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Floral biology of *Nuphar pumila* (Timm) DC. (Nymphaeaceae) in China

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Abstract. Anthesis in individual flowers of *Nuphar pumila* (Timm) DC. occurs for four consecutive days. First-day flowers are protogynous and functionally female. Flowers can open completely on the first day of anthesis. This contrasts with all previous reports, which state that first-day flowers of *Nuphar* are characterized by partial expansion of the calyx, leaving a distal small triangular opening just above the stigmatic disc. Flowers close completely on the first night of anthesis and remain partially open on the subsequent three nights. During the entire anthesis period the stigmas emit a sweet, fruity odor and the petal nectaries produce visible nectar drops. The stigma of *N. pumila* is secretory and unicellular-papillate. Pollen grains are monosulcate with long spines. Our observations on the mating system of *N. pumila* indicate that neither asexual seed production nor spontaneous self-pollination occurs. Cross-pollination of second-, third- and fourth-day flowers produced few seeds. Flowers of *N. pumila* were mainly pollinated by sweat bees, with flies playing a minor pollination role. No beetle visits were observed. Our insect-pollination observations substantiate the view that the relative contribution of flies, bees, and beetles to pollination in a single *Nuphar* population depends on two factors: the relative abundance of the insects, and presence of alternative food sources.

Key words: Floral biology, *Nuphar pumila*, Nymphaeaceae.

Nuphar Sm. (spatterdock or yellow pond-lily) is a small genus of perennial hydrophytes that inhabits freshwater ponds and slow-running streams throughout temperate regions of the Northern Hemisphere (Fu and Padgett 2001). Contemporary morphological and molecular studies continue to support the association of *Nuphar* with *Barclaya*, *Euryale*, *Victoria*, *Nymphaea*, *Ondinea* in the family Nymphaeaceae (Salisbury 1806; Caspary 1891; Ito 1987; Les et al. 1991, 1997; Moseley et al. 1993; Padgett et al. 1999; Schneider et al. 2003), a member of the ANITA clade that constitutes the three most basal angiosperm lineages [*Amborella*, Nymphaeales, and Austrobaileyales (Austrobaileyaceae, Illiciaceae, Schisandraceae, and Trimeniaceae)] (Les et al. 1999, APG II 2003, Qiu et al. 2005). Recent phylogenetic analyses of the genus *Nuphar* in North America and Europe recognized 13 distinct lineages (excluding hybrids), five in Europe and Asia and eight in North America (Padgett 1997, Padgett et al. 1999). *Nuphar* has been divided into two sections (*Nuphar* and *Astylus*) corresponding to largely Old World and New

World species respectively (Padgett et al. 1999, Padgett 1999). *N. pumila* (Timm) DC., an Eurasian species of section *Nuphar*, possesses pistils with elongated necks and lobed stigmatic disks, and belongs to the Old World clade.

There are considerable existing data on the pollination biology of *Nuphar*. Early observations were summarized by Schneider and Moore (1977). Their studies on *N. advena* native to central Texas (recognized as *N. lutea* ssp. *macrophylla* [Small] Beal) suggested that *Nuphar* is closely adapted for pollination by *Donacia* beetles, which represent the most effective pollinators of *Nuphar* flowers. Although other investigations highlighted the association between *Donacia* and *Nuphar* (Schneider and Moore 1977, Lippok et al. 2000), few other workers considered *Donacia* beetles to be important pollinators of *Nuphar*. Robertson (1889) considered *N. advena* in Illinois and Florida to be mainly pollinated by sweat bees (*Halictus pectoralis*) and shore flies (*Notiphila* sp.). Despite observing an abundance of *Donacia piscatrix* in older flowers, Robertson (1889) rejected *Donacia* beetles as likely pollinators, and did not consider the *Nuphar* flower to be adapted for beetle pollination; indeed, he regarded *Donacia piscatrix* as "worse than useless when it comes to pollination."

Nuphar lutea and *N. pumila* in the Netherlands, Norway, and Germany are pollinated by flies and bees rather than by *Donacia* or other beetles (van der Velde 1986, Ervik et al. 1995, Lippok and Renner 1997). In both species, flies are the primary pollinators; these include several apparent *Nuphar* specialists, such as the scatophagid *Hydromyza livens* and ephydrids *Hydrellia* and *Notiphila*. Robertson (1889) also recorded *Notiphila* as among the pollinators of *N. advena* in Florida. Based on comparative studies of pollinator spectra in two Old World and three New World species of *Nuphar*, Lippok et al. (2000) did not support the widely accepted view that beetle pollination is the predominant pollination mode in the genus, but suggested that the relative contribution of flies, bees, and beetles in any one population depends on their relative abundance and the availability of alternative food sources.

Despite considerable study on flower-insect relationships in *Nuphar*, there are relatively few previous reports on floral behavior during anthesis and those that exist are often inconsistent in different species and different places studied. For example, some authors have reported that flowers close at night (Schneider and Moore 1977, Lippok et al. 2000), others that they remain open (Robertson 1889, Schneider and Moore 1977, van der Velde 1986, Ervik et al. 1995). Some workers found that the petal nectaries secrete nectar drops (Robertson 1889, Schneider and Moore 1977, van der Velde 1986), but others did not (Lippok et al. 2000).

Our aim is to contribute detailed observations on the floral biology of *N. pumila* to improve our understanding of the floral biology of *Nuphar*. This investigation is part of an ongoing series of studies on the floral biology and embryology of Nymphaeaceae, designed to contribute new evidence for determining the phylogenetic relationships of the family.

Material and methods

Investigations on the floral biology of *Nuphar pumila* were conducted during the summers of 2003 and 2004 in an outdoor pond in Beijing Botanical Garden (Chinese Academy of Sciences). Field observations were made during summer 2005 in two freshwater ponds in Wuhan, Hubei Province, central China. Flowers were marked with a colored line and observed during both day and night. The neutral red technique (Esau 1965) was applied for determining the site of floral odor emission.

Flowers at various developmental stages were collected and immediately fixed in a solution of 95% ethanol and glacial acetic acid (3:1) and stored in 70% ethanol. Specimens for scanning electron microcopy (SEM) were dehydrated in an ethanol-amyl acetate series, critical-point dried, coated with gold palladium and observed with SEM S800.

Paraffin sections of stigma and anther for light microscopy (LM) were prepared using standard procedures (Johanson 1940), stained with Heidenhain's iron-alum hematoxylin and counterstained with fast green. Micrographs were taken using an Olympus BH light microscope.

To elucidate the reproductive mechanism of *N. pumila* we bagged about 50 flowers prior to anthesis and these were then subjected to one of the following treatments: (1) To test for spontaneous selfing, 10 flower buds were bagged without further manipulation, (2) To test for presence of agamospermy, 10 flowers were emasculated before anther dehiscence, (3) To test for cross pollination and stigma receptivity, 10 first-day flowers were emasculated and artificially pollinated with pollen of second-day flowers from other plants, and (4) To test for stigma receptivity, 5 second and about 15 succeeding day flowers were cross-pollinated. Developing fruits were collected two weeks after treatment and pollination; they were fixed in a solution of 95% ethanol and glacial acetic acid (3:1) and stored in 70% ethanol. Developing seeds and aborted ovules were counted to determine percentage seed set.

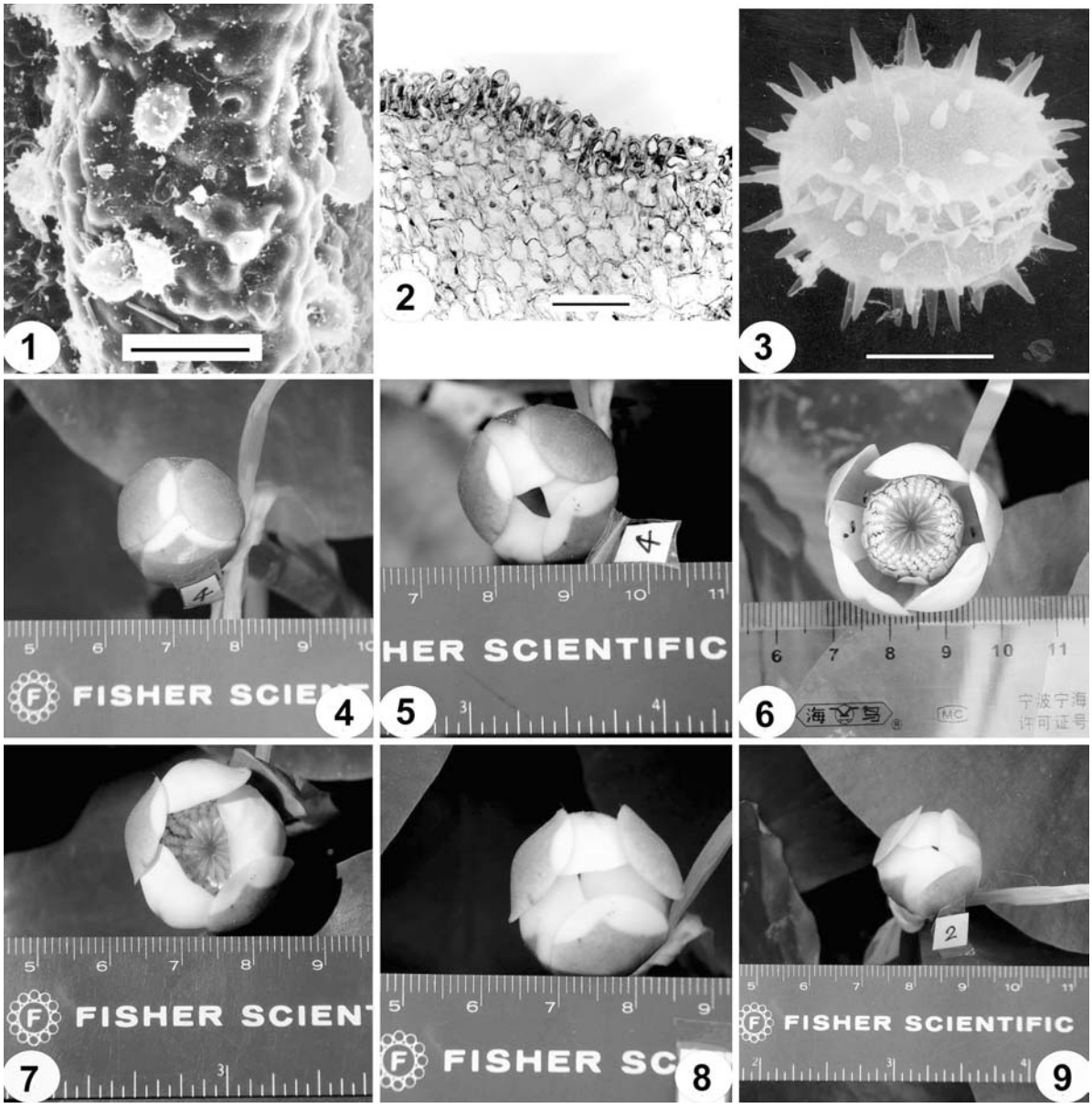
Results

Flowers of *Nuphar pumila* are solitary, subglobose to bowl-shaped and borne on green rigid peduncles ~23 cm above the water surface. They have five or six broadly spatlulate, yellow sepals, which are tinged green on the base. Inserted above the sepals are 12–15 small, yellow, thick, scale-like structures which sometimes are interpreted as petals. Two small inner yellow sepals occasionally occur between the sepals and petals. Each petal bears a circular, slightly raised nectary. The ~103 stamens with elongated and paired anther-sacs are packed below the stigmatic disk prior to anthesis. The yellow compound gynoecium is swollen basally, but narrows distally and then flares outward to form a circular flattened disk with 12–14 rays of red-yellow and shiny stigmatic tissue. The receptive surface of the stigma is papillate; papillae are unicellular (Figs. 1, 2). Pollen grains of *N. pumila* are anasulcate (Fig. 3). The pollen surface is echinate and long stout echinae are not arranged in patterns (Fig. 3).

Individual flowers bloom for four consecutive days. They begin to open during the morning from 7:30 to 9:00 am. Anthesis is first indicated when the tightly imbricated sepals begin to loosen and the yellow coloration of the upper part of the sepals is revealed (Fig. 4). The moving sepals form a triangular opening over the stigmatic disk around 8:00 am on the first day (Fig. 5). The size of the opening continues to increase until the sepals are fully expanded by about 10:00 am (Fig. 6). At this time, the flower appears bowl-shaped, and the stigmatic disk, stamens and petals are completely exposed. During the first day of anthesis, the petals and staminal parts remain tightly pressed together, the anthers are indehiscent and the stigmatic disk is covered with a sticky, mucilaginous secretion. We consider the stigma to be pollen-receptive during this stage and therefore the flowers to be protogynous. The petals produce visible nectar droplets on the abaxial surface at this stage. First day flowers also emit an intense, sweet-smelling odor, somewhat like immature apricots. When flowers were treated with neutral red, the sepals, petals and staminal parts did not stain, whereas the stigmatic rays in the stigmatic disc exhibited intense staining, thus indicating the site of intense odor emission.

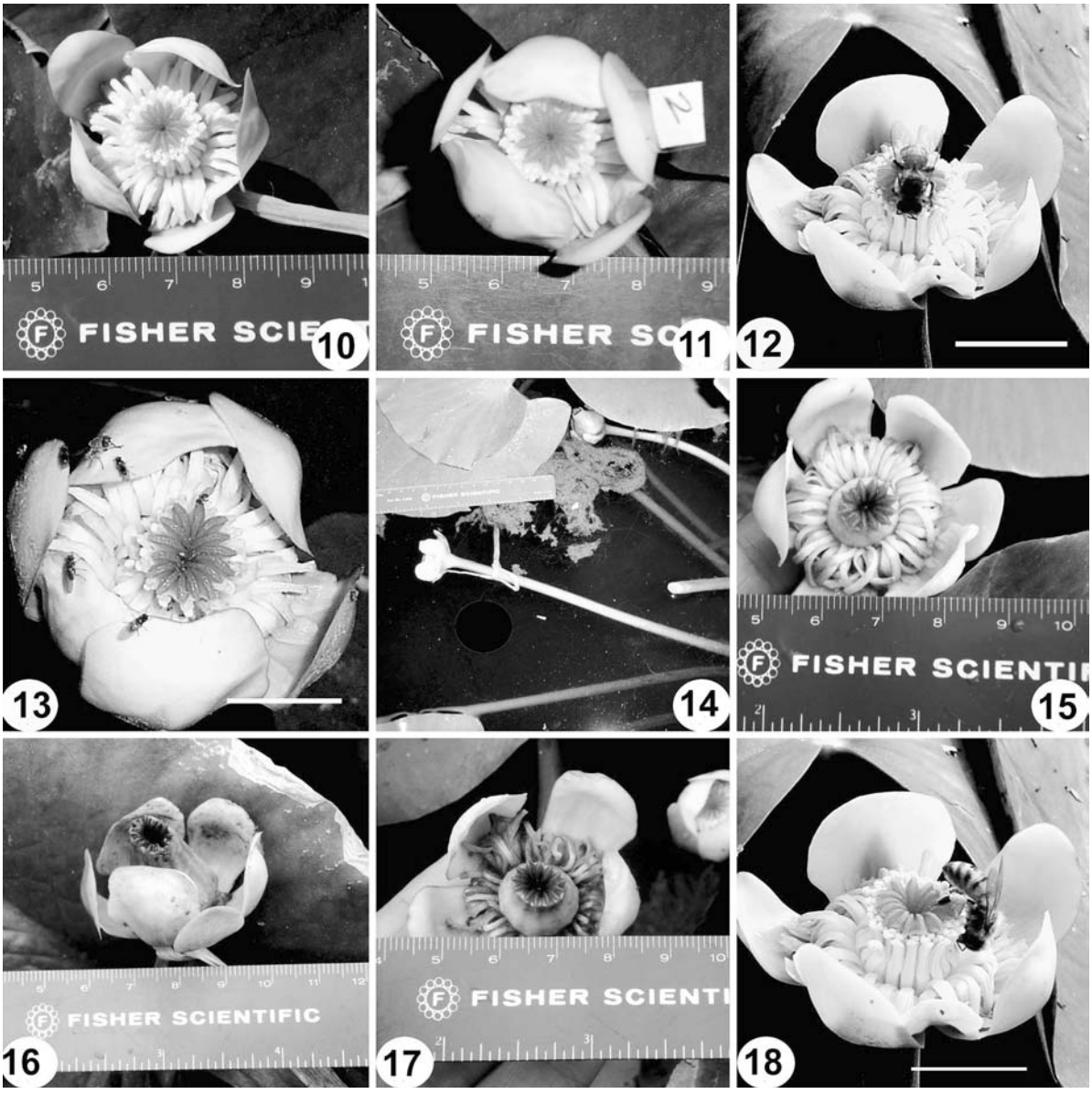
First-day flowers begin to close at about 12:00 (Fig. 7). Retraction and imbrication of the sepals over the stigmatic disc is so sluggish that the flowers are not fully closed until between 17:50 and 19:30 (Fig. 8). During the first night the petals and stamens do not expand extrorsely, nor do the anthers dehisce to release pollen.

On the second day of anthesis, flowers typically begin to open slightly earlier than first-day flowers (Fig. 9). As the sepals become reflexed, the petals and outer rows of stamens bend away from the stigmatic disc, with anthers releasing pollen (Fig. 10). During the second and succeeding days the petals continue to secrete nectar droplets. The stigmatic surface is still wet in the early morning of the second day, but it becomes dry and the stigmatic rays appear less shiny after 10:00. We consider this



Figs. 1–9. Stigma, pollen, and flowers of *Nuphar pumila*. **1** Scanning electron microscopic (SEM) micrograph of stigma surface showing unicellular papillae. Bar = 70 μm. **2** Light microscopic micrograph of stigmatic longitudinal section showing papillae. Bar = 40 μm. **3** SEM of anasulcate pollen with long spines. Bar = 16.7 μm. **4** First-day flower begins to loosen at 7:47 and yellow parts of sepals are revealed. **5** The moving sepals form a small triangular opening just above the stigmatic disc at 8:26 on the first day of anthesis. **6** Fully opened flower at 9:43 on the first day. **7** First-day flower is closing at 13:15 on the first day. **8** First-day flower is just completely closed at 17:45. **9** Second-day flower begins to open at 7:45

sequence of stigmatic changes to be indicative of a non-pollen-receptive state. During the second and subsequent two days, flowers continue to emit a sweet smell, but the intensity of the odor gradually reduces. The second-day flowers partly close at night (Fig. 11), and the extent of sepal retraction and imbrication are variable in different flowers.



Figs. 10–18. Flowers of *Nuphar pumila*. **10** Second-day flower at 13:13 showing the petals and outer rows of stamens reflexing. **11** Second-night flower remains partly open at 21:01. **12** Opening third-day flower at 11:30. Bar = 20 mm. **13** Third night flower at 9:30 showing big opening. Bar = 20 mm. **14** Flower 1 day after anthesis float at the water surface at 19:44. **15** Flower 2 days after anthesis at 12:28. **16** The sepals remain 2 weeks after anthesis. **17** Flower 3 days after anthesis at 12:30. **18** Sweat bee visiting flower first land on the stigmatic disc. Bar = 20 mm

On the third and fourth days, opening flowers clearly increase in size (Fig. 12). The stamens continue to reflex with concomitant dehiscence of the anthers in a centripetal manner. The reflexed stamens conspicuously elongate and arch extrorsely. On the third and fourth nights, sepals form a large opening over the stigma (Fig. 13).

During anthesis the flower is held above the water surface by the peduncle. After the last

day of flowering the peduncles lose their rigidity and consequently the flowers float on the surface of the water (Fig. 14). Subsequently the ovary rapidly enlarges and gradually turns green (Fig. 15). The petals and staminal parts do not abscise but rapidly decay after anthesis (Figs. 15–17). The sepals persist for about four weeks and finally also decay (Fig. 16). The fruit rapidly develops and ripens at the water surface.

Sweat bees were observed to visit first-day flowers, but soon departed to older flowers when they noted the absence of pollen in first-day flowers. First-day flowers were also visited by flies. Shortly after the second-day flowers opened, there was considerable activity with an abundance of bees and a few flies; this was also the case during the third day and fourth day of anthesis, when the remaining anthers dehisce, releasing large amounts of pollen. After the fifth day of anthesis there was little insect activity on the flowers owing to absence of pollen and nectar. Bees that entered the flowers frequently landed on or crawled directly onto the stigmatic disc (Figs. 12, 18) then moved further into the flower in search of pollen and nectar. Our night observations revealed that there was often an abundance of syrphid flies in the flowers on the last three days of anthesis (Fig. 13).

The flowers that were bagged throughout anthesis did not yield seeds. Experimental cross-pollination of first day flowers and natural pollination produced 67 and 59 % seed set, respectively. Flowers that were cross-pollinated prior to 10:00 on the second day produced slightly fewer seeds than first-day cross-pollinated flowers. Few seeds were produced in flowers that were cross-pollinated on the afternoon of the second day and on the succeeding days of anthesis, indicating that stigmas are less receptive at these stages.

Discussion

Our studies show that anthesis lasts four consecutive days in individual flowers of *N. pumila*. First-day flowers are protogynous and functionally female, because pollen is released only on the subsequent three days, as in other species of *Nuphar* such as *N. lutea* (van der Velde 1986), *N. ozarkana* and *N. advena* (Lippok et al. 2000). Our observations contradict reports in previous investigations that on the first day of anthesis of *Nuphar* flowers, sepals expand to only a small distal triangular opening over the stigmatic disc (Robertson 1889, Schneider and Moore 1977, van der Velde 1986, Ervik et al. 1995, Lippok et al. 2000). By contrast, we found that flowers of *N. pumila* open completely at about 10:00 on the first day, though early first-day flowers possess triangular openings over the stigmatic disc when they begin to open at about 8:00. This aspect requires confirmation in other *Nuphar* species.

Our observations show that flowers of *N. pumila* close completely during the first night, but the amount of flower closure gradually reduces over the subsequent three nights. This is in accordance with the observations of Lippok et al. (2000) on *N. ozarkana* and *N. advena*, but contrasts with many other reports. For example, van der Velde (1986) and Ervik et al. (1995) suggested that flowers of *Nuphar* do not close at night, based on observations on *N. lutea* (L.) Sm. Ervik et al. (1995) considered that the absence of flower closure in the Norwegian *N. lutea* populations was probably not simply the result of light night. Heslop-Harrison (1955) was the first to report that flowers of *Nuphar* close at night; he suggested that such closure protects the pollen. Schneider and Moore (1977) observed that first-day flowers of *N. advena* (Aiton) W. T. Aiton close at night and many *Donacia* beetles became trapped in these flowers; they also noted that the second-, third- and fourth-day flowers close at night, trapping further *Donacia* beetles. Such conflicting reports about nocturnal flower closure could result either from incorrect interpretations, distinction of different species, or different environment conditions. Schneider and Moore (1977) and Lippok et al. (2000) both observed *N. advena* from central Texas, but found different results.

Odor is apparently variable between different species. Flowers of *N. pumila* emit sweet,

fruity odor during anthesis, as in *N. lutea* (van der Velde 1986, Ervik et al. 1995) and *N. advena* (Schneider and Moore 1977, Lippok et al., 2000). In contrast, flowers of *N. ozarkana* emit no perceptible odor (Lippok et al. 2000). Experimental tests consistently indicate that the stigmatic rays of *Nuphar* flowers are the sites of the most intense odor emission (Schneider and Moore 1977, Lippok et al. 2000, present study). Petal nectaries of *N. pumila* produce visible nectar drops during the entire period of anthesis, as in *N. lutea* (L.) Sm. (van der Velde 1986, Ervik et al. 1995), *N. advena* (Schneider and Moore 1977, Lippok et al. 2000). However, Lippok et al. (2000) found that petal nectaries of *N. ozarkana* do not secrete visible nectar drops.

We observed that flowers of *N. pumila* were visited by sweat bees and flies, the former being the most frequent visitors. No beetle visits occurred during the entire study period. We did not observe the presence of *Donacia* beetles or other beetles around the ponds studied. Sweat bees fly from one flower to another collecting pollen and nectar; on first-day flowers, they first land on the stigmatic disc and if carrying pollen (as they were observed to do) they achieve cross-pollination. Sweat bees may well be more efficient cross-pollinators than flies, because they visibly carry more pollen from older flowers to first day flowers, and also visit more flowers in given amount of time. Our insect pollination observations substantiate the view of Lippok et al. (2000) that the relative contribution of flies, bees, and beetles to pollination in any one *Nuphar* population depends on these insects' relative abundance and alternative food sources.

All species of *Nuphar* possess bowl-shaped flowers with apparently readily accessible pollen and nectar rewards. Padgett et al. (1999) noted that flowers of the two *Nuphar* clades (New World and Old World) differ markedly in anther length and stigmatic disk size. Different-sized reproductive parts or different amounts of nectar might be differentially attractive to flies, bees, or beetles. *Nuphar* species appear to have different pollinator spectra (Schneider and Moore 1977, Ervik et al. 1995, Lippok and Renner 1997, Lippok et al. 2000). Padgett et al. (1999) suggested that pollinator spectra shift is associated with differences in floral morphology between Old World and New World species. However, comparative studies of Lippok et al. (2000) on pollinator spectra in the two Old World and three New World *Nuphar* species did not support Padgett et al:s hypothesis. Lippok et al. (2000) suggested that pollinator spectra shift mainly depends on the relative abundances of flies, bees, and beetles and alternative food sources in any one population rather than stamen length differences between Old World and New World pond-lilies.

The flowers that were bagged throughout anthesis did not yield seeds, as also observed by Ervik et al. (1995) in *N. luteum* and by Lippok et al. (2000) in *N. advena*, though Schneider and Moore (1977) found that bagged flowers of *N. advena* produced some seeds. Our observations on *N. pumila* are consistent with the observations of Ervik, Renner, and Johanson (1995) and Lippok et al. (2000) that neither asexual seed production (agamospermy) nor spontaneous self-pollination (autogamy) occurs in *Nuphar*. Cross-pollination of second and succeeding day flowers produced few seeds, indicating absence of stigmatic receptivity at this stage, as observed on other species of *Nuphar* (Ervik et al. 1995, Lippok et al. 2000). The stigma of *N. pumila* is secretory and unicellular-papillate, in contrast to the two other water lily genera *Nymphaea* and *Ondinea*, in which the receptive stigmatic surface is covered with numerous crowded multicellular papillae (Schneider 1983, Capperino and Schneider 1985).

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