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The effect of bat (Rousettus aegyptiacus) dispersal on seed germination in eastern Mediterranean habitats

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Abstract The fruit-bat Rousettus aegyptiacus (Pteropodidae) in Israel consumes a variety of cultivated and wild fruits. The aim of this study was to explore some of its qualities as a dispersal agent for six fruit-bearing plant species. The feeding roosts of the fruit-bat are located an average of 30 m from its feeding trees and thus the bats disperse the seeds away from the shade of the parent canopy. The bat spits out large seeds but may pass some (2%) of the small seeds (<4 mm) through its digestive tract. However, neither the deposited seeds nor the ejected seeds (except in one case) had a significantly higher percentage germinating than intact seeds. Although the fruit-bat did not increase the percentage germinating, seeds of three plant species subject to different feeding behaviors (deposited in feces or spat out as ejecta) had a different temporal pattern of germination from the intact seeds. The combined seed germination distribution generated by these different treatments is more even over time than for each treatment alone. It is suggested that this increases asynchronous germination and therefore enhances plant fitness by spreading the risks encountered during germination, especially in eastern Mediterranean habitats where the pattern of rainfall is unpredictable.

Key words Frugivory · Seed dispersal · Rousettus aegyptiacus · Germination · East Mediterranean

Introduction

Bats have long been known as important seed dispersal agents, especially the phyllostomids of the New World (Vazquez-Yunes et al. 1975; August 1981; Fleming 1981; Heithaus 1982; Estrada et al. 1984; Dinerstein 1986; Marinho-Filho 1991). Despite the far longer history of frugivory in pteropodids of the Old World, little is known of their role in seed dispersal and seedling recruitment (Howe 1986).

The efficiency of an animal as a successful dispersal agent depends on many attributes, such as its ability to remove a large portion of the crop at the appropriate time or its ability to move seeds away from parent trees to a suitable new microhabitat. This study focuses on the effect of the feeding behavior of the fruit-bat Rousettus aegyptiacus on the probability of seeds being removed from the parent tree and germinating in semi-arid microhabitats of the eastern Mediterranean.

Several studies in the tropics (Morrison 1978; Fleming and Heithaus 1981; Charles-Dominique 1986) indicated that two types of fruits are eaten by bats: (1) fruits containing many very small seeds, which are swallowed and pass through the digestive tract and (2) fruits containing a relatively large seed, which are dropped at some distance from the tree after the pulp has been removed. However, the bat may treat a small-seeded fruit species in both ways, either passing the seeds through the digestive tract or spitting them out as compact fibrous pellets. To our knowledge, only two studies have analyzed the effect of these different feeding behaviors on seed dispersal and germination in pteropodid bats (Thomas 1982; Uzurrum and Heideman 1991).

The effect of the dispersal agent upon seed germination may include two components. The first is the total germination percentage, which sometimes depends on the length of the study period and is usually compared to seeds which were not treated by animals. In this context it should be mentioned that selection should not always favor prompt high germination (Janzen 1981, 1984). The second component is the temporal distribution of germination. In an unpredictable environment, selection probably favors asynchronous germination which spreads mortality risk over a longer time (Harper 1977; Ng 1978). The length of seed dormancy and the temporal pattern of germination vary among different species and individuals of avian dispersers, probably due to different mechanical and chemical treatments of seeds in their guts.

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(Izhaki and Safran 1990). Therefore, it is expected that the different feeding behaviors of bats will result in different patterns of seed germination as well. Moreover, intraspecific differences in the digestion process among individuals may also affect the pattern of seed germination.

The fruit-bat Rousettus aegyptiacus (body mass: 140-160 g) is widely distributed in tropical and subtropical regions of Africa and Asia; its northernmost distribution reaches southern Turkey (see review by Kuitzner 1979). It is the only frugivorous bat in Israel. This bat consumes a variety of wild and cultivated fruits such as Ficus retusa, F. sycomorus, Melia azedarach, Phoenix dactylifera, dates, mango and banana (Kuitzner 1979) and therefore is a potential seed disperser. However, our knowledge regarding its actual role as dispersal agent is still very limited. Its role as dispersal agent is especially interesting since we have a unique situation where a tropical old-world fruit-bat serves as seed disperser in an eastern Mediterranean ecosystem.

To investigate the potential role of the fruit-bat in seed dispersal of several plant species in eastern Mediterranean habitats, we performed a series of field observations and experiments. Specifically, we had six objectives: (1) to compare characteristics of fruits whose seeds were passed through the digestive tract with those that were spat out; (2) to determine the proportion of seeds that were spat out with those that passed through the digestive tract; (3) to determine the distances of feeding roots from feeding trees; (4) to compare percentage germination of seeds that were subject to three feeding-behavioral treatments: passed through the digestive tract (feces), ejected in pellets, and intact; (5) to compare percentage germination of seeds eaten by different individual bats; and (6) to compare the temporal patterns of seed germination among different treatments (feces, pellets, and control).

Methods

Germination experiments

Ripe fruits from six species of plants (carob, Ceratonia siliqua L.; loquat, Eriobotrya japonica; fig, Ficus carica L.; mulberry, Morus nigra, which are naturally consumed by bats in Israel, and arbutus, Arbutus andrachne L. and jujube, Ziziphus spinosa-christi (L.) Desf., for which we have no record of consumption by bats in the wild) were collected for the experiments. The freshly collected fruits were fed to six bats caged individually except in two cases (Z. spinosa-christi and A. andrachne) in which the bats were fed in groups of six individuals. Each individual or group was fed ad lib before sunset for 6 days and the remains were collected every morning. The remains were divided into feces and pellets (ejecta). Seeds removed from feces and pellets and from un eaten fruits (controls) were placed on damp filter paper in sterile petri dishes in the shade and checked every 3 days for germination until 2 weeks after the last germinated seed was observed. In each observation the number of germinated and ungerminated seeds was recorded for each dish. Emerging seedlings were immediately removed to reduce their effect on the remaining, ungerminated seeds. Germination was defined as the emergence of any seedling part from the seed. Length of dormancy was defined as the time (days) from sowing until germination.

In order to assess the number of seeds which passed through the digestive tract, we estimated the number of seeds in the mulberry fruits given to the bats (Table 1), we counted the number of seeds in 20 pellets that were dropped and estimated it for all the pellets, and counted the seeds in the feces of each bat.

Field observations

The distance (m) between the feeding tree and feeding roost was determined by direct observations (3-5 days for 2-3 h per night) beginning from the arrival of the first bat with binoculars on flights of bats. One of the feeding roosts was a cave which contained seeds of C. siliqua and M. azedarach. We could not determine the trees from which the bats picked the fruits and flew to the cave. Instead, we mapped all the trees near the cave and calculated the average distance from the trees to the cave.

Scanning electron microscope

Dry seed coats of six randomly selected seeds from feces, pellets, and controls of A. andrachne and dry seed coats from pellets and control of C. siliqua were examined with a scanning electron microscope (Jeol, JSM-T300). The seeds were gold-coated in a vacuum (Polaron SEM coating system), photographed and compared.

Data analysis

Mean percentage of germination was calculated for each plant species, treatment (control, feces and pellets) and individual (when the experiment was performed on each individual separately). In the two cases where the experiments were carried out in groups, the average was calculated per group. In both cases, each day of each experiment was treated as a replicate. One-way analysis of variance (ANOVA) was used to test differences in percentage germination among individuals and between treatments in each plant species. All proportions were arcsin-square-root transformed before analysis.

In order to reveal differences among temporal distributions of seed germination which were treated differently (feces, pellets and control), we used a simple linear, rank non-parametric analysis. We used the Kolinogorov-Smirnov two-sample test to examine whether the length of dormancy of the seeds from two different treatments (pellets and control) was from populations with the same distribution. This test is sensitive to differences such as dispersion, skewness, etc. in the compared distributions (Siegel and Castellan 1988). When we had seeds from three different treatments (pellets, feces, and control), we used the Kruskal-Wallis one-way ANOVA of ranks. This technique tests whether the three samples come from the same population or from identical populations with the same median (Siegel and Castellan 1988). Differences were significant when P < 0.05.

The cumulative percentage of germination was calculated and drawn in order to demonstrate the different germination patterns between treatments. The quantitative evaluation of seed germination was based on additional two parameters: germination rate (GR) and germination start (GS). Germination rate was calculated by the equation: GR = (d/P)/(T1-T0), where P is the final germination percentage, T0 is the time interval (days) between sowing and emergence of 1/60P of the seedlings, and T1 is time interval (days) between sowing and emergence of 4/60P of seedlings. Germination start (GS) was defined as the time interval (days) between sowing and emergence of 1/60P of the seedlings.

Results

Seed classification according to feeding behavior

The seeds of three of the six species of the C. siliqua, E. japonica, and Z. spinosa-christi) were always ejected while some of the seeds of the other species (F. carica, M.
Table 1 Comparison of several fruit and seed characteristics between fruits whose seeds have only been ejected by the fruit bat and those whose seeds may either be defecated or ejected. Data are presented as means±SD (in parentheses)

<table>
<thead>
<tr>
<th></th>
<th>Ceratonia</th>
<th>Eriobotrya</th>
<th>Ziziphus</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>(n=22)</td>
<td>(n=22)</td>
<td>(n=20)</td>
</tr>
<tr>
<td>Fruit wet mass (g)</td>
<td>12.1 ± 3.6</td>
<td>32.3 ± 6.6</td>
<td>1.2 ± 0.2</td>
</tr>
<tr>
<td>Seed wet mass (mg)</td>
<td>192 (11)</td>
<td>2175 (781)</td>
<td>594 (99)</td>
</tr>
<tr>
<td>No. seeds per fruit</td>
<td>8.3 ± 2.9</td>
<td>3.1 ± 1.7</td>
<td>1.0 ± 0.6</td>
</tr>
<tr>
<td>Seed wet mass/pulp wet mass</td>
<td>0.15 (0.02)</td>
<td>0.22 (0.08)</td>
<td>0.93 (0.12)</td>
</tr>
</tbody>
</table>

Different significances among treatments (P<0.05, using Duncan test) are indicated by different letters: a>b>...>d.

* One-way ANOVA among the six fruit species; *** P<0.001. Significantly different among the six fruit species (P<0.05, using Duncan test) are indicated by the superscripts a-d: a>b>c>d.

![Germination Graph](image)

**Fig. 1** Percent seed germination during the study period. The origins of the seeds were from intact fruits (control, lightly spotted), pellets (ejecta, heavily spotted) and defecations (feeces, open bars). Significantly different percentages among treatments (P<0.05, using Duncan test on arcsin √proportion) are indicated by different letters: A>B.

**Arbutus** Fiq. Mulberry Carica Loguat Jujube

nigra and A. andrachne) passed through the digestive tract and appeared in the feces. These two categories of fruits are significantly different in several morphological attributes (Table 1). Fruits whose seeds were always ejected had much heavier seeds, had only a few seeds per fruit, and had a relatively lower ratio of seed wet mass/pulp wet mass than the other group (Table 1). However, fruit wet mass did not differ between these two groups.

Six bats which were fed *M. nigra* ejected many more seeds (5386 ± 212, SD) than they dropped in their feces (87 ± 11 per night). Thus, more than 98% of the consumed seeds were not passed through the digestive tract.

**Germination percentage**

**Comparison among treatments**

In most cases there were no significant differences in percent germination among different treatments (Fig. 1).

However, germination percentage of *E. japonica* seeds that were ejected was higher than that of intact ones. Although germination percentages of seeds in feces were usually higher than those of intact ones, the differences were not significant (Fig. 1).

**Intraspecific comparisons**

Different germination percentages of seeds that had been ejected by different individuals were observed only in the case of *C. siliqua* (Kruskall-Wallis one-way ANOVA, df = 5, P<0.04). No other significant differences among conspecific individuals in germination percentages were found in any other plant-treatment combination.

**Temporal distribution of germination among treatments**

*Plants whose seeds were only ejected*

Germination in *E. japonica* and *C. siliqua* occurred over 4 weeks (Fig. 2a) while germination in *Z. spina-christi* lasted 8 weeks. In *E. japonica*, the germination distribution for seeds which were spat out in pellets was different from that of the control (Kolmogorov-Smirnov two-sample test, P<0.001). The germination of the control seeds was skewed to the right (skewness = 0.37) while the germination of seeds from pellets was slightly skewed to the left (skewness = -0.09). The mode of the control seeds was much lower than that of the seeds from the pellets (13 vs. 25 days, respectively). Germination start of control seeds preceded the ejecta seeds by 3 days (Table 2). Different patterns of accumulative seed germination (Fig. 2a) were detected for this species although the average rate of germination was similar (Table 2).

In *C. siliqua*, no difference was found between the germination distributions of ejected and control seeds (Kolmogorov-Smirnov two-sample test, P>0.05). Both were strongly skewed to the right (skewness = 1.02, 1.21, respectively). Although similar patterns of accumulative seed germination (Fig. 2b), and similar germina-
Seed germination patterns in *Z. spin-a-christi* were bimodal in both the ejected and the control seeds. The two distributions were similar (Kolmogorov-Smirnov two-sample test, *P* > 0.05). The accumulative seed germination pattern was also similar between ejecta and control seeds (Fig. 2c). Germination rate was double in ejecta seeds (Table 2).

Plants whose seeds were ejected and defecated

Germination in *Morus* occurred in 2 weeks in all treatments, while *F. carica* seeds germinated over 6 weeks and *A. andrachne* seeds germinated over 8 weeks (Fig. 3). While the germination distribution of the control seeds of *M. nigra* was skewed to the right (skewness = 0.75), the germination patterns of the ejected and defecated seeds were bimodal. Germination distributions of seeds from these three treatments differed significantly (Kruskal-Wallis, *P* < 0.05). The patterns of accumulative seed germination were different among the three treatments (Fig. 3a) and significant differences between germination starts of ejecta seeds versus the feces and control seeds were also observed (Table 2).

Distribution patterns of germination of seeds of all treatments in *F. carica* were strongly skewed to the right, had the same mode (13 days) and the differences between them were not significant (Kolmogorov-Smirnov test, *P* > 0.05). The patterns of accumulative seed germination were similar (Fig. 3b) as well as the germination starts (Table 2).

While the germination patterns of the *A. andrachne* control and ejected seeds were skewed to the right (skewness = 0.66, mode = 25 for both), the germination distribution of the defecated seeds was skewed to the left (skewness = -0.27, mode = 40). The pattern of the accumulative seed germination of ejecta was different from that in the other two treatments (Fig. 3c). The start of germination of seeds of feces was later than in the other two treatments, and the germination rate was quite similar among all treatments (Table 2).

Table 2 The average germination start (GS, time interval in days) between sowing and emergence of 1/6x(total seed germination) and germination (GR, % of germination per day). See Methods for more details.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Treatment</th>
<th>Ejecta</th>
<th></th>
<th></th>
<th>Feces</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Control</th>
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<tbody>
<tr>
<td></td>
<td>GS (d)</td>
<td>GR (%/d)</td>
<td>GS (d)</td>
<td>GR (%/d)</td>
<td>GS (d)</td>
<td>GR (%/d)</td>
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<tr>
<td><em>E. japonica</em></td>
<td>13</td>
<td>5.0</td>
<td></td>
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<tr>
<td><em>C. siliqua</em></td>
<td>9</td>
<td>8.7</td>
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<td><em>Z. spin-a-christi</em></td>
<td>57</td>
<td>0.5</td>
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<td><em>M. nigra</em></td>
<td>7</td>
<td>0.5</td>
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<tr>
<td><em>F. carica</em></td>
<td>11</td>
<td>5.0</td>
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<tr>
<td><em>A. andrachne</em></td>
<td>17</td>
<td>1.6</td>
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<td>10</td>
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<td>6</td>
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<td>16</td>
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</table>
Distance between the feeding tree and the feeding roost

This range indicates the average straight-line distance that a bat commutes between its feeding tree and its feeding roost. The feeding roosts of bats that fed on these trees were pine trees (*Pinus halepensis*), one *Casuarina torulosa*, and a cave (Table 3). The average distance from a feeding tree to another tree as a feeding roost was <30 m while the average distance to the cave as a feeding roost was 400 m (Table 3, $t_3 = 7.86, P<0.01$).

The effect of ingestion and ejection on the sculpture of seed coats

There were differences in seed coats among ingested, ejected and control seeds of *A. andrachne* (Fig. 4c–e). The coat of the control and ejected seeds had several holes and the cell wall is evident (Fig. 4c,d), whereas the coat of ingested seeds (Fig. 4e) had many holes and the cell wall was destroyed. In the case of *C. siligua* (Fig. 4a,b), the cell wall and the waxy substance which fills the cells of the control seed (Fig. 4a) is clear, whereas in the control ejected seeds (Fig. 4b), the cell wall is smoother.

**Discussion**

Feeding behavior of *R. aegyptiacus*

The behavior, physiology, and morphology of frugivores may influence the dispersal of a particular fruit species. Food handling, processing, and gut passage time affect the viability of a seed and the size of the clump in which it is deposited; home range and movement patterns affect the location where a seed is likely to be deposited with respect to microhabitat conditions and the prevalence of natural enemies, and therefore, the fate of the seeds and the seedlings (Rowell and Mitchell 1991).

Most of the studies of frugivory are those of bats that feed on small-seeded fruits in the New World tropics.

<table>
<thead>
<tr>
<th>Feeding tree</th>
<th>Feeding roost</th>
<th>(m)</th>
<th>Distance (m)</th>
<th>Averages SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Melia azedarach</em></td>
<td><em>Pinus halepensis</em></td>
<td>(9)</td>
<td>26±10</td>
<td>11–41</td>
<td></td>
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<tr>
<td></td>
<td><em>Casuarina torulosa</em></td>
<td>(1)</td>
<td>45</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Cave ^b^</td>
<td>(4)</td>
<td>400±94</td>
<td>259–459</td>
<td></td>
</tr>
<tr>
<td><em>Ceratonia siliqua</em></td>
<td><em>Pinus halepensis</em></td>
<td>(2)</td>
<td>32±4</td>
<td>29–34</td>
<td></td>
</tr>
<tr>
<td><em>Eriobotrya japonica</em></td>
<td><em>Casuarina torulosa</em></td>
<td>(1)</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Morus nigra</em></td>
<td><em>Casuarina torulosa</em></td>
<td>(1)</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total without the cave ^c^</td>
<td></td>
<td>(14)</td>
<td>11–45</td>
<td>28±10</td>
<td></td>
</tr>
</tbody>
</table>

* Number of distances from feeding tree of feeding roost

^b^ See Methods
(Howe 1986; Fleming 1988; Fleming et al. 1977), especially with respect to their movement pattern in the habitat (Fleming 1988). In eastern Mediterranean bat, it is the availability of fruits which are preferred by *R. aegyptiacus* varies seasonally with a very low availability in winter. This is in contrast with its tropical distribution where fruit diversity and availability is relatively high during all seasons (Kullitzer 1979).

Under laboratory conditions, *R. aegyptiacus* consumes between 50–150% of its body mass per day on carob and loquat diets, respectively (unpublished data). Frugivorous bats such as *Artibeus lituratus* and *A. jamaicensis* in Panama consume 81 g of figs daily, which is equivalent to 200% of their body mass (Morrison 1978, 1980). *Carollia perspicillata* in French Guiana consumes 18–22 g of fruit per day which is 100–120% of its body mass (Charles-Dominique 1991). Other Paleotropical fruit-bats (*Epomops huertorii* and *Micropterus pusillus*) ingested 63–359 g of fruit (140–250% of their body mass) (Thomas 1984). Hence, it seems that the Old and New World frugivorous bats are similar in the ratio between their food intake and body mass. However, since all New World frugivorous bats (family Phyllostomidae) weigh less than 100 g, whereas many Old World frugivores (family Pteropodidae) weigh much more than this (up to 1500 g; Fleming et al. 1987), it is suggested that the individual quantitative role of the Old World bat as seed disperser may be more significant. For instance, by consuming 150 g of mulberry fruits an individual *R. aegyptiacus* may remove >3000 seeds daily.

Dispersal distances

The post-dispersal fate of seeds depends partly on the distance that seeds are moved away from the vicinity of the parent plant (Howe et al. 1985; Levey 1987; Fleming 1988). Seeds in this study may be spat out or deposited anywhere from 25 to 400 m away from the parent tree. The seed shadow generated by tropical fruit-bats was found to be highly leptokurtic, with two-thirds of the seeds deposited under night roosts within about 50 m of parent plants (Fleming 1988). Moreover, this distribution of dispersal distances was based on fruit-bats which pass the seeds through the gut and stay for 1.5 h in the same feeding location. *R. aegyptiacus* does not pass through its gut any of the relatively large seeds that were tested, and passes only 2% of the total small seeds (<4 mg) ingested. *R. aegyptiacus* may pick a single fruit and carry it to its feeding roost or may consume the fruit on the parent tree (C. Korine, personal observations). This feeding behavior may alter the pattern of the seed shadow distribution toward a bimodal one with relatively high seed density beneath the parent tree and beneath the feeding roost. Neotropical bats use wind-dispersed trees.

*Fig. 4a–e* Micrographs of seed coats of *A. andrachne* and *C. siliqua*. a,b Control and ejected seeds of *C. siliqua* (magnified 200 times); c,d,e Control, ejected and defecated seeds of *A. andrachne* (magnified 200 times)
as well as fruiting trees as feeding roosts which serve as foci of recruitment (Fleming and Heithaus 1981; McDonnell and Stiles 1983). *R. aegyptiacus* uses mainly non-fruiting species (such as *Ficus*) as feeding roosts and therefore may increase the probability that the seedlings avoid parent and sibling intraspecific competition.

It has been suggested that predation risks force fruit bats to eat the fruits at feeding roosts (Morrison 1980). We suggest that feeding roosts, such as caves, as was found in this study, may also serve as feeding shelters during rain.

The effect of feeding behavior on seed germination

The results of the seed germination experiments indicated that the seed passage through the entire digestive tract did not enhance germination. However, in the case of *E. japonica*, the percent of seed germination of the ejected seeds was significantly higher compared to the control intact seeds. Hence, *R. aegyptiacus* is very similar in this respect to the New World frugivorous bats in which gut passage did not depress seed germination probability (Fleming 1988). However, it is still unknown whether the removal of the fruit pulp by *R. aegyptiacus* increases seed survival by reducing seed predation as suggested for neotropical bats (Janzen 1982).

However, this is not the case with respect to the effect of the bats on the pattern of germination distribution. In three of the six plant species we studied (*M. nigra*, *A. andrachne*, and *E. japonica*) there was some evidence that seeds which experienced different treatments had different germination rates, germination patterns, as well as different patterns of accumulative germination. The combined seed germination distribution generated by these different treatments is more even over time than each treatment alone. One of the most important survival mechanisms of plants growing in unpredictable conditions such as in the eastern Mediterranean habitats is the ability of one plant to produce a population of seeds with considerable variety in their germination (heteroblasty). This will ensure that, even under optimal conditions, only part of the seed population will germinate at one time (Koller 1972; Guttman 1985). An additional way of circumventing the unpredictability in the temporal distribution of rains in eastern Mediterranean habitats is to spread germination relatively evenly over a long time. Therefore, these three plant species that use bats for seed dispersal also enjoy an added benefit in that frugivory results in both spatial and temporal risk-spreading (Izhaki and Saffri 1990).

There were no clear-cut differences between small and large seeds with regard to this phenomenon. Interestingly, at least some of the defecated seeds of *M. nigra* (as was shown in the sculpture of the seed coats) and *A. andrachne* seeds exhibited delayed germination, in contrast to most other studies which showed that gut passage caused earlier germination (Swank 1944; Noble 1975; but see McDirmid et al. 1977). The delayed germination may indicate that germination inhibitors in the pulp may be washed out with the feces and therefore remain close to the seeds after deposition. Alternatively, it may indicate that some inhibition was caused by physical and chemical treatment in the gut.

The other three fruit species demonstrated relatively high germination and similar distribution patterns regardless of the different treatments. However, in this case, differences were detected in germination rate. The germination of *F. carica* seeds was not affected by the bat even when the seeds passed through the gut. These results contradict the observed improvement of seed germination of *F. chrysophlea* after ingestion by priopodid bats in the Philippines (Utzurrum and Heideman 1991).

The overall efficiency of the fruit-bat as dispersal agent

The significance of the fruit-bat to the dispersal of a specific plant species is a consequence of several attributes, of which only a few were studied here. Our data demonstrate that the fruit-bat at least serves as a seed carrier which carries seeds away from the parent plant without affecting the ability of the seeds to germinate. However, the different feeding behaviors which were documented here for small-seeded fruits, such as passing the seed through the gut or spitting it out, creates different patterns of seed germination which may enhance the probability of seedling establishment in unpredictable environments. There are still many open questions which are essential for the understanding of the quality of the disperser for plant fitness, such as how much of the crop does the bat remove? What are the chances of seeds germinating and establishing in a specific microhabitat to which the bats carry them?

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