

# NECTAR FEEDING ACTIVITY OF *Aedes* MOSQUITOES, WITH SPECIAL REFERENCE TO *Aedes communis* FEMALES

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**ABSTRACT.** A total of 5,721 mosquitoes (6% males) of 16 species were collected with an aerial net, when attracted to the investigator, during May–August 1984 at 2 sites in central Sweden. The majority of the mosquitoes collected (63%) were *Aedes communis*. *Aedes communis* females at both localities showed peak flight activity at evening twilight. At one site, a diel pattern of nectar feeding was correlated with host seeking activity; at the other site no correlation was found. Seasonal differences in mean fructose content of the mosquitoes were found. Among the 94 blood-fed females (belonging to 6 species) that were collected, 71% were fructose positive ( $n = 67$ ) and in different ovarian stages.

## INTRODUCTION

Adult mosquitoes have daily rhythms with specific periods of activity and rest. The flight activity period for mosquitoes includes various behaviors such as host seeking, nectar and blood feeding, mating and ovipositing (Service 1971).

Flight activity is triggered by daily changes in light intensity, e.g., at dusk and dawn, heavy cloud cover, etc. The response of the mosquitoes is further modified by other climatic factors, such as temperature, relative humidity, rain and wind velocity (Wright and Knight 1966).

Mosquito flight may be classified as migratory, appetential or consummatory (Bidlingmayer 1985). Migration is rare among mosquitoes, whereas appetential and consummatory flights are very common (Provost 1952, 1953). Most species are crepuscular and show peak flight activity at dusk (Service 1971, Jaenson 1988). This flight period includes both males and females, and is correlated with host seeking and blood feeding behaviors (Service 1971, 1977).

For prolonged flights, e.g., host seeking or swarming, mosquitoes need extra energy. Sugar is an important source of energy for flight dispersal, reproduction and survival (Nayar and Sauerman 1975a, 1975b) and is available as nectar from flowers or honeydew from aphids.

The purpose of my study was to determine if diel host seeking and nectar feeding activities are correlated. I also wanted to clarify if different species of mosquitoes nectar feed at different times. Data about species composition in 2 different habitats, seasonal occurrence of species and blooming periods of flowering plants abundant in the areas are also presented.

## MATERIALS AND METHODS

**Study areas:** Mosquitoes were collected approximately once a week from late May through the first week in August, 1984, at 2 localities

(Marielund and Florarna) in the province of Uppland, Sweden.

1) Marielund (59°51'N, 17°60'E) is a small deciduous forest surrounded by farms. In June sloe (*Prunus padus* L.), wood cranesbill (*Geranium sylvaticum* L.) and cow parsley (*Anthriscus sylvestris* (L.) Hoffm.) are the dominant blooming plants. In July these are replaced by blooming meadow sweet (*Filipendula ulmaria* (L.) Maxim.) and ground elder (*Aegopodium podagraria* L.). Most of the mosquitoes at this site emerged from shallow snow-melt pools.

2) Florarna (60°17'N, 17°60'E) is a large bog surrounded by coniferous forest. It is a nature reserve and relatively unaffected by human activity. In early June blueberry (*Vaccinium myrtillus* L.), bog bilberry (*V. uliginosum* L.) and crystal tea (*Ledum palustre* L.) are flowering. In late June–early July cloudberry (*Rubus chamaemorus* L.) and cow parsley are the most abundant nectar sources. Most of the mosquitoes developed in deep pools at the edges of the bog.

**Collection and processing of the mosquitoes:** On May 31 (Marielund) and on June 2 (Florarna), 24-h studies were carried out to determine the times of greatest flight activity. Adult mosquitoes, attracted to the sedentary collector, were sampled with an aerial net. Samplings were carried out for 5–10 min at 30-min intervals during the studies, the shorter period used when mosquitoes were more abundant. Based on these preparatory studies, collection on the other dates (Table 1, a and b) were carried out, in a similar fashion, between 1600 h and 0300 h local time. Because of the sampling method, the majority of mosquitoes caught were host seeking, anthropophilic females, whereas ornithophilic species, like *Culex pipiens* Linn. and *Cx. torrentium* Martini were underrepresented in the samples (Jaenson and Niklasson 1986, Jaenson 1988).

Temperature and relative humidity were measured with a hygromograph continuously during the studies. Wind velocity and

Table 1a. Seasonal occurrence of empty, nulliparous (N) and parous (P) female mosquitoes at Marielund.

Species	Parity state	May		June				July			August	Total captured
		31	10	18	26	4	17	30	22			
<i>Aedes cantans</i>	N	4	18	70	58	13	2	0	4	169		
	P	0	5	13	13	5	18	14	14	82		
<i>Ae. cinereus</i>	N	5	2	45	22	2	0	1	0	77		
	P	0	0	6	8	3	2	14	7	40		
<i>Ae. communis</i>	N	498	68	52	33	0	0	0	0	651		
	P	12	12	56	49	25	25	0	0	179		
<i>Ae. diantaeus</i>	N	4	7	4	0	0	0	0	0	15		
	P	0	1	1	2	5	0	0	0	9		
<i>Ae. punctor s.l.</i>	N	16	14	7	0	0	0	1	0	38		
	P	1	5	0	4	0	1	0	0	11		

Table 1b. Seasonal occurrence of empty, nulliparous (N) and parous (P) female mosquitoes at Florarna.

Species	Parity state	June				July		August	Total captured
		2	12	20	29	10	24	20	
<i>Aedes cantans</i>	N	0	10	12	36	3	0	0	61
	P	0	0	10	12	28	9	3	62
<i>Ae. cinereus</i>	N	0	4	31	45	15	4	0	99
	P	0	0	6	27	96	47	6	182
<i>Ae. communis</i>	N	659	353	228	71	0	0	0	1,311
	P	24	94	196	387	198	118	24	1,041
<i>Ae. diantaeus</i>	N	60	2	10	16	5	0	0	93
	P	0	4	8	34	36	19	0	101
<i>Ae. intrudens</i>	N	92	10	0	0	0	0	0	102
	P	19	47	28	13	0	6	0	113
<i>Ae. punctor s.l.</i>	N	279	110	26	0	0	0	0	415
	P	0	36	48	40	28	36	0	188

cloud cover were estimated and recorded every hour. During the 24-h studies mean nectar content in flowers of the 2 most abundant flowering plants (wood cranesbill at Marielund and bog bilberry at Florarna) was measured with a capillary tube. Nectar was collected from 20 fresh flowers every hour and mean nectar content per flower was calculated.

The mosquitoes collected were immediately killed with cyanide, put in vials kept on ice and later stored at -70°C. Within 2-15 months the specimens were identified according to species and sex. Females were classified according to abdominal stages of blood feeding (E = empty, FF = freshly fed, LF = late stage fed, HG = half gravid, SG = subgravid, G = gravid) and dissected to determine parity (Detinova 1962) and ovarian stage (Christophers 1911). The remainder of each mosquito was tested for fructose using cold anthrone (Van Handel 1972). The intensity of blue color, which depends on the amount of fructose in the sample, was scored from 0 to 3 after 30 min.

*Measurements of feeding activity:* The diel host seeking activity was calculated as the mean number of individuals caught per minute with the aerial net, since sampling periods varied between 5 and 10 min.

Nectar feeding activity was measured as the percentage of mosquitoes, within each aerial net sample, containing fructose. Numbers of samples per collection day varied slightly, between 10 and 15, depending on mosquito activity. To study changes in nectar feeding activity during the season, mean fructose content (based on blue color scoring in the anthrone test) was calculated for each sampling date.

Due to the characteristics of the samples (non-normality and ordinal level of measurement), non-parametric statistics were used to analyse the data (Siegel 1956).

## RESULTS

*Species composition and seasonal occurrence:* Species composition of mosquitoes differed significantly between the 2 localities ( $\chi^2$ ,  $P < 0.0001$ ,  $n = 5,721$ ). *Aedes communis* (DeGeer) and *Ae. cinereus* Meigen were common in both habitats (Table 2). *Aedes cantans* (Meigen) was significantly more abundant at Marielund ( $P < 0.01$ ,  $n = 400$ ), whereas black-legged *Ochlerotatus* mosquitoes such as *Ae. diantaeus* Howard, Dyar and Knab ( $P < 0.05$ ,  $n = 228$ ) and *Ae. punctor* (Kirby) ( $P < 0.01$ ,  $n = 769$ ) were more typical for the coniferous habitat at Florarna.

Table 2. Species composition at Marielund and Florarna.

Species	Marielund			Florarna		
	Number		% of total catch	Number		% of total catch
	♀	♂		♀	♂	
<i>Anopheles claviger</i>	2	0	0.1	0	0	0
<i>An. maculipennis s.l.</i>	1	0	0.06	0	0	0
<i>Aedes cantans</i>	255	25	17.1	126	1	3.1
<i>Ae. cataphylla</i>	1	0	0.06	1	0	0.02
<i>Ae. cinereus</i>	122	5	7.7	290	4	7.2
<i>Ae. communis</i>	834	240	65.4	2,384	105	61.0
<i>Ae. dianiaetus</i>	24	2	1.6	194	8	5.0
<i>Ae. excrucians s.l.</i>	21	0	1.3	13	0	0.3
<i>Ae. intrudens</i>	2	0	0.1	219	3	5.4
<i>Ae. punctor s.l.</i>	51	10	3.7	620	108	17.8
<i>Culex pipiens</i>	9	0	0.6	1	0	0.02
<i>Cx. torrentium</i>	2	0	0.1	0	0	0
<i>Culiseta alaskaensis</i>	1	0	0.06	1	0	0.02
<i>Cs. bergrothi</i>	1	0	0.06	0	0	0
<i>Cs. morsitans</i>	0	0	0	1	0	0.02
<i>Coquillettidia richiardii</i>	15	0	0.9	1	0	0.02
Total	1,358	282		3,852	229	

The adults of *Ae. communis* emerged early in the season, both at Marielund and Florarna (Table 1, a and b). With one exception, each species had similar emergence and peak abundance periods in the 2 habitats. Peak abundance of *Ae. cinereus* was 3 weeks earlier at Marielund than at Florarna (Kolmogorov-Smirnov,  $P < 0.001$ ,  $n = 411$ ).

**Diel pattern of host seeking and nectar feeding:** Both at Marielund and Florarna *Ae. communis* females showed peak flight activity, i.e., host seeking, at evening twilight about ½ hour after sunset (Fig. 1, A and B). At Florarna, *Ae. punctor* showed a similar pattern of behavior (Fig 1c). No activity at morning twilight was found at either site, perhaps due to low temperatures (5–7°C). Females of other species were not caught in sufficient numbers to determine the specific patterns of diel flight or feeding activities.

For *Ae. communis* at Florarna, nectar feeding (percentage fructose positive) was positively correlated with host seeking activity during the whole season (Table 3). At Marielund, however, this species fed on nectar sporadically throughout daytime and nectar feeding was not correlated with host seeking (Table 3). *Aedes cinereus* at Florarna showed increasing host seeking activity with rising temperature and decreasing relative humidity (Table 3).

Nectar feeding activity was also correlated with falling temperature and increasing relative humidity for *Ae. communis* at Florarna (Table 3). *Aedes dianiaetus*, *Ae. intrudens* and *Ae. punctor* showed an increase in nectar feeding activity with falling temperature (Table 3).

Neither nectar feeding or host seeking activities showed any significant correlation with

wind velocity or cloud cover. Amounts of nectar collected from the most common flowering plant in each habitat peaked at 1400–1500 h at Marielund (wood cranesbill), and at 2300–2400 h at Florarna (bog bilberry) (Fig. 2).

**Nectar feeding in relation to blood feeding and ovarian development:** Time of nectar feeding and host seeking did not differ significantly between nulliparous (= females that have not laid eggs) and parous (= females that have laid eggs) females with one exception. On June 20 at Florarna, parous females of *Ae. communis* sought hosts and also fed on nectar later in the evening than nulliparous females of the same species (Kolmogorov-Smirnov  $P < 0.001$ ,  $n = 344$ ).

Also, over the season, parous females contained significantly more fructose (higher anthrone test score) than nulliparous females caught on the same day, in both Marielund (Wilcoxon,  $P < 0.01$ ,  $n = 830$ ) and Florarna ( $P < 0.01$ ,  $n = 2,352$ ). This was not correlated with the fluctuations of mean fructose content in mosquitoes over the season (Fig. 3, A and B).

Most females caught were empty, i.e., they did not contain vertebrate blood. Ninety-four individuals (1.6% of the mosquitoes collected) contained host blood and were in different stages of ovarian development (Table 4). Nectar fed *Ae. communis* in several different stages of follicular development were found. The other species, except *Ae. cinereus*, had some fructose positive specimens in some stages of ovarian development (Table 4).

**Seasonal pattern of nectar feeding:** Individuals were pooled by species for each sampling date and mean fructose contents were calculated for each sample (Fig. 3, A and B). In *Ae. communis*

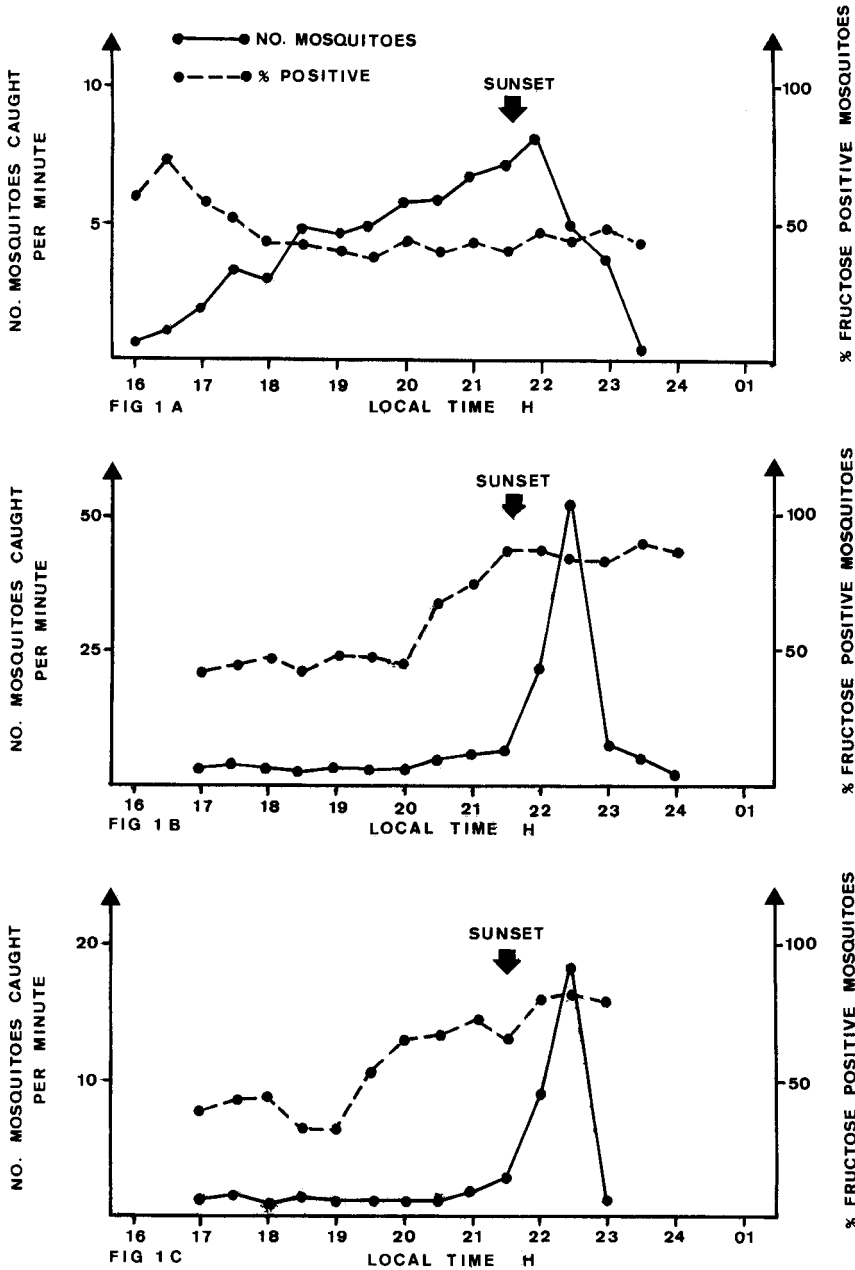


Fig. 1A. Diel flight and nectar feeding activity of empty, nulliparous *Aedes communis* females ( $n = 510$ ) at Marielund on May 31. B. Diel flight and nectar feeding activity of empty, nulliparous *Aedes communis* females ( $n = 659$ ) at Florarna on June 2. C. Diel flight and nectar feeding activity of empty, nulliparous *Aedes punctor* females ( $n = 279$ ) at Florarna on June 2.

a significant difference in fructose content between all dates was found, both at Marielund (Kruskal-Wallis,  $P < 0.001$ ,  $n = 830$ ) and at Florarna ( $P > 0.0001$ ,  $n = 2,352$ ). These significant differences did not correspond to differing proportions of parous females in the samples,

differing numbers of mosquitoes caught on different dates or differing times of peak flight activity over the season (Spearman rank correlation). In the other less abundant species, no significant differences in fructose content during the season were found. Mosquitoes were

Table 3. Nectar feeding correlated with temperature, relative humidity and host seeking activity. Host seeking correlated with temperature and relative humidity in both Marielund (M) and Florarna (F) (Spearman rank correlation).

Species	Locality	Temperature		Rel. humidity		Host seeking		Temperature		Rel. humidity	
<i>Aedes cantans</i>	M	-0.24	N.S.	-0.04	N.S.	0.05	N.S.	0.022	N.S.	0.26	N.S.
	F	-0.15	N.S.	0.15	N.S.	0.21	N.S.	0.04	N.S.	-0.31	N.S.
<i>Ae. cinereus</i>	M	0.15	N.S.	-0.15	N.S.	0.11	N.S.	0.21	N.S.	0.21	N.S.
	F	-0.20	N.S.	0.19	N.S.	-0.16	N.S.	0.70	***	-0.51	**
<i>Ae. communis</i>	M	0.18	N.S.	0.02	N.S.	-0.05	N.S.	0.07	N.S.	-0.16	N.S.
	F	-0.61	***	0.50	***	0.40	***	-0.27	*	-0.19	N.S.
<i>Ae. diaantaeus</i>	M	-0.16	N.S.	0.61	*	0.25	N.S.	0.23	N.S.	0.22	N.S.
	F	-0.34	*	0.07	N.S.	0.21	N.S.	0.01	N.S.	-0.10	N.S.
<i>Ae. intrudens</i>	M	—	—	—	—	—	—	—	—	—	—
	F	-0.50	***	0.24	N.S.	0.18	N.S.	-0.10	N.S.	-0.11	N.S.
<i>Ae. punctator</i>	M	0.11	N.S.	0.27	N.S.	0.14	N.S.	-0.21	N.S.	0.05	N.S.
	F	-0.32	**	0.19	N.S.	0.22	N.S.	-0.16	N.S.	0.07	N.S.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ . Correlation between temperature and relative humidity varied between -0.58 and -0.98,  $P = 0.001$ , sample sizes between 16 and 67. No correlation between wind velocity and nectar feeding or host seeking activities were found.

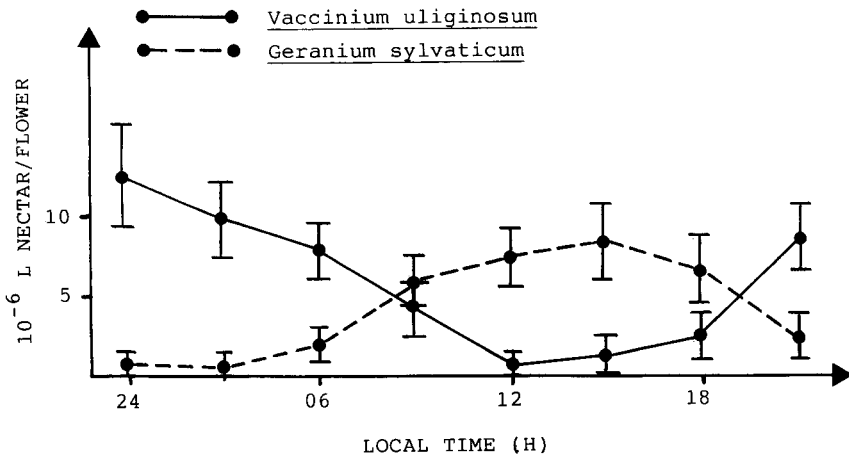


Fig. 2. Mean nectar content  $\pm$  SD in single flowers of *Vaccinium uliginosum* ( $n = 160$ ) and *Geranium sylvaticum* ( $n = 160$ ) during the day.

observed to nectar feed on all flowers listed in Fig. 3, A and B, except *Geranium sylvaticum* (wood cranesbill) and *Filipendula ulmaria* (meadow sweet).

DISCUSSION

*Species composition and seasonal occurrence:* *Aedes cantans* was a typical species for the deciduous habitat at Marielund, whereas *Ae. diaantaeus* and *Ae. punctator* were more typical for the coniferous habitat at Florarna. Species like *Ae. cinereus* and *Ae. communis* seem to be more opportunistic in their choice of habitat. One likely explanation for this is that the latter species are more tolerant in their larval requirements, e.g., pH of water and microorganisms for food, and/or less susceptible to larval predators or parasites.

The only species that showed a difference in peak abundance time was *Ae. cinereus*. It was the last species to emerge during the season, and therefore *Ae. cinereus* larvae at Marielund were exposed to pools drying up. This accelerated the larval development and resulted in an earlier peak abundance period for *Ae. cinereus* at Marielund compared with Florarna.

*Diel pattern of nectar feeding and host seeking activities:* At Florarna host seeking and nectar feeding activities of *Ae. communis* were correlated, which confirms earlier findings (Grimstad and DeFoliart 1975). The nectar feeding activities were also correlated with falling temperature and increasing relative humidity; these climatic changes apparently enhancing the nectar feeding behavior. At Marielund, however, no correlation between nectar and host seeking activities could be found on any date.

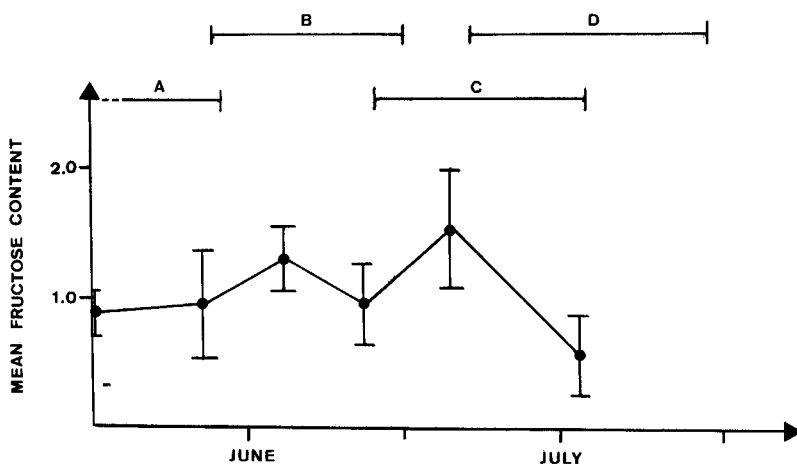


FIG 3 A

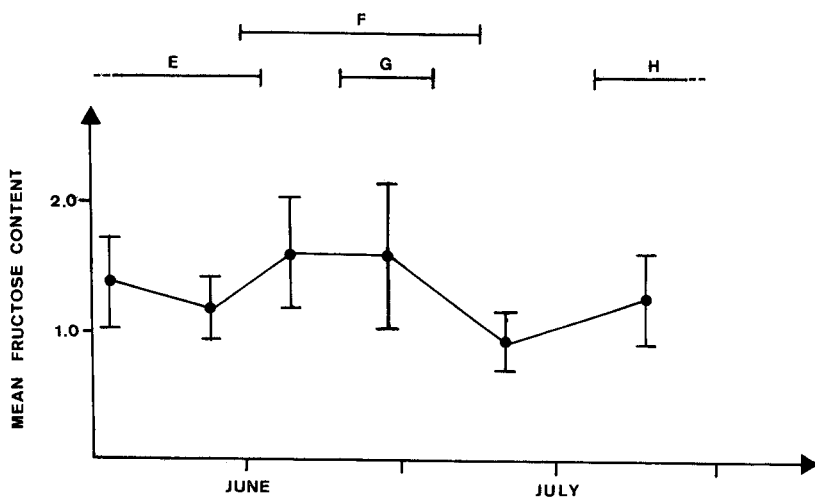


FIG 3 B

Fig. 3A. Mean fructose content  $\pm$  SD (ordinal scale 0-3) in samples of *Aedes communis* females ( $n = 830$ ) from Marielund during the season. Blooming periods for A = *Geranium sylvaticum* and *Myosotis arvensis*, B = *Anthriscus sylvestris*, C = *Aegopodium podagraria* and D = *Filipendula ulmaria*. B. Mean fructose content  $\pm$  SD (ordinal scale 0-3) in samples of *Aedes communis* females ( $n = 2,352$ ) from Florarna during the season. Blooming periods for E = *Vaccinium uliginosum* and *Ledum palustre*, F = *Anthriscus sylvestris*, G = *Rubus chamaemorus* and H = *Achillea millefolium*.

Table 4. Nectar feeding in mosquito females in relation to abdominal stages. Mosquitoes from Marielund and Florarna are pooled. + = fructose positive, - = fructose negative specimens.

Species	Freshly blood-fed		Late stage fed		Half gravid		Sub-gravid		Gravid		Total
	+	-	+	-	+	-	+	-	+	-	
<i>Aedes cantans</i>	3	2				1	1				7
<i>Ae. cinereus</i>		7		1						2	10
<i>Ae. communis</i>	7	2	7	1	8	3	4		16	4	53
<i>Ae. diantaeus</i>					1						1
<i>Ae. intrudens</i>	1				1		2				4
<i>Ae. punctor s.l.</i>	2		5	1	4				5	2	19
Total	13	11	12	3	14	4	7	0	21	8	94

Grimstad and DeFoliart (1975) also suggested that nectar feeding is controlled by an endogenous circadian rhythm. If this rhythm could be modified within different populations of the same species, i.e., *Ae. communis*, due to adaptations to floral composition and times of peak nectar production, this could explain the difference in nectar feeding times between the 2 habitats.

A negative correlation between nectar feeding and temperature was found for 4 species at Florarna. This indicates: 1) nectar feeding activity increases when the temperature is falling, or 2) nectar digestion rates decrease with falling temperature.

Times of host seeking activities were similar in both habitats for *Ae. communis*, suggesting that this behavior was not affected by the habitat differences. Most likely the host seeking behavior was triggered by the onset of dusk, i.e., decreasing light intensity.

*Seasonal pattern of nectar feeding:* Mean fructose content in females of *Ae. communis* varied over the season. On all the sampling dates, except June 20, there were no differences in flight activity due to parity, time of nectar feeding or fructose content. It appears that these differences in mean fructose content depend on availability of flowering plants and their differing nectar sugar concentrations.

*Nectar feeding in relation to blood feeding and ovarian development:* The different nectar feeding and host seeking periods of parous and nulliparous *Ae. communis* females on June 20 is interesting. This is also the only sampling date when nulliparous and parous females were collected in similar numbers ( $n = 228$  and  $n = 196$ , respectively). The nulliparous females started their nectar feeding and host seeking activities earlier than the parous females. One likely explanation for this is that parous females, having already oviposited, delay their host seeking until climatic conditions are optimal.

Parous females were shown to contain more fructose than nulliparous females caught on the same date. This could imply that: 1) parous females rely more on carbohydrates for energy than do nulliparous, as Leprince and Lewis (1986) found for *Tabanus quinquevittatus* (Macquart), or 2) parous females might be bigger and therefore take larger sugar meals. Haramis (1983) and Nasci (1986) found that parous females tend to be larger than nulliparous females.

An earlier investigation showed that host seeking *Culex* females had fed on nectar shortly before they started to seek a blood meal (Andersson and Jaenson 1987). Vargo and Foster (1984) found that *Aedes vexans* (Meigen) and *Culex restuans* Theobald nectar feed after host seeking. In the present study, however, high

scorings with the anthrone test (indication of recent nectar feeding) were most common before host seeking started in all species investigated. Since fructose is important for flight energy, this could be a good strategy. Walker and Edman (1985) also noted that sucrose fed females were more persistent in their attempts to blood feed.

There are no exact data on how often blood-fed females feed on nectar in nature. Both Magnarelli (1978) and Nasci and Edman (1984) found gravid females that contained fructose. I found blood-fed females of *Ae. communis* that contained nectar in all different phases of the gonotrophic cycle and I also observed some blood-fed females feeding on flowers. Therefore I support the hypothesis that blood-fed females actively seek nectar during oogenesis.

### ACKNOWLEDGMENTS

I am indebted to Thomas G. T. Jaenson, who read the manuscript and provided helpful discussions. I am also very grateful to Erik Petersson for statistical advice. The study was financially supported by Stiftelsen for Zoologisk Forskning, Regnells Fond and Hierta-Retzus' Stipendiefond.

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