

Release-Recapture Experiments with Canopy Mosquitoes in the Genera *Haemagogus* and *Sabethes* (Diptera: Culicidae) in Brazilian Amazonia

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ABSTRACT In 2 forested areas near Belém (Para State, Brazil), 2 *Haemagogus* and 6 *Sabethes* species were marked released and recaptured in May 1989 and in April 1993. The recapture rates were high, 4.9 and 13.1% for *Haemagogus* and *Sabethes* spp., respectively. For *Haemagogus janthinomys* Dyar, females were recaptured until 27 d after release. The duration of the gonotrophic cycle was between 5.0 and 9.5 d and the survival rate was 0.90-0.92. *Haemagogus leucocelaenus* (Dyar & Shannon) was recaptured once, 21 d after release. Twelve *Sabethes chloropterus* (Von Humboldt) were recaptured, with a peak at 15-18 d; 1 female was recaptured at 44 d, indicating extended survival. Seven *Sabethes amazonicus* Gordon & Evans and 7 *Sabethes cyaneus* (F.) were recaptured, mostly at 14-39 d. These results indicate that *Haemagogus* and *Sabethes* spp. have a gonotrophic cycle in nature longer than inferred from laboratory studies, and that cycle length varies seasonally. The capacity of these species to sustain epizootics or epidemics of arboviruses may depend on local weather, with risk greatest at the end of the rainy season.

KEY WORDS *Haemagogus janthinomys*, *Sabethes chloropterus*, *Sabethes cyaneus*, *Sabethes belisarioi*, gonotrophic cycle, survival

Haemagogus AND *Sabethes* mosquitoes are important maintenance and amplifying vectors of arboviruses in Brazilian Amazonia (Hervé et al. 1986, Vasconcelos et al. 1992). Many species are primatophagic and therefore may transmit these agents to humans.

Haemagogus janthinomys Dyar and *Sabethes chloropterus* (Von Humboldt) are the main vectors of sylvatic yellow fever (YF) virus in Central and South America (Dégallier et al. 1992a, Vasconcelos et al. 1997). *Sabethes glaucodaemon* (Dyar & Shannon) recently was found to be infected naturally with YF during an epidemic in Minas Gerais State (Anonymous 1996). YF is of prime health importance because of the close proximity between its endemic or emergence zone and cities infested by the domestic vector, *Aedes aegypti* (L.) (Dégallier et al. 1992b, Vasconcelos et al. 1997). Mayaro (MAY) virus has been isolated repeatedly from *Hg. janthinomys* during human epidemics (Hervé et al. 1986, Vasconcelos et al. 1992). *Sa. chloropterus* is also a vector of other arboviruses, including Chagres, Ilheus, and St. Louis encephalitis (SLE) viruses (Karabatsos 1985; Rodaniche and Galindo 1957a, b; Rodaniche et al. 1957). This species also may be a good candidate as a vector of emergent viruses because it has been collected in urban areas (Carvalho et al. 1995). *Sabethes belisarioi* Neiva was

found infected naturally with SLE (Causey et al. 1964, Vasconcelos et al. 1991) and *Sabethes quasicyaneus* Peryassu probably is a maintenance host of Sororoca, Wyeomyia, and Tucunduba viruses (Hervé et al. 1986, Vasconcelos et al. 1998). Mosquito pools containing 1 or more of these *Sabethes* spp. have been positive for other arboviruses pathogenic for humans: Bussuquara, Mucambo, Murutucu, Oriboca, and Mayaro (Hervé et al. 1986, Anonymous 1996).

Despite the importance of these mosquitoes in the transmission of human emergent or reemergent viruses, they have been little studied in the field, because of their canopy-dwelling habits and the lack of an effective sampling method other than human bait. Galindo (1958) and Galindo et al. (1956) worked on the bionomics of various species in the laboratory and in nature. Others investigated seasonality (Bates 1944, Gast-Galvis and Bates 1945, Galindo et al. 1956), diel biting (Kumm and Novis 1938, Galindo et al. 1950, Pinheiro et al. 1981, Chadee et al. 1992), oviposition (Chadee and Tikasingh 1989), or vertical (Galindo and Trapido 1955, Trapido and Galindo 1957) patterns of *Hg. janthinomys*. Dégallier et al. (1990) studied the landing behavior of anthropophagic *Haemagogus* and *Sabethes* species.

The only available data on epidemiologically important traits, such as survival and duration of the gonotrophic cycle, were based on laboratory obser-

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vations (Bauer and Hudson 1928; Bates 1946, 1947; Bates and Roca-Garcia 1946 a-c; Hervé et al. 1985; Mondet 1997). Dégallier et al. (1991), using the results of laboratory studies, estimated the survival rate of vector populations shortly after an epizootic in low Amazonia. To determine the influence of weather on survival, and therefore the risk of disease transmission, evaluations are needed in nature during different seasons.

Herein, we describe the results of 2 mark-release-recapture experiments to determine the duration of the gonotrophic cycle and survival of *Haemagogus* and *Sabethes* species under field conditions.

Material and Methods

Mark-release-recapture studies were from 8 May to 6 July 1989 and from 12 April to 14 May 1993 in 2 densely forested areas: the Instituto de Pesquisas Agropecuárias do Norte (IPEAN) forest in the suburbs of Belém and at Benevides, 30 km east of Belém (Belém-Brasilia Highway), Para State, respectively. Both sites were terra firme forest (=not inundated), and surrounded by patchy cultivated areas and secondary forest. Monthly rainfall was recorded at the meteorological station of the IPEAN in Belém. Daily maximum and minimum temperatures were measured at canopy level.

Landing mosquitoes were collected daily between 1000 and 1400 hours by 3 collectors (volunteers immunized against YF), each sitting on a platform at canopy level (between 10 and 20 m in height and 25-50 m apart). During the first 5 d, females were allowed to blood feed to repletion, and then were dusted with a different color of fluorescent dye (Day-Glo, Paris, France) each day, and released at canopy level at 1600 hours the same day. Mosquitoes were examined daily for the presence of dust from the 2nd d onward.

After the end of the 1st experiment, recaptured, marked females and a sample of unmarked females of *Hg. janthinomys* (stored at -70°C) were dissected in the laboratory to determine parity by the degree of coiling of the ovarian tracheoles and follicular development by using Christophers' stages (Detinova 1963).

Results

Weather. Average minimum and maximum temperatures during the 1989 and 1993 experiments were 22.9 and 30.3°C and 24.4 and 29.8°C, respectively. Although the 2 studies were at the end of the rainy season, the total amount of rain was much lower during the year preceding the 1993 than the 1989 experiment (2,581 mm versus 4,126 mm), and the mean range of temperature was greater during 1989 than 1993 (6.4° versus 5.4°C).

Recapture Patterns. *Haemagogus.* Table 1 shows the numbers of *Haemagogus* mosquitoes collected, released and recaptured during the 1989 and 1993 experiments. The relative abundance of *Hg. janthinomys*

Table 1. Females of *Haemagogus* and *Sabethes* species, collected, marked and released, and recaptured in Brazilian Amazonia during 2 experiments

Species	Collected	Marked and released	Recaptured (%)
First experiment (8 May-6 July 1989)			
<i>Haemagogus</i>			
<i>janthinomys</i>	193	74	8 (10.8)
<i>leucocelaenus</i>	44	12	1 (8.3)
<i>Sabethes</i>			
<i>chloropterus</i>	458	59	12 (20.3)
<i>cyaneus</i>	260	62	7 (11.3)
<i>belisarioi</i>	226	34	2 (5.8)
<i>amazonicus</i>	216	32	7 (21.8)
<i>quasicyaneus</i>	48	20	1 (5.1)
<i>glauco-daemon</i>	55	21	0 (0)
<i>Sabethes</i> total	1,263	228	29 (12.7)
Second experiment (12 April-14 May 1993)			
<i>Haemagogus</i>			
<i>janthinomys</i>	1,884	575	24 (4.1)
<i>leucocelaenus</i>	30	12	0 (0)
<i>Sabethes</i>			
<i>chloropterus</i>	189	51	8 (15.6)
<i>cyaneus</i>	92	18	2 (11.1)
<i>Sabethes</i> total	281	69	10 (14.5)

was 10.4 times greater during the 2nd than 1st experiment (0.5 versus 5.2 females per bait per hour).

The patterns of *Hg. janthinomys* recapture are shown in Fig. 1 A and B. During the 1989 experiment, 8 females were recaptured between days 8 and 19 (recapture rate of 10.8%), despite continued collecting until the 59th d. The 1st female recaptured probably completed 1 gonotrophic cycle of 8 d. Its gut did not contain any trace of dark blood, whereas the last female probably completed 2 cycles of 9.5 d each. Therefore, the duration of the gonotrophic cycle probably ranged between 8.0 and 9.5 d. Only 1 marked

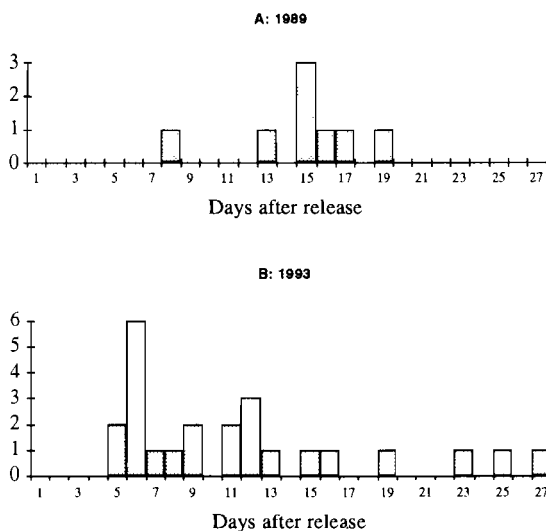


Fig. 1. Number of marked *Hg. janthinomys* recaptured per day. (A) 8 May-6 July 1989 and (B) 12 April-14 May 1993.

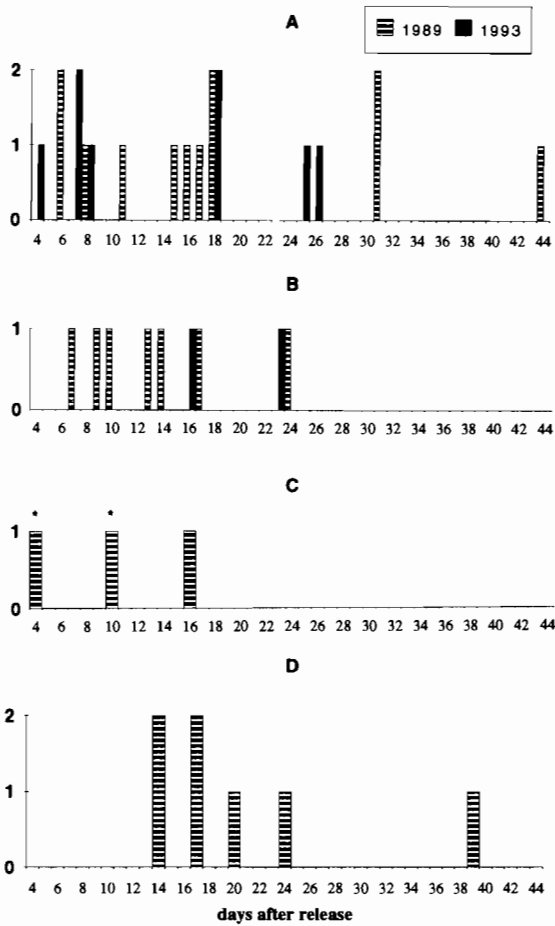


Fig. 2. Number of marked *Sabethes* spp. mosquitoes recaptured per day. (A) *Sa. chloropterus*, (B) *Sa. cyaneus*, (C) *Sa. belisarioi* (*, same individual collected twice), and (D) *Sa. amazonicus*.

Hg. leucocelaenus was recaptured 21 d after release during the 1st experiment.

During the 1993 experiment, 24 *Hg. janthinomys* were recaptured (recapture rate of 4.1%), showing a trimodal pattern (Fig. 1 B). The duration of successive gonotrophic cycles may be inferred from the beginning and end of each peak in the recapture rate (i.e., 5.0–9.0 d, 5.5–6.5 d, and 5.0–6.3 d, respectively). Therefore, the female recaptured on the 27th d may have completed up to 4 gonotrophic cycles (6.8-d duration).

Sabethes. Table 1 shows the numbers of *Sabethes* mosquitoes collected, released, and recaptured during the 1989 and 1993 experiments. The temporal patterns of the *Sabethes* recaptured are shown in Fig. 2 A–D.

Only 1 specimen of *Sa. quasicyaneus* was recaptured 21 d after release, also showing long survival. None of 21 released *Sa. glaucodaemon* was recaptured. The survival of *Sa. amazonicus* was of the same order as that of *Sa. chloropterus*. Two females of *Sa. cyaneus* were recaptured during the 2nd experiment, 16 and 23 d

after release, showing the long survival of this species in nature.

Sabethes chloropterus. In 1989, 75% of the recaptured females was collected between 6 and 18 d after release, possibly following their 1st cycle after release (Fig. 2A). However, it is possible that at least the females recaptured the 6th, 8th, and 11th d had not completed 1 cycle. Two and 1 females were collected 31 and 44 d after release, respectively, showing rather long survival at the beginning of dry season (collecting continued until the 59th d). These females may have completed 2 and 3 cycles of 14–15 d, respectively.

The recapture rate during experiment 2 was not significantly different than that in experiment 1 (15.6 versus 20.3%) ($\chi^2 = 0.08$, $df = 1$, $P > 0.05$), but the duration of the gonotrophic cycle was possibly shorter, between 7 and 9 d. Females recaptured on 18th and 25–26th d may have completed 2 and 3 gonotrophic cycles, respectively. *Sabethes chloropterus* relative abundance was significantly greater during the 1st experiment (1.0 versus 0.7 females per bait per h) ($\chi^2 = 7.00$, $df = 1$, $P < 0.01$), when the weather was hotter and previous year more rainy. This pattern agreed with the preference of this species for breeding in large tree cavities with small openings (Galindo 1958).

Sabethes cyaneus (F.). During the 1st experiment, the females were recaptured regularly from days 7–16 after release (Fig. 2B). Although the pattern shows no defined peak, we presumed a 7- to 10-d duration gonotrophic cycle.

Sabethes belisarioi Neiva. Only 2 females were recaptured, 1 of them twice (on the 4th and 10th d) and the other after 16 d (Fig. 2C). The duration of the gonotrophic cycle tentatively was 8–10 d.

Sabethes amazonicus Gordon & Evans. More than half of the females was recaptured on days 14–17 after their release (Fig. 2D) but the pattern of recapture did not allow the inference of a gonotrophic cycle duration.

Survival. *Haemagogus*. The parity rate of the unmarked *Hg. janthinomys* population based on the ovarian tracheoles of 105 females collected between the 25 May and the 5 July 1989 was 49% (44 pars of 89 readable females) and remained fairly constant (Table 2).

Recaptured females were at follicular stages IIb (days 13 and 19), IIIa (day 16), and IIIb (day 17) with dark blood; 4 were not readable. The follicular stages of biting females from the unmarked population were as follows: IIa (44), IIb (32), IIc (8), and III (8). Females ($n = 105$) with retained stage V eggs were at stage IIa (8 eggs), IIb (2 eggs), and III (1 egg, 4 eggs, and 1 egg) with a mean of 0.11 eggs retained per female. Egg retention is not an experimental artifact and availability of suitable breeding places may be an important factor in the variation of the duration of the gonotrophic cycle. In contrast, *Hg. janthinomys* does not seem to need more than 1 blood meal to mature each egg batch (gonotrophic concordance). The age structure of the population was assumed to be stationary during this period and amenable to survivor-

Table 2. Parous rates of females of *Hg. janthinomys* collected in Brazilian Amazonia, 25 May–5 July 1989

Date	Collected	Dissected	Read	Parous
25 May	9	9	8	4
29 May	11	11	11	5
31 May	9	9	7	5
1 June	4	4	4	3
2 June	6	5	2	1
5 June	11	11	10	5
13 June	4	5	4	1
14 June	6	6	4	2
16 June	4	4	4	2
19 June	4	4	3	2
20 June	12	12	10	4
21 June	8	8	7	1
23 June	7	7	5	2
28 June	8	1	1	1
29 June	4	3	3	1
4 July	2	2	2	2
5 July	4	4	4	3
Total	113	105	89	44

ship estimation by using vertical methods. Assuming an 8.0- to 9.5-d gonotrophic cycle (g) as presently inferred, parous rate (p) = 0.494, and gonotrophic concordance (most mosquitoes are landing with their ovarioles at stage II of Christophers), the survival rate of the population during our 1st experiment ranged from 0.90 to 0.92 (formula of Coz et al. 1961 modified by Germain et al. 1977: $g\sqrt{p}$). The parity status of the unmarked population was not determined during the 2nd experiment. Further studies are needed to provide data on the survival rate of *Hg. janthinomys* in different seasons.

Discussion

The release–recapture experiments showed high recapture rates (4.9 and 13.1% for *Haemagogus* and *Sabethes* spp., respectively). Such values may be explained by low dispersal following the release of engorged mosquitoes, or by the presence of suitable oviposition sites near the release and recapture points. However, the recapture patterns indicated considerable variability in the duration of the gonotrophic cycle, depending upon the availability of oviposition sites.

Under constant temperatures (27–29°C), Hervé et al. (1985) showed that egg laying by *Hg. janthinomys* females occurred between the 5th and 26th d after feeding, with a mean duration of 10 d for the gonotrophic cycle. They attributed this high variability to the unsuitability of the laboratory oviposition surface (filter paper) that resulted in a high proportion of females (9 of 43 = 20.9%) retaining 1 or more eggs after oviposition. Egg retention did not seem frequent during the current experiments. Mondet (1997), working with a new type of breeding tube, reported a shorter-duration gonotrophic cycle (minimum of 7 d), despite lower experimental temperatures (24–25°C) and no egg retention. Availability of suitable oviposition substrate and temperature therefore may be important factors that influence the duration of the gonotrophic

cycle in the laboratory. Under natural conditions, the interval between 2 successive blood meals may vary greatly.

Larval habitats require rainfall for filling, but it remains unclear if heavy rainfall (>400 mm/mo) may inhibit oviposition as Pajot et al. (1985) hypothesized in French Guiana. In Trinidad, Chadee et al. (1992) found fewer mosquitoes with retained eggs during the dry season than during the wet season. In our study the variability of the recapture intervals was greater during the 1993 experiment, when the previous amount of rain was less (2,873 versus 1,778 mm) and the temperature hotter and less variable (mean daily minimum temperature = 24.4°C). Dégallier et al. (1991) showed that *Hg. janthinomys* may have a mean daily survival rate as high as 0.96 (parous rate, 60%), shortly after an epizootic during the dry season in low Amazonia. During the wet season, parous rates between 55% (Chadee et al. 1992) and 61% (Hervé et al. 1985) have been reported. Pajot et al. (1985) have reported parous rates from 43 to 70% during the same season in French Guiana.

During studies of dispersal, Causey and Kumm (1948) collected 1 *Hg. leucocelaenus* on the 12th d after release. The survival of this species may be much longer (21 d) as was shown in the current study.

Sabethes chloropterus, *Sa. cyaneus*, and *Sa. amazonicus* showed greater recapture rates and survival than the other species. This may be due either to less dispersal or more strict primatophagic feeding habits. Under laboratory conditions (21.7–30°C, 70–100% RH), Galindo (1958) found that the mean longevity of *Sa. chloropterus* ranged from 32.5 and 46.8 d after 1 blood meal and that the duration of the gonotrophic cycle was 11 d at room temperature (23–30°C). Our results indicate that such long life spans and gonotrophic cycles also occur in nature, where these mosquitoes are effective maintenance hosts of various arboviruses.

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