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OBSERVATIONS ON THE DISTRIBUTION OF ANOPHELINES IN SURINAME WITH PARTICULAR REFERENCE TO THE MALARIA VECTOR *ANOPHELES DARLINGI*

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A study was made on the distribution of anophelines in Suriname with special emphasis on the principal malaria vector Anopheles darlingi *and on the occurrence of other possible vector species. Peridomestic human bait collections of adult mosquitoes and collections of larvae were made in many localities with a recent history of malaria transmission.*

Stable populations of An. darlingi *were only found in the interior, south of the limit of tidal influence, due to year-round availability of breeding habitats in quiet partly sunlit places in flooded forest areas and along river banks. In the area with tidal movement of the rivers, breeding is limited to flooded areas in the wet season.* Anopheles darlingi *was only incidentally collected in low densities. In the interior, malaria transmission occurred in all places where* An. darlingi *was found. The absence of malaria transmission along the Upper Suriname River could be explained by the absence of* An. darlingi. *In the malaria endemic areas,* An. darlingi *was the most numerous mosquito biting on man. In the tidal region, malaria outbreaks are infrequent and might be explained by the temporary availability of favourable breeding habitats for* An. darlingi. *However, evidence is insufficient to incriminate* An. darlingi *as the vector of malaria in this region and the possible vectorial role of other anophelines is discussed.*

Key words: Suriname – malaria vectors – *Anopheles darlingi* – distribution – breeding habitats – tidal influence

Suriname has usually been divided in three zones with different ecological and malariological characteristics: in the North, the coastal plain which is partly cultivated and inhabited and became free of malaria during 1950-1960; in the South, the primary rainforest area of the interior with a small population of Amerindians and Bushnegroes. In the mid-latitudes lies the white sands formation, botanically characterized as "savanna belt", mainly populated by Amerindians. Historically, malaria transmission in this area was more severe than in the coastal area but less intense than in the interior. After the eradication of malaria in the coastal area malaria in the savanna region only occurs in small epidemics.

The anophelines suspected as vectors of malaria in the three regions differ. In the northern coastal plain *Anopheles aquasalis* was considered the vector by Bonne & Bonne-Wepster (1925). Van der Kuyp (1950) also attributed malaria transmission along the lower courses of the Saramacca, Suriname and Commewyne rivers to *An. aquasalis.* However, New Nickerie on the coast where a very high number of *An. aquasalis* occur, has always been free of malaria except for a few epidemics which were related by Van der Kuyp to periodic invasions of *An. darlingi* from the interior in periods of excessive rainfall. However, *An. darlingi* was never collected in New Nickerie. A few epidemics in Coronie were also correlated with large *An. aquasalis* populations (Van der Kuyp, 1950; Stage & Geyskes, 1946; Van der Kaay, 1976). Giglioli (1963) considered *An. aquasalis* as a vector in the coastal area of Guyana, which borders New Nickerie to the West. In French Guyana, it was suspected to play a minor role in malaria transmission by Floch & Abonnenc (1943); Goarant (1970) and Pajot (1978). Silvain & Pajot (1981) concluded that *An. aquasalis* females were too short-lived to be important vectors. In Brazil (Deane et al.,

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1948; Ferreira, 1964; Forattini, 1962) and Trinidad (Downs et al., 1943), it was considered an important vector.

In the savanna area, several anopheline species have been considered as possible vectors. In Moengo, which is not far from the savanna belt, Bonne & Bonne-Wepster (1925) collected, during a period of malaria transmission, numerous *"An. argyritarsis"*, demonstrated the presence of oocysts, and incriminated *"An. argyritarsis"* as the local primary vector of malaria. *"Anopheles argyritarsis"* was later considered a complex of species. According to Van der Kuyp (1950), who re-examined the collections of Bonne & Bonne-Wepster, this *An. argyritarsis* was similar to *An. darlingi.* During another epidemic in Moengo, Geyskes (1946) could not collect any *An. darlingi* and he considered *An. aquasalis* as the vector. Panday (1977) also could not collected any *An. darlingi* shortly after an epidemic in Moengo and considered *An. nuneztovari* a possible vector. After an outbreak in Tibitibrug, he primarily collected *An. nuneztovari* and again considered this species as a possible, incidental vector. Additional evidence for a vectorial role of *An. darlingi* in the savanna was provided by Van der Kuyp (1954) who collected this species during periods of malaria transmission in Donderskamp and Tapoeripa, in the Western part of the savanna. Bruyning (1952) collected *An. darlingi* near Matta. He suggested that malaria outbreaks in the savanna region might be related to periodic invasions of *An. darlingi* whose larvae had floated downstream from the interior in the big rivers which traverse the savanna.

In the interior, south of the savanna, malaria has always been endemic and *An. darlingi* has generally been considered the principal or only vector of malaria (i. e. Van der Kuyp, 1950; Bruyning, unpublished report, 1952; Fleming, unpublished report, 1963; Hudson (1984); Rozendaal, 1987; 1989; in press). Bruyning (unpublished report, 1952) found oocysts in *An. darlingi* on the Tapanahony. Rozendall (1987; 1989) demonstrated anthropophilic behaviour in *An. darlingi*. A relation between seasonal fluctuations in riverwater level, *An. darlingi* biting densities and malaria incidence was demonstrated by Rozendaal (in press).

This paper adds new data on the distribution and relative densities of man-biting *Anophelines* to the already available data, by attempting to define the natural habitat of *An. darlingi* and the role of this species and other *Anophelines* in the transmission of malaria.

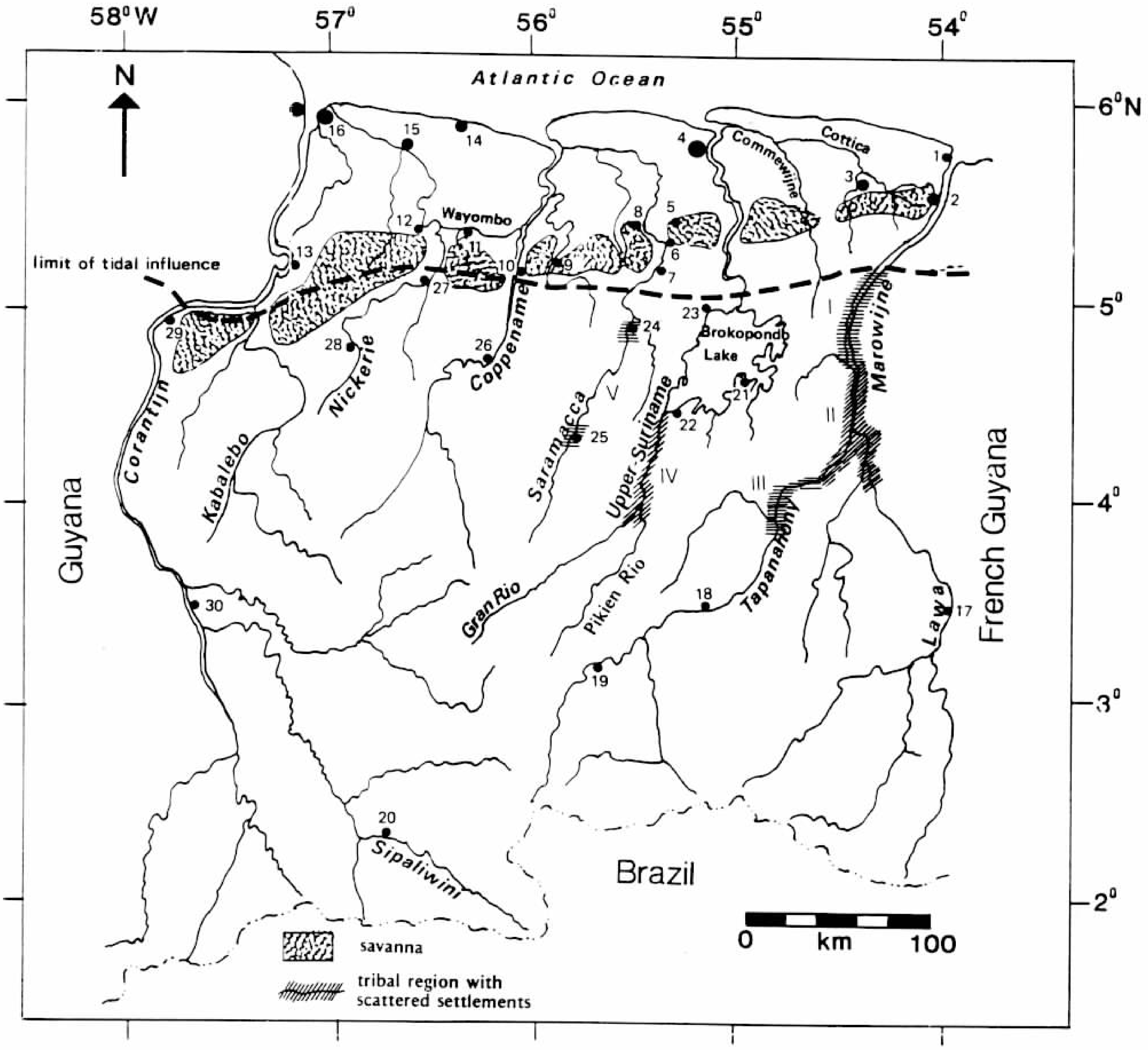
STUDY AREA, PEOPLE AND METHODS

Study area – Although the term interior is often used to indicate the forests south of the savanna belt it is preferable to use the limit of the tidal influence on the rivers as a more well defined border (Fig. 1). On most rivers this limit is just below the first rapids in an upstream direction. It is thought that this limit is of relevance for the distribution of mosquito species which have their breeding habitats in or along the rivers. In this paper, "interior" will refer to the area south of the limit of tidal influence. The savanna belt or white sand formations are mainly located north of this limit and intersected by rivers which are lined with forests. North of the savanna belt is the coastal plain which consists of cleared and cultivated land, open swamps and hydrophytic forests.

Of the total population in Suriname, which is estimated at 400,000 people, about 350,000 live in the coastal area. Of the remainder, an estimated 33,000 people live in the interior, in settlements along the rivers upstream of the first rapids. Of these 31,000 are Bushnegroes and 2,000 are Amerindians. The latter live in four isolated villages in the southern part of Suriname. The Bushnegroes are organized in several tribes which live mainly along the Upper-Marowijne (33%), Upper-Suriname (63%) and Upper-Saramacca (4%) rivers. Other localities in the interior are a few isolated tourist posts and hydrological stations, which are permanently staffed, i. e. Raleighfalls, Stondansie, Blanche Marie and Mataway (Fig. 1).

In the savanna region, most villages are populated by Amerindians. Moengo is an exception since it is a bauxite mining town situated at some distance from the savanna belt in a hilly area in the tidal zone.

The climate – The climate is a tropical rainforest climate, usually with a major rainy season from April to August, a major dry season from September to November, a minor rainy season from December to January and a minor dry season from February to March.



Villages in tidal zone	malaria transm.	An.darl. density	Villages/regions in non-tidal zone	malaria transm.	An.darl. density
1. Galibi	±	±	17.Kawemhakan	++	++
2. Albina	±	±	18.Puleowime	++	++
3. Moengo	±	±	19.Peleloe Tepoe	++	++
4. Paramaribo	-	-	20.Kwamalasamoetoe	++	++
5. Matta	±	±	21.Lebidoti	?(-)	-
6. Pikien Saron	±	±	22.Pikien Pada	?(-)	-
7. Kwakoegron	±	±	23.Brownsweg	-	-
8. Bigi Poika	±	-	24.Njoen Jacobkondre	++	++
9. Tibitibrug	±	±	25.Poesoegroenoe	±	-
10.Witagron	±	-	26.Raleigh falls	±	++
11.Donderskamp	±	±	27.Stondansie	±	++
12.Tapoeripa	±	±	28.Blanche Marie	-	++
13.Apoera	?	-	29.Mataway	-	-
14.Coronie	-	-	30.Amotopo	±	++
15.Wageningen	-	-	Upper-Marowijne Region	++	++
16.New Nickerie	-	-	Upper-Suriname River	±	±(+)
			Gran and Pikien Rio	+	++

Malaria transmission:
++ moderate
\+ low, interrupted
± incidental, normally without
\- none

An.darlingi density:
++ medium or high
\+ very low
± one or two times coll. over many years
\- never collected

tribal regions: I. Paramaccans; II. Bilo-Djukas; III. Opo-Djukas;
IV. Saramaccans; V. Mataway.

Fig. 1: map os Suriname. Indicated are: the limit of tidal influence, the savanna belt, the places mentioned in the text and, per place, the intensity of malaria transmission and the occurrence of *Anopheles darlingi.*

The malaria situation – Most of the *Plasmodium falciparum* cases were detected in the Upper-Marowijne River area (92% from a total of 2,500 in 1984) where transmission occurs throughout the year. Only 1% of all *P. falciparum* cases were found in the Upper-Suriname River area, mainly along its tributaries the Gran and Pikien Rio. Both *P. vivax* and *P. falciparum* cases were detected throughout the year in the Amerindian villages in the south. Along the Upper-Saramacca River, malaria outbreaks occur yearly in Njoen Jacobkondre but not in Poesoegroenoe. All other localities which are small and isolated in the interior and savanna region, are usually free from malaria except for a few outbreaks between 1983 and 1988 in Pakira creek, Raleighfalls, Stondansie, Tapoeripa, Donderskamp, Tibitibrug, Witagron and Pikien Saron. In all other areas, no indications of local malaria transmission existed.

Data collections – During the period 1983 to 1986, entomological surveys were made by human bait collection at peridomestic sites in settlements in the savanna region and in the interior south of the limit of tidal influence. Collection hours were 18.30 – 20.30; 22.30 – 01.30 and 04.30 – 06.30 hours to cover known peaks in biting activity. Along the Upper-Marowijne River and Upper-Suriname River, collections were made every month during the period March 1983 to May 1984 independently from reported malaria cases. In the malarious Amerindian village Kwamalasanoetoe in the far south, collections during eight months covered all seasons of the year. In all other localities, collections were made one to two months after the detection of autochtonous cases of malaria. Human bait collections were also made in Kwakoegron, Poesoegroenoe and Apoera, from which no autochtonous cases were detected since 1982 when the Medical Mission started data collection. From Boslanti, downstream of the Brokopondo Lake, and Lebidoti, a few malaria cases were reported by the end of 1982 but their autochtonous nature remained unconfirmed. In a radius of 1-2 km around the investigated isolated localities, larval collections were made. Mosquitoes were preserved dried on naphthaline paper, larvae were preserved in alcohol (70%). Identifications were made in the laboratory with the keys of Faran & Linthicum (1981) and Cova Garcia & Sutil (1977).

RESULTS

General – Results of the larvae and adult mosquito collections are shown in Table I for the area without tidal influence and in Table II for the area with tidal influence. Results of a literature study of previous observations on the occurrence and distribution of anophelines in Suriname are also shown in Tables I and II. All the results refer to the author's collections unless literature is cited. Since collection methods differed, no distinction is made between collections by previous investigators of larvae or adults.

In the discussion below, reference will only be made to the anopheline species which belong to the subgenus *Nyssorhynchus* because of their suspected or proven role as vectors of malaria in South America. It appears that the non-*Nyssorhynchus* species only occur in small numbers and were only collected in a few localities.

The interior (area without tidal influence)

Adult man-biting collections – Throughout the interior, *An. darlingi* was the most common man-biting mosquito, followed by *An. nuneztovari* and *An. oswaldoi. Anopheles braziliensis* and *An. triannulatus* were also detected but only a few specimens at 2 or 3 localities with the exception of the high biting densities recorded for *An. braziliensis* at the Sipaliwini savanna by Bruyning (unpubl. rep., 1952).

Upper Marowijne River Region (including Lower-Lawa and Lower-Tapanahony): *An. darlingi* reached its highest biting densities in this area and occurred throughout the year. *Anopheles nuneztovari* was second in number but was almost only collected in the dry season. Hudson (1984) obtained similar results. Bruyning (unpubl. rep., 1952) detected an *An. darlingi* specimen with oocysts along the Tapanahony.

Brokopondo (storage) Lake: collections in Pikien Pada and Rediddoti on the bank of the lake yielded high numbers of *An. nuneztovari* and to a lesser extent, *An. oswaldoi* but no *An. darlingi.* The only locality where Panday (1977) collected *An. nuneztovari* in very high numbers was near Brownsweg.

Upper-Suriname River: collections in all seasons did not yield any *An. darlingi* specimen.

TABLE I

Collections of larvae and adult (human bait) anopheline mosquitoes at peridomestic sites in the interior (no tidal influence) of Suriname

	Upper Marowijne	Brokopondo Lake	Upper Suriname	Gran Rio Pikien Rio	Upper Saramacca	Coppename	Nickerie	Corantyn	Sipaliwini	South-East
Month of collection (Jan 1 – Feb 2 etc.)	1-12	2, 3, 6, 8	1-12	1-12	4, 6, 11, 12	9, 10	9, 10	11, 12	1, 12	4, 5, 9
Number of manhours	1698	114	642	792	198	96	48	198	186	36
An. (Nys.) braziliensis	d		s						d	
An. (Nys.) darlingi	+, 2737 (1.6) d, h, i		h, f, s	+, 115 (0.2) s	+, 91 (0.5) h	64 (0.7)	+ 50 (1.0) h	k, l, m	+, 248 (1.3) h	11 (0.3)
An. (Nys.) nuneztovari	+, 440 (0.3) d, f, h, i	+,1167 (10.2) i, k	+, 171 (0.3) f, h, s	+, 670 (0.9)	+, 51 (0.3) h	+, 6 (0.1) i	h	+, 4 (0.0) k, l, m	40 (0.2)	2 (0.1)
An. (Nys.) oswaldoi	+, 32 (0.0) d, f, h, i	325 (2.9) s	+, 39 (0.1) f, s	+, 49 (0.1)	+, 4 (0.0)		3 (0.1)	k, m	+ 4, (0.0)	5 (0.1)
An. (Nys.) triannulatus	d, f, h		f	+, 2 (0.0)						
An. (Ano.) apicimacula	h		+, 2 (0.0) q, s					m		
An. (Ano.) mediopunctatus	+, 1 (0.0) d, f, h	1 (0.0)	+, 1 (0.0) f, q, s			+			1 (0.0)	
An. (Ker.) neivai	1 (0.0) b, h		f, s							
An. (Ano.) peryassui								k, m		
An. (Ano.) punctimacula	+, 2 (0.0) d, i	1 (0.0)						m	1 (0.0)	
An. (Ano.) eiseni	b, d		b							
An. (Ano.) intermedius	d, f		f					m		
An. (Ste.) nimbus	+ b, d		b							

The number of sampling sites, the months during which the collections were carried out and the total number of nights and manhours for which adult collections were made are indicated per location. For each *Anopheles* species a + denotes if larvae were collected. The total number of adult specimens collected (the number collected per manhour) is shown for each species collected in this study. Where previous investigators have made collections, letters a to s refer to the records of these investigators as follows: a) Baboeram (pers. comm.) coll. 1988, b) Bonne & Bonne-Wepster (1925), c) Bruyning (1952), d) Bruyning (unpublished report + unpubl. data, 1952), e) Burgos (pers. comm.) coll. 1983-1987, f) Fleming (unpublished report, 1963), g) Geyskes (1946), h) Hudson (1984), i) Panday (1977), j) Panday (1979), k) Panday (1980), l) Rambajan (1985), m) in: Rambajan (1987), n) Rozendaal & Slootweg (1984), o) Swellengrebel & Van der Kuyp (1940), p) Van der Kuyp (1950), q) Van der Kuyp (1954), r) Van der Kuyp (1985), s) Van Thiel (1962). Because the collection methods of these investigators differed the letters a to s may refer to both adult or larvae collections.

TABLE II

Collections of larvae and adult (human bait) anopheline mosquitoes at peridomestic sites in the savanne and coastal areas (with tidal influence) of Suriname

	Albina[1]	Moengo	Greater Paramaribo[2]	Pikien Saron Matta[3]	Kwakoegron	Tibitibrug[4]	Witagron	Donderkamp[5]	Tapoeripa[6]	Apoera	New Nickerie[7]	New Amsterdam[8]
Month of collection (Jan 1 – Feb 2 etc.)					4	8	8, 10, 11	8, 11	8, 11	11		
Number of manhours					12	24	103	78	60	48		
An. (Nys.) albitarsis											e, f, r	
An. (Nys.) allopha				h							h	m
An. (Nys.) aquasalis	e, i, n	b, g, i	b, f, p		p	6 (0.3) a	5 (0.1), +	+	+	5 (0.1), +	e, f, h, q, r	m
An. (Nys.) braziliensis	e	b, g, i, o										m
An. (Nys.) darlingi	p	b		a, c	p	+ a		+ d	a, d, q			m
An. (Nys.) nuneztovari	i	i	p			40 (1.7), + i	23 (0.2), +	4 (0.1)				m
An. (Nys.) oswaldoi	e, i	g, i	f, p	c	4 (0.3) p	3 (0.1), + j	10 (0.1), +	a		4 (0.1)	p, q, r	
An. (Nys.) triannulatus			f, p		p	1 (0.0)						m
An. (Ker.) neivai		b										
An. (Ano.) apicimacula	e	b, g, i	p					3 (0.0)	9 (0.2)	52 (1.1), +		
An. (Ano.) eiseni		b										
An. (Ano.) intermedius		b										
An. (Ano.) mediopunctatus		b, g, i		c			5 (0.1)					
An. (Ano.) peryassui	e	b, g, i		c, n								
An. (Ano.) punctimacula		i				+ a	1 (0.0)	a		+		
An. (Ano.) shannoni		g		c								
An. (Ste.) nimbus		b, p	b	b, c				b	b			

1) also: Erowarte, Galibi, Papatam, Bigiston 2) also: Meerzog, Kwatta, 3) also: Bigi Poika 4) also: Sabana, Kabo 5) also: Corneliskondre 6) also: Arrawarra monding 7) also: Coronie, Wageningen 8) lower Corantyn section in Guyana.

The number of sampling sites, the months during which the collections were carried out and the total number of nights and manhours for which adult collections were made are indicated per location. For each *Anopheles* species a + denotes if larvae were collected. The total number of adult specimens collected (the number collected per manhour) is shown for each species collected in this study. Where previous investigators have made collections, letters a to s refer to the records of these investigators as follows: a) Baboeram (pers. comm.) coll. 1988, b) Bonne & Bonne-Wepster (1925), c) Bruyning (1952), d) Bruyning (unpublished report + unpubl. data, 1952), e) Burgos (pers. comm.) coll. 1983-1987, f) Fleming (unpublished report, 1963), g) Geyskes (1946), h) Hudson (1984), i) Panday (1977), j) Panday (1979), k) Panday (1980), l) Rambajan (1985), m) in: Rambajan (1987), n) Rozendaal & Slootweg (1984), o) Swellengrebel & Van der Kuyp (1940), p) Van der Kuyp (1950), q) Van der Kuyp (1954), r) Van der Kuyp (1985), s) Van Thiel (1962). Because the collection methods of these investigators differed the letters a to s may refer to both adult or larvae collections.

Anopheles nuneztovari was the most numerous species with a pronounced peak in the dry season. Hudson (1984) collected 2 *An. darlingi* specimens after 27 hours of collection. Van Thiel (1962) also mentioned having problems in finding *An. darlingi*. Van der Kuyp (1950) collected numerous adults and larvae but these collections were made in a village which is currently covered by the Brokopondo Lake.

Gran and Pikien Rio: *An. darlingi* was collected throughout the year, but it was outnumbered by *An. nuneztovari* which reached a peak in biting density during the dry season, although almost disappearing during the rainy season.

Upper-Saramacca River: during a period of malaria transmission in Njoen Jacobkondre, *An. darlingi* was the most numerous *Anopheles* collected. In malaria-free Poesoegroenoe, only a few *An. oswaldoi* were collected. Hudson (1984) also collected *An. darlingi* at Njoen Jacobkondre. After two outbreaks of malaria in Goenzie, *An. darlingi* was the most numerous species collected.

Coppename River: *An. darlingi* was common and almost the only anopheline during an outbreak of malaria at Raleighfalls.

Nickerie River: during an outbreak of malaria at Stondansie, *An. darlingi* was relatively abundant and was the most common anopheline collected. *An. darlingi* was also collected at upstream Blanche Marie falls. Hudson (1984) found similar results.

Corantijn River: at Mataway, no *An. darlingi* and only a few *An. nuneztovari* were collected. Panday (1980) collected numerous *An. darlingi* at Amotopo. Rambajan (1985) collected *An. darlingi* and *An. nuneztovari* on the Guyanese side of the river during a period with malaria transmission.

Sipaliwini River and South-East: *An. darlingi* was collected in all four Amerindian villages where malaria is endemic, it was the most numerous *Anopheles* and could be collected in all seasons. *Anopheles nuneztovari* was second in number but occurred only in the dry season. Hudson (1984) also recorded *An. darlingi* from Kwamalasamoetoe.

Larvae collections – Larvae of *An. darlingi* were found in the following habitats throughout the interior:

creeks – at partly sunlit places in small forest streams protected from the current by obstacles such as roots and fallen trunks;

river edge – between floating debris and water plants or protrusions from the river bank which provide protection from the current, these habitats were partly shaded by the nearby forest;

flooded forest – in open, partly sunlit places between emergent plants or floating debris in swamps created during the rainy season when the river overflows its banks;

pools – formed during the dry season in or near the river bed following a drop in the river waterlevel, pools near the river bank were partly shaded, although those in the riverbed were unprotected and did not yield any *An. darlingi* larvae.

The pH in all four habitats was between 6 and 7, the average water temperature was approximately 26 °C, except for sunlit pools in the riverbed where temperatures of up to 40 °C were recorded. In Kwamalasamoetoe *An. darlingi* larvae were found in an open swamp which contained water during almost the whole year. Larvae of *An. nuneztovari* and *An. oswaldoi* were also collected in the four above mentioned habitats but *An. nuneztovari* showed preference for the sunlit pools in the riverbed during the dry season while *An. oswaldoi* was more commonly found in shaded habitats.

The savanna and coast (area with tidal influence) – The collection sites are indicated in Table II by using the names of the villages where collections were made and not by using the river names because the rivers cross different ecological zones in the savanna and coastal areas.

Albina and neighbouring villages: no investigations were made in this study in villages along the lower course of the Marowijne River. Swellengrebel & Van der Kuyp (1940) found high spleen rates in Bigiston and Galibi (close to Albina) and collected *An. darlingi*. Van der Kuyp (1950) also found *An. braziliensis*. The most recent outbreak of malaria in Galibi occurred in 1972. According to Oostburg (report border meeting French Guyana-Suriname, 1973) *An. aquasalis* was the responsible vector. Many years later, Rozendaal & Sllotweg (1984) found only *An. aquasalis* after 77 hours of human bait collection. Panday (1977) collected *An. aquasalis, An. nuneztovari* and *An. oswaldoi* near Albina. More upstream along the Marowijne, at Pakira creek, Burgos (pers. comm.) collected only *An. darlingi* shortly after an outbreak of malaria (not shown in Table II).

Moengo: following the start of the bauxite mining activities in 1920, Bonne (1924) reported from the interior of houses numerous *An. argyritarsis,* including specimens with oocysts. Larvae were found in extensive permanent swamps close to the village. He described a decline in number of *An. argyritarsis* and malaria incidence during the first years of development of the settlement. Re-examination by the author of the Bonne collection in the State Museum of Natural History in Leiden, Netherlands confirmed Van der Kuyp's (1950) earlier determinations of "*An. argytarsis*" as *An. darlingi* but in addition a few *An. braziliensis* specimens were discovered. Swellengrebel & Van der Kuyp (1940) also recorded *An. braziliensis* from Moengo. During or shortly after a period of malaria transmission, Geyskes (1946) collected *An. braziliensis* and also *An. aquasalis* and *An. oswaldoi.* Panday (1977) collected *An. aquasalis, An. nuneztovari, An. braziliensis,* and *An. oswaldoi* shortly after the last outbreak recorded from Moengo.

Greater Paramaribo: malaria transmission has not been reported from the city itself but transmission occurred until the first half of the 20th century in the surrounding areas. *Anopheles darlingi* has never been reported but *An. aquasalis* is commonly found. *Anopheles nuneztovari, An. oswaldoi,* and *An. triannulatus* have also been collected.

In Boslanti, downstream of the lake along the Suriname River 4 nights of human bait collections did not yield any anophelines (not shown in Table II).

Pikien Saron: collections shortly after an outbreak of malaria in 1988 yielded *An. darlingi* as the only *Anopheles* species (Baboeram, pers. comm.).

In Matta, *An. darlingi* was collected by Bruyning (1952) in the absence of malaria transmission. Hudson (1988) collected *An. braziliensis* in nearby Bersaba.

Kwakoegron: two nights of collection only yielded a few *An. oswaldoi* specimens in this malaria free village. Van der Kuyp (1950) collected *An. darlingi, An. aquasalis,* and *An. oswaldoi.*

Tibitibrug: after an outbreak of malaria, *An. nuneztovari* was the most numerous *Anopheles* followed by *An. aquasalis.* A few larvae of *An. darlingi* were collected in temporary swamps. Panday (1977) collected numerous *An. nuneztovari* and a few *An. oswaldoi* after a period with malaria transmission.

Witagron: after an outbreak of malaria *An. nuneztovari* was most numerous followed by *An. aquasalis* and *An. oswaldoi*. No *An. darlingi* was collected.

Donderskamp and Tapoeripa: after a period with malaria transmission, human bait collections were negative but *An. aquasalis* larvae could be collected and, in Donderskamp, also *An. nuneztovari* larvae. A study one year later yielded *An. darlingi* larvae in a temporary swamp near Donderskamp. Van der Kuyp (1954) collected *An. darlingi* in both villages during a period with malaria transmission. Bruyning (unpubl. data, 1953) also collected adult *An. darlingi* in these villages.

Apoera: in this village with no recent records of malaria transmission, *An. aquasalis* was the only species which could be collected.

New Nickerie: collections in this malaria free coastal town by several investigators never yielded any *An. darlingi* but *An. aquasalis* was collected in very high numbers. In Wageningen and Coronie *An. aquasalis* was also collected in high numbers. Burgos (pers. comm.), Fleming (unpubl. rep. 1963) and Van der Kuyp (1985) also reported *An. albitarsis* from this region. Hudson (1984; 1988) reported *An. albitarsis* as "*An. allopha*" from Wageningen and New Nickerie.

CONCLUSIONS AND DISCUSSION

Possible impact of tidal movement of the rivers on the distribution of An. darlingi –

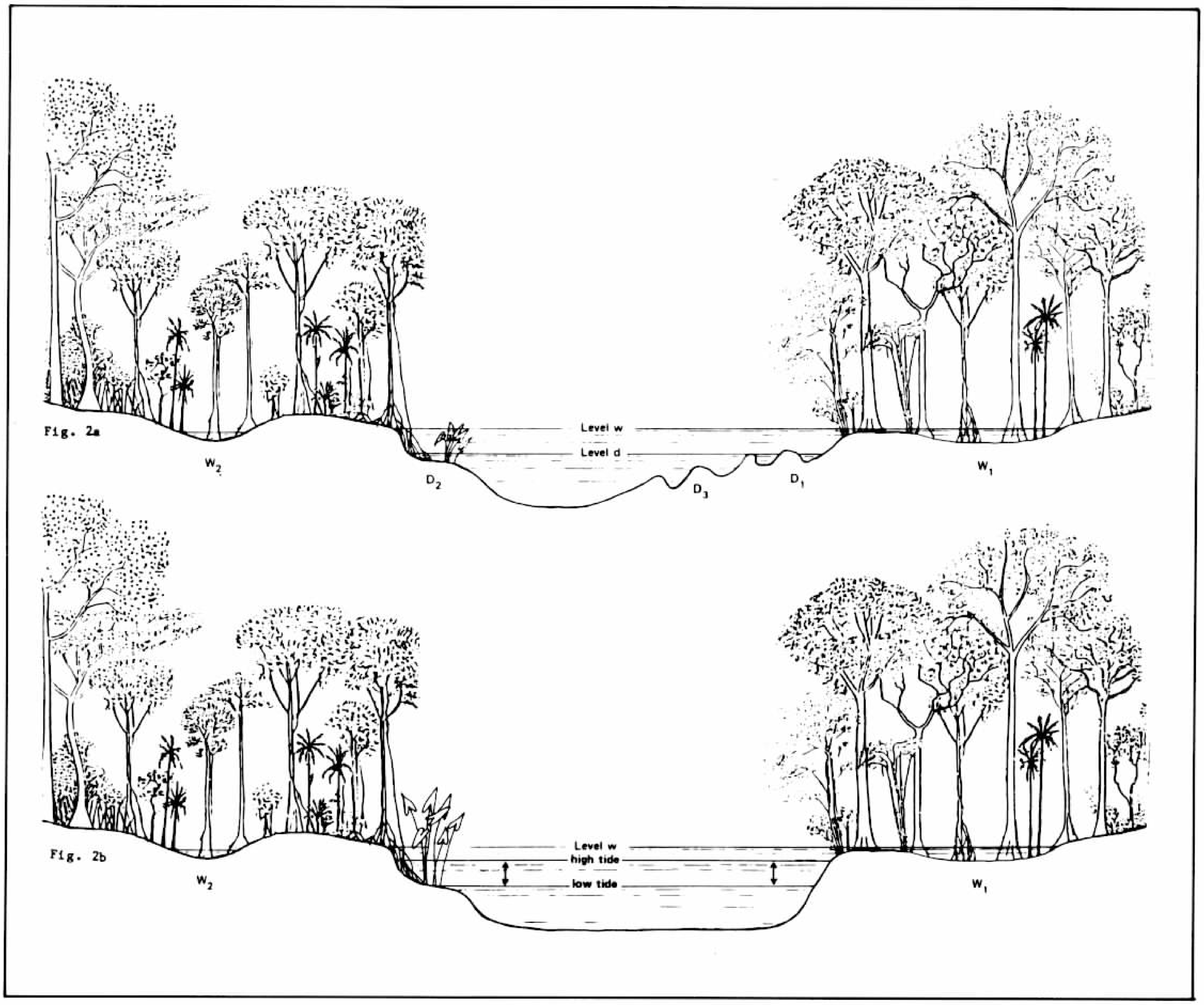


Fig. 2 (a, b): the relation between the river water level, rainfall, tidal movements and the availability of breeding habitats for *Anopheles darlingi.* (a) the area without tidal influence: in the wet season with river water level w forest areas are flooded (W1) and pools are filled by rainwater (W2). In the dry season with river water level d pools D1 and calm water near the riverbank (D2) are suitable breeding habitats. Pools (D3) become available with a further fall in river level, but these places are unshaded and do not constitute suitable breeding places for *An. darlingi* (Fig. from Rozendaal, in press). (b) area with tidal influence: in the wet season when the high tide is as high as river water level w similar breeding habitats will be created as in the non-tidal area. Due to the daily fluctuations between high and low tide breeding habitats of type D will not occur in the dry season.

While *An. darlingi* occurred in stable populations in most parts of the interior, it was rarely collected in the villages downstream of the limit of the tidal influence. Absence of suitable breeding habitats is the most plausible explanation for this phenomenon. Of the four categories of breeding habitats found in the interior, three categories are favoured by or dependent on a retreat in the river waterlevel during the dry season (Fig. 2a). These places are never available in the tidal region where the daily movement of the water will prevent the development of quiet and stable larval habitats. The only potential breeding places occurring in the tidal region are the flooded forest areas and wet season swamps which are independent of the tidal movement of the river waterlevel (Fig. 2b). The larvae collected in Tibitibrug and Donderskamp and by Bonne (1924) in Moengo were found in this habitat. The limited and temporary availability of this habitat probably accounts for the few collections of *An. darlingi* in the tidal zone.

According to Bruyning (1952), the savanna region acts as a natural barrier and prevents *An. darlingi* from spreading from its permanent breeding places south of the savanna belt. Primarily because of the acidity of this swamps and creeks, the savanna region seems to be unsuitable as a habitat for *An. darlingi* (Stage & Giglioli, 1947; Giglioli, 1951; Bruyning, 1952). However, this theory only provides a secondary explanation since the main rivers of the savanna have a suitable pH. Tidal movement is probably most likely the main limitating factor. Whether *An. darlingi* populations survive periods without favourable breeding habitats in very low densities which are below detection level or whether it disappears altogether is not known. Bruyning (1952) suggested that *An. darlingi* reinvades areas with temporary breeding habitats by downstream floatation of larvae between patches of waterhyacinth along the great rivers which originate south of the savanna region. Migration by adults is not likely since they were reported to have a flight range of only a few km (Deane et al., 1948). However, the collections of *An. darlingi* in Moengo cannot be explained by an invasion of this species by means of downstream floating larvae since the Cottica River does not originate south of the limit of tidal influence. This also seems to be true for the collections along the Wayombo near Donderskamp, along the Troeli creek near Matta and along the Pakira creek. However, larvae may have drifted "upstream" into these creeks with the upcoming tidal current from the nearby main rivers, the Nickerie River, Saramacca River and Marowijne River respectively.

In Guyana, Giglioli (1951) and Giglioli & Charles (1954) observed a progressive invasion of the coastlands by *An. darlingi* along the banks of the Demarara River. *Anopheles darlingi* was collected in the tidal region of Guyana but breeding occurred only in non-tidal manmade habitats such as irrigation and drainage channels. From the tidal region in French Guyana, *An. darlingi* was only reported from non-tidal breeding places such as ponds, and swamps (Pajot, 1978). However, comparison with French Guyana is complicated, since the hilly tropical rainforest area limits tidal influence to the area of the coast.

Distribution of An. darlingi *in the Interior (non-tidal area) and its relation to malaria transmission* – Additional evidence on the role of *An. darlingi* as the primary vector of malaria in the interior of Suriname is provided by data on its distribution and relative abudance.

The occurrence of malaria transmission and *An. darlingi* appeared to be closely related to each other. Biting densities were highest in the Upper-Marowijne River area which is also the focus of malaria transmission in Suriname. Near the Brokopondo Lake and along the Upper-Suriname River *An. darlingi* was not collected and for many years no autochtonous malaria cases originated from this area. Along the tributaries of the Suriname River, the Gran Rio and Pikien Rio, a low degree of malaria transmission was observed together with a low *An. darlingi* biting density. Along the Upper-Saramacca River, malaria transmission and *An. darlingi* coincided in Njoen Jacobkondre but not in Poesoegroenoe. After outbreaks at Stondansie and Raleighfalls, *An. darlingi* was also present. In the malarious Amerindian villages in the far south *An. darlingi* was also abundant.

The low density of *An. darlingi* along the Upper-Suriname River is difficult to explain. Van Thiel (1962), Fleming (unpubl. rep., 1963), Hudson (1984) and this author have observed this phenomenon. After an epidemic had occurred in 1980 along the Upper-Suriname River, this area has been almost free of malaria. Rozendaal (1987) suggested that along the Upper-Suriname River breeding conditions for *An. darlingi* are unfavourable. The Upper-Suriname River is for the greater part, a narrow river with steep banks which seldom overflow. By contrast, in the Upper-Marowijne River area, the river basin consists of river flood plains which readily flood. Moreoever, the river is very wide with many islands. Both the flooded forest areas and the extensive river banks were found to be favourable breeding places for *An. darlingi* on the Upper-Marowijne River. Between the habitat availability, near Njoen Jacobkondre and Poesoegroenoe (Saramacca River) a similar difference exists. River floodplains occur near Njoen Jacobkondre, where *An. darlingi* and malaria transmission occur, but not near Poesoegroenoe, where no *An. darlingi* or malaria transmission were reported and where the river is narrow with steep banks. The Sipaliwini River near Kwamalasamoetoe was also narrow, with steep river banks but the year round presence of *An. darlingi* could possibly be explained by the availability of a permanent, partly shaded swamp in a depression between the hills near the village.

In contrast to the predictions by van Thiel (1962) the hydropower scheme which created the Brokopondo Lake by 1971, did not cause a malaria problem. No *An. darlingi* have been found in this area where the unshaded shores of the Lake are evidently unsuitable habitats. Carvalho (1953) observed a decline in *An. darlingi* densities and malaria transmission after the construction of the Lages dam in Brazil which he attributed to the variations in water level which destroyed the preferential breeding places of *An. darlingi*.

Apart from the fact that *An. darlingi* is the *Anopheles* species whose geographical distribution correlates well with the occurrence of malaria, it is also the only *Anopheles* which occurs throughout the year. For the Marowijne Region, Rozendaal (in press) demonstrated a relation between the seasonal availability of *An. darlingi* breeding habitats and fluctuations in malaria incidence. As was discussed by Rozendaal (1987), *An. oswaldoi* and *An. nuneztovari* are unlikely to act as vectors since both species prefer to feed themselves in the forest, moreover, *An. oswaldoi* has only been collected in very low numbers, while the more numerous *An. nuneztovari* was mainly collected during a few months in the dry season.

Information about the occurrence of *An. darlingi* in uninhabited areas is scarce. The collections by Panday (1980) along the Upper-Corantijn River were made in an uninhabited area. At Aselikamp, Lawa River, during the rainy season, high biting densities of *An. darlingi* were observed during five consecutive years (1979-1983) by Hudson (1984) and Rozendaal (1987). After the human population left only a few *An. darlingi* could be collected by the author in the rainy season of 1986. Giglioli (1956) discussed the dependance of *An. darlingi* on man in Guyana: *An. darlingi* is anthropophilic and prospers in the presence of human blood but is able to survive as a "wild" population in much lower numbers on animal blood. In French Guyana (Pajot, 1978) and in Brazil (Deane et al., 1948) *An. darlingi* was also collected in uninhabited areas.

The distribution of An. nuneztovari *and its possible role as a vector in the Interior* – *Anopheles nuneztovari* was the most frequent manbiting *Anopheles* in human settlements after *An. darlingi.* According to Panday (1977) this species has increased in number and spread considerably after the construction of the Brokopondo Lake which was filled in 1971. Breeding was observed by Panday (1977) and by the author after an increase of the water level of the Lake between the submerged grass stems along the shore. After a drop in the water level during the dry season, these habitats disappear. As a result, peak biting activities are highest during the wet season. However, along the rivers in the interior, the author observed a peak in biting activity during the dry season and the almost total absence of biting *An. nuneztovari* during the wet season. This was due to extensive breeding in sunlit rock pools in the dry river beds. This habitat is eliminated when there is a rise in river water level. An increase in the number of *An. nuneztovari* after the filling of the lake might be explained by a diversification of suitable breeding habitats.

The absence of malaria transmission in the settlements surrounding the Brokopondo Lake, which are exposed to high biting densities of this mosquito, and along the Upper-Suriname River where *An. nuneztovari* is the most common *Anopheles* provide additional evidence against its role as a vector of malaria.

Elliott (1972) suspected the existence of at least two sibling species of *An. nuneztovari* of which one is a primary vector of malaria in parts of Venezuela and Colombia. It bites near midnight, mainly inside houses. The other occurs in Brazil, Ecuador and the Guyanas (which includes Suriname), is not known as a vector, has a peak in biting activity soon after sunset, and prefers feeding on animals. Rozendaal (1987) and Panday (1977) also observed a peak in biting activity immediately after sunset, in addition Rozendaal (1987) observed a strong preference to bite in a forested environment over biting in villages. Kitzmiller et al. (1973) studied the arrangement of chromosome banding of both varieties and according to Panday (1979) the X-chromosome arrangement of the population in Suriname has the same arrangement as the Brazilian non-vector population. In a recent study in Brazil (Arruda et al., 1986) sporozoites and oocysts of *P. vivax* were found in *An. nuneztovari* which suggests that even this supposedly non vector sibling might at least incidentally act as a malaria vector.

Possible vectors of malaria in the tidal region – When evaluating the results of mosquito collections from localities in the tidal region, it has to be realized that the collections often occurred after and not during the period of actual transmission of malaria, and may not reflect the composition of the anopheline fauna at the time of transmission. As was discussed above, the populations of *An. darlingi* are probably very short-lived because of the temporary availability of breeding habitats. The occurrence of *An. darlingi*, although in unstable populations, has been sufficiently proven and in a few cases this species has been collected in association with an outbreak of malaria, i. e. Pikien Saron and Tibitibrug, 1988; Pakira creek (upstream of Albina), 1986. It is likely therefore that *An. darlingi* is at least partially responsible for the transmission of malaria in this region.

It should also be noted that the outbreaks of malaria in the period 1983-1988 mainly occurred during or shortly after the long wet season. This might suggest a relation with the availability of breeding habitats of *An. darlingi* in the wet season although the other *Anopheles* species occuring in the tidal region are also favoured by the wet season.

Special reference has to be made to the observations of *An. albitarsis*, *An. allopha* and *An. braziliensis.* Faran & Linthicum (1981) distinguished within what they called an Albitarsis Group two subgroups, the monotypic Braziliensis Subgroup *(An. braziliensis)* and the Albitarsis Subgroup. They divided *An. albitarsis* into two species: *An. albitarsis* and *An. allopha* of which the first is restricted to the South-East of South-America and the second occurs in the tropical parts of South-America.

"Anopheles albitarsis" has been mentioned as a minor vector in a limited area of Venezuela by Gabaldon (1956) and as a potential vector of malaria in the savanna region of Guyana by Giglioli (1948). Since both Giglioli and Gabaldon did not record *An. braziliensis,* although this species is known to occur in both countries, it is possible that their *"An. albitarsis"* refers to the whole *Albitarsis* Subgroup. Recently, Arruda et al. (1986) found in northern Brazil *P. vivax* sporozoites in what they called *An. albitarsis.* In the same study, uninfected *An. braziliensis* specimen were also recorded. It is likely that their *"albitarsis"* is similar to what Faran & Linthicum (1981) considered as *An. allopha.*

Rambajan (1984) reported *An. allopha* and *An. braziliensis* from Guyana where both occurred in the coastlands and the interior. He did not consider these species as vectors of malaria in Guyana. The *An. albitarsis* specimen recorded from the coastal area in Suriname by Burgos (pers. comm.), Fleming (unpubl. rep., 1963) and Van der Kuyp (1985) might be similar to Faran & Linthicum's *An. allopha* since these authors have also reported *An. braziliensis* in other collections. Hudson (1984) also recognized *An. allopha* among collections from the coastal region. However, recently Oliveira & Deane (1984) questioned the validity of the name *allopha* and treated it as a nomen nudum. Hudson (1988) therefore renamed his earlier collections of *An. allopha* as *An. albitarsis.* Linthicum (1988) also considered *allopha* no longer as a valid name and proposed *marajoara* Galvão and Damasceno as the next available name for this species.

When analyzing the data from Moengo, it appears that *An. braziliensis* is the only *Anopheles* which was collected in all four published studies which were conducted during or shortly after periods with transmission of malaria. From the few collections of this species which have been made elsewhere in Suriname, it can be concluded that as in Guyana (Rambajan, 1984) it occurs in the coastlands, the savannas and the interior. Pajot (1978) reported *An. braziliensis* from the coastal savanna areas of French Guyana, where it was found breeding in open swamps, but also in the forest. He observed an anthropophagic and partly endophagic behavior and considered this species as a secondary vector of malaria, after *An. darlingi.* Deane et al. (1948) also observed an endophagous behaviour in Amazonia, Brazil, moreover they found a specimen with sporozoites. They also believed that *An. braziliensis* could act as a secondary vector when certain favourable conditions were met. *Anopheles aquasalis* remains a potential vector in view of its widespread distribution in the tidal regions and its previous role as a vector in the coastlands of Suriname and other countries. It has probably been the vector in places such as Galibi where it was the only Anopheles found. As Giglioli (1963) pointed out, environmental changes may cause *An. aquasalis* to shift from feeding on livestock to feeding on man, thus increasing its vectorial capacity.

It is possible that *An. nuneztovari* acts as an incidental vector in the tidal region although it is unlikely that is plays a vectorial role in the interior as was discussed above.

Summarizing it can be concluded that in the tidal region more research will be needed to be able to determine the most important malaria vector(s). However, it seems probable that *An. darlingi* was responsible for some of the outbreaks while *An. braziliensis* and *An. aquasalis* might have played a role in some other outbreaks of malaria where *An. darlingi* was absent.

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