Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region

A. Dafni, P. Bernhardt, A. Shmida, B. Y. Ivri, S. Greenbaum, Ch. O'Toole and L. Losito

1990

Israel Journal of Botany

39: 81-92
RED BOWL-SHAPED FLOWERS: CONVERGENCE FOR BEETLE POLLINATION IN THE MEDITERRANEAN REGION

A. DAFNI*, P. BERNHARDTI, A. SHIMIDA*, Y. IVRI*, S. GREENBAUM*, CH. O'TOOLE* AND L. LOSITO*

*Institute of Evolution, University of Haifa, Haifa 31999, Israel
bDepartment of Biology, St. Louis University, St. Louis, MO 63103, USA
cDepartment of Botany, The Hebrew University of Jerusalem, Givat Ram, Jerusalem 91904, Israel
dKibbutz Ayelet Hashahar, D. N. Galil Elyon 12200, Israel
*Hope Entomological Collections, University Museum, Parks Road, Oxford OX13PW, UK

ABSTRACT

Anemone coronaria, Papaver rhoeas, Ranunculus asiaticus, and Tulipa agenensis are pollinated primarily by scarabaeid beetles (Amphicoma, Glaphyridae) and secondarily by bees (Lasioglossum marginatum Br., Halictidae, and Synhalonia plumigera Kohl, Anthophoridae). The four plant species have large bowl-shaped flowers which are orange-red in color with a black center, radial symmetry, weak scent (to humans), and filamentous stamens. It is suggested that there is a convergent evolution of red bowl-shaped flowers in the East Mediterranean region, concordant with a center of diversity in the genus Amphicoma. The floral phenology of these “Poppy guild” species correlated positively with the amount of edible pollen produced by each of them and with the visiting frequencies of their pollinators. Field experiments showed that Amphicoma beetles also preferred red, odorless flower models over odorless models of different colors, and models with a dark center over plain red ones. This evidence extends the classic concepts of beetle pollination, suggesting a “shift” from scent to color as a primary attractant and the domination of orange-red (typical “bird-flower” colors) as the visual cue.

If a plant taxon is cross-pollinated primarily by beetles, the range of floral attractants usually stresses scent production over pigmentation (Pellmyr & Thien, 1986). Beetle blossoms (Faegri & van der Pijl, 1979) are usually chambered flowers or inflorescences bearing many laminate stamens that extrude pollen (Vogel, 1978). Peaks of scent emission are intense, often crepuscular, and reminiscent of dung, fermentation, decay, and/or ripened fruit. However, floral pigmentation has been described as “dull” due to the dominance of cream, greenish white, and/or maroon-iodine hues. This syndrome of cantharophily has been described most frequently in relictual magnolioids and monocots.

1Author to whom correspondence should be addressed.
Received April 1, 1989 and in revised form July 3, 1989
in the order Aracales (Gottsberger, 1970; Bernhardt & Thien, 1987), but is rather understudied in more advanced families of angiosperms (Grant & Grant, 1968; Armstrong, 1979). In fact, many beetle taxa bear structures modified specifically for the collection and digestion of pollen and nectar (Crowson, 1981).

Bright red flowers, many of which are zygomorphic and long-tubed, are typical to tropical regions (Paegri & van der Pijl, 1979) and are pollinated mainly by hummingbirds (Raven, 1973). In the Mediterranean basin, red flowers are relatively rare. Although they comprise only 2% of the Israeli flora (Shmida & Dafni, in preparation), red flowers are a very prominent feature of the Israeli landscape, especially during the spring (February–April). The species forming these displays belong to the genera Anemone, Papaver, Tulipa, Ranunculus, Gladiolus, and Adonis, all of which have large, bowl-shaped, scentless (to the human nose), and nectarless flowers. These flowers are radially symmetrical and frequently occur in large very showy populations. The flowers of the "Poppy guild" species have a dark center which is created by the stamens (e.g., Anemone coronaria and Ranunculus asiaticus) or by coloration of the perianth (Papaver rhoes and Tulipa agenensis).

An initial report by Ivri (1985) suggested that beetle species of the Amphilota genus prefer red flowers. This diverges sharply from the classic view of beetle pollination (Diel, 1916; Takhtajan, 1969) as mentioned before. In the following, we address several issues to establish the interrelationships between red flowers and Amphilota beetles:

1) Demonstration of convergent evolution towards red bowl-shaped flowers in the East Mediterranean region.

2) Quantification of flowering phenology and flowering replacement among the red-flower species in relation to the temporal abundance of Amphilota species during the season.

3) Since all the species of red-flower guilds have a dark center, we hypothesize that the red–black contrast is more attractive to Amphilota beetles than plain red.

4) Determination of the extent of relative attraction of the different red-flower species in terms of pollen exposure as a reward and the frequency of pollination visits.

MATERIALS AND METHODS

Study Site and Plant Species

During the spring of 1985, a 400 × 200 m plot was established at Ein Hashophet (15 km east of Haifa, Israel). Four 100-m transects were roped off within the plot and the numbers of open red flowers along each transect were recorded every 3 days from February 1 to May 30. The transects contained four spring-flowering species (Table I): Anemone coronaria (Ranunculaceae), Papaver rhoes (Papaveraceae), Ranunculus asiaticus (Ranunculaceae), and Tulipa agenensis (Liliaceae). Additional sites used for the red model experiment (see below) were: Horshat Tal Orchid Reserve (25 km north of Tiberias, Dan Valley) and Haifa University (500 m east of the campus, Mt. Carmel).

*The local form is also known as Papaver carmelit Feinbr.
TABLE I
Comparative floral and pollen exposure characters of the red-flower guild species

<table>
<thead>
<tr>
<th>Species</th>
<th>Flower size (cm)</th>
<th>Number of stamens</th>
<th>Flowering period of the population (days)</th>
<th>Floral lifespan (days)</th>
<th>Daily pollen exposure (hours)</th>
<th>Number of exposed pollen grains per flower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anemone coronaria</td>
<td>4–8</td>
<td>&gt;50</td>
<td>60</td>
<td>5–12</td>
<td>4–8</td>
<td>&lt;500&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Tulipa agenensis</td>
<td>3–6</td>
<td>6</td>
<td>33</td>
<td>4–6</td>
<td>1–2</td>
<td>1000–4000&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Ranunculus asiaticus</td>
<td>3–5</td>
<td>&gt;50</td>
<td>35</td>
<td>6–12</td>
<td>3–6</td>
<td>1000–4000</td>
</tr>
<tr>
<td>Papaver rhoeas</td>
<td>5–7</td>
<td>&gt;50</td>
<td>60</td>
<td>1</td>
<td>4</td>
<td>&gt;5000</td>
</tr>
</tbody>
</table>

<sup>a</sup>Pollen does not accumulate on anthers as it is removed and dispersed by air currents.

<sup>b</sup>Pollen is extruded from anthers and collects on perianth and floral base.

The reflectance range was measured with a Bausch and Lomb Spectronic 15 spectrophotometer with attachment for reflectance assessment.

**Insect Observations**

Insect numbers on red-flower species and the specific diversity and foraging movements of the insects were recorded within the study plot. A capture and release program on species of *Amphicoma* was instituted by labelling beetles with commercial numbered bee labels applied to the right elytron of each insect (*n* = 500). A representative collection of foraging insects was deposited in the Hope Entomological Collections, University Museum, Oxford, and in the Institute of Evolution at the Haifa University. The genus *Amphicoma* is currently under revision by L. Losito (Oxford).

**Field Experimentation To Determine Color Preferences of Beetles**

Colored odorless plastic cups (red, blue, yellow, green, brown, and white) of the average size of a red-guild flower (ca. 4 cm in diameter and 5 cm deep) were employed as models of the floral system and placed within the study sites during the spring flowering season. Each replicate contained four models of each color. On each date and at every locality, they were employed three times (3 × 1 h). Cups were mounted on 15–25 cm sticks (the average height of a red-guild flower). Beetles were rarely captured in cups above 40 cm high. The number of beetles landing in each color model was recorded over a total of 12 h. Beetles were timed within a cup model vs. a red-guild flower.

**The Attractiveness of Red-and-Black Models**

A second set of experiments comprised red 9-cm petri dishes arranged on the ground in triplets. Each triplet included: (1) a plain red dish; (2) a red dish with a dead *Amphicoma* female glued to its center; (3) a red dish with a black spot (1 cm in diameter)
in the center. The dishes were filled with water containing a few drops of detergent to catch the landing beetles and to prevent any possible emission of volatiles. Every captured beetle was removed and immediately placed in a separate vial for determination of species and sex. Each replicate included four sets of triplets which were exposed for 1 h during the peak activity period of the beetles. For each date and locality, four replicates ($4 \times 1$ h) were designed.

RESULTS

In order to demonstrate the concentration of the "Poppy guild" species around the Mediterranean, we compared the proportion of red flowers in each genus (Fig. 1) in various geographical parts of their distribution areas. Figure 1 demonstrates that species with red flowers within each genus of the "Poppy guild" are more abundant in the Mediterranean region and especially in Israel. Such a distribution pattern is especially stressed in *Anemone* and *Ranunculus*. The genus *Ranunculus* comprises about 400 species in the world (Willis, 1973); only three of them are red and centered in the East Mediterranean region. These red species are nectarless, in contrast to the rest of the members of the genus, and each has a corolla at least twice as broad as that found in the

Fig. 1. The occurrence of red flowers in the genera to which the "Poppy guild" species belong. Compiled from Komarov, 1935; Mouterde, 1966; Tutin et al., 1980; Davis, 1984; Meikle, 1985. In Israel there is only one polymorphic species of *Anemone*; about half of the populations are not red.
yellow and white species. The color distribution in the genus Tulipa (Fig. 2A) shows a close association of red flowers with hilly habitats in comparison to other floral colors in this genus. The geographical distribution (Fig. 2B) shows the dominance of red Tulipa species in the Mediterranean region, while the yellow species are more frequent in Europe.

Colorimetric measurements of the reflectance (Fig. 3) of the four red-flower species show a striking similarity of the reflectance curves. All the species have a peak between 655 and 700 nm, the same as the red paint used for the model experimental dishes. The phenology of members of the red-flower guild and of the various Amphilcoma beetles is
illustrated in Figure 4A and B. *A. coronaria* was the early flowering species which appeared in the largest mass. *R. asiaticus* is very similar to *T. agenensis* in its flowering course as well as in its quantity. *P. rhoeas* was the latest species showing a long flowering period with a small and fluctuating population.

There was also a temporal succession among the *Amphicoma* beetles, which showed several peaks. The earliest were *Amphicoma aleppensis* and *Amphicoma libanonensis* which appeared about 4 weeks after the commencement of *A. coronaria* flowering. Their peak coincided with those of *R. asiaticus* and *T. agenensis*, 8 weeks after the peak flowering of *A. coronaria*. *Amphicoma syriaca* and *Amphicoma genel* showed clear peaks, while *Amphicoma hyrax* and *Amphicoma papaveris* were present in low quantities without showing any clear pattern. While *Amphicoma syriaca* appeared with the decline of *Amphicoma aleppensis* and *A. libanonensis*, *R. asiaticus*, and *T. agenensis*, all the rest of the *Amphicoma* species were limited to various durations within the long flowering range of *P. rhoeas*.

The effective visitation rates of the pollinators to the various species of the "Poppy

---

**Fig. 4.** A. Flowering course of members of the red-flower guild in Ein Hashophet, 1985. B. The abundance of *Amphicoma* spp. in Ein Hashophet, 1985.
guild" are presented in Table II. It can be seen that *P. rhoeas* is the most attractive species as is inferred from the relative visitation frequency. *T. agenensis* and *R. asiaticus* are similarly attractive, but both are visited more frequently than *A. coronaria*. These results reflect the amount of exposed pollen available in each plant species (Table I).

All *Amphicoma* beetles have long dense hairs on their legs and ventral segments (Fuchs, 1975) on which pollen accumulates from all four red-flower guild species. Female beetles (of *Amphicoma syriaca*) remain on open flowers (of *R. asiaticus*) for an average of 15.7 ± 4.6 min (n = 250). Male beetles (of the same species) remain on open flowers of *R. asiaticus* for only 3.3 ± 1.7 min (n = 250). Besides foraging for edible pollen, male beetles frequently search the flowers for mates (±200 beetle pairs recorded *in copula*). *Amphicoma* species were found only on flowers of the red-flower guild within the Ein Hashophet study site. However, at another site near Haifa University, about 100 *Amphicoma* beetles, including mating pairs, were found on blue flowers of *Centaurea cyanoides* Berg. et Wallenb. (Asteraceae). This was towards the end of the flowering season of the red species, when their pollen was largely depleted (confirmed by microscopic examination of the empty anthers of *R. asiaticus*).

Beetles contact the stigmas of members of the red-flower guild while foraging actively on anthers (i.e., "mess and soil foraging"; Faegri & van der Pijl, 1979) or while

<table>
<thead>
<tr>
<th>Insect taxon</th>
<th>Flower species</th>
<th>Anemone coronaria (n = 15)</th>
<th>Tulipa agenensis (n = 20)</th>
<th>Ranunculus asiaticus (n = 27)</th>
<th>Papaver rhoeas (n = 27)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coleoptera</td>
<td><em>Amphicoma libanensis</em> and <em>A. aleppensis</em></td>
<td>4.8 ± 0.8</td>
<td>5.2 ± 1.0</td>
<td>9.0 ± 1.0</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td><em>Amphicoma syriaca</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>9.4 ± 4.4</td>
</tr>
<tr>
<td></td>
<td><em>Amphicoma papaveris</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>8.1 ± 6.5</td>
</tr>
<tr>
<td></td>
<td><em>Amphicoma hyrax</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.5 ± 0.2</td>
</tr>
<tr>
<td>Total beetles</td>
<td></td>
<td>4.8</td>
<td>5.2</td>
<td>9.0</td>
<td>18.0</td>
</tr>
<tr>
<td>Apoidea</td>
<td><em>LasioGLOSSum (Evlyaeus)</em></td>
<td>4.2 ± 0.6</td>
<td>6.6 ± 0.8</td>
<td>11.4 ± 0.8</td>
<td>9.1 ± 2.0</td>
</tr>
<tr>
<td></td>
<td><em>marginum</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2.7 ± 3.1</td>
</tr>
<tr>
<td>Total pollinators</td>
<td></td>
<td>9.0</td>
<td>11.8</td>
<td>20.4</td>
<td>29.8</td>
</tr>
</tbody>
</table>

*The rate is expressed by the mean number of times each insect species contacts the pollen-receptive gynoecia (stigma or stigmata). The observation unit includes 20 flowers of each plant species within a foraging bout of 20 min (n = number of replicas; mean and standard deviation). Ein Hashophet 15–18.iii.85 for *A. coronaria*, *T. agenensis*, and *R. asiaticus* and 20.iv.–1.v.85 for *P. rhoeas*. 
searching for pollen that falls from the anther onto the floral base. When an *Amphicoma* species contacts the gynoecium of *A. coronaria* or *R. asiaticus*, its body may cover 10–30 receptive stigmata in a single touch. When removed from *R. asiaticus*, a single *Amphicoma aleppensis* carries an average of 1900 ± 830 pollen grains (*n* = 100). *A. coronaria* appears to represent the red-flower guild species visited least by beetles, while *P. rhoes* is visited most often (Table II).

*Lasioglossum (Evarleus) marginatum* Br. (Halictidae) is a small-bodied (7–9 mm) bee which visits almost all plants in flower within the study site regardless of floral color. *L. marginatum* spends an average of 0.9 ± 0.5 min on a single *R. asiaticus* flower (*n* = 250). Although *L. marginatum* contacts the stigma of a red-flower species as often as *Amphicoma* species (Table II), an individual bee carries an average of only 110 pollen grains (±67, *n* = 27). Furthermore, an individual of *L. marginatum* will contact only 5–10 stigmata each time it touches the gynoecium of *R. asiaticus* or *A. coronaria*.

In contrast, *Synhalonia plumigera* Kohl (Anthophoridae) is a large bee (15–22 mm) which also visits red flowers for short periods (average 0.8 ± 0.7 min, *n* = 100). *S. plumigera* carries approximately ten times as many pollen grains as a *Lasioglossum* forager (1200 ± 380, *n* = 18). However, *S. plumigera* is uncommon within the study site, visits only *P. rhoes*, and does not contact the stigmata of this species as often as *Amphicoma syriaca* or *Amphicoma genet* (Table II).

Out of the beetles found in colored cups, 87% were found in the red models (Table III). The remaining 13% were evenly distributed throughout the other color models. Beetles remain in the red flowers of *R. asiaticus* and *T. agenensis* for an average of 9.5 ± 4.1 min (*n* = 150), while in the red models they only stay for 1.1 ± 2.3 min (*n* = 136).

---

### TABLE III

The attraction of *Amphicoma* beetles to colored flower models

<table>
<thead>
<tr>
<th>Locality and date</th>
<th>Average temperature (°C)</th>
<th>Average relative humidity (%)</th>
<th>Presence of red-flower species*</th>
<th>Number of <em>Amphicoma</em> beetles landing on flower models</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Red</td>
</tr>
<tr>
<td>Ein Hashopet (8.iii.86)</td>
<td>20</td>
<td>62</td>
<td><em>R, T, A</em></td>
<td>33</td>
</tr>
<tr>
<td>Haifa (15.iii.86)</td>
<td>20</td>
<td>62</td>
<td><em>R, A</em></td>
<td>19</td>
</tr>
<tr>
<td>Haifa (16.iii.86)</td>
<td>19</td>
<td>67</td>
<td><em>R, A</em></td>
<td>26</td>
</tr>
<tr>
<td>Horshat Tal (17.iii.86)</td>
<td>23</td>
<td>48</td>
<td><em>R, A</em></td>
<td>24</td>
</tr>
<tr>
<td>Horshat Tal (18.iii.86)</td>
<td>22</td>
<td>51</td>
<td><em>R, A</em></td>
<td>26</td>
</tr>
<tr>
<td>Total</td>
<td>128</td>
<td>4</td>
<td>2</td>
<td>3</td>
</tr>
</tbody>
</table>

*A = Anemone coronaria; R = Ranunculus asiaticus; T = Tulipa agenensis.*
The results of the red dishes experiment (Table IV) show that males of all the involved *Amphicoma* species were significantly more attracted than females \((p \leq 0.003\) using a significance test). Application of the paired *t*-test revealed that (a) there was no significant difference in attraction of beetles by the plain red petri dishes vs. dishes containing a female beetle in the center; (b) there was significantly more attraction of beetles to dishes with a dark spot in the center than to those with a beetle in them \((t = 2.76, p \leq 0.05)\) or to the plain red dishes \((t = 9.9, p \leq 0.001)\).

### Table IV

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Horshat Tal 21.iii.86</th>
<th>Haifa 14.iii.86</th>
<th>Haifa 16.iii.86</th>
<th>Ein Hashophet 15.iii.86</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average temperature (°C)</td>
<td>24</td>
<td>19</td>
<td>19</td>
<td>21</td>
</tr>
<tr>
<td>Average relative humidity (%)</td>
<td>47</td>
<td>64</td>
<td>67</td>
<td>63</td>
</tr>
<tr>
<td>Presence of red-flower species(^a)</td>
<td>A, R</td>
<td>A, R</td>
<td>A, R</td>
<td>A, R, T</td>
</tr>
<tr>
<td><em>Type of red dish</em></td>
<td><em>Sex of beetles</em></td>
<td><em>Number of beetles</em></td>
<td><em>Mean ± SD</em></td>
<td></td>
</tr>
<tr>
<td>Plain red</td>
<td>M</td>
<td>3</td>
<td>4</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>With female</td>
<td>M</td>
<td>9</td>
<td>15</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>4</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>With black spot</td>
<td>M</td>
<td>14</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>8</td>
<td>9</td>
<td>13</td>
</tr>
<tr>
<td>Total no. of beetles</td>
<td></td>
<td>38</td>
<td>61</td>
<td>80</td>
</tr>
<tr>
<td>Female:male ratio</td>
<td>1:1.22</td>
<td>1:1.17</td>
<td>1:2</td>
<td>1:3.7</td>
</tr>
</tbody>
</table>

\(^a\) *A* = *Anemone coronaria*; \(R\) = *Ranunculus asiaticus*; \(T\) = *Tulipa agenensis*.  
\(^b\) *S* = *A. syriaca L*; \(G\) = *A. genei* Truq.; \(H\) = *A. hyax* Truq.; \(L\) = *A. ibononensis* Petr. and *A. aleppensis* Petr.

**DISCUSSION**

The analysis of the geographical color distribution within the genera to which the "Poppy guild" species belong (Figs. 1, 2) and the colorimetric examination (Fig. 3) demonstrate that there is a convergence towards red bowl-shaped flowers around the Mediterranean (e.g., in *Adonis, Anemone, Tulipa, Glaciurn, Papaver*, and *Ranunculus*). Species of these genera rarely bear red flowers outside the Mediterranean basin. In general, red-scarlet flowers are related to hummingbird pollination (Raven, 1973) especially in tropical and subtropical regions. They are also fairly common in California and the temperate zone.
of North America (Grant & Grant, 1968). However, in the Old World red bird-pollinated flowers are very rare.

It is noteworthy that all members of the "Poppy guild", including *P. rheas*, do not reflect at the UV range (Menzel & Shmida, in preparation). In Europe, *P. rheas* does reflect UV light (Daumer, 1958) and is pollinated by bees (Proctor & Yeo, 1973, p. 64). It seems that the lack of UV reflectance in the East Mediterranean *P. rheas* populations reflects a convergence to beetle pollination.

In the Mediterranean basin, red flowers are quite common, but they are bowl-shaped pollen-flowers. These species, most of which belong to the "Poppy guild", are pollinated by insects. It is noteworthy that the East Mediterranean basin is also a center of speciation of the genus *Amphicoma* (L. Losito, in preparation), the main pollinator of the guild.

The evidence presented here expands our knowledge on visual perception in the genus *Amphicoma* and it also questions the preconceptions regarding the beetle-pollination syndrome. The four herbaceous species studied possess some of the morphological traits of a standard "beetle flower" with an herbaceous habit, e.g., erect, bowl-shaped blossoms, many stamens (polyandry) with a single flower, and/or semi-extrusive pollen encouraging "mess and soil" pollination (Pellmyr, 1984; Bernhardt & Thien, 1987). On the other hand, the roles of scent and color are reversed in importance when the red-flower guild is compared with magnolioids and palm-like plants. Even in the nectar-producing beetle-pollinated angiosperms of Australia (e.g., Myrtaceae and Sapindaceae) the flowers are strongly scented, and the perianth and stamens reflect the trend towards dull-discrete pigmentation or white blossoms (Armstrong, 1979; Hawkeswood, 1982). Moreover, Willemstein (1987, p. 152) concluded that "there is no evidence from the literature that Coleoptera can see red." Vivid red-orange flowers with weak scents are characteristically associated with pollination by nectar-foraging birds (Grant & Grant, 1968; Bernhardt, 1983). Here, however, results of spectrophotometry (Fig. 2) and field experimentation (Table III) show that the pigmentation of red flowers in the Mediterranean basin attracts beetles of the genus *Amphicoma*.

The fact that *Amphicoma* spp. beetles were attracted to red cups (Table III) and red petri dishes (Table IV) indicates that the red color is more important than the shape of the flower in attracting *Amphicoma* beetles. This may explain the low discriminative ability of the beetles which were observed moving freely between the different red-flower species.

The experiment with the red dishes (Table IV) showed an enhancement (nonsignificant) of the attraction ability when a female was glued in the center of the dish (in reality, the actual size of the floral center is larger than a single beetle). This difference became highly significant when a black spot (1 cm in diameter) was added on the red background. The conclusion is that the black–red contrast is more attractive to species of *Amphicoma* than plain red. It was also found that males are more active than females in search for new models since the females stay on the flowers longer than the males, and the males are very active in cruising among the flowers in search of mates. This result corresponds with the effect of the dark center of the red flowers of the "Poppy guild" and demonstrates its attractive value for beetles.

In Israel, as well as in other parts of the East Mediterranean region, *P. rheas* has a
prominent black spot at the base of the corolla. However, in Germany (and in all of West Europe), such populations are very rare (J. Kadereit, personal communication). *P. rhea*us originated in the East Mediterranean and has expanded in the last millennia to the West Mediterranean and West Europe. *Amphicoma* spp. beetles are very rare or absent in these regions; hence, it can be hypothesized that *P. rhea*s lost the dark coloration of the center in West Europe in the absence of these beetles as main pollinators. The same type of behavior was observed in several species of *Amphicoma* (Table IV), which indicates a common pattern of behavior among beetles. The sequential flowering peaks (Fig. 4A) of the various members of the “Poppy guild” may support the view that there is a characteristic displacement of flowering phenologies of these sympatric species. Such a phenomenon may be interpreted in terms of competition for pollinators (Gleeson, 1981; Feinsinger, 1987).

ACKNOWLEDGMENTS

We cordially thank S. Vogel, D. Cohen, D. Eisdikowitch, P.H. Raven, G. Gottsberger, and A. Horovitz for their constructive comments and criticism, and for their encouragement.

REFERENCES


