*Functional Ecology* 2001
**15**, 669–675

# Passage through bird guts causes interspecific differences in seed germination characteristics

A. TRAVESET,*† N. RIERA* and R. E. MAS‡

*Institut Mediterrani d'Estudis Avançats (CSIC-UIB), *C/Miquel Marqués 21, 07190 Esporles, Mallorca, Balearic Islands, Spain and ‡C/Bisbe Sastre 26, 07011 Palma de Mallorca, Balearic Islands, Spain*

## Summary

**1.** Seed germination characteristics are often modified after seeds are ingested by frugivores. Factors that are intrinsic either to the plant or to the frugivore's digestive tract are responsible for the great variation observed in germination response.
**2.** Our objectives were to determine whether and how the seed germination patterns of five common western Mediterranean plant species are affected by seed passage through the guts of their major dispersers, and to elucidate the mechanism by which such patterns are changed.
**3.** We used captive birds (*Turdus merula* and *Sylvia melanocephala*) to obtain ingested seeds and compared their germination rate (speed) and germinability (final percent germination) with those of controls (uningested, pulp-removed seeds), controlling for seed age, size and source. Germination was monitored for 2 years in an experimental garden. We evaluated the possible changes in seed traits after ingestion by measuring weight and coat thickness, and by observing seed coat sculpture.
**4.** Rate of seed germination, but not germinability, changed in all species after gut treatment. The greatest effect was in *Osyris*, in which germination was much enhanced. A great acceleration of germination, which is likely to translate into a seedling size advantage, was also found in *Asparagus*. In the other three species tested, germination was slower for ingested than for control seeds.
**5.** For *Rubus* and *Rubia* seeds, we found a different germination response depending upon the frugivore species tested. A different degree of seed coat scarification caused by differences in gut retention time, chemical and/or mechanical abrasion probably account for such responses.
**6.** In three of the species (*Osyris*, *Rubia* and *Phillyrea*), seed weight decreased after gut treatment. Such weight loss was not caused by any change in coat thickness, but may have been because of the scarification and consequent alteration of the seed coat structure.
**7.** The five Mediterranean species studied germinate when rains are most likely to fall (mostly autumn and spring). The different speed of germination promoted by gut treatment within frugivores may increase the probability that seeds can recruit successfully at a given time and in a given place.
**8.** This study suggests that frugivores contribute to the heterogeneity in germination characteristics not only within plant populations but also within plant communities, each frugivore species having a particular effect on the seeds of each plant consumed.

*Key-words*: Frugivory, Mediterranean shrubs, seed ingestion by birds, seed traits

*Functional Ecology* (2001) **15**, 669–675

## Introduction

The effect that the ingestion of fruits by vertebrate frugivores has on seed germination has received considerable attention (reviewed in Traveset 1998 and Traveset & Verdú 2001). Many studies show that germination is more successful after seeds pass through the digestive tract of frugivores (mostly birds). However, such enhancement is not universal, and several (usually uncontrolled) factors (e.g. retention time in guts, seed size, seed age, seed source) cause the great variation found in germination response. The conditions under which germination tests are performed also influence germination success, and contrasting results are often found when comparing treated and

†Author to whom correspondence should be addressed. E-mail: ieaatv@clust.uib.es

control (uningested) seeds of the same species under different conditions (Bustamante *et al.* 1992, 1993; Figueiredo & Perin 1995; Yagihashi *et al.* 1998; Traveset *et al.* 2001). Most studies are performed in the lab, testing germination in Petri dishes usually in growth chambers, yet these favourable conditions may sometimes obscure significant differences between treatments (Herrera 2000; Traveset *et al.* 2001).

We studied the seed germination response of five plant species, commonly found in western Mediterranean scrubland, after passage through the digestive tracts of their major avian dispersers. As germination responses, we considered (i) length of seed dormancy ($T_0$, defined as the time elapsed from sowing until first germination); (ii) rate of germination (defined as the speed at which seeds germinate, i.e. the number or proportion of seeds germinated in certain periods of time), and (iii) germinability (or final proportion of germination, i.e. proportion of seeds that germinate in a period long enough to obtain total germination). Our first goal was to test the hypothesis of Izhaki & Safriel (1990) that frugivores modify the length of seed dormancy and rate of germination and that by doing so, they may be spreading the chances of seedling survival over time, mainly in environments with unpredictable rain patterns (e.g. the Mediterranean). Our second objective was to identify the mechanism(s) by which seed germination responses are modified after passage through a frugivore. The specific questions of the study were the following:

1. To what extent does seed passage through avian guts affect germination responses?
2. Does the same plant species respond similarly to different frugivore species?
3. Do the germination responses of plants to avian ingestion depend upon seed traits such as size or seed coat thickness?
4. In plant species where birds modify germination responses of the ingested seeds, is there any seed trait (in particular weight and coat thickness) that changes significantly when compared with uningested (control) seeds?

## Materials and methods

During the summer of 1997, we collected fruits from five bird-dispersed plant species common in western Mediterranean scrubland: *Rubus ulmifolius* (Rosaceae), *Rubia peregrina* (Rubiaceae), *Asparagus acutifolius* (Liliaceae), *Osyris alba* (Santalaceae) and *Phillyrea* spp. (these included the species *latifolia* and *angustifolia*, which usually hybridise, Oleaceae). Hereafter, we will refer to them by generic names only. The fruits of all species were collected from a minimum of 10 individuals.

Recently collected fruits were fed to captive sedentary birds caught in Mediterranean scrubland. These birds were *Turdus merula* (blackbird) and *Sylvia melanocephala* (Sardinian Warbler), the most important dispersers of these plants in the Balearic Islands. Between three and 10 individuals of each species were tested for each plant. Birds were kept in separate cages ($60 \times 60 \times 60$ cm) and were maintained on a diet consisting of beetle larvae, commercial food for insectivorous birds and fruits of various fleshy-fruited species. At the time of experimental seed passage, only fruits of the particular species studied were given to them to avoid any seed-mixing effect on the results. A random sample of the fruits was depulped manually and the seeds served as controls. Therefore, we tested the direct effect of seeds passing through the guts rather than the effect of pulp removal. Different studies have already demonstrated the important role that frugivores play by freeing seeds from the germination inhibitors present in the pulp (e.g. Temple 1977; Izhaki & Safriel 1990; Barnea *et al.* 1991; Bustamante *et al.* 1993; Fukui 1995, 1996; Yagihashi *et al.* 1998; Engel 2000; Traveset *et al.* 2001). All fruits were collected on the same day and from the same site to avoid any seed age or source effect on germination.

Five hundred seeds of each species were used as controls, with the exception of *Phillyrea*, for which only 150 seeds could be obtained. For *Rubus* and *Rubia*, 500 seeds defecated by each bird species were gathered, whereas for *Osyris*, *Phillyrea* and *Asparagus*, a sufficient number of seeds to test was obtained only with blackbirds (warblers did not usually swallow these larger fruits; see Table 1). For these three species, we had 500 seeds of only the 'blackbird' treatment.

All seeds were kept in paper bags in dark and dry conditions until the date of sowing (6 October 1997). Seeds were planted in pots (12 cm in diameter) previously filled with horticultural mixture. We spread a total of 50 seeds on each pot and covered them with a 2 mm layer of the potting mixture. Pots, randomly assorted in four trays, were covered with a lid of 1 cm wire mesh to prevent seed predation by rodents. The trays were placed on the floor of an experimental garden and surrounded by a fence to reduce possible animal disturbances. Pots were watered periodically (with the same amount of water), only when rain was scarce (mainly in summer) to avoid seed death through desiccation. An unknown number of seeds was removed

**Table 1.** Average seed diameter (± SD) of the species tested and fresh weight of control (uningested) seeds and seeds ingested by either *Turdus* (blackbird) or *Sylvia* (warbler) ($n = 25$ seeds)

| Species | Seed diameter (mm) | Seed weight (mg) | | |
|---|---|---|---|---|
| | | Control | *Turdus* | *Sylvia* |
| *Rubus* | 1·98 ± 0·03 | 3 ± 1 | 3 ± 1 | 4 ± 1 |
| *Rubia* | 3·45 ± 0·07 | 20 ± 5 | 15 ± 5** | 15 ± 5** |
| *Asparagus* | 4·37 ± 0·05 | 44 ± 6 | 45 ± 6 | – |
| *Osyris* | 5·72 ± 0·04 | 92 ± 14 | 81 ± 9** | – |
| *Phillyrea* | 4·21 ± 0·06 | 50 ± 9 | 44 ± 8* | – |

$*P < 0·05$; $**P < 0·01$ (indicate differences between treatment and control).


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from different pots by ants soon after being planted. When ants were detected, an insect trapping adhesive (Tanglefoot Co., Gran Rapids, MI, USA) was placed around the edge of each pot. At the end of the experiment, all remaining ungerminated seeds were counted in each pot. Pots from which most seeds had been removed were eliminated from the analyses, leaving a total of 109 pots.

Seedlings began emerging 1 month after planting; from that time, they were counted every week or every month (depending upon season). The experiment ended in the spring of 1999 (5 May), when no seedlings had emerged for about a month. Germinated seeds were removed as they were counted.

To identify the mechanisms by which seed germination may be modified after gut passage through a frugivore, the possible changes that seeds suffer in both weight and coat thickness were evaluated. A sample of 25 fresh seeds from each treatment and control group was weighed individually (to the nearest mg). Seed coat thickness was measured from a minimum of 10 seeds from each treatment and control by means of a dissecting microscope connected to a computer using Optimas 6·1 software (Media Cybernetics, L.P., Silver Spring, MD, USA). Further observations on seed coat sculpture were made using a scanning electron microscope (Hitachi S-530).

### DATA ANALYSIS

Differences in germination rate between treated and control seeds were examined for each species with a repeated-measures analysis of variance (RMANOVA), whereas dormancy length, final germination percentage and an additional measure of germination rate used by several authors ($T_{50}$, or time elapsed from sowing until 50% germination, e.g. Barnea *et al.* 1991) were compared by means of ANOVAS. Each pot was considered as a replicate. The angular (arc-sin square root) transformation was used to normalize the proportions. Weights of ingested and control seeds were compared using a one-way ANOVA for each plant species, whereas coat thickness (six measurements per seed) was compared with a nested ANOVA, using treatment as a fixed effect and seed as a random effect nested within treatment. All means are accompanied by their standard errors unless otherwise indicated. Data were analysed using SYSTAT V. 10·0 (SPSS, Chicago, IL, USA).

## Results

### GERMINATION CHARACTERISTICS

*Rubus ulmifolius*

Rubus ulmifolius began germinating soon after planting (towards the end of autumn), continuing throughout the winter until the spring of the following year (Fig. 1). The rate of germination varied significantly among treatments in the RMANOVA ($F_{2,14} = 4{\cdot}3$, $P = 0{\cdot}035$, time × treatment not significant), although it was not until day 94 (8 January 1998) that differences became apparent. $T_0$ did not vary among treatments ($F_{2,14} = 0{\cdot}87$, $P = 0{\cdot}44$), although $T_{50}$ did ($F_{2,14} = 3{\cdot}68$, $P = 0{\cdot}05$). A Tukey's test showed that control seeds germinated significantly faster than those ingested by warblers (Table 2). In contrast, seeds ingested by blackbirds did not differ from control seeds, with the exception of day 115, when germination in the former was significantly lower (Fig. 1). Regardless of differences in germination rate, final percentage germination was not significantly greater for control than for ingested seeds ($F_{2,14} = 1{\cdot}15$, $P = 0{\cdot}34$).

*Rubia peregrina*

Most germination occurred during the winter of 1998. Only a minor fraction of seeds germinated during winter and spring of the following year (after day 220; Fig. 1). A highly significant effect of seed ingestion by birds on germination rate was found in this species ($F_{2,19} = 6{\cdot}47$, $P = 0{\cdot}007$, time × treatment not significant), although the number of germinated seeds at the end of the experiment did not differ significantly among treatments ($F_{2,19} = 2{\cdot}11$, $P = 0{\cdot}15$; Fig. 1). Seeds ingested by blackbirds began germinating later ($T_0$: $F_{2,19} = 2{\cdot}86$, $P = 0{\cdot}08$) and $T_{50}$ was also longer for ingested than for control seeds ($F_{2,19} = 6{\cdot}38$, $P = 0{\cdot}008$) (Table 2). Warblers did not significantly affect either $T_0$ or $T_{50}$; however, seeds ingested by these birds germinated faster than those ingested by blackbirds (Tukey's test).

*Asparagus acutifolius*

Most germination took place from January to April 1998 (between days 121 and 191; Fig. 1). Seed germination of this species appeared to be marginally affected by ingestion in the RMANOVA ($F_{1,14} = 3{\cdot}51$, $P = 0{\cdot}08$, time × treatment not significant), seeds passed through blackbirds germinating faster than uningested seeds. $T_{50}$ was also greater for control than for ingested seeds, although $T_0$ was very similar between the two (Table 2). In winter and spring of 1999 (days 479–595; Fig. 1), a smaller fraction of seedlings emerged, although controls caught up with the ingested seeds. Final percentage germination did not differ between treatment and control ($F_{1,14} = 1{\cdot}54$, $P = 0{\cdot}24$).

*Osyris alba*

The influence of avian ingestion on germination responses in this plant was the greatest of all species tested. Germination rate was much greater for seeds passed through blackbirds ($F_{1,17} = 103{\cdot}84$, $P < 0{\cdot}001$, significant time × treatment interaction; Fig. 1). $T_0$ did not differ between control and ingested seeds

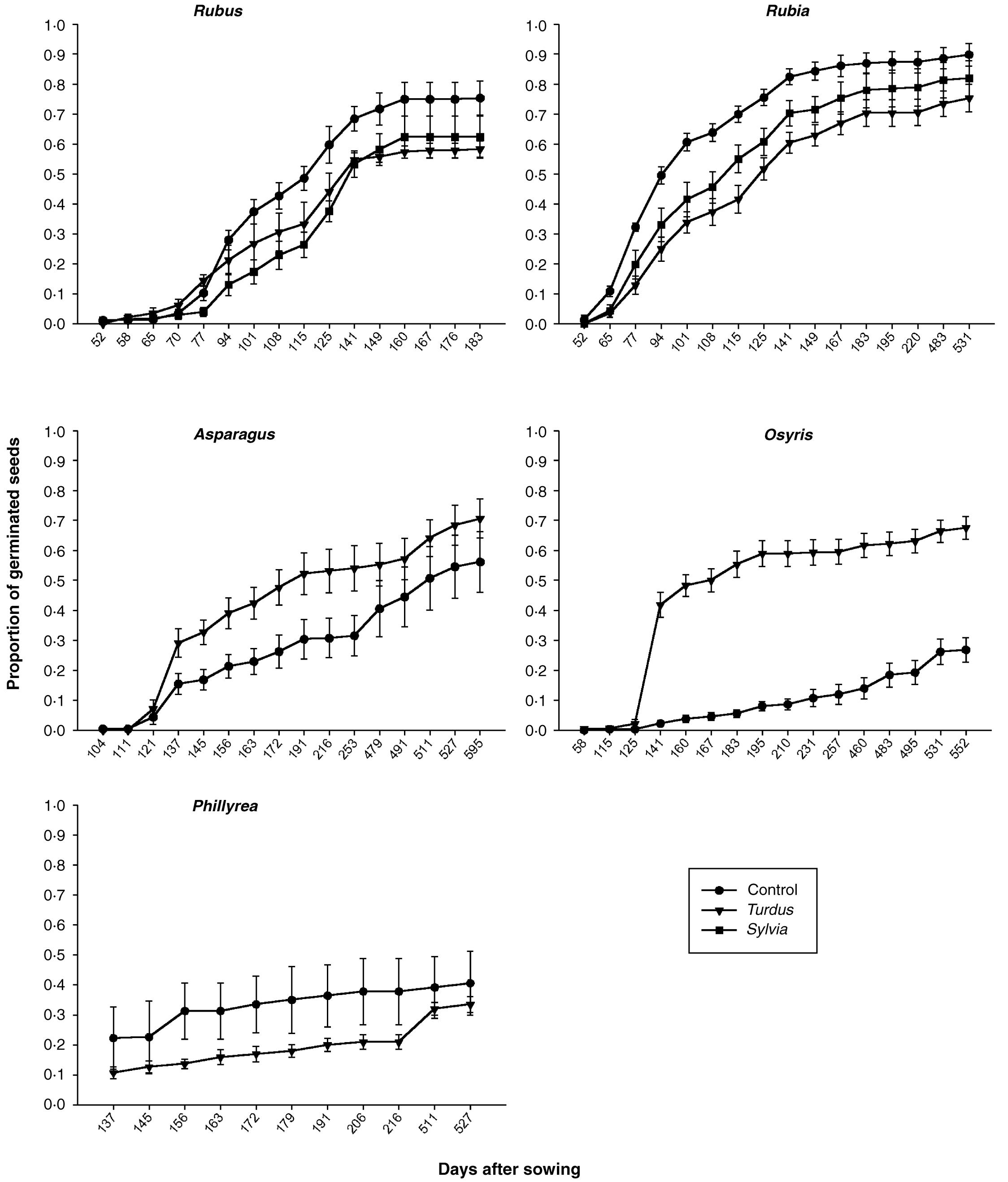


**Fig. 1.** Cumulative proportion of seeds per pot germinating from each treatment and for each of the study species. Mean and standard error bars (calculated from the original data) are shown. Note different horizontal scales for each species.

**Table 2.** Dormancy length ($T_0$) and time elapsed to 50% of total germination ($T_{50}$) for control (extracted manually from the pulp) and treated [ingested by either *Turdus merula* (blackbirds) or *Sylvia melanocephala* (warblers)] seeds of five species from the Mediterranean scrubland. Data are means ± SD; number of pots in parentheses. Each pot contained 50 seeds

| | $T_0$ (days) | | | $T_{50}$ (days) | | |
|---|---|---|---|---|---|---|
| Plant species | Control | *Turdus* | *Sylvia* | Control | *Turdus* | *Sylvia* |
| *Rubus* | 72 ± 13·6 (6) | 63 ± 5·9 (4) | 74 ± 16·2 (7) | 100 ± 5·3 (6) | 106 ± 10·5 (4) | 116 ± 13·8* (7) |
| *Rubia* | 57 ± 2·4 (6) | 70 ± 14·3 (9) | 66 ± 8·7 (7) | 94 ± 0·09 (6) | 109 ± 11·9** (9) | 99 ± 5·3 (7) |
| *Asparagus* | 129 ± 13·2 (7) | 131 ± 8·4 (9) | – | 215 ± 113·0 (7) | 185 ± 111·8[a] (9) | – |
| *Osyris* | 153 ± 26·0 (9) | 132 ± 26·5 (10) | – | 387 ± 134·2 (9) | 140 ± 8·5*** (10) | – |
| *Phillyrea* | 138 ± 0·0 (3) | 138 ± 0·8 (4) | – | 144 ± 9·82 (4) | 186 ± 24·5* (3) | – |

*$P \leq 0·05$; **$P < 0·01$; ***$P < 0·001$; [a]$P = 0·08$ (indicate differences between treatment and control).

($F_{1,17} = 2{\cdot}96$, $P = 0{\cdot}10$) but $T_{50}$ was significantly greater for the former ($F_{1,17} = 33{\cdot}91$, $P < 0{\cdot}001$; Table 2). Most germination took place during the winter of 1998; only about 10% of seedlings emerged in the winter and spring of the following year (days 460–552; Fig. 1). The final germination percentage was also much higher for ingested than for control seeds ($F_{1,17} = 50{\cdot}67$, $P < 0{\cdot}001$). Due to these differences, non-germinated seeds of each treatment were dissected at the end of the experiment to examine whether they were intact or aborted. A large fraction (> 85%) of seeds were filled with endosperm and appeared viable, and there were no differences between control and ingested seeds ($t = -0{\cdot}56$, df = 10, $P = 0{\cdot}59$).

*Phillyrea*

*Phillyrea* spp. began germinating in February 1998 and continued to do so gradually until the end of spring, although never reaching 40%. A very small fraction germinated the following winter (days 511–527; Fig. 1). The germination curves of control and ingested seeds were not significantly different in the RMANOVA ($F_{1,5} = 2{\cdot}91$, $P = 0{\cdot}15$, time × treatment not significant). Seed ingestion by blackbirds did not influence $T_0$, although $T_{50}$ was longer for ingested than for control seeds ($F_{1,5} = 8{\cdot}95$, $P = 0{\cdot}03$; Table 2). At the end of the experiment, however, no differences were apparent between ingested and control seeds, as a greater number of ingested seeds had emerged during the second winter (Fig. 1).

### SEED WEIGHT, COAT THICKNESS AND SCULPTURE

Seed weight was influenced by passing through the digestive tracts of birds in at least three of the five species tested (Table 1). In *Rubia*, *Osyris* and *Phillyrea*, control seeds always weighed slightly more than defecated seeds. This weight loss might be attributed to the abrasion that seed coat can suffer when passing through the bird's digestive tract. However, this change in weight does not explain consistently the differences in germination rates found between treated and control seeds, as germination patterns in *Osyris* were the opposite of those in *Rubia* or *Phillyrea*.

When we compared seed coat thickness, we found no significant differences between control and treatments (*Rubus*: $0{\cdot}20 \pm 0{\cdot}05$ *vs* $0{\cdot}23 \pm 0{\cdot}05$ mm (*Turdus*) and $0{\cdot}25 \pm 0{\cdot}05$ (*Sylvia*); *Rubia*: $0{\cdot}06 \pm 0{\cdot}01$ *vs* $0{\cdot}06 \pm 0{\cdot}01$ mm (*Turdus*) and $0{\cdot}05 \pm 0{\cdot}01$ (*Sylvia*); *Asparagus*: $0{\cdot}04 \pm 0{\cdot}01$ *vs* $0{\cdot}04 \pm 0{\cdot}004$ mm; *Osyris*: $0{\cdot}18 \pm 0{\cdot}03$ *vs* $0{\cdot}16 \pm 0{\cdot}02$ mm; *Phillyrea*: $0{\cdot}22 \pm 0{\cdot}04$ *vs* $0{\cdot}20 \pm 0{\cdot}03$ mm). This indicated that the loss in seed weight in *Rubia*, *Osyris* and *Phillyrea* after ingestion was not because their seed coat became thinner.

Scanning electron microscopy of the seed coat sculpture added relatively little information to the effect of birds' gut treatment on germination. Slight differences were observed in only *Osyris* and *Asparagus*, the two species in which germination was enhanced after passing through blackbirds. In both species, the coats of ingested seeds appeared somewhat modified (more dilated or with scars and crevices) compared with those of controls.

## Discussion

The passage of seeds through the digestive tracts of vertebrates – particularly birds – is important in determining their future germination behaviour. Although it did not affect dormancy length, seed ingestion by birds modified, to a large or small extent, the speed at which seeds germinated in all five species examined. The greatest effect was in *Osyris*, a result consistent with that reported by Izhaki & Safriel (1990), who tested the same species with different frugivorous birds. *Osyris* was also the only species that showed a significant effect of ingestion on final percentage germination; however, most ungerminated seeds were still viable after almost 2 years, suggesting that they might have germinated eventually had the experiment lasted longer. Our ongoing experiments with this species planted in the field will assess this possibility. The ingestion of *Asparagus* seeds greatly accelerated their germination as well, and at the end of the germination period of the first year, the number of seedlings that emerged from defecated seeds was double that from uningested seeds. This is likely to translate into a seedling size advantage and, in turn, into a greater probability of survival – although we would need data on the mortality factors (dessication, herbivory etc.) acting on those seedlings to test this hypothesis. Also, a faster germination implies less exposure to seed predators, which may represent an important mortality factor for some species. In the other three species (*Rubus*, *Rubia* and *Phillyrea*), seed passage through the digestive system of a bird had the opposite effect: it reduced the germination rate. The greatest 'delaying' effect was for *Phillyrea*: during the first year, only 21% of ingested seeds germinated compared with 38% of the controls. A germination delay in ingested seeds is uncommon (see reviews in Traveset 1998; Traveset & Verdú 2001), and the mechanism by which it occurs remains unknown.

Consistent with the results reported by Barnea *et al.* (1991) from the eastern Mediterranean, we found that even though most of the plant species grow in the same habitat, their seeds respond differently to ingestion by birds. Even the same species of bird can affect the germination patterns of closely related species quite differently (reviewed in Traveset 1998; Mas & Traveset 1999). One possible reason is that seed coats are affected differently (scarified) after exposure to grinding in a bird's gizzard. The degree of such scarification probably varies greatly among plant species, perhaps as a function of seed coat thickness, texture or sculpture. Likewise, the effect on a particular seed species may vary among frugivores (Traveset 1998). In the two cases in which we compared the effect of blackbirds with that of Sardinian Warblers, we found significant differences in germination rates: ingestion by the former affected *Rubia* but not *Rubus* seeds, whereas the opposite was found with ingestion by the latter. These differences can sometimes be attributed to different retention times in the guts (Barnea *et al*. 1991; Murphy *et al*. 1993), but not always (Barnea *et al*. 1990). Gut passage times reported for blackbirds (15–74 min; Barnea *et al*. 1991) encompass those reported by warblers (Traveset, unpublished). All these studies assume that longer retention times result in increased abrasion of the seed coat. However, no data exist to support this hypothesis. Alternatively, some gizzards may cause a greater scarification than others, regardless of seed retention time. Besides mechanical abrasion, the chemical composition of food ingested along with seeds (with variable water content, pH, secondary compounds) may also modify seed coat traits, either directly or indirectly, by affecting retention time in the guts (e.g. Levey & Karasov 1994; Murray *et al*. 1994; Witmer 1996; Cipollini & Levey 1997).

A striking result of this study was that seeds that had passed through the birds' guts lost weight, at least in three of the five species studied. For *Rubia*, this has been confirmed with fruits gathered in 2000 from another site and tested with other bird individuals (Traveset *et al*. unpublished). This contrasts with the only other study (Paulsen 1998) in which seed weight of control and ingested seeds was compared. Paulsen found that seeds of *Sorbus aucuparia* increased in mass by ≈ 9% after passing through the digestive system of thrushes (*Turdus* spp.), and explained this weight change by water uptake after the mechanical abrasion of the seed coat; that water uptake accelerated germination, which led to a greater seedling growth (Paulsen 1998). From our results, we could explain weight loss in ingested seeds if we observed that the seed coat had been abraded, either becoming thinner or more porous. However, we found no evidence that coat thickness had changed in any of the species, observing a slightly altered structure only in *Osyris* and *Asparagus*. An alternative explanation for the smaller seed weight of ingested seeds compared with controls is that birds selected fruits containing smaller seeds. To test this, we compared the seed diameter of these species in the control and treated groups. We rejected this hypothesis, as we found significant differences only for *Phillyrea*, and in the opposite expected direction [i.e. control seeds appeared to be slightly smaller ($4{\cdot}64 \pm 0{\cdot}07$ mm, $n = 53$) than ingested seeds ($4{\cdot}88 \pm 0{\cdot}05$ mm, $n = 93$)]. This supports the idea that seed coat does not become thinner after ingestion but becomes lighter.

If the weight loss of ingested seeds in *Rubia*, *Osyris* and *Phillyrea* reflects greater seed coat abrasion, we might expect that germination rate increased in these species; but as mentioned above, we found this result only in *Osyris*. In the other two species, germination rate was reduced. In the case of *Rubia*, this is consistent with Izhaki & Safriel's (1990) report for *Rubia tenuifolia*, a species closely related to *R. peregrina*, but inconsistent with the results of Barnea *et al*. (1991).

Seed size is another trait that influences the effect of ingestion by frugivores on future germination. A recent meta-analysis (Traveset & Verdú 2001) showed that large seeds are more likely to be affected positively (with greater germination percentages in ingested seeds compared with uningested ones) than small seeds. Our findings are consistent with this pattern, as *Osyris* and *Asparagus* are the species with the largest seeds and are, in turn, the only ones that increased their germination rate after being passed through birds. If retention time in the gut is important in influencing seed coat abrasion, we might expect that small seeds are more likely to be abraded than large ones, as the former are often retained for longer periods in an animal's digestive tract than the latter (e.g. Garber 1986; Levey & Grajal 1991; Gardener *et al*. 1993; Izhaki *et al*. 1995). However, seed coat traits that may ultimately determine the likelihood of being abraded are not necessarily associated with seed size. In our study species, for instance, there was no relationship between seed size and coat thickness.

The five species examined in this study germinate when rains are likely to fall (mostly autumn and spring), although such rainfall is rather unpredictable in Mediterranean ecosystems. The different speed of seed germination that ingestion by frugivores usually promotes in these environments (Izhaki & Safriel 1990; Barnea *et al*. 1991; Mas & Traveset 1999; Traveset *et al*. 2001; this study) may increase the chances that seeds can establish and survive as seedlings within those seasons. Under some circumstances, seedling survival will be greater if seeds take several weeks to germinate, whereas in others, an early germination will be more beneficial. Ingestion by different frugivorous species, each having a particular effect on germination performance, may represent an even greater increase in the chances of seedling survival (Izhaki & Safriel 1990). We need more data on the stage from seed to seedling to assess whether seed passage through frugivores' guts is adaptive in these environments. The possibility that the passage of seeds of different plant species through the guts of different birds leads to heterogeneity in germination characteristics, not only within plant populations but also within plant communities, certainly deserves further exploration.

## Acknowledgements

We are indebted to Javier Rodríguez for his assistance in the field and laboratory, to Ferràn Hierro for his help with the scanning electron microscope photographs, and to Beatriz Morales-Nin for letting us use her Optimas software. We are also grateful to Gene Schupp and an anonymous reviewer for their valuable comments on an earlier version of the manuscript. This work was supported by project DGICYT PB97-1174 financed to A.T.

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*Received 12 January 2001; revised 15 May 2001; accepted 24 May 2001*