 200 vertebrate-seed interactions, most of which (N = 83; 41.5%) involved birds (mainly pigeons and tinamous), followed by small mammals (N = 55; 27.5%) or other mammals (N = 12; 6.0%). We

could not identify the seed removers for 50 visits, mostly because two or more vertebrate species visited the seed stations between daily inspections. Three total exclusion treatments had their seeds removed by small mammals.

Seed removal by rodents differ among controls and selective exclusions for Model I cages (Wilcoxon-paired sample test: $T = 6.5$; $P = 0.032$; $N = 21$), but this did not occur either to Model II ($T = 3.0$; $P = 1.0$; $N = 14$) or Model III cages ($T = 5.0$; $P = 0.249$; $N = 20$) (Figure 1). Despite the difference between treatments, seed removal by rodents in selective exclusions was highly correlated with controls for all models of cages used (Spearman rank correlation: $r_s = 0.78$ or higher for all models of cages, all significant $P < 0.001$) (Figure 1). Five species of large mammals also removed seeds from treatments: Brazilian rabbit (*Sylvilagus brasiliensis*), Capuchin monkey (*Cebus apella*), South American coati (*Nasua nasua*), White-lipped peccary (*Tayassu pecari*), and one unidentified marsupial. Their visits could be easily recognized because they usually turned the cages over when trying to reach the seeds and trampled the vegetation around the seed station.

Although the selective exclusions were used to tell apart the small mammal seed removal from that of other animals, birds could persistently remove up to ten seeds within selective exclusions (Figure 1). Moreover, seed removal by birds in selective exclusions was always correlated with controls (Model cage I: $r_s = 0.56$, $P < 0.001$; Model cage II: $r_s = 0.74$, $P < 0.001$; Model cage III: $r_s = 0.73$, $P < 0.001$) (Figure 1). In many studies (see above) seed removal from selective exclusions have been compared with controls (open treatments) using correlations in order to find the most important animals that remove seeds. Thus, studies using selective exclusions to investigate the removal of small seeds (< 6 mm) in Neotropical areas may overlook the role of birds as seed removers (but see Pizo and Vieira 2004). Other traits that help birds to be potentially important seed removers in the Neotropics are the abundance and biomass of species that usually consume seeds on the forest floor (tinamous, pigeons, doves, and finches) (Willis and Oniki, 1981; Terborgh et al., 1990), and their flexible foraging behavior that enable them to feed on seeds of quite variable size, shape and nutritional content (Pérez and Bulla, 2000; Christianini, 2001). Most plant species in tropical forests produce small seeds (Foster and Janson, 1985), which are especially prone to be eaten by granivorous birds. Also, most of these birds swallow the seeds whole, thereby removing evidence of their foraging on seed removing experiments. Thus, the role of birds interacting with seeds on the floor of tropical forests (see Hulme 1998 for a review) may be underestimated for some plant species, due to an artifact of the observational or the exclusion method employed. Although just in the Atlantic forest of Brazil 116 plant species have fruits and/or seeds recorded in the diet of columbids and tinamids (Christianini, 2001), experimental evidence pointing to the role of birds as seed removers in forest habitats is still

scarce (Pizo and Vieira, 2004; A. V. Christianini and M. Galetti unpubl. data).

Birds removed no seed from total exclusions, but rodents removed seeds from three total exclusions by digging under the cages or just passing through the wire mesh. Despite these discrepancies, total exclusions were in general effective to deter the removal of seeds by vertebrates (first quartile – median – third quartile of the number of seeds removed: controls 4-10-10; selective exclusions 0-6-9; total exclusion 0-0-0; Friedman ANOVA $\chi^2 = 101.65$; $P < 0.001$; $N = 65$). There was no correlation between seed removal along total exclusions and controls ($r_s = 0.08$; $P = 0.67$) or between total exclusions and selective exclusions ($r_s = 0.17$; $P = 0.17$). Because the wire mesh on top of the Model III cages was the same as that of the wire mesh of the total exclusion cages, we suggest that birds were removing seeds from the sides of selective exclusions, where the mesh was larger (Table 1). Many bird footprints were observed surrounding the selective exclusions, with signs of several stopping places (footprints facing the cage). This type of behavior was frequently observed, where birds inspected seeds inside these cages, but were unable to get at them (A.V. Christianini pers. obs.). Birds did not go inside the cage to remove seeds, since no footprints of birds were recorded inside cages. A bird would bend down close to the side of the selective exclusion and put its head and neck inside the cage to pick up seeds (the bills of the local granivorous bird species are too short to reach the seeds in the Petri dishes from outside the cage). When experimental seeds are placed at the center of the cage, the wider the cage, the lower the chance of seed removal by birds through the sides of the cage. Exclusions measuring 40 x 40 x 40 cm should prevent the removal of seeds by birds, while allowing the consumption of the seeds by small mammals. Several trials using captive birds have shown that even large granivorous birds, such as Solitary Tinamou (*Tinamus solitarius*), cannot remove seeds from such exclusions (A. V. Christianini pers. obs.).

Until a selective exclusion treatment that allows seed removal exclusively by birds is developed, we suggest the employment of four treatments in the experimental design in the Neotropics - open controls, exclusive rodent access, exclusive invertebrate access, and a closed control (no access to animals) (see Orrock et al., 2003 for a similar approach) - instead of the usual pair of treatments normally used (open controls and invertebrate access only, see references above). Correlations among treatments can provide some evidence of the most important guild of seed removers. For example, seed stations that have seed removal at open controls weakly correlated with the seed removal at the exclusive rodent access and at the exclusive invertebrate access can indicate that birds or large mammals are removing the seeds. In this case, additional cues like footprints or tooth marks can help to correctly identify the guild. Another option is to combine a temporal exclusion approach, when inferences of seed removal are based on

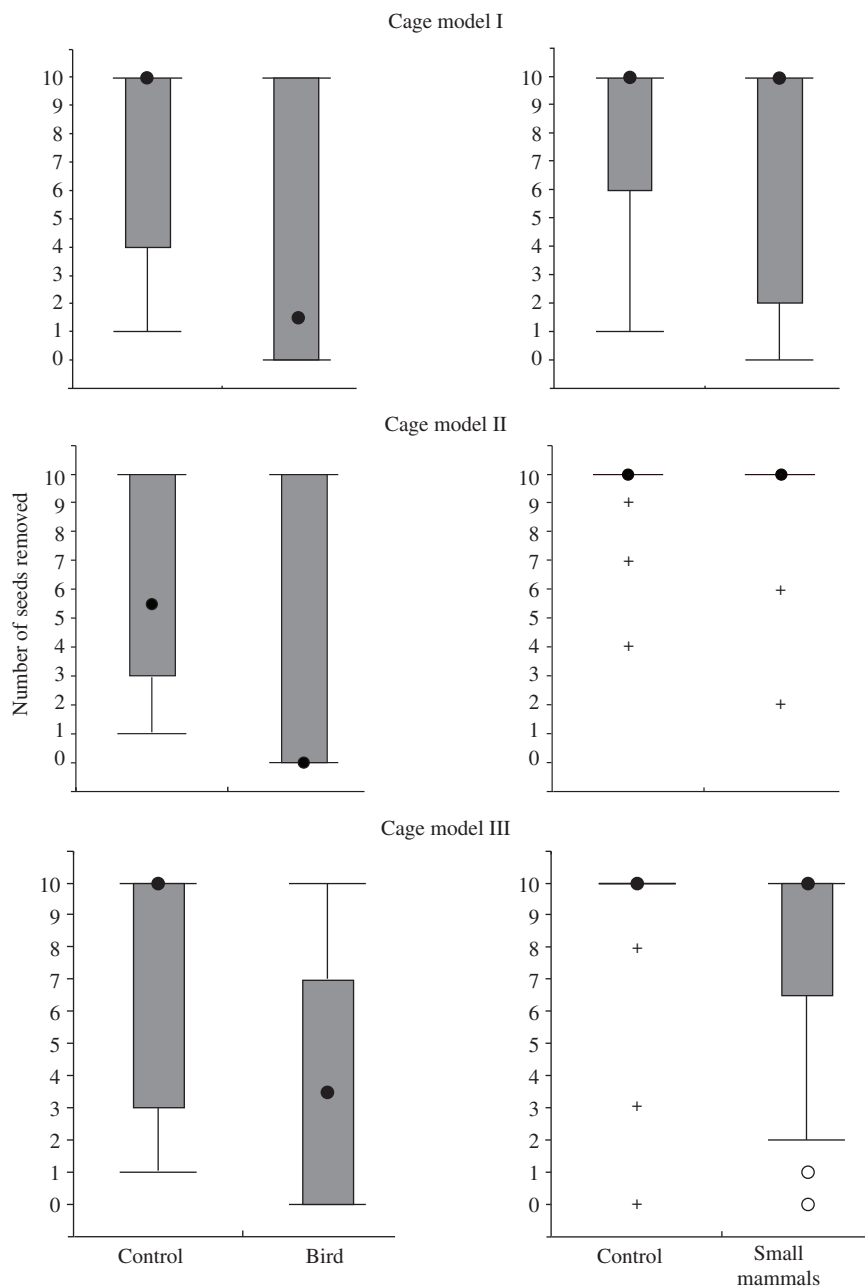


Figure 1. Comparative seed removal from paired treatments to test the effectiveness of different models of selective exclusions. Seed removal events from birds (left side) or from small mammals (right side) were compared to seed removal from paired, open controls (no exclusion for vertebrates). Filled circle is the median; lower and upper boxes are 25-75% percentiles; bars show minimum and maximum non-outlier values; open circles are outliers, while crosses are extreme values. Sample sizes for bird and rodent seed removal, respectively: Cage Model I: $n = 18$, and $n = 21$; Cage Model II: $n = 18$, and $n = 14$; Cage Model III: $n = 47$, and $n = 20$.

previously known circadian rhythms of the local animal species. With the monitoring of the seed stations at dawn and dusk it is possible to infer the amount of seeds taken by diurnal (e.g. birds) or nocturnal (e.g. rodents) animals (e.g. Thompson et al. 1991; Pizo and Vieira, 2004). However the application of temporal exclusions are subject to several constraints: 1) the study plot has to be relatively small,

allowing the monitoring of seed stations at short intervals of time; 2) long-term studies are difficult, because seed removal must be recorded twice a day; and 3) some animals like agoutis and squirrels have activity schedules during the day, violating the assumption of diurnal seed removal only by birds. For tropical savannas, another alternative could be the use of selective exclusions over large areas

(Brown and Heske, 1990). In forest habitats however, several rodent species have arboreal or semi-arboreal behavior (Malcolm, 1991) which make these rodents able to pass over the exclusions, biasing the conclusions derived from such studies.

This paper illustrates how small selective exclusions can be used in studies of seed removal in the Neotropics, and some of the insights given by their use. A proper use of selective exclusions can clarify if birds are interacting with more seeds on the floor of Neotropical forests than we think.

Acknowledgments — We are grateful to the Museu de Zoologia da Universidade de São Paulo, Fundação Parque Zoológico de São Paulo, and the Instituto Florestal de São Paulo for authorization to carry out research in areas under their control. We also thank Keith S. Brown, Jeff Himmelstein, Pedro Jordano, Milene M. Martins, Jeremy Minns, Marco A. Pizo, and an anonymous reviewer for their comments on the manuscript. This study was undertaken while the authors were receiving fellowships from the Brazilian Research Council (CNPq). We also thank FAPESP and PROAP-CAPIES for financial support.

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