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Visitation of a specialist pollen feeder *Althaeus hibisci* Olivier (Coleoptera: Bruchidae) to flowers of *Hibiscus moscheutos* L. (Malvaceae)¹

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SHIMAMURA, R., N. KACHI (Department of Biological Sciences, Graduate School of Sciences, Tokyo Metropolitan University, Hachioji 192-0397, Japan), H. KUDOH (Department of Biology, Faculty of Science, Kobe University, Kobe 657-8501, Japan), AND D. F. WHIGHAM (Smithsonian Environmental Research Center, Edgewater, MD 21037). Visitation of a specialist pollen feeder *Althaeus hibisci* Olivier (Coleoptera: Bruchidae) to flowers of *Hibiscus moscheutos* L. (Malvaceae). *J. Torrey Bot. Soc.* 132: 197–203. 2005.—We investigated visitation of a bruchid seed beetle, *Althaeus hibisci* Olivier, to flowers of *Hibiscus moscheutos* L. (Malvaceae) under natural conditions. We examined movement of the beetle among flowers that were in different developmental stages, the correlation between corolla size and pollen production, and the correlation between beetle density and corolla size. Beetles moved diurnally from wilted *Hibiscus moscheutos* flowers that had opened on the previous day to newly open flowers. Beetles did not move to unopened flowers as long as petals were covered by sepals. The results demonstrate that the beetles use corollas as a cue to locate flowers. *Hibiscus moscheutos* flowers produced pollen in proportion to corolla size; therefore, beetles visiting larger flowers had a high probability of finding larger amounts of pollen. We detected positive correlations between beetle density and petal area when beetles were abundant. Although the correlation coefficients were small ($r = 0.24$ – 0.32), they were statistically significant or marginally significant. On the other hand, the correlations were not significant when the density of beetles was low suggesting that the preference for larger flowers is not always detectable and its strength varies with beetle density under natural conditions.

Key words: *Althaeus hibisci*, bruchid beetle, floral attraction, flower size, foraging, freshwater wetland, *Hibiscus moscheutos*, Maryland, pollen production.

In many plant species, corolla size varies among and within individuals (Bell 1985, Galen 1999, Wolfe and Krstolic 1999). Theoretically, if corolla size correlates with the amounts of resources provided by flowers, then insect visitors should select flowers based on corolla size to reduce the costs of movement and maximize their rates of resource gain. Previous studies have shown that pollinators prefer to visit flowers with larger corollas (Bell 1985, Young and

Stanton 1990, Stanton et al. 1991, Johnson et al. 1995).

Corolla size might also be important in determining the preference and behavior of small insect visitors (e.g., thrips, flies, small bees, and small beetles). Small insects are found to serve as pollinators in some systems (Momose et al. 1998a, b; Sakai et al. 1999). As pollen/ovule feeders, small insects may considerably reduce reproductive success of larger flowers (Brody 1992, Mutikainen and Delph 1996). Furthermore, small insects often use flowers as a site of mating and oviposition (Feller et al. 2003).

In this study, we investigated the responses of a bruchid seed beetle, *Althaeus hibisci* Olivier (hereafter referred to as *A. hibisci*), to natural corolla size variation in *Hibiscus moscheutos* L. (hereafter referred to as *Hibiscus*) flowers. Adults of *A. hibisci* visit *Hibiscus* flowers and forage for pollen (Spira 1989, Kudoh and Whigham 1998). Kudoh and Whigham (1998) reported that the density of *A. hibisci* on *H. moscheutos* flowers decreased when petal size was

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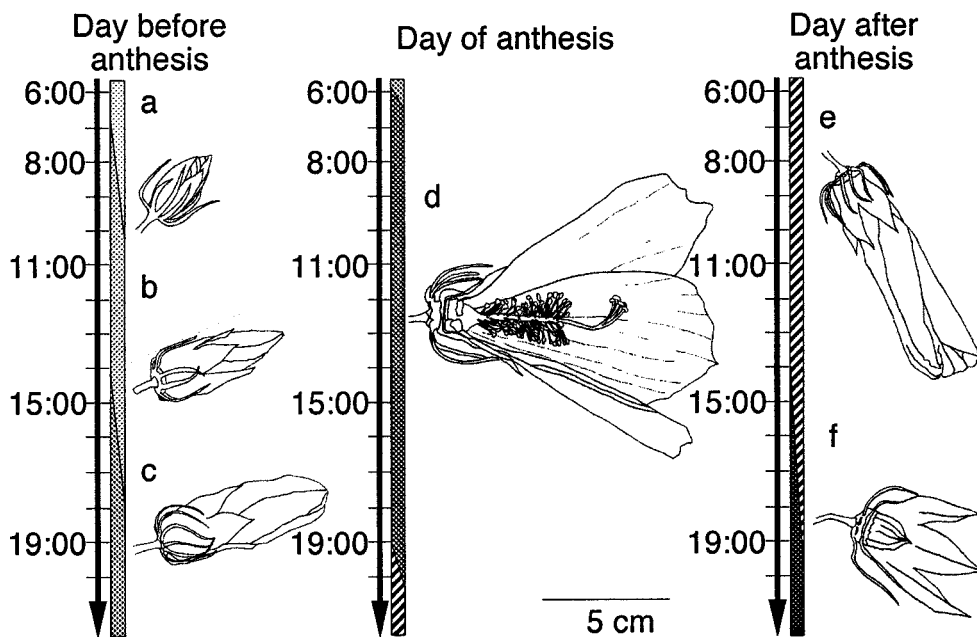


FIG. 1. Typical schedule of anthesis of a *Hibiscus moscheutos* flower. The corolla is covered by sepals until the morning of the day before anthesis (a). The corolla begins to appear from the sepals in the morning (b) and develops in the afternoon (c) of the day before anthesis. Flowers open at about 0600 hr (d). The flower closes in the night (e), and the wilted corolla falls by the evening of the next day (f). Two petals and two sepals were removed in (d) and (f) to show the inside of the flower. Shaded bars on the left side of each figure show the approximate periods of each flowering stage.

artificially reduced to the smallest size class found in natural populations. Under natural conditions, *H. moscheutos* exhibits continuous variation in corolla size. To understand the impact of *A. hibisci* on seed production it is necessary to understand how these beetles respond to the natural variation in a floral trait.

To evaluate the effects of corolla size on flower preference by *A. hibisci*, we addressed the following questions: (1) Does *A. hibisci* arrive at *Hibiscus* flowers before or while they are open? (2) Is corolla size used as a cue in flower choice by *A. hibisci*? (3) Does corolla size correlate with the amount of pollen in *Hibiscus* flowers? (4) Does the density of *A. hibisci* in flowers correlate with corolla size?

Materials and Methods. STUDY SYSTEM. *Hibiscus moscheutos* L. (Malvaceae) is a herbaceous perennial native to freshwater and brackish marshes of eastern North America (Brown and Brown 1984). Plants have few to many upright stems, 1–2 m tall. The flowering season extends from late July to early September, and the flowers are relatively large (10–15 cm across), with white or pink petals that open

for a single day (Spira 1989). Flowers open at dawn and close by night (Fig. 1). Time of anthesis may depend on temperature because anthesis is delayed on rainy days and later in the flowering season (Ryouji Shimamura, personal observation). Flowers are pollinated mainly by an anthophorid bee, *Ptilothrix bombiformis* Cresson, and by a bumblebee, *Bombus pennsylvanicus* DeGeer (Spira 1989). The flowers are self-compatible, but spatial separation of the stigmas and the anthers prevents automatic self-pollination (Spira 1989).

Adults of *A. hibisci* Olivier are 2.0–2.5 mm in length and feed on *Hibiscus* pollen (Weiss and Dickerson 1919). Female *A. hibisci* oviposits on the outside of the green ovary. Larvae enter ovules in developing fruits and consume the entire content of the seed, except for the seed coat. Larvae pupate in the seed and emerge as adults from late September to November. Another seed predator, the curculionid weevil *Conotrachelus fissunguis* Lec., also visits flowers to forage on pollen and females oviposit into the developing fruits (Weiss and Dickerson 1919, Kudoh and Whigham 1998).

The study site was located in a freshwater

wetland in the Smithsonian Environmental Research Center, Maryland, USA (38° 53' N, 76° 33' W), locally known as Mill Swamp. Our study site corresponds to the site No. 2 in Kudoh and Whigham (1997) and to the site where corolla-size manipulation experiments were performed by Kudoh and Whigham (1998). The shoot density of *H. moscheutos* averaged 19.4 stems m⁻² at the study site (Kudoh and Whigham 1997).

MOVEMENT OF *A. HIBISCI* AMONG DIFFERENT FLOWER STAGES. To determine the density of *A. hibisci* among different flower stages, at four sampling times per day (0800 hr, 1100 hr, 1500 hr, and 1900 hr), we collected 12 samples each of flowers in three developmental stages: flower buds that would open on the next day (Fig. 1a, b), open flowers (Fig. 1d), and closed flowers that had opened on the previous day (Fig. 1e). We set four 60 m line transects crossing the *Hibiscus* population in the study site. At each sampling time, we collected flowers in three stages at 5 m intervals among one of the transects. Each flower, including any *A. hibisci* beetles, was carefully put into a plastic bag. The number of *A. hibisci* in each flower was counted in the laboratory. Collections were made on 20 August 1995 and 2, 17, and 26 August 1998. We selected sunny days for flower collections.

A three-way analysis of variance (ANOVA) was conducted to determine the effects of flower stage, time of day, and date on density of *A. hibisci* per flower (Sokal and Rohlf 1995). Two variables, flower stage and time of day, were treated as fixed factors and one variable, date was as a random factor (mixed model ANOVA). Data were log-transformed for the analysis to ensure data normality and variance homogeneity.

CORRELATIONS BETWEEN PETAL AREA AND POLLEN PRODUCTION. To examine correlations between petal area and pollen production, 25 flower buds that would open the next day (Fig. 1b, c) were bagged to preclude pollen removal. On the next day, the flowers were collected after anthesis. Collections were performed on 2, 18, and 25 August 1998. In the laboratory, individual flowers were divided into three groups: (1) stigmas, styles, ovary, and staminal column; (2) parts of stamens above the point of attachment to the staminal column (hereafter referred to as stamens); and (3) petals. We also separated other supporting/protection parts (sepals, a receptacle with epicalyx) but did not include them in the

analyses. We measured petal area of each flower with an area meter (Model LI-3100; Li-Cor Inc., Lincoln, Nebraska, USA). The three groups for each flower were dried at 60 °C in a forced air oven for two days. Dried materials were weighed to the nearest 0.1 mg. We treated dry weight of stamens as approximation of pollen production. Pearson's correlation coefficients were calculated between the dry weights of stamens and the petal area. Dry matter allocation to petals and stamens was calculated for each flower as proportions of the total dry weight of reproductive parts (total of the above mentioned three groups). Significant deviations of correlation coefficients (*r*) from zero were tested using Fisher's *z* transformation (Sokal and Rohlf 1995).

RESPONSES OF *A. HIBISCI* TO COROLLA SIZE VARIATIONS. To examine the relationship between corolla size and density of *A. hibisci*, we collected 53, 52, 52, 25 and 25 open flowers at 1500 hr during five sunny days; 25, 26, and 27 August 1997, and 21 and 27 August 1998, respectively. Flowers were collected at approximately 5-m intervals along multiple 60-m line transects across the *Hibiscus* population. The collection was made on 1500 hr because petals become fully open around 1200 hr and the beetle density was highest at the 1500 hr based on a 1995 survey. Each flower was carefully put into a plastic bag. We measured petal area of each flower and counted the number of *A. hibisci* per flower. Pearson's correlation coefficients between petal area and the number of *A. hibisci* were calculated for each sampling date. A nested ANOVA was conducted to test difference between years on petal area (Sokal and Rohlf 1995). In the nested ANOVA, sampling dates were nested within year.

Results. **MOVEMENT OF *A. HIBISCI*.** The number of *A. hibisci* per flower changed with time and the changes differed among flower stages as indicated by a significant time × flower stage interaction in the three-way ANOVA (Fig. 2, Table 1). The number of *A. hibisci* captured in open flowers tended to increase with time of day but the pattern was temporally variable (Fig. 2). On 20 August 1995, the proportion of open flowers with *A. hibisci* increased from 50% at 0800 hr to 100% at 1100 hr. The number of beetles decreased with time in closed flowers (Fig. 2). There were few *A. hibisci* on flowers in the bud stage at any time of day.

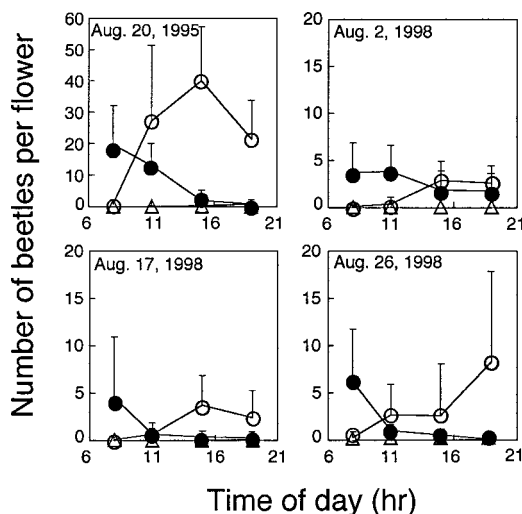


FIG. 2. Daytime changes in the average number of *Althaeus hibisci* per *Hibiscus moscheutos* flower in the following developmental stages: flower buds (open triangles), open flowers (open circles), and closed flowers (closed circles). Flowers and flower buds were harvested on 20 August 1995, and on 2 August, 17 August, and 26 August 1998. Bars show one standard deviation.

The ANOVA also showed a significant effect of sampling date on beetle numbers (Table 1). The number of *A. hibisci* per flower ranged from 0 to 77 in 1995 and from 0 to 31 in 1998. The mean numbers of *A. hibisci* per flower on each date were 10.5 on 20 August 1995, and 1.4 on 2 August, 1.0 on 17 August, and 1.8 on 26 August 1998. The mean density on 20 August 1995 was significantly higher than those on any of the sampling dates in 1998 (Scheffé's multiple comparison test, $P < 0.001$). In the ANOVA, time was not significantly related to beetle numbers (Table 1).

CORRELATIONS BETWEEN POLLEN PRODUCTION AND PETAL SIZE. On average, petals and stamens

Table 2. Pearson's correlation coefficients (r) between stamen weight and petal area for three different sampling dates. Asterisks indicate significance levels: ***, $P < 0.001$; **, $P < 0.01$. Number of examined flowers (N) and Fisher's z -transformation statistics (z) are also listed.

Sampling dates (1998)	N	r	z
2 August	25	0.61	0.71***
18 August	26	0.87	1.34***
25 August	26	0.59	0.69**

accounted for approximately 67% and 15% biomass, respectively, of the reproductive parts of flowers. Stamen dry weight showed significant positive correlations with petal area for all three sampling dates (Table 2).

RESPONSES OF *A. HIBISCI* TO COROLLA SIZE. Petal area per flower varied from 62.3 to 273.4 and from 98.5 to 335.2 cm² (mean = 175.2 and 200.9 cm²) in 1997 and 1998, respectively. The nested ANOVA showed no significant difference between years in petal area although the date within year term was significant (Table 3). The beetles were found in 85%, 100%, 99%, 80%, and 84% of the flowers sampled on 25, 26 and 27 August 1997, and 21 and 27 August 1998, respectively. In 1997, correlations between petal area and the number of *A. hibisci* per flower were weak ($r = 0.24$ – 0.32) but statistically significant or marginally significant ($P = 0.02$ – 0.09 , Figs. 3a, b, c). In 1998, no significant correlation was found between the petal area and the number of *A. hibisci* (Figs. 3d, e).

Discussion. FLOWER VISITATION BY *A. HIBISCI*. The diurnal changes in the densities of *A. hibisci* (Fig. 2, Table 1) indicates that the beetles moved from closed flowers to open flowers after they began to open. The data suggest that *A. hibisci*

Table 1. Three-way ANOVA (mixed model) on number of *Althaeus hibisci* per *Hibiscus moscheutos* flower. Degrees of freedom (df), sum of squares (SS), mean squares (MS) and F values were listed. Adjusted coefficient of determination was 0.71. Asterisks indicate significance levels: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. Data were log₁₀ transformed.

Source	df	SS	MS	F
Flower stage	2	658.2	329.1	15.4**
Time	3	11.2	3.9	0.8
Date	3	304.5	101.5	87.7***
Time × Flower stage	6	451.2	75.2	15.3***
Flower stage × Date	6	127.9	21.3	18.4***
Time × Date	9	46.1	5.1	4.4***
Time × Flower stage × Date	18	88.6	4.9	5.3***
Residual	536	620.6	1.2	

Table 3. Nested ANOVA on petal area of *Hibiscus moscheutos* flowers. Degrees of freedom (df), sum of squares (SS), mean squares (MS) and *F* values were listed. Adjusted coefficient of determination was 0.10. Asterisks show levels of significance: ***, $P < 0.001$.

Source	df	SS	MS	<i>F</i>
Year	1	24977.4	24977.4	2.8
Date (Year)	3	26320.8	8773.6	4.4***
Residual	202	399137.1	1975.9	

stays in an individual flower during the day that it opens and the night following anthesis. This behavior is suggested by our observations that in the morning (0800 hr), just after anthesis of new flowers, most beetles were found in closed flowers that had been open during the previous day. Non-significant effect of time of day on the beetle densities in the ANOVA (Table 1) infers that population density of the beetles is more or less constant within the sampling days in the study site.

We rarely found *A. hibisci* on flowers that were in the bud stage (Fig. 2). This result sug-

gests that *A. hibisci* use corollas as a cue for locating flowers. The finding is also supported by the results of petal size manipulation experiments reported by Kudoh and Whigham (1998) who found that no *A. hibisci* visited flowers without corollas. Many insects use combined visual and chemical information to locate potential hosts (Kevan and Baker 1983; Prokopy and Owens 1983). Some beetle species locate flowers by sight (Goldblatt *et al.* 1998). We do not know whether *A. hibisci* uses sight, scent, or both senses to locate and select flowers. The diurnal habit of *A. hibisci* suggests that these beetles use visual cues, at least in part, to locate flowers.

RESPONSE OF *A. HIBISCI* TO FLOWER SIZE. The results indicated that beetles visiting larger flowers had a high probability of encountering larger amounts of pollen. Petal area was positively related to the amount of pollen (Table 2). The *r*-values (0.59–0.87) found in this study were comparable to or greater than those detected in previous studies, e.g., $r = 0.93$ for *Amaryllis*

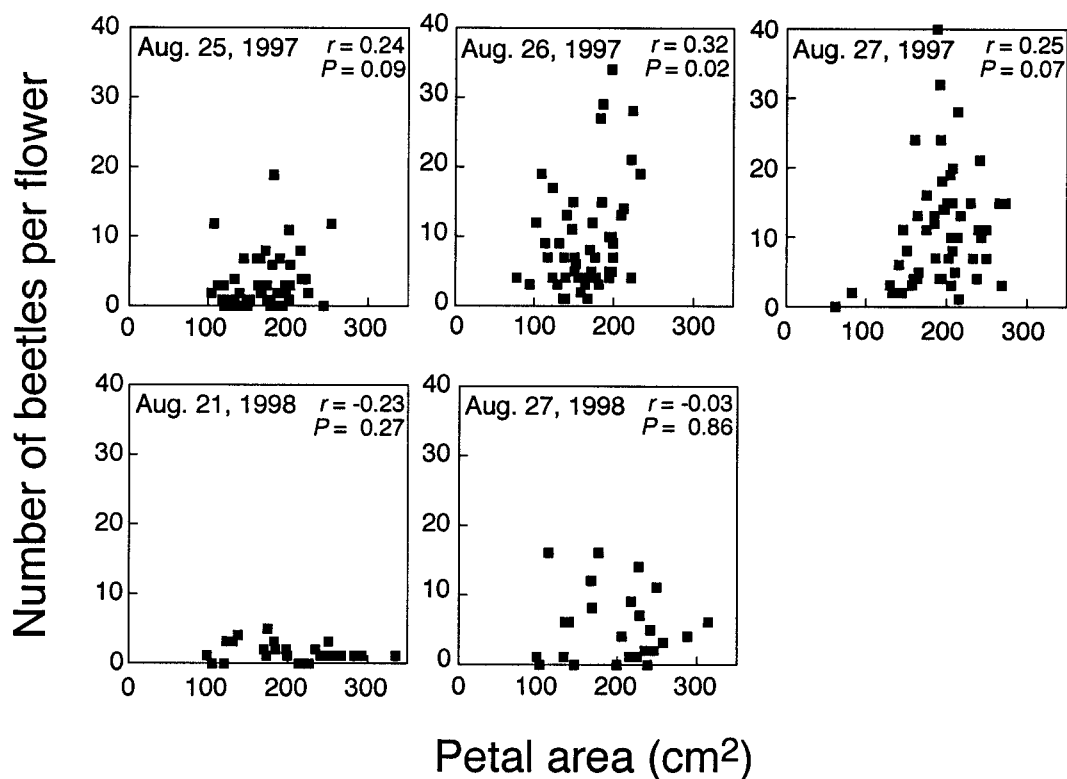


FIG. 3. Correlations between petal area and number of *Althaeus hibisci* per flower on 25 August, 26 August, and 27 August 1997, and on 21 August and 27 August 1998. Number of examined flowers were 53, 52, 52, 25, 25, and 25 for August 25, 26 and 27, 1997, and August 21 and 27, 1998. Pearson's correlation coefficients (*r*) and significance levels (*P*) are shown.

spp. (Smith and Evenson 1978), 0.37–0.78 for *Impatiens capensis* (Bell 1985), 0.34–0.57 for *Raphanus sativus* (Stanton and Preston 1988), and 0.19–0.39 for *Wurmbea dioica* (Vaughton and Ramsey 1998). The preference for larger flowers in petal-manipulated flowers (Kudoh and Whigham 1998) suggests that *A. hibisci* does not respond directly to the amount of pollen but to the corolla size.

Our results, however, show that a preference for larger flowers by *A. hibisci* does not always result in higher beetle densities in larger flowers under natural conditions. Our data suggest, however, that a positive correlation between petal size and beetle density occurs when beetle abundance is high. The number of beetles per flower was greater in 1997 (mean = 8.1 and maximum = 40) than in 1998 (mean = 3.5 and maximum = 16). We only detected positive correlations between the number of beetles on a flower and the petal area in only 1997 (Fig. 3). In years of low beetle densities, even small flowers may have enough pollen resources and may allow beetles to visit flowers irrespective of corolla size. In other pollinator-flower systems, it has been reported that response of pollinators to corolla size appeared under high pollinator densities (Eckhart 1991, Conner and Rush 1996). Various factors, such as number of host flowers in the previous year, densities of competing insect species, and climatic conditions during winter, can be responsible for yearly changes in density of insect visitors (Young and Stanton 1990, Johnson et al. 1995, Krupnick et al. 1999). We were unable to detect any simple correlates between density of *A. hibisci* in 1998 and climatological data (air temperature and precipitation) from the SERC Weather Station.

Although corolla size of *Hibiscus* flowers can be used by *A. hibisci* as an indicator of pollen quantity, we need further studies to determine whether or not the beetles has evolved a preference to larger flowers as a foraging response. Because *Hibiscus* flowers are also used for the mating site of *A. hibisci*, the beetles may prefer a larger flower if mating success is greater in larger flowers. Further studies should also elucidate how *A. hibisci* responds to corolla size under various beetle abundances and whether the behavior of *A. hibisci* affects reproductive success of *Hibiscus*.

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