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REMOVAL OF THE GREEN FRUIT OF ASPARAGUS APHILLUS BY BIRDS —
SEED PREDATION OR DISPERSAL?

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INTRODUCTION

The development of fleshy-fruits includes morphological and
chemical changes such as an increase in the sugar content of
the pulp, a decrease in the amount of secondary compounds in
the pulp, and alteration of the green color to bright colors.
It is believed that frugivorous birds are able to respond to
such changes while foraging. Several studies have demonstrated
the role of fruit colors (see review in Willson and Whelan
1990), and fruit taste in fruit selection (Sorensen 1983).
However, only a few studies have reported that birds remove
unripe fruits (Sherburne 1972, Core 1974, Postar 1977) and
therefore may act as seed predators rather than legitimate seed
dispersers. Viable seeds with germination ability have been
found in unripe fruits (Gould 1966, Forbes 1972) but these
studies did not deal with the effect of seed passage through
the digestive tract of the dispersal agents (Izhaki and Safriel
1990, Barnea et al. 1991). It is expected that soft seeds in
the first development stages will be more vulnerable than the
hard-shell seeds in later stages which are protected against
mechanical and chemical damage in the digestive tract (Barnea
et al. 1990).

Izhaki (1986) observed consumption of unripe green-fruits
of ASPARAGUS APHILLUS in Israel. The aims of the present study
were (1) to explore the significance of this phenomenon; (2) to
determine whether the consumption of green fruits is predation
or legitimate dispersal; and (3) to search for correlations
between the seed state and external morphological characters
and chemical features of the pulp throughout the ripening
season.

STUDY SITE AND METHODS

The study was carried out in two consecutive fruiting seasons
southern edge of Mount Carmel, Israel (34°57' E, 32°33' N).
The dominant species in the scrub is PHILLYREA LATIFOLIA
accompanied mainly by PISTACIA LENTISCUS, CLITUS INCANUS, and
CALYCOTOME VILLOSA.
**Plant study.** All *Asparagus* individuals were marked at the beginning of the fruiting seasons and divided randomly into three groups: (1) An observation group was used for the estimation of fruit removal by birds. Branches with fruit were marked 20 cm below their tips and an accurate diagram of the location of each individual fruit was drawn for each branch to detect the removal of individual fruit. Fruit presence, diameter, color, and damage by insects were recorded every 5-7 days. Fruit was classified as removed by birds where the peduncle and the calyx remained, or where several adjacent fruit disappeared simultaneously. (2) A control group was used to estimate natural fruit shedding and the appearance rate of black fruit. Branches with fruit were covered by plastic bags with ten 1 cm² holes which enabled normal photosynthesis, respiration, and fruit development. Every 7 days the fallen fruit was collected, counted, measured, and their color recorded. (3) A sample group was used to study fruit characteristics during fruit ripening and for germination experiments. Every 7 days fruit was sampled at random and analyzed for water and sugar content. Fruit diameter, color, mass and seed mass were also recorded. Fruit hardness was measured with a pressing instrument of 60 units of force (1-hard fruit; 50-very soft fruit).

**Germination study.** Fruit from the sample group described above were sown with their pulps in a greenhouse a few days after they were collected. Each fruit was sown in a different germination cell. Sown fruit remained in the soil during the following spring and summer. Germination cells were watered at the beginning of the rains of the following winter when they also germinated. Germinated seeds were counted every 3-4 days. The number of days from first watering was used as the time duration for germination.

**RESULTS**

**Fruit size.** Three weeks after blooming the fruits achieved 90% of their final diameter. They continued growing two weeks more through mid-December when their growing stopped. There was some variation in fruit size among plants in the observation group with minimum and maximum final diameters of 5 and 7.7 mm, respectively.

**Fruit color.** In the 1988-1989 season during first ten weeks of their development, most fruit was still green. After an additional four weeks only 60% of the fruit was black and, at the end of the fruiting season (after more two weeks, in 15 February), 20% of the fruit was still green. The appearance of black fruit in 1989-1990 season lagged three weeks relative to the previous season (Fig. 1).
Fig. 1. Proportion of black fruit from the total crop of *Asparagus officinalis* in two fruiting seasons in Israel.

**Fruit hardness.** At the beginning of the fruiting season the fruits were relatively soft with watery seeds. The fruit became hard three weeks after blooming and stayed in this state additional three weeks until the first week in January. Then the fruits rapidly became soft with minimum solidity at the end of January.

**Sugar content of pulp.** Sugar content increased with fruit development in both seasons and reached a maximum of 3% when fruits were soft.

**Seed and pulp dry mass.** Seed dry mass was doubled from mid December to the end of January when pulp dry mass increased by 89% during the same period.

**Seed and pulp water content.** Water contents of both seed and pulp decreased during fruit development down to 42% and 71% respectively at the end of the first fruiting season.

**The relationships between fruit color, hardness, and sugar content of the pulp.** In the 1988-1989 fruiting season the color shift from green to black took place prior to fruit softening. No differences were detected at the beginning of January between the solidity of green vs. black fruit ($F_{1,16}=9.2$, $P<0.05$), while green fruits were much more solid than the black ones at the end of January ($F_{1,16}=10.2$, $P<0.001$). However, the fruits in the second fruiting season became soft with almost no color change. No difference was detected in sugar content between green fruit (30.4±2.7%) and black fruit (30.3±4.8%, $P>0.05$).
Seed germination. No germination was observed in seeds collected from the plants at the end of November until mid-December. Low germination percentages (<30%) were detected for seeds collected at 15th December and 22nd December 1989 and high percentages (>30%) for seeds collected from 28th December through 25th January (Fig. 2).

Fig. 2. Percentage of germination of *Asparagus* seeds picked from the plants on different dates. Sample size is indicated above bars.

Fig. 3. Percentage of *Asparagus* individuals with fruit removal record in different dates during (a) the 1988-1989 fruiting season and (b) 1989-1990 season.
fruit removal. The green solid fruit at the beginning of the first studied season (until 8 January) was occasionally eaten by birds (Fig. 3a). As of this date birds preferred the black fruit over the green. In this year most fruit changed color before it became soft and was not consumed until fruits became soft few days later. In the second studied year fruit removal in the first period was marginal. From the beginning of January fruit was consumed in more individual plants with maximum in the beginning of February (Fig. 3b). In this season most fruit was eaten in the green state, perhaps after some softening had occurred. In both years fruit removal by birds was significantly correlated with fruit softness rather than with fruit color or sugar content of pulp.

DISCUSSION

This study demonstrates that legitimate dispersal may occur much before the plant advertises its crop by bright colors. The consumption of green fruits toward the end of the season, as reported by Ishaki (1986) and which occurred in 1989-1990, is not predation. At this stage the seeds are completely ripe and germinable. Once the seeds have reached approximately half-maximum dry mass they are able to germinate. However, seedlings survival also depends on seed size since large seeds contain more reserves.

Fruit removal by birds is related to the softening process rather than changes in color and in sugar content. Therefore, it is suggested that color may entice birds to the fruit crop from long distances (Wills and Whelan 1990) but fruit softness gives the bird information on food quality. The Sardinian warbler (Sylvia melanocephala) was observed assessing fruit solidly by lightly pressing the beak on green Asparagus fruits (Ishaki, pers. obs.). It is notable that the Asparagus has a relatively moderate fruit display since fruit is green almost throughout the whole fruiting season. It is also notable that the dispersal of Asparagus schulii seed is fairly efficient since all of the healthy fruit present on the plants at the end of the season was taken by birds. The evolution of such display might be explained by the timing of its fruiting season which is during winter after the massive bird migration. It is expected that all-year and winter resident birds who are familiar with the habitat are able to locate even cryptic Asparagus crops rapidly. Thus, the plant probably utilizes the green fruits for photosynthesis up to the end of the fruiting season.

Fruit predation was detected in both seasons. Young fruit whose seeds were still soft comprised 20% of the fruits consumed in the first studied season, and 14% in the second. Fruit consumption in this development stage may be enhanced by the fact that the seeds are soft and digestible and the frugivore may digest the seed itself. Moreover, the pulp of