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# Effect of frugivorous birds on seed dispersal and germination of multi-seeded fruits

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**Abstract**

This work involves multi-seeded fruits which are ingested by frugivorous birds. We investigated the patterns of temporal and spatial seed deposition and their effects on germination success.

Multi-seeded fleshy-fruits of *Morus nigra* and *Solanum luteum* were offered to two species of frugivorous birds: *Pycnonotus xanthopygos* and *Turdus merula*. The fruits were swallowed whole but the seeds were gradually defecated during a period of a few hours in numbers per feces significantly lower than those within the complete fruit. This pattern of temporal seed deposition might have a positive implication on seed dispersal in space.

Different retention times of *S. luteum* seeds had no effect on their germination success. However, as number of seeds per group increases their germination success decreases in both plant species. Therefore, we suggest that in the case of multi-seeded fruits, bird ingestion plays an important role by reducing the number of seeds per group, which in turn may enhance germination.

**Keywords:** Frugivorous birds, multi-seeded fruits, seed deposition, germination success.

**Résumé**

Ce travail traite des fruits à plusieurs graines mangés par les oiseaux frugivores. Nous avons étudié les modalités temporelles et spatiales de dispersion des graines, et leurs effets sur le succès de la germination.

Des fruits charnus à plusieurs graines de *Morus nigra* et *Solanum luteum* ont été proposés à deux espèces d'oiseaux frugivores : *Pycnonotus xanthopygos* et *Turdus merula*. Les fruits ont été consommés immédiatement, mais les graines ont été déféquées peu à peu au cours de quelques heures, en nombre nettement inférieur à celui du fruit entier. Cette forme de dispersion temporelle des graines pourrait élargir la distribution spatiale des graines.

Les différentes périodes de rétention des graines de *S. luteum* n'ont aucun effet sur le succès de la germination. Néanmoins, nous avons établi une relation inverse entre la densité des graines et le succès de la germination pour les graines des deux espèces. Nous suggérons donc que, dans le cas des fruits à plusieurs graines, l'ingestion par les oiseaux joue un rôle important en réduisant la densité de graines, ce qui peut en fin de compte augmenter la germination.

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## INTRODUCTION

Studies on seed dispersal by birds have focused mainly on dispersal in response to bird behavior, e.g. the time the bird remains on the parent plant (PRATT & STILES, 1983), the patterns of departure flights from the parent plant (HOWE, 1979, 1986), or the influence of bird migration (RIDLEY, 1930). Nevertheless, additional factors, such as retention time of seeds within the digestive system of the bird, number of seeds in the droppings and the frequency seeds are distributed when released, must also be considered.

Preliminary observations on 15 fleshy-fruited species that are consumed by blackbirds (*Turdus merula*, Turdidae), and bulbuls (*Pycnonotus xanthopygos*, Pycnonotidae) in the Mediterranean maquis had indicated that fruits are swallowed whole (BARNEA, 1988). In field observations we noticed that when multi-seeded species (e.g. *Morus nigra*, *Myrtus communis*, *Solanum luteum*, or *S. nigrum*) are consumed, their seeds are defecated in numbers smaller than those within the complete fruit. These observations suggested that seeds which had been swallowed together are not defecated at the same time, but are gradually dispersed. Such a pattern of temporal seed dispersal might have a positive implication on seed dispersal in space.

The spatial pattern of seed deposition influences both germination success and seedling establishment (HOWE, 1977; HERRERA, 1984; HOWE *et al.*, 1985). For example, there is evidence that seed density decreases as a function of the distance from the parent plant (HARPER, 1977; WHEELWRIGHT, 1983; DEBUSSCHE *et al.*, 1985). The advantage of seeds that are removed from their parent plant relative to those which are dropped underneath is a result of density-dependent mortality, escape of the seeds from predators and pathogens (CONNELL, 1971; JANZEN, 1970, 1983; SMITH, 1975) or seedling competition (HARPER, 1977; CLARK & CLARK, 1984; BECKER & WONG, 1985).

The spatial pattern of seed dispersal is a consequence of many factors, such as behavior (HERRERA & JORDANO, 1981; SORENSEN, 1981; DAVIDAR, 1983; DEBUSSCHE *et al.*, 1985; KREBS & HARVEY, 1986), the duration of each visit (DAVIDAR, 1983; KREBS & HARVEY, 1986), and also the factor that is studied here – variation in retention time of ingestion and seed delivery.

Therefore, the aims of this work were to answer the following questions:

1. What is the pattern of temporal seed deposition in multi-seeded fruits?

2. Do differences in retention times of various seeds have any effect on their germination success?

3. Does the number of seeds per feces/fruit have any effect on their germination success?

## MATERIALS AND METHODS

### Plant and Bird Species

Two plant species whose fruits contain many seeds were selected: *Solanum luteum* Miller (Solanaceae) is a ruderal, annual plant, and has orange fleshy fruits (SAARISALO-TAUBERT, 1967). Fresh mass of a single fruit is $0.27 g \times 10^{-3} \pm 0.01$ ($n = 15$), and the mean number of seeds per fruit is $34.2 \pm 4.3$ ($n = 10$). *Morus nigra* L. (Moraceae) is an introduced tree from the Far East (ZOHARY, 1973). Fresh mass of a single fruit is $1.45\,g \times 10^{-3} \pm 0.18$ ($n = 30$), and the mean number of seeds per fruit is $56.8 \pm 15.7$ ($n = 5$). Both species occur in the Mediterranean region of Israel. These species were chosen because they are common, their fruits are consumed by birds, and the seeds are excreted in the feces (DANIN, 1983).

We chose two species of resident frugivorous birds for the study: bulbuls and blackbirds. Both were observed to consume fruits of *S. luteum* and *M. nigra* in the wild. The bulbul is a tropical species common in most parts of Israel, while the blackbird is a palaearctic bird, found in the northern and central parts of the country (PAZ, 1986). Ripe fruits of *S. luteum* and *M. nigra* were collected from at least 3 individual plants of each species in November and May-June 1987 respectively, in the northern part of Israel (33°40'N, 35°35'E), and offered to birds within 24 hours of collection.

## The pattern of seed deposition in time

For each bird species four individuals were tested. Each bird was kept separately in a cage (100 × 30 × 50 cm). On the day of the experiment birds were offered 10 fruits of the tested species, plus water. After 5 minutes the number of eaten fruits was recorded, the remains removed, and the birds were offered regular food (eggs, flies larvae, and other kinds of fruits). Feces of the birds were collected every half an hour during the first 4 hours and then again after 24 hours. The number of seeds in each feces was recorded.

Each bird was tested once for the whole period of 24 hours. However, most birds were tested more times for shorter periods. Each bird was given at least 3 days of acclimatization before and between the feeding trials. Before and after each feeding trial the birds were weighted to ensure that they maintain good condition.

## The influence of seed retention time on germination

Preliminary experiments showed no significant differences between germination of *S. luteum* seeds which were ingested by different individuals from the same species – bulbuls or blackbirds (for details see BARNEA *et al.*, 1990). Hence seeds from the same class of retention time, ingested by all birds from the same species, were kept together.

Germination success as a function of retention time was compared with that of control uningested seeds. Before sowing, seeds were rinsed under running water for 10 minutes and then set to germinate in 1-8 replicate petri dishes (5 cm diameter) of 10 seeds per dish. Petri dishes were used with two filter papers and 2 ml of distilled water for each dish. The dishes were kept at a temperature of 25 ± 2°C with continuous illumination (GIVELBERG *et al.*, 1984). The number of seedlings in each dish was recorded every morning until none appeared at two consecutive observations.

## Germination success as a function of number of seeds per group

As seeds which were ingested by different individuals from the same species (bulbuls or blackbirds) showed no significant differences in their germination success (BARNEA *et al.*, 1990), seeds were kept collectively from feces of all four individuals from each bird species. Germination success as a function of number of seeds in a group was tested for each type of seeds (uningested, ingested by bulbuls, and ingested by blackbirds) in different groups. Each group (four replicate petri dishes) contained a different number of seeds placed together in the center of the dish. Seven groups were tested for *S. luteum* (2, 5, 10, 20, 40, 60, and 80 seeds), and eight for *M. nigra* (2, 4, 6, 10, 20, 40, 60, and 80 seeds). These groups cover the range between two possible natural germination situations: seeds which are defecated by birds (few seeds per group, see table 2), and seeds which are left in an uneaten dried fruit that falls on the ground (many seeds per group). Germination conditions were as described above.

## RESULTS

### The pattern of seed deposition in time

This pattern was determined only for *S. luteum* (fig. 1). Seeds that had been swallowed together are gradually defecated during a period of 24 hours. Some seeds

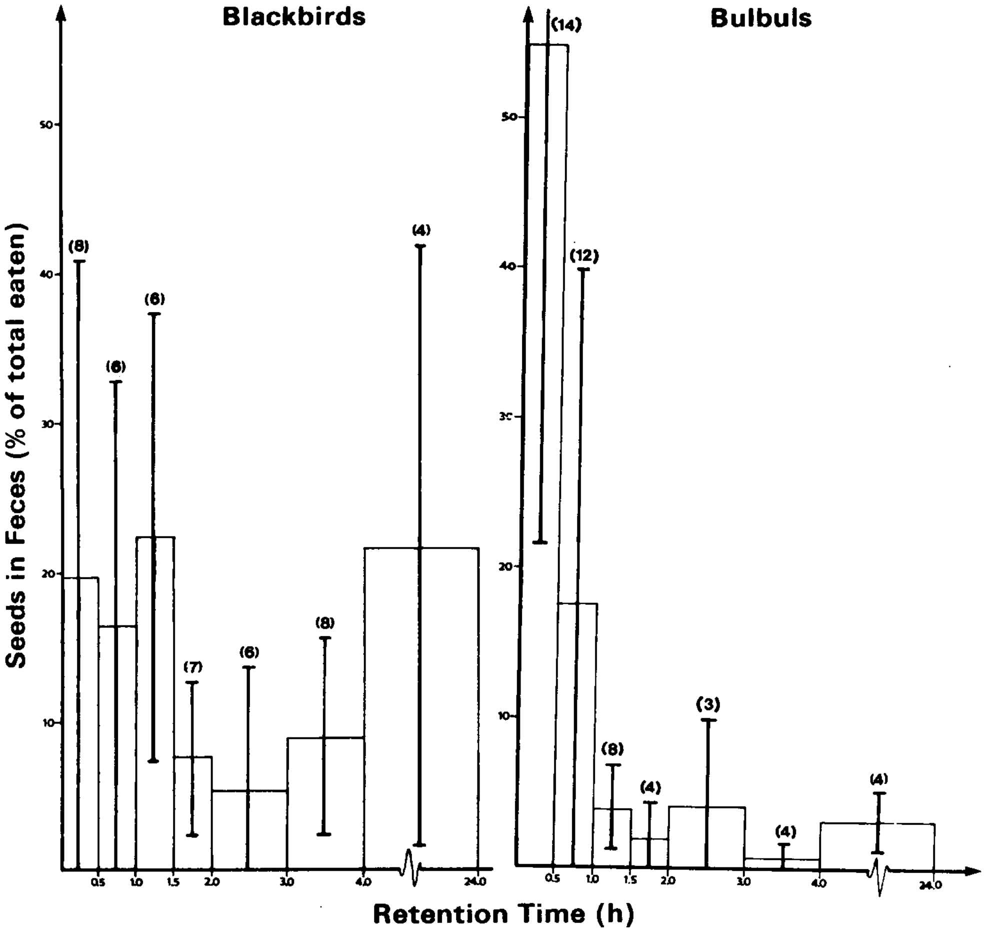


FIG. 1. – Percentage of *Solanum luteum* seeds (%$\bar{X} \pm$ S.E. of total eaten) in feces of blackbirds and bulbuls as function of retention time. ($n$) = number of observations of different feeding trials.

remain a few minutes, whereas others are defecated later, sometimes even 24 hours after consumption.

### The influence of seed retention time on germination

Germination percentages of seeds of *S. luteum* that remained for different periods in the digestive tract of either bulbuls or blackbirds were compared with

TABLE I. — *Germination percentages (%$\bar{X} \pm SE$) of seeds of* Solanum luteum *as a function of retention time in digestive systems of either bulbuls or blackbirds. (N = number of petri dishes,* 10 *seeds per dish).*

| Retention time (*h*) | Germination percentages of: | | |
|---|---|---|---|
| | Uningested seeds | Seeds ingested by: | |
| | | Bulbuls | Blackbirds |
| 0.0 | 97.5 ± 4.3 (8) | | |
| 0.5 | | 98.3 ± 3.7 (6) | 96.7 ± 7.5 (6) |
| 1.0 | | 95.0 ± 5.0 (2) | 98.3 ± 3.7 (6) |
| 1.5 | | 100.0 (1) | 100.0 ± 0.0 (6) |
| 2.0 | | 100.0 (1) | 100.0 ± 0.0 (3) |
| 3.0 | | 80.0 ± 23.5 (2) | 90 (1) |
| 3.5-24.0 | | 85.0 ± 5.0 (2) | 98.3 ± 3.7 (6) |

those of control, uningested seeds (table I). The data were analyzed by one way ANOVA, after angular transformation. The results suggest that retention time has no effect on germination success ($p < 0.05$, $F_{(6.15)} = 1.93$ for bulbuls and $F_{(6,29)} = 0.19$ for blackbirds).

## The influence of number of seeds per group on germination success

Average number of seeds per feces of both bulbuls and blackbirds (collected over 24 hours), were determined for *S. luteum* and *M. nigra* and compared with the

TABLE II. — *The number of seeds of* Solanum luteum *and* Morus nigra *in fruits and feces of bulbuls and blackbirds* ($\bar{X} \pm$ S.E.). *N = number of fruits or birds.*

| Plant species | Number of seeds in: | | |
|---|---|---|---|
| | Intact fruits | Bulbul's feces | Blackbird's feces |
| *Solanum luteum* | 34.1 ± 5.0 (10) | 8.1 ± 0.3 (3) | 8.2 ± 1.9 (3) |
| *Morus nigra* | 56.8 ± 15.7 (5) | 4.9 ± 2.0 (3) | 3.6 ± 0.7 (3) |

average number of seeds per fruit, respectively (table II). Results of a one way ANOVA show that there is a significant difference in the number of seeds between the three tested groups (intact fruits, bulbuls' and blackbirds' feces) in both plant species; $p < 0.001$, $F_{(2,13)} = 63.94$ for *S. luteum* and $F_{(2,8)} = 24.35$ for *M. nigra*). Multiple unplanned comparison among pairs of mean for unequal sample size (the T′-method) showed no significant difference between the two birds species for both plant species ($MSD_{(2,3)} = 12.96$ for *S. luteum* and 30.15 for *M. nigra*). However, in both bird species and for both plant species, number of seeds/feces was found to be significantly smaller than the number per fruit ($p<0.01$, MSD values as mentioned above). This number is 23% of the average number of seeds per fruit for *S. luteum* and 7% for *M. nigra*.

The results of experimental germinations at different seed numbers indicate that ingestion by bulbuls and blackbirds has a differential effect on germination

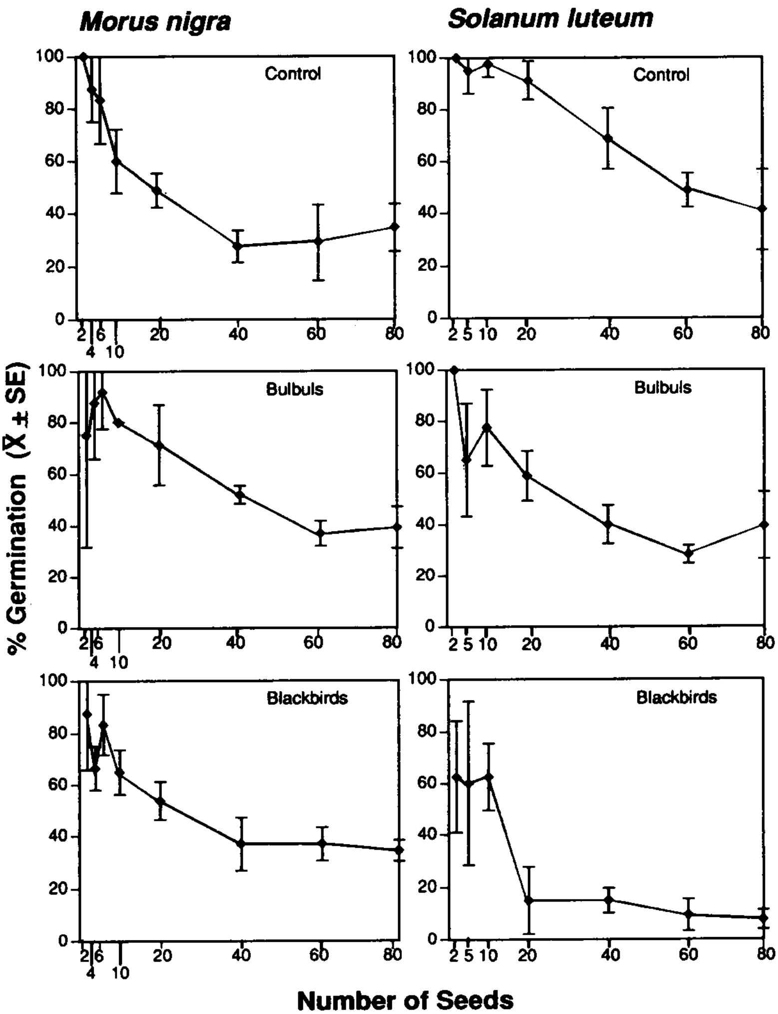


FIG. 2. – Germination percentages (%X̄ ± S.E.) of uningested and ingested seeds of *Solanum luteum* and *Morus nigra* as a function of number of seeds per group. Each mean is based on four replicates.

success of seeds of the two plant species: in *S. luteum* (fig.2), control uningested seeds yield the highest germination percentages, followed by seeds ingested by bulbuls, while seeds ingested by blackbirds show the lowest germination success. In contrast, control seeds of *M. nigra* (fig. 2) yield the lowest germination percentages, while seeds ingested by both bulbuls or blackbirds show higher germination success. The effect of seed ingestion by bulbuls and blackbirds on germination in both plant species, compared with that of control uningested seeds, was previously described in details (Barnea *et al.*, 1990, 1991), and therefore it is neither tested nor discussed here.

However, figure 2 indicates another finding, which is common to both plant species and to all three types of germinated seeds: when the number of seeds per group increases their germination success decreases. The data presented in figure 2 were transformed by angular transformation and then tested for each treatment from each plant species using a one way ANOVA test. The results, presented in

Table III. — *Results of one-way ANOVA examining the effect of number of seeds in a group on germination success of control and ingested seeds in* S. luteum *and* M. nigra.

| Plant species | *df* | $F_s$ | P< |
|---|---|---|---|
| *S. luteum*: | | | |
| Control seeds | 6,21 | 3.84 | 0.01 |
| Seeds ingested by bulbuls | 6,21 | 12.62 | 0.001 |
| Seeds ingested by blackbirds | 6,21 | 6.15 | 0.001 |
| *M. nigra*: | | | |
| Control seeds | 7,24 | 15.62 | 0.001 |
| Seeds ingested by bulbuls | 7,24 | 3.02 | 0.05 |
| Seeds ingested by blackbirds | 7,24 | 7.36 | 0.001 |

table III, show that germination success is significantly different within the experimental groups, in all treatments and both plant species. Planned comparisons between means of groups which contained number of seeds similar to that in a bird feces and in a fruit were carried out for both plant species and all treatments. In the case of *S. luteum* the compared groups were 10 seeds (closest to the average of 8.1 seeds per feces in bulbuls and 8.2 in blackbirds, see table II), and 40 seeds (closest to the average of 34.1 seeds per fruit). For *M. nigra* the compared groups were four seeds (closest to 4.9 and 3.6 seeds per feces, respectively), and 60 seeds (closest to 56.8 seeds per fruit). The results of these comparisons are presented in table IV. In all cases germination success of groups which contain number of seeds similar to the number per feces, is significantly higher than germination success of groups which have seed numbers similar to that in a single fruit.

## DISCUSSION

We found that in the case of *Solanum luteum* and *Morus nigra*, which have multi-seeded fruits (30-60 seeds per fruit), the mean number of seeds that are defecated each time is significantly smaller than the mean number of seeds per fruit. Defecation of all the seeds from fruits that are swallowed whole occurs gradually over a period of a few hours. Our results correlate with those of a previous work by Levey (1986): small seeds were placed in more defecations and

TABLE IV. – *Results of planned comparisons of germination success of groups which contain number of seeds similar to that in a bird feces and in a fruit, in control and ingested seeds of* S. luteum *and* M. nigra.

| Plant species | *df* | $F_s$ | P< |
|---|---|---|---|
| *S. luteum*: | | | |
| (Tested groups: 10 vs. 40 seeds) | | | |
| Control seeds | 1, 21 | 4.33 | 0.05 |
| Seeds ingested by bulbuls | 1, 21 | 9.60 | 0.01 |
| Seeds ingested by blackbirds | 1, 21 | 7.2 | 0.05 |
| *M. nigra*: | | | |
| (Tested groups: 4 vs. 60 seeds) | | | |
| Control seeds | 1, 24 | 29.44 | 0.001 |
| Seeds ingested by bulbuls | 1, 24 | 8.93 | 0.01 |
| Seeds ingested by blackbirds | 1, 24 | 4.6 | 0.05 |

passed over a long period of time, sometimes several hours after the last trace of pulp or skin was found in the defecations. LEVEY suggests that birds have the ability to give a different gut treatment to pulp or seeds. This ability partially depends on seed size, and when seeds are too small the mechanism does not operate. In such cases, seeds are defecated along with the pulp over a long period of time. Our results seem to support this hypothesis, as both *Solanum luteum* and *Morus nigra* have small seeds (average of 0.82 and 1.58 mg per seed, respectively).

The data presented here are based on experiments with captive birds, feeding in 5 minutes bouts and lacking "normal" diet-mixing with other fruit species. Nevertheless, we believe that they represent the situation in nature, where birds are foraging continually, mixing fruits of different species (LOISELLE, 1990), and/or additionally consuming insects. This assumption is supported by results of another work: WHITE and STILES (1990) studied the co-occurrences of foods in stomachs and feces of wild frugivores in eastern North-America and showed that the mean number of seeds per dropping increases with body size. It was found to be 3.9 and 9.2 for bird species with a similar size as bulbuls and blackbirds, respectively. Furthermore, in seven out of eight multi-seeded species (containing more than three seeds per fruit), the mean number of conspecific seeds per egestion was found to be smaller than the mean number of seeds per fruit (table IV in the above-mentioned work). Similar tendency is found in another study of seeds in dropping of tropical fruit-eating birds (LOISELLE, 1990). Out of five multi-seeded fruit species, four had a smaller number of seeds per dropping, compared with the number per fruit.

Patterns of temporal seed dispersal by animals were previously recorded by other authors (MCKEY, 1975; JANZEN, 1982, 1983; JOHNSON *et al.*, 1985; LEVEY, 1986). However, the question of the effect of different retention times on germination success was not sufficiently investigated. We know of only one work that examined germination success of seeds as a function of retention time in the digestive system (RICK & BOWMAN, 1961). Retention time of tomato seeds was found to be 12-20 days in the gut of a tortoise. A negative correlation existed between retention time of these seeds and germination success. These results differ from ours, which showed no correlation in that respect. However, it is obvious that this example involves a different class of vertebrate as well as different retention times.

Nevertheless, variation in temporal seed dispersal might have other positive implications, such as on seed dispersal in space. Even though the dispersal agents in this study are territorial and usually do not fly long distances, the fact that the seeds are defecated in small groups over a period of a few hours may result in their dispersal to different niches within the territory borders. Such seed scattering to many sites may prevent various factors of interference, e. g. predation, or pathological damage (DAVIDAR, 1983; HOWE *et al.*, 1985), as well as increase the number of potential safe sites reached by seeds of a particular maternal plant.

Our data also indicate that when number of seeds per group increases their germination success decreases in both *S. luteum* and *M. nigra*. Viability of seeds was tested and found to be $85.3 \pm 3.4\%$ in *S. luteum* (150 seeds from 4 fruits) and $92.9 \pm 7.5\%$ in *M. nigra* (130 seeds from 3 fruits). Therefore, the existence of such a negative relationship between the number of seeds per group and germination success in both plants might be due to a mechanism operating at the seed level (e. g. autotoxicity). We suggest that in the case of multi-seeded fruits, the defecation of the seeds in small groups, rather than together, might be advantageous in nature. The frugivores reduce seed density of such fruits, thus reducing the levels of intraspecific and sib-competition among genetically similar seeds, and promoting seed establishment. The greater number of defecations containing seeds was also previously discussed to be of importance for a successful dispersal and a higher potential of seedling establishment (LEVEY, 1986).

Nevertheless, in order to better establish the above mentioned conclusions, further experiments need to be carried out:

1. Field observations have clearly shown that birds vary considerably in their pattern of seed deposition. Some species defecate from certain preferred sites, a behavior that might cause accumulation of the seeds (HARPER, 1977; WILLSON, 1986), while others appear to scatter seeds widely (HOWE, 1977; MCDIARMID *et al.*, 1977). Therefore, the ecological implications of our study should be checked in a behavioral field-work that will determine the dispersal pattern, in respect with the tested birds and plants species.

2. The negative relationship between germination success and number of seeds per group was proven only in petri dishes. There is a need to examine this effect (which might be a result of autotoxic intraspecific competition) in soil also.

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