

# Does ingestion by birds affect seed germination?

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**Abstract.** Fleshy fruits from 14 plant species were fed to bulbuls (*Pycnonotus xanthopygos*) and blackbirds (*Turdus merula*). Minimal retention times of seeds in the digestive systems were recorded. Ingested seeds were placed in soil to germinate and their germination rate compared to that of intact seeds, as well as to seeds artificially extracted from the fruit pulp. Only nine of the 14 species germinated. Freeing the seeds from the pulp had a variable effect on germination: in 14 out of 28 combinations seed germination was not affected by pulp removal, while in the other 14 cases germination increased significantly when seeds were extracted from the pulp.

Mostly, the bird species did not produce a specific effect on germination. However, seeds ingested by blackbirds usually showed substantially higher germination percentages than those ingested by bulbuls. This tendency can be partially explained by the longer retention times of seeds in digestive systems of blackbirds, compared with those for bulbuls, which might cause a stronger effect of seed coat abrasion and hence better germination.

Generally, seed ingestion had no consistent influence on germination. However, we suggest that a certain predictable tendency does exist concerning the response of seed germination of different species to bird ingestion: affected seeds were those which stayed longer in the birds' digestive systems, compared with unaffected ones. Presumably, abrasion of their seed coat increased permeability and consequently enhanced germination.

*Key-words:* Avian ingestion, fleshy fruits, mediterranean scrubland, perennial species, seed germination

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## Introduction

Bird dispersal is a process in which a frugivorous bird consumes the pulp and regurgitates or excretes all or some of the seeds unharmed (Ridley, 1930). It has been suggested that this process is advantageous as, among other effects, it enhances germination (Turcek, 1961; Van der Pijl, 1972). Removal of the seed from the pulp which contains germination inhibitors (Evenari, 1949), or the modification of the coat structure of the seeds (Agami & Waisel, 1988) are both considered as factors which may enhance germination. Nevertheless, when subjected to experimental analysis, enhancement has not always been confirmed (Lieberman *et al.*, 1979; Debussche, 1985; Lieberman & Lieberman, 1986) and in some cases seeds which had been left in intact fruits successfully germinated (Adams, 1927).

Despite the fact that species producing fleshy fruits represent a very prominent fraction of the vegetation in the mediterranean region (Zohary, 1962; Herrera, 1984), and most of the annual fruit crop is eaten by birds (Herrera, 1984; Izhaki & Safriel, 1985), only a few studies have been carried out on bird dispersal in this region. In this study we investigated the germination response of seeds which had passed through avian digestive tracts, comparing them with either intact seeds or seeds extracted from fleshy fruits in order to answer the following three questions:

- 1 Is the germination process of seeds released from the pulp different from that of the seeds left inside it?
- 2 Is the germination of seeds affected by previous ingestion?
- 3 Do birds produce a specific effect on germination?

## Materials and methods

### *The area under study*

Our field areas were two localities in the maquis of the mediterranean region of Israel: Mount Carmel (32° 47' N, 34° 58' E) and the Judean hills (centre approximately 31° 48' N, 35° 15' E). Mean annual rainfall at these areas is around 600–700 mm and occurs between November and April. Mean

annual temperature is 17°C, and that of the hottest month (August) and the coldest (January) are 27 and 11°C, respectively (Amiran *et al.*, 1985).

#### Plant and animal material

The collected fruits had been observed to be eaten by birds or were reported as the staple food of frugivorous birds in the study area by Izhaki & Safriel (1985). Ripe fruits of 14 species (Table 1) were collected mostly during the summer (July–September) and were offered to birds within 48 h after their collection. Two widespread and well-known frugivorous passerine species were offered the ripe fruits: Bulbul (*Pycnonotus xanthopygos* Linné, Pycnonotidae) and blackbird (*Turdus merula* Linné, Turdidae). In one test, robin (*Erithacus rubecula* Linné, Turdidae) was also included. Each individual bird was kept in a separate cage (100 × 30 × 50 cm) for at least 5 days prior to the experiment.

#### Experimental procedure

*Determination of minimal seed retention time.* Preliminary observations indicated that seeds of different species can be either defecated, regurgitated or excreted in both ways. In order to ascertain the minimal retention time of the seeds each bird was offered only 10 ripe fruits of one of the plant species, plus water *ad libitum*. The first appearance of the seeds, either by defecation or by regurgitation, was recorded. Fruits of each plant species were offered to four to seven birds (replicates) of each species. At the end of the experi-

ment, each bird was offered regular food plus water.

*Germination experiments.* On the day of feeding, each experimental bird was offered ripe fruits of only one species, plus water *ad libitum*. For simulating the fate of the ingested seeds in nature, faeces or regurgitated seeds from each bird were collected the following day and were allowed to dry in the shade for a few days. Fruits of each plant species were offered to at least four individuals (replicates) of each species.

In the mediterranean climate of Israel seeds germinate only during the rainy winter and spring (November–April). In the present study we tried to simulate the natural conditions that prevail in the mediterranean maquis under a favourable rainy winter. The dried faeces, dried ripe fruits and seeds that were extracted uneaten from the pulp were kept in small bags of plastic netting (2 × 2 cm). The bags were inserted into containers filled with dried soil, which, in turn, were kept in the dark at ambient temperature until November 1985. Then, when ambient temperatures and the day length approximated those in the natural habitat during winter and the rainy season started, seeds were set to germinate in soil.

Prior to sowing, the seeds had been rinsed under running water for 10 min. This simulated, to some extent, the rinsing of the seeds by the first rains, and was also necessary for the exact counting of the seeds. For the most part, 500 seeds from each treatment category were apportioned and sown into 10 pots of 12 cm diameter (i.e. 50 seeds per pot), and filled with a brown–red sandy soil. The

**Table 1.** List of the tested plant species, their family, life form and chorotype\*.

No.	Plant species	Family	Life form	Chorotype
1	<i>Arum hygrophilum</i>	Araceae	g	EM
2	<i>Asparagus aphyllus</i>	Liliaceae	c	M
3	<i>Ephedra campylopoda</i>	Ephedraceae	c	EM
4	<i>Morus nigra</i>	Moraceae	t	Far East (introduced)
5	<i>Morus alba</i>	Moraceae	t	Iran (introduced)
6	<i>Myrtus communis</i>	Myrtaceae	s	M
7	<i>Rhamnus alaternus</i>	Rhamnaceae	t	M
8	<i>Rhamnus palaestinus</i>	Rhamnaceae	s	M
9	<i>Rubia tenuifolia</i>	Rubiaceae	c	EM, IT
10	<i>Rubus sanctus</i>	Rosaceae	s	M, IT, ES
11	<i>Smilax aspera</i>	Liliaceae	c	M, Tr
12	<i>Tamus communis</i>	Dioscoreaceae	c	M, ES, IT
13	<i>Tamus orientalis</i>	Dioscoreaceae	c	EM
14	<i>Viscum cruciatum</i>	Loanthaceae	p	SM

\* According to Zohary, Feinbrun & Eig (1962) and Zohary (1973).

EM, east mediterranean; ES, euro-siberian; IT, irano-turanean; M, mediterranean; SM, south mediterranean; Tr, tropic; c, climber; g, geophyte; p, parasite; s, shrub; t, tree.

pots were covered with metal nets to exclude rodents. To provide conditions similar to those in mediterranean maquis, the pots were placed outdoors on shaded shelves and were watered with tap water, two to three times a week, in order to keep the soil continuously moist. Watering lasted from November to April, the same period as the naturally occurring rainy season.

Germination was recorded when cotyledons emerged, and seedlings were counted every 5 days. Recording continued until no more seedlings appeared for two consecutive observations (10 days). When watering was terminated, the pots were kept dry under the same ambient conditions until the autumn. In November 1986, the pots were rewatered and emergence of new seedlings were counted as outlined above.

The germination process of all the species listed in Table 1 was monitored. Each species was subjected to the following treatments which simulated the likely fate of the seed of a fleshy fruit. Only in two cases (*Morus nigra* L. and *Rubus sanctus* auct.) the treatment of intact fruits had not been carried out, as will be explained later:

**1** Intact fruits. Under natural conditions, a fruit that is not eaten may dry out and either remain on the plant or fall off. In the rainy season the dried pulp of fallen fruit is subjected to microbial activity. We simulated the latter by the sowing of dried intact fruits.

**2** Control seeds. Seeds deliberately extracted from the pulp were used as control, thus preventing the possibility of germination inhibitors and/or high osmotic microenvironment. This manipulation resembled ingestion only partly, because the seeds were merely freed from the pulp but did not actually pass through a bird's alimentary canal. A situation like this sometimes exists, as certain bird species (e.g. blackbirds) regurgitate some seeds.

**3** Seeds that passed through avian digestive tracts. Within bird intestines the seeds are subjected to morphological and/or chemical changes that may affect their ultimate germination. Since different bird species affect the seeds in transit in various ways, fruits of each species were offered separately to each of the bird species and seed germination, if any, was monitored.

*Data analysis.* Mean cumulative germination percentages ( $\bar{x} \pm SE$ );  $n = 10$  pots were calculated for each observation and plotted for each treatment and every tested species as a function of the number of days from the onset of the experiment. In order to compare the different curves obtained

for the tested plants, we determined the following for each pot:

**1** Days elapsed from sowing until emergence of the first seedling ( $G_0$ ). Determined either by reading the actual data, or by extrapolating from the line connecting the first day on which emergence of seedlings was noticed with the previous observation.

**2** Per cent of total cumulative germination ( $\%G_t$ ). Determined from the actual data, derived from the final observation.

**3** Days for sowing until 50% of total germination ( $G_{50}$ ). Determined by the actual data or by extrapolating from the line connecting the two observations in which germination was respectively higher and lower than 50%.

**4** Duration of germination, i.e. the interval between emergence of the first and last seedlings ( $G_t$ ). Determined by calculating the number of elapsed days between  $G_0$  and the last day on which seedlings appeared.

The significance of the differences among the treatments for each parameter was evaluated by a one-way analysis of variance (ANOVA). Data on the  $\%G_t$  parameter were first transformed using an angular transformation.

The three listed treatments were not applied to all the plant species. In *Rubus sanctus* and *Morus nigra*, the pulp of the intact dry fruits crumbled, so that there was no real difference between seeds within or outside the pulp. If there was no evidence that a tested bird species consumed the fruits of a particular plant species in the wild, fruits were not offered to the tested bird in captivity. Contrariwise, according to our field observations we also included robins in the case of *Asparagus aphyllus* L.

## Results

### *Minimal retention times of seeds in the birds' digestive systems*

As described above, seeds are excreted either by defecation or by regurgitation. Generally, in species whose seeds had been both defecated and regurgitated, no significant difference had previously been found between retention times (A. Barnea, Y. Yom-Tov & J. Friedman, unpublished observations). Therefore, for each species, an overall minimal retention time was calculated, regardless of the way of excretion. The results and a comparison of the differences in seed retention times in digestive systems of bulbuls and blackbirds are presented in Table 2.

**Table 2.** Retention times ( $\bar{x} \pm \text{SE}$ ) of seeds in digestive system of bulbuls and blackbirds and the significance of the differences between them.

Plant species	Retention time (min) ( $\bar{x} \pm \text{SE}$ ) of seeds in:		Significance
	Bulbuls	Blackbirds	
<i>Arum hygrophilum</i>	—	30.7 $\pm$ 29.28 (r;3)	—
<i>Asparagus aphyllus</i>	20 (d;1)	13.0 $\pm$ 5.66 (d+r;4)	NS
<i>Ephedra campylopoda</i>	12.0 $\pm$ 3.92 (d;4)	16.5 $\pm$ 4.93 (d+r;4)	NS
<i>Morus nigra</i>	16.4 $\pm$ 13.06 (d;8)	44.4 $\pm$ 29.10 (d;5)	*
<i>Myrtus communis</i>	27.3 $\pm$ 28.05 (d;4)	30.9 $\pm$ 17.65 (d+r;7)	NS
<i>Rhamnus alaternus</i>	17.1 $\pm$ 4.26 (d;8)	20.5 $\pm$ 6.59 (d+r;8)	NS
<i>Rhamnus palaestinus</i>	32.8 $\pm$ 9.09 (d;5)	40.7 $\pm$ 23.31 (d+r;6)	NS
<i>Rubia tenuifolia</i>	16.5 $\pm$ 5.86 (d;6)	15.0 $\pm$ 11.99 (r;7)	NS
<i>Rubus sanctus</i>	13.5 $\pm$ 10.61 (d;2)	20.8 $\pm$ 7.09 (d;4)	NS
<i>Smilax aspera</i>	21.0 $\pm$ 16.33 (d+r;5)	16.2 $\pm$ 12.99 (r;5)	NS
<i>Tamus communis</i>	8.7 $\pm$ 3.21 (d;3)	17.9 $\pm$ 5.70 (r;7)	*
<i>Viscum cruciatum</i>	20.8 $\pm$ 11.08 (d;5)	73.7 $\pm$ 49.14 (d;3)	*

\* Significant at  $P < 0.05$ ; NS, not significant; n, no of replicas; r, regurgitation; d, defecation.

#### Seeds germination

Of 14 plants tested, eight species (*Morus nigra*, *Arum hygrophilum* Boiss., *Rubia tenuifolia* D'urv., *Rhamnus palaestinus* Boiss., *Rhamnus alaternus* L., *Rubus sanctus*, *Myrtus communis* L. and *Ephreda campylopoda* C.A. Mey.) germinated during the first winter (1985). One, *Asparagus aphyllus*, germinated during the second winter (1986), and another, *Smilax aspera* L., only during the third winter (1987). In the latter species, an unknown number of seeds were eaten or damaged by rodents so these data are missing. The remaining species, *Tamus orientalis* Thiebaut, *Tamus communis* L., *Viscum cruciatum* Sieb. ex. Boiss. and *Morus alba* L., either did not germinate at all, or less than 5% of their seeds did so, and therefore, these data are also missing.

**Germination of uningested seeds.** Seeds of *Rhamnus alaternus* in intact fruits did not germinate at all, whereas control seeds liberated from their fruits germinated readily (average  $G_{50}$  was 52.0 days  $\pm$  4.0, see Table 3). An opposite response was demonstrated by *Rhamnus palaestinus*: when the pulp was removed, the germination of seeds was significantly inhibited in comparison with that of

seeds in intact fruits (26.5%  $\pm$  2.7 and 52.1%  $\pm$  7.4, respectively; Table 3).

Excluding *Rhamnus alaternus*, out of the 28 combinations of tested parameters  $\times$  plant species, 14 were not affected when the pulp was removed. The other 14 were affected and seed germination of intact fruits was significantly lower than that of control seeds extracted from the pulp.

**Germination of ingested seeds.** Out of the 34 combinations of tested parameters  $\times$  plant species, 16 were not affected by bird ingestion. The other 18 were affected, and seed germination of ingested seeds was in most cases significantly improved compared with that of uningested control seeds.

However, when each species is examined separately, it can be seen that in *Arum hygrophilum*, *Myrtus communis*, *Rubus sanctus*, *Rhamnus palaestinus*, *Rhamnus alaternus* and *Morus nigra* all, or three out of the four studied germination parameters were significantly ( $P < 0.05$ ) affected, mostly positively, by the passage through bird intestines, compared to seeds that were liberated from their pulp but had not passed through the avian alimentary canal. In the remaining species

**Table 3.** Germination data (mean  $\pm$  SE) for seeds of intact fruits (IF), control seeds (deliberately extracted from the pulp), and ingested seeds (IS) of nine species of mediterranean maquis in Israel.

Life form	Plant species	Parameter											
		Total germination percentages (%G <sub>0</sub> )			Days until onset of germination (G <sub>0</sub> )			Duration of germination (G <sub>1</sub> )			Days until 50% of total germination (G <sub>50</sub> )		
		IF	Control	IS	IF	IS	Control	IF	IS	Control	IF	IS	
Geophyte	<i>Anem hydropichilum</i>	71.8 $\pm$ 6.8 NS	85.4 $\pm$ 1.9 NS	87.4 $\pm$ 3.4 NS	31.9 $\pm$ 1.2 NS	29.3 $\pm$ 0.4 *	33.5 $\pm$ 1.2 NS	34.3 $\pm$ 2.7 NS	36.5 $\pm$ 3.2 *	51.1 $\pm$ 4.4 NS	40.4 $\pm$ 1.3 NS	38.9 $\pm$ 1.5 *	45.8 $\pm$ 1.5
Climber	<i>Asparagus aphyllus</i>	76.0 $\pm$ 5.6 NS	73.8 $\pm$ 6.5 NS	74.1 $\pm$ 5.1 NS	43.3 $\pm$ 2.8 NS	39.0 $\pm$ 2.4 NS	44.7 $\pm$ 0.8 NS	45.5 $\pm$ 3.4 NS	54.8 $\pm$ 2.1 NS	46.6 $\pm$ 2.4 NS	58.3 $\pm$ 3.8 NS	53.0 $\pm$ 0.9 NS	54.9 $\pm$ 1.3
Climber	<i>Epiphecta campylopoda</i>	36.0 $\pm$ 7.1 *	73.6 $\pm$ 4.3 NS	80.8 $\pm$ 1.4 NS	12.3 $\pm$ 0.8 *	2.0 $\pm$ 0.3 NS	1.0 $\pm$ 0.0 NS	28.3 $\pm$ 4.4 NS	29.4 $\pm$ 1.8 NS	29.4 $\pm$ 1.7 NS	15.5 $\pm$ 5.3 NS	14.7 $\pm$ 1.0 NS	12.1 $\pm$ 0.4
Climber	<i>Rubia tenuifolia</i>	24.8 $\pm$ 0.2 *	63.7 $\pm$ 0.3 NS	56.8 $\pm$ 4.3 NS	54.0 $\pm$ 3.0 NS	48.4 $\pm$ 2.0 *	41.4 $\pm$ 1.5 NS	58.0 $\pm$ 2.6 NS	62.2 $\pm$ 5.4 NS	57.1 $\pm$ 3.1 NS	77.4 $\pm$ 3.4 *	64.6 $\pm$ 1.8 NS	61.8 $\pm$ 1.8
Shrub	<i>Myrtus communis</i>	23.3 $\pm$ 6.2 *	56.3 $\pm$ 6.8 NS	59.4 $\pm$ 3.5 NS	62.3 $\pm$ 3.8 *	58.6 $\pm$ 2.2 *	42.5 $\pm$ 2.1 NS	23.3 $\pm$ 3.8 *	38.9 $\pm$ 2.8 *	53.5 $\pm$ 2.2 NS	77.3 $\pm$ 1.4 NS	73.4 $\pm$ 1.6 *	60.0 $\pm$ 1.9
Shrub	<i>Rubus sanctus</i>		62.6 $\pm$ 2.4 *	51.8 $\pm$ 1.9 NS		54.0 $\pm$ 1.8 NS	47.0 $\pm$ 2.7 NS		61.5 $\pm$ 1.4 *	60.7 $\pm$ 2.9 NS		80.2 $\pm$ 1.4 *	69.1 $\pm$ 2.9
Shrub	<i>Rhamnus palaestinus</i>		52.1 $\pm$ 7.4 *	26.5 $\pm$ 2.7 *	60.1 $\pm$ 3.7 NS	22.9 $\pm$ 1.6 NS	21.1 $\pm$ 0.7 NS	54.6 $\pm$ 5.6 NS	65.0 $\pm$ 5.0 *	26.9 $\pm$ 1.2 NS	38.1 $\pm$ 1.0 *	47.3 $\pm$ 3.4 *	28.5 $\pm$ 0.6
Tree	<i>Rhamnus alaternus</i>		0.0 $\pm$ 0.0 *	20.6 $\pm$ 3.1 *	39.6 $\pm$ 4.5 NS	0.0 $\pm$ 0.0 *	18.1 $\pm$ 1.4 NS	0.0 $\pm$ 0.0 *	59.6 $\pm$ 7.5 NS	60.5 $\pm$ 3.8 NS	0.0 $\pm$ 0.0 *	52.0 $\pm$ 4.0 *	32.1 $\pm$ 1.6
Tree	<i>Morus nigra</i>		2.0 $\pm$ 0.0 *	33.9 $\pm$ 3.4 NS		18.3 $\pm$ 5.8 *	10.2 $\pm$ 1.5 NS		(a)	48.3 $\pm$ 2.9 NS		(a)	29.3 $\pm$ 1.1

NS, not significant; \* significant at  $P < 0.05$  by one-way analysis of variance test (ANOVA).

(a) In control seeds of *Morus nigra* total germination percentage reached only 2%, so evaluation of G<sub>1</sub> and G<sub>0</sub> in this case was impossible.

(*Asparagus aphyllum*, *Ephedra campylopoda* and *Rubia tenuifolia*) passage through bird intestines exerted no, or only minimal, effect (Table 3).

*The effect of bird species on seed germination.* In most cases (28 out of 32), passage of the seeds through the intestines of blackbird, bulbul or robin yielded no significant difference insofar as the various germination parameters were concerned (Table 4). However, in the remaining four cases ingestion by blackbirds significantly enhanced the germination process, compared with bulbuls.

## Discussion

In the mediterranean region, birds play an important role in seed dispersal since they consume a major part of the fleshy fruit crop (Herrera, 1984; Izhaki & Safriel, 1985). The remaining fruits, and also some that are dropped by feeding birds, fall underneath the parent plant. Hence, the seed of a fleshy fruit can begin germination either within the pulp or, if ingested by a bird, outside it.

It is sometimes assumed that when the pulp is digested by a frugivore, the seed is freed from high osmotic pressures and germination inhibitors (Mayer & Poljakoff-Mayber, 1982; Janzen, 1983; Debussche, 1985). However, our results show that this is true only in some cases, and generally, the act of freeing the seed from the pulp has a variable effect on germination of seeds of different species (Table 3).

Out of the seven tested species, seeds of two (*Asparagus aphyllus* and *Arum hygrophilum*) showed no significant difference in germination between the intact fruits and control seeds. In two other species (*Ephedra campylopoda* and *Rubia tenuifolia*) only two ( $%G_t$  and  $G_0$ ;  $%G_t$  and  $G_{50}$ , respectively) showed an improvement of germination when the pulp was removed. Nevertheless, in two other species (*Myrtus communis* and *Rhamnus alaternus*), removal of the pulp did cause a significant enhancement of the germination process, compared with seeds in intact fruits. In *Myrtus communis* there was a significant difference in the values of three out of four parameters between the two types of seeds. The latter, *Rhamnus alaternus* showed the most extreme possible response as seeds in intact fruits did not germinate at all; only seeds which were released from their pulp germinated. To these contrasting responses one should also add the seventh species *Rhamnus palaestinus*. This species was the only one in which germination was significantly inhibited when the pulp was

removed, compared with that of seeds in intact fruits.

Therefore, the general conclusion is that the act of freeing the seeds from the pulp does not have a uniform and consistent impact on different species. Some of the tested species were not affected by the process whilst others were, although in different ways.

Mostly, the species of the disperser did not have a significant effect on germination success of the ingested seeds (Table 4). However, seeds which were ingested by blackbirds usually showed substantially higher final germination percentages than those ingested by bulbuls. In four cases ( $G_t$  in *Rubus sanctus*,  $%G_t$  and  $G_0$  in *Rhamnus alaternus* and  $%G_t$  in *Morus nigra*) this tendency was found to be significant.

This differential effect might be explained by the differences in minimal retention times in digestive systems of the two tested bird species, as shown in Table 2. Even though most values do not differ significantly, retention times in digestive systems of bulbuls tend to be shorter than those for blackbirds. Therefore, it might be assumed that longer retention times cause a stronger reduction of seed coat, and hence better germination.

However, results of another experiment suggest that retention time is probably not the only factor involved: seeds of *Solanum luteum* which were ingested by blackbirds also yielded higher germination percentages in comparison with seeds ingested by bulbuls, although retention times of these seeds in the digestive systems of the two bird species did not differ significantly (Barnea, Yom-Tov & Friedman, 1990).

When discussing the effects of birds as a group, the results show that even though most of the studied plant species grow in the same habitat, their seeds respond differently to ingestion by birds. Out of the 34 combinations of ingested seeds (for the nine species and four tested parameters), values of 18 were significantly different (showing either enhancement or suppression of the germination process) when compared with the adequate values of the control uningested seeds. The remaining 16 combinations showed no significant difference between the two types of seeds, proving that, generally, seed ingestion by birds has no clear and consistent influence on the germination process.

There are few studies in which germination of ingested seeds has been compared with that of fresh, uningested ones. Moreover, in these few studies the seeds had been sown in petri dishes rather than in soil. We performed preliminary

**Table 4.** Data on the tested germination parameters (mean  $\pm$  SE) for seeds ingested by robins, blackbirds and bulbuls.

Plant species	Parameter															
	Total germination percentages (%G <sub>t</sub> )				Days until onset of germination (G <sub>0</sub> )				Duration of germination (G <sub>i</sub> )				Days until 50% of total germination (G <sub>50</sub> )			
	Ingestion by:		Ingestion by:		Ingestion by:		Ingestion by:		Ingestion by:		Ingestion by:		Ingestion by:			
	Robins	Blackbirds	Bulbuls	Robins	Blackbirds	Bulbuls	Robins	Blackbirds	Bulbuls	Robins	Blackbirds	Bulbuls	Robins	Blackbirds	Bulbuls	
<i>Asparagus ophyllus</i>	77.4 $\pm$ 11.9	NS	72.2 $\pm$ 5.0	45.0 $\pm$ 1.4	NS	44.5 $\pm$ 1.1	47.2 $\pm$ 4.0	NS	46.3 $\pm$ 3.1	56.0 $\pm$ 3.0	NS	54.3 $\pm$ 1.2				
<i>Ephedra campylopoda</i>																
<i>Rubia tenuifolia</i>																
<i>Myrtus communis</i>																
<i>Rubus sanctus</i>																
<i>Rhamnus palaestinus</i>																
<i>Rhamnus alaternus</i>																
<i>Morus nigra</i>																

NS, not significant; \* significant at  $P < 0.01$  by one-way analysis of variance test (ANOVA).*Arum hygrophilum* is not included as we used only seeds removed from faeces of blackbirds for this species.

experiments for comparison of germination process of seeds of perennials in soil and in petri dishes. Germination success in the soil was significantly higher than that obtained in petri dishes (A. Barnea, Y. Yom-Tov & J. Friedman, unpublished observations), unlike the results of similar experiments carried out on seeds of annuals (Barnea *et al.*, 1990). Yet, to the extent that germination in petri dishes reflects ecological reality, the investigation by Debussche (1985), carried out in the French mediterranean region, concurs with our results: Debussche examined the effect of bird ingestion on seed germination of three species (*Asparagus acutifolius*, *Hedera helix* and *Pyracantha coccinea*). He concluded that the process of ingestion does not affect germination.

Two other studies had been carried out in tropical Ghana: Lieberman *et al.* (1979) found that ingestion by baboons improved germination in three out of four species tested. Lieberman & Lieberman (1986) also examined germination of seeds of 16 species following ingestion by birds, bats or primates, and found a wide range of responses to bird ingestion.

We suggest, however, that a certain predictable tendency does exist concerning the response of seed germination of different species to bird ingestion, except that this tendency is not the same for all species. If the results which are given in Table 3 are examined separately for each plant species, the nine tested species can be divided into two categories:

1 Species in which at least three out of four parameters were unaffected by ingestion – *Asparagus aphyllus*, *Ephedra campylopoda* and *Rubia tenuifolia*.

2 Species in which at least three out of four parameters were significantly affected by ingestion – *Arum hygrophilum*, *Myrtus communis*, *Rubus sanctus*, *Rhamnus palaestinus*, *Rhamnus alaternus* and *Morus nigra*.

As already discussed above, different retention times might be the cause of differential germination. And indeed, a comparison of mean retention times of the seeds of the three species which were unaffected by ingestion with those of which germination was enhanced (see Table 2) shows that the former were excreted earlier than the latter (Mann-Whitney *U*-test,  $U_{S(11,6)} = 58$ ;  $P < 0.01$ ). Presumably abrasion of the seed coat occurred only in seeds which stayed longer in the digestive systems. This abrasion probably increased seed coat permeability and consequently enhanced germination. Scanning electron micrographs of

ingested and uningested seeds of all the nine tested species support this hypothesis. These micrographs show that seed coat sculpture of seeds of all the affected species was abraded compared to the control, uningested seeds (A. Barnea, Y. Yom-Tov & J. Friedman, unpublished observations). A similar response was also found in seeds of the annual *Solanum luteum* (Barnea *et al.*, 1990). As a result, for some plant species, the only role of birds is probably in seed dispersal, but for others, birds serve both as seed dispersers and germination mediators. Needless to say, this hypothesis requires confirmation on a larger number of plant species.

Another ecological implication, evident from Table 3, is that there are two differences between east-mediterranean species and ones of more temperate origin (*Morus nigra*, being an adventive plant in Israel, is excluded from consideration here), namely the former species start germinating earlier and show a faster germination than do the latter. We found significantly ( $P < 0.05$ ) lower values of the  $G_0$  (number of days till onset of germination) in control seeds of the east-mediterranean *Ephedra campylopoda*, *Rhamnus palaestinus* and *Arum hygrophilum*, than in control seeds of the more temperate *Rhamnus alaternus*, *Asparagus aphyllus*, *Rubia tenuifolia*, *Rubus sanctus* and *Myrtus communis*. Presumably species which penetrate semi-arid areas (as *Ephedra campylopoda* and *Rhamnus palaestinus* do) should profit from early and fast germination. In contrast, in areas with a predictably continuous rainy season during the winter, suitable conditions for germination last longer and therefore early and fast germination is not so crucial. This is especially evident for *Rubus sanctus* and *Myrtus communis*, which present high  $G_0$  and  $G_{50}$  values and often grow near streams where there is less chance of desiccation.

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