EFFECTS OF NECTAR STATUS ON FLOWER AVAILABILITY TO POLLINATORS IN NYMPHAEA AMPLA

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ABSTRACT (DKS)

Flowers of the water lily, Nymphaea ampla, exhibit diurnal patterns in nectar levels, corolla aperture, and stamen corona aperture. We hypothesized that these diurnal patterns function to regulate pollinator access. We found that artificial nectar removal caused the corollas to close 2-6 hours earlier in the day, but delayed closure of the stament corona 3 hours. Stamen corona collapse did not preclude insect visitation, however, appeared to increase pollinator contact with the anthers. Exclusion of insects by bagging did not affect either corolla aperture stamen corona aperture. High nectar levels may be employed as a cue by N. ampla to indicate that pollination has not occurred. Further studies are needed to clarify the pollination biology of N. ampla.

Key Words: Nymphaea ampla, pollinator access, water lily

INTRODUCTION (JLB)

The water lily, Nymphaea ampla, at Palo Verde contains about 4ml of nectar at the base of the corolla. Surrounding this nectar pool is a stamen corona (Figure 1). We observed that stamens remained upright in some lilies, exposing the nectar, in others, coronas had collapsed. Lilies with open corollas were visited by at least three species of insects. Presumably, the lilies produce nectar to attract insect pollinators.

We predicted that the aperture of the stamen corona was a response to the amount of nectar with collapse indicating nectar removal by potential pollinators. We expected that stamen corona collapse impaired pollinator access to the base of the corolla, therefore minimizing pollinator contact with the stigma.

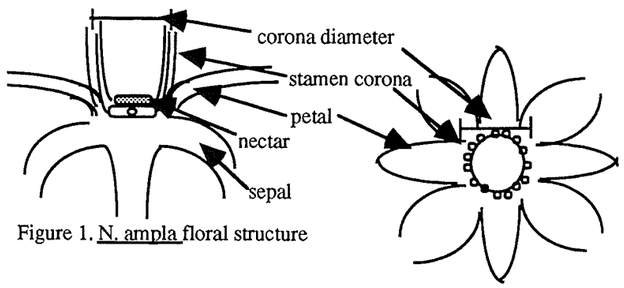

Figure 1. N. ampla floral structure

METHODS (JLB)

We conducted experiments in the marsh adjacent to the airstrip at Palo Verde National Wildlife Refuge, Costa Rica. At dawn on 13 January, 1994, we selected 40 flowers that were blooming, contained nectar and had open stamen coronas. Each flower was assigned to one of four treatments: 1) nectar removed, flower bagged, 2) nectar present, flower bagged, 3) nectar removed, flower unbagged, and 4) nectar present, flower unbagged. Nectar was removed using cotton swabs, without disturbing stamen coronas. Bagging treatments involved covering flowers with fine-mesh netting to prevent pollinator access.

We monitored flowers hourly from 09:00 to 16:00. At each observation, we measured stamen corona diameter and assessed whether petals were open or closed. Corona aperture (the extent to which the stamen corona was open) was expressed as follows.

$$\text{Corona aperture} = \frac{\text{corona diameter at time t}}{\text{maximum corona diamter observed for flower.}}$$

Data were analyzed with a repeated measures ANOVA.

Table 1: Repeated measures ANOVA for effect of nectar removal on stamen collapse over time for N. ampla.

	df	MS	F	p
bag treatment	1	0.209	1.32	0.26
nectar treatment	1	3.915	24.63	<0.0001
bag trt. x nectar trt.	1	0.223	1.40	0.24
time	8	5.740	166.16	<0.0001
time x bag trt.	8	0.036	1.03	0.41
time x nectar trt.	8	1.583	45.82	<0.0001
time x bag trt.x nectar trt.	8	0.034	0.98	0.45

RESULTS (JLB)

Our control flowers (nectar present, flower unbagged) suggest the temporal pattern that N. ampla corollas are open approximately seven hours daily, from dawn until early afternoon. Stamen coronas remained open longer in flowers where nectar had been removed compared to the control ($p < 0.001$; Figure 2). However, the corolla closed earlier when nectar was artificially removed ($p < 0.001$; Figure 3). Pollinator exclusion (bagging) did not affect either corolla or stamen corona closure ($p = 0.41$, Table 1; $p = 0.17$; Table 2). Stamen corona closure did not interfere with pollinators' access to the base of the corolla, as they were able to crawl between the pollen coated anthers.

DISCUSSION (DKS)

Our data generally support our hypothesis relating nectar levels to pollinator access. We observed opposite trends for aperture of stamen corona and proportion of flowers with an

Table 2: Repeated measures ANOVA describing effects of nectar removal on petal closure over time for N. ampla.

	df	MS	F	p
bag treatment	1	0.078	0.41	0.53
nectar treatment	1	2.628	13.69	0.0007
bag trt. x nectar trt.	1	1.128	5.88	0.02
time	7	5.671	69.42	<0.0001
timex bag trt.	7	0.121	1.48	0.17
time x nectar trt.	7	0.714	8.74	<0.0001
time x bag trt. x nectar trt.	7	0.285	3.50	0.0014

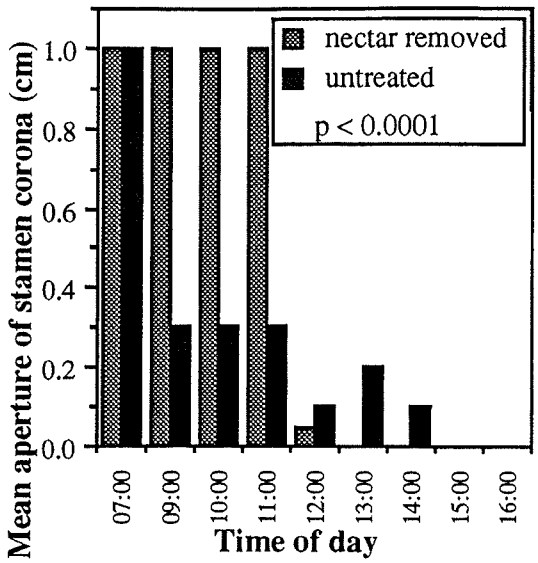

Figure 2. Effect of nectar removal on N.ampla stamen collapse (repeated measures ANOVA).

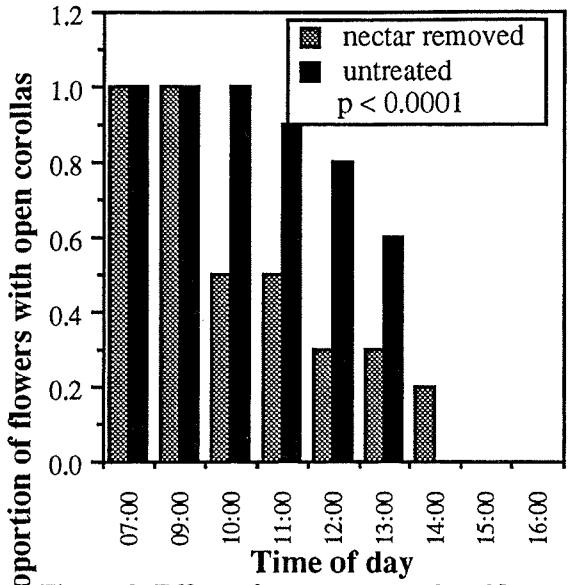

Figure 3. Effect of nectar removal on N. ampla corolla closure (repeated measures ANOVA).

open corolla in treated vs. untreated flowers. This suggests that two different mechanisms are at work.

We speculate that low nectar levels serve as a cue that enough pollinators have visited to pollinate the flower. If nectar levels are high, as in untreated flowers, visitation has not been sufficient to guarantee pollination. In this case, stamen coronas close earlier, forcing increased contact between pollinators and anthers and the ovary. This is consistent with the idea that cross-pollination is favorable to self pollination, but self-pollination is better than no pollination.

In contrast to stamen corona closure patterns, corolla closure is delayed in untreated flowers. We suggest that here also, as described above high nectar levels signal a lack of pollination, and the corolla is therefore left open to allow pollinators to enter. Both stamen coronas and corollas close by 14:00, possibly because the preferred pollinator is active in the morning.

Pollinator exclusion had no effect on time of stamen corona or corolla closure in either treatment. This suggests that mechanical disturbance or pollination does not affect the aperture of either the corolla or the stamen corona.

There still exist fundamental gaps in our knowledge of N. ampla pollination biology. Flowers are probably open for several days, and we do not know whether the trends we observed repeat every day. It would be interesting to study whether petal closure signals that pollination has occurred and triggers the development of the fruit. Manual pollination experiments could be used to test the effects of pollination on flower closure and determine whether the population is obligatorily outcrossing.