# Comparison of Behavior and Vector Efficiency of *Anopheles gambiae* and *An. arabiensis* (Diptera: Culicidae) in Barkedji, a Sahelian Area of Senegal

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J. Med. Entomol. 34(4): 396–403 (1997)

**ABSTRACT** The ecology, population dynamics, and malaria vector efficiency of *Anopheles gambiae* and *An. arabiensis* were studied for 2 yr in a Sahelian village of Senegal. Anophelines were captured at human bait and resting indoors by pyrethrum spray. Mosquitoes belonging to the *An. gambiae* complex were identified by polymerase chain reaction. Of 26,973 females, *An. arabiensis* represented 79% of the mosquitoes captured and remained in the study area longer than *An. gambiae* after the rains terminated. There were no differences in nocturnal biting cycles or endophagous rates between *An. gambiae* and *An. arabiensis*. Based on an enzyme-linked immunosorbent assay test of bloodmeals, the anthropophilic rate of these 2 vectors were both ≈60%, when comparisons were made during the same period. Overall, 18% of the resting females had patent mixed bloodmeals, mainly human–bovine. The parity rates of *An. gambiae* and *An. arabiensis* varied temporally. Despite similar behavior, the *Plasmodium falciparum* circumsporozoite protein (CSP) rates were different between *An. gambiae* (4.1%) and *An. arabiensis* (1.3%). *P. malariae* and *P. ovale* only represented 4% of the total *Plasmodium* identified in mosquitoes. Transmission was seasonal, occurring mainly during 4 mo. The CSP entomological inoculation rates were 128 bites per human per year for the 1st yr and 100 for the 2nd yr. Because of the combination of a high human biting rate and a low CSP rate, *An. arabiensis* accounted for 63% of transmission. Possible origin of differences in CSP rate between *An. gambiae* and *An. arabiensis* is discussed in relation to the parity rate, blood feeding frequency, and the hypothesis of genetic factors.

**KEY WORDS** *Anopheles gambiae*, *Anopheles arabiensis*, malaria transmission, bloodmeal sources, population dynamics, Senegal



THE MAIN VECTORS responsible for malaria transmission in Africa are *Anopheles gambiae* Giles and *An. arabiensis* Patton, 2 of 6 species comprising the *An. gambiae* complex, as well as *An. funestus* Giles. In numerous regions of West Africa, *An. gambiae* and *An. arabiensis* are sympathric (Robert et al. 1989, Lindsay et al. 1993, Toure et al. 1996).

With a long-term goal of using transgenic mosquitoes with reduced malaria vector competences for control, data are being collected on intra- and interspecific gene flow within the *An. gambiae* complex (Lanzaro et al. 1995, Lehmann et al. 1996). The Sahelian area, with its short rainy season, could be a useful area for studying the population genetics of malaria vectors, because vector populations here probably are more isolated from each other both spacially and temporally than in regions where mosquitoes are present throughout the year.

Few studies have been conducted in the Sahelian region to compare population dynamics, biology, behavior and vector efficiency among *Anopheles* species. Some surveys evaluated malaria transmission (Hamon et al. 1965, Omer and Cloudsley-Thompson 1970, Haridi 1972, Vercruysse 1985, Gazin et al. 1988, Faye et al. 1993, Taylor et al. 1993). Following the definition of the WHO, vector efficiency is defined as the "ability of a mosquito species, in comparison to another species in a similar climatic environment, to transmit malaria in nature. A rough estimate of relative efficiency may be made by comparison of sporozoite rates taken in comparable conditions." (WHO 1963). This is, of course, different from vectorial capacity which does not take into account the sporozoite rate (Garret-Jones and Shidrawi 1969).

Generally, *An. arabiensis* is considered to have an anthropophilic rate, life expectancy, and vectorial capacity lower than *An. gambiae* (Coluzzi 1984, Gillies and Coetzee 1987). Because of the methods of capture, the methods of identification of species

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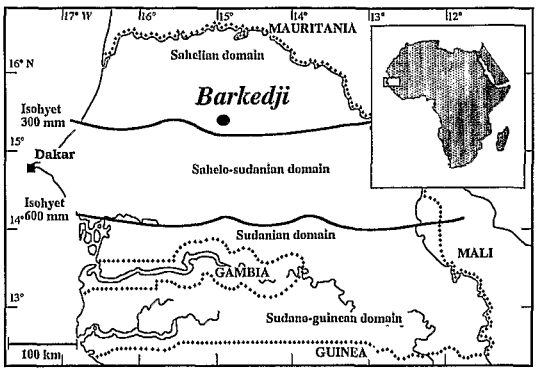


**Fig. 1.** Location of study village in Senegal.

of the *An. gambiae* complex, variations in vector density, and the availability of vertebrate hosts over time, comparison between *An. gambiae* and *An. arabiensis* may be distorted, as it was shown in Kenya (Petrarca et al. 1991) and in Dielmo, another region of Senegal (unpublished data).

The aim of our longitudinal study was to assess the differences in biology, behavior, and circumsporozoite protein (CSP) rate of *An. gambiae* and *An. arabiensis* in relation to malaria transmission, and to estimate the intensity and periodicity of transmission, and respective roles of each vector over time. Availability of a polymerase chain reaction (PCR) technique, which allowed identification of all the specimens of the *An. gambiae* complex, allowed us to reach these objectives.

## Materials and Methods

**Study Area.** The study was carried out in the village of Barkedji (15° 17′ N, 14° 53′ W) (Fig. 1). This village of 700 inhabitants is situated in the Ferlo, in the Sahelian region of Senegal. It is representative of villages in the area. The dominant ethnic group is Peuhl, mainly cattle and sheep farmers, and some Wolof farmers. The rainy season is short, extending from July to October. Rainfall varies annually: 215 mm in 1991, 347 mm in 1992, 335 mm in 1993, 301 mm in 1994, and 404 mm in 1995, with extraordinary downpours of 26 mm in December 1995. The village of Barkedji is situated in the fossil valley river bed of the Ferlo and is surrounded by clay hollows which collect water as soon as the rains start. During the last 2 yr, these temporary ponds dried by November 1994 and by January 1996. The average minimum and maximum monthly temperature, recorded by the national meteorological service, were constantly high, ranging from 16.4–32.3°C in January 1995 to 22.6–41.2°C in May 1995.

**Mosquito Collections.** Adult mosquitoes were captured biweekly from June to December 1994 and from July 1995 to March 1996. A survey was conducted in June 1995 at the end of the dry season. The following 2 collection techniques were used: (1) Hourly human bait collections were made on adult volunteers from 1900 to 0700 hours at the same sites for 2 consecutive nights. One indoor collector and outdoor collector were positioned at each site. In total, 8 human-nights were done every 2 wk. The human biting rate was expressed as the number of mosquito bites per person per night during each 2-wk sample. (2) During 1994, pyrethrum spray collections were made in the early morning inside 16 bedrooms, which were different from houses used for human bait collections. Houses were divided into 4 groups of 2 compounds with 2 bedrooms per compound, situated in different parts of the village. Only 6 of these were used during the following year.

**Field Processing of Anophelines.** Anophelines were identified using the morphological characteristics and identification key of Gillies and De Meillon (1968). Ovaries from a portion of female anophelines captured on human bait were dissected to determine parity (Detinova 1962). All the mosquitoes from the *An. gambiae* complex, dissected or not, were stored individually in a numbered tube with dessicant for laboratory processing in Dakar.

**Laboratory Processing of Anophelines.** Bloodmeal sources of a sample of females captured biweekly by pyrethrum spray were identified by an enzyme-linked immunosorbent assay (ELISA) (Beier et al. 1988). The technique identified human, bovine, ovine or caprine (sheep and goat), equine (horse and donkey), or chicken host.

The head and thorax of female anophelines were tested for circumsporozoite protein of *Plasmodium falciparum*, *P. malariae*, and *P. ovale* by the ELISA as described by Burkot et al. (1984) and modified by Wirtz et al. (1987). The circumsporozoite protein rate, and the 95% CI were calculated. *P. vivax* is not present in this region of Africa. The entomological inoculation rate was calculated by multiplying the human biting rate by the circumsporozoite protein rate for each 2-wk period.

Females belonging to the *An. gambiae* complex were identified to species using the PCR technique described by Scott et al. (1993). A leg or a wing was placed directly into the reaction mixture containing the species-specific primers, dNTPs, buffer, and polymerase. The length of the amplified sequences was 315 nucleotides for *An. arabiensis*, 390 for *An. gambiae*, and 464 for *An. melas*. This technique has been validated in West Africa (Fontenille et al. 1993). When >20 anophelines of the *An. gambiae* complex were captured during each 2-wk period by each of the capture methods, a minimum of 20 specimens were randomly identified by PCR. The probable number of specimens per species for each method of capture then was extrapolated. All mosquitoes found positive by circumsporozoite protein ELISA were identified by PCR.

**Table 1. Number and percentage of malaria vectors caught from July 1994 to March 1996 by different methods in Barkedji**

| No. or % | Feeding on humans outdoors | Feeding on humans indoors | Resting in bedrooms | Total |
|---|---|---|---|---|
| No. *An. gambiae* s.l. captured | 3,309 | 4,451 | 19,213 | 26,973 |
| No. *An. gambiae* s.l. tested by PCR | 504 | 601 | 1,728 | 2,833 |
| Estimated No. *An. gambiae* | 616 | 796 | 4,285 | 5,697 |
| Estimated No. *An. arabiensis* | 2,693 | 3,655 | 14,928 | 21,276 |
| % *An. gambiae* | 18.6 | 17.9 | 22.3 | 21.1 |
| % *An. arabiensis* | 81.4 | 82.1 | 77.7 | 78.9 |

## Results

**Capture of Mosquitoes.** From July 1994 to March 1996, 26,973 *Anopheles* were collected by spray collections in bedrooms, and 264 man-nights on human volunteers. No *An. funestus* were caught. Of the *An. gambiae* complex females captured, 2,833 were identified by PCR. The number and percentage of females of *An arabiensis* and *An. gambiae* captured by each method are shown in Table 1. Non malaria-vector species captured included *An. pharoensis* Theobald, *An. rufipes* (Gough), *An. ziemanni* Grünberg, *An. coustani* Laveran, and *An. squamosus* Theobald.

Considerable differences were observed each year. During 1994, *An. gambiae* represented 27.3% of total *An. gambiae* complex females captured; but during 1995, only 12.3%, using the same techniques. The number of resting mosquitoes varied greatly among rooms. During 1994, 140 females of the *An. gambiae* complex were captured by 12 pyrethrum spray collections in the least productive room (maximum 54 females in October), whereas the most productive room produced 1,901 anophelines (maximum 555 females in October). The percentage of *An. gambiae* was significantly higher among females collected resting than biting indoors or outdoors ($\chi^2 = 6.7$, df = 1, $P < 0.01$). No anophelines were found during the survey conducted in June 1995 at the end of the dry season.

**Seasonality and Biting Cycles.** The human biting rate for each species varied temporally depending on the rainy season (Fig. 2). In 1994, the biting rate was maximum in October for *An. gambiae*, with a peak of 27 bites per human per night during the 1st wk of October. For *An. arabiensis* the maximum rate was in November with a peak of 107 bites per human per night during the 2nd wk of November. In 1995, the human biting rate for *An. gambiae* was always low, with a maximun average of 7.5 bites per human per night during the last week of October. For *An. arabiensis* the maximum rate was in October with a peak of 104 during the last week of the month. *An. gambiae* disappeared from collections earlier in the year than *An. arabiensis*.

Night-biting cycles were similar for *An. gambiae* and *An. arabiensis* (Fig. 3), and did not vary during the year (data not shown). A biting peak was observed consistently between 0300 and 0500 hours for both species.

**Host-Seeking Behavior.** Overall, 56.4% of *An. gambiae* and 57.6% of *An. arabiensis* were cap-

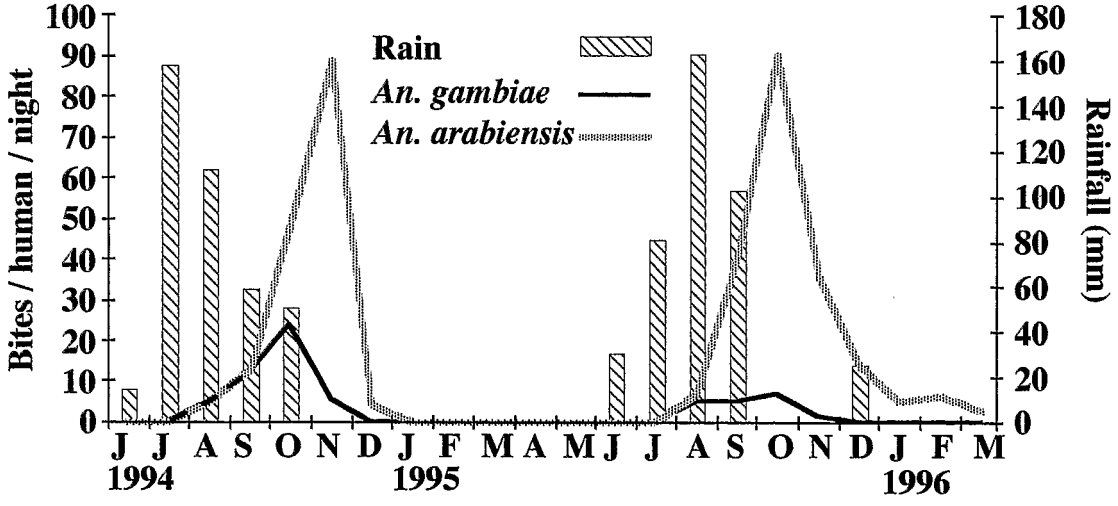


**Fig. 2.** Monthly total rainfall and human biting rate for *An. gambiae* and *An. arabiensis* in Barkedji from June 1994 to March 1996.

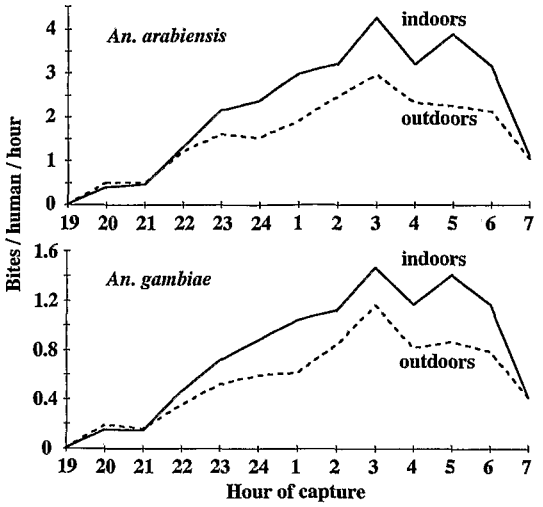


**Fig. 3.** Average number of bites per human per hour indoors and outdoors for *An. gambiae* and *An. arabiensis* during the rainy season in Barkedji.

tured on humans indoors. The endophagous rate was similar for both species ($\chi^2 = 0.68$, df = 1, $P = 0.41$).

In total, 2,029 bloodmeals from resting females of the *An. gambiae* complex were tested by ELISA, including 264 from PCR identified *An. gambiae* and 859 *An. arabiensis* (Table 2). The anthropophilic rate of *An. gambiae* and *An. arabiensis* were similar only during the rainy season (61.9% versus 58.5%, $\chi^2 = 0.71$, df = 1, $P = 0.40$) (Fig. 4). Over 2 yr, including rainy and dry seasons, the anthropophilic rate was 62.1% for *An. gambiae* and 68.0% for *An. arabiensis* ($\chi^2 = 3.12$, df = 1, $P = 0.08$). In addition 35.2% of *An. gambiae* and 28.1% of *An. arabiensis* fed on cattle. Overall, 8% of anophelines had fed on ovine and 11.7% on equine. Only 2 females (0.1%) had taken chicken bloodmeals. Overall, 17.7% of bloodmeals were taken from 2 different host species. The most frequent combinations were human–cow bloodmeals (6.4% for *An. gambiae* and 7.5% for *An. arabiensis*), then human–equine bloodmeals (1.1% for *An. gambiae* and 4.1% for *An. arabiensis*). Four mosquitoes fed on 3 different species (0.2%). The percentage of mixed bloodmeals was the same for 1994 and 1995 (18.1% versus 17.4%, $\chi^2 = 0.18$, df = 1, $P = 0.67$). Over the 2-yr study, 17.0% of *An. gambiae* tested had taken patent mixed bloodmeals compared with 18.6% for *An. arabiensis* ($\chi^2 = 0.28$, df = 1, $P = 0.60$).

**Parity Rates of Vectors.** In 1994 the parity rate was 79.4% ($n = 107$) for *An. gambiae* ($CI_{95\%}$ = 71.4–87.4), and 60.7% ($n = 211$) for *An. arabiensis* ($CI_{95\%}$ = 54.1–67.3). This difference was highly significant ($\chi^2 = 11.3$, df = 1, $P < 0.001$). In 1995, the parity rate was 40.4% ($n = 57$) for *An. gambiae* ($CI_{95\%}$ = 27.7–53.1), and 80.2% ($n = 323$) for *An. arabiensis* ($CI_{95\%}$ = 75.9–84.5). This difference was highly significant ($\chi^2 = 40.2$, df = 1, $P < 0.001$).

**Circumsporozoite Protein Rates.** The circumsporozoite protein rate was calculated monthly for each species. Overall, 96% of identified *Plasmodium* were *P. falciparum* (Table 3). In 1994, 4.5% ($CI_{95\%}$ = 3.5–5.9) of *An. gambiae* and 1.3% (0.9–1.8) of *An. arabiensis* tested positive for *P. falciparum*. This difference was highly significant ($\chi^2 = 39$, df = 1, $P < 0.0001$). In 1995, 2.8% ($CI_{95\%}$ = 1.3–5.1) of *An. gambiae* and 1.3% (0.9–1.8) of *An. arabiensis* tested positive for *P. falciparum*. This difference also was significant (Fisher exact test, $P = 0.047$). If the circumsporozoite protein rates were calculated only with mosquitoes captured from July to October, when *An. gambiae* and *An. arabiensis* both were present, the circumsporozoite protein rates were 2.9 and 1.8% for *An. gambiae* and *An. arabiensis*, respectively, and were not different ($\chi^2 = 2.1$, df = 1, $P = 0.15$).

Adjusting for years, this difference was highly significant (4.1% for *An. gambiae* versus 1.3% for *An. arabiensis*, Mantel–Haenszel chi-square for stratified analysis = 40.7, df = 1, $P < 0.0001$). For each species the circumsporozoite protein rates over the 2 yr were not significantly different (4.5% versus 2.8% for *An. gambiae*, $\chi^2 = 2.0$, df = 1, $P = 0.16$, and 1.3% versus 1.3% for *An. arabiensis*, $\chi^2 = 2.10^{-5}$, df = 1, $P > 0.99$). Little *P. malariae*

**Table 2. Percentage of indoor resting mosquitoes fed on each vertebrate host during the rainy season from July to October when *An. gambiae* and *An. arabiensis* were present simultaneously, as well as over the whole year (in brackets) (Barkedji July 1994 to March 1996)**

| Mosquito species | No. of mosquitoes | Mosquitoes fed on each vertebrate host, % | | | | | % mixed bloodmeal |
|---|---|---|---|---|---|---|---|
| | | Human | Bovine | Ovine | Chicken | Equine | |
| *An. gambiae* | 257 (264) | 61.9 (62.1) | 35.4 (35.2) | 11.3 (11.0) | 0.0 (0.0) | 8.6 (8.7) | 17.1 (17.0) |
| *An. arabiensis* | 376 (859) | 58.5 (68.0) | 41.5 (28.1) | 7.2 (7.9) | 0.0 (0.1) | 11.4 (14.6) | 18.6 (18.6) |
| Not determined *An. gambiae* s.l. | 750 (906) | 66.1 (69.1) | 35.2 (30.9) | 6.5 (7.2) | 0.0 (0.1) | 9.7 (9.8) | 17.6 (17.1) |
| Total | 1,383 (2,029) | 63.3 (67.7) | 36.9 (30.3) | 7.6 (8.0) | 0.0 (0.1) | 10.0 (11.7) | 17.8 (17.7) |

Mixed bloodmeal: 2 different vertebrate species detected in the bloodmeal of the same mosquito.

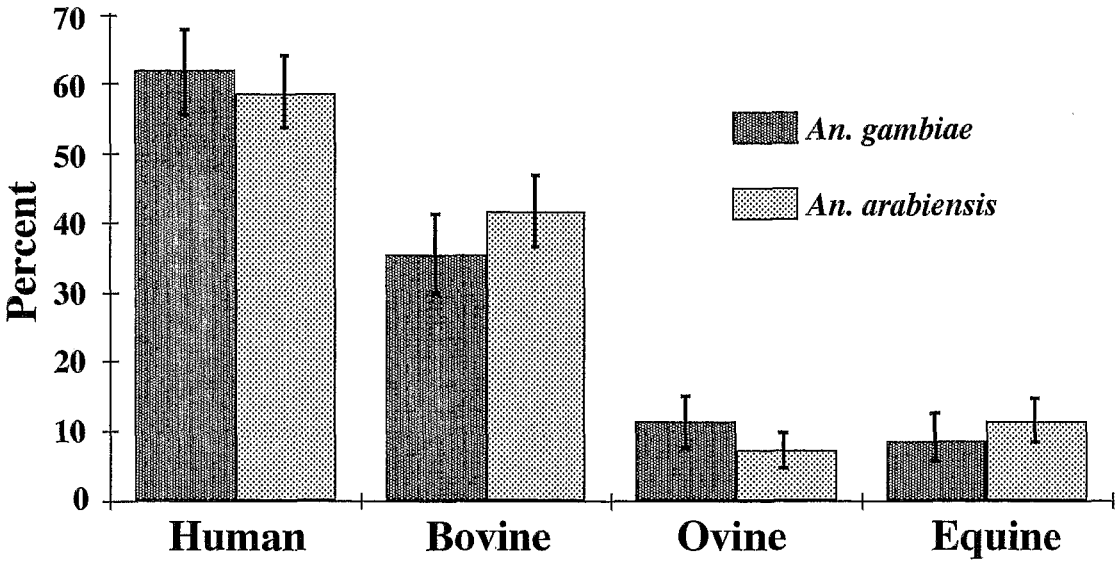


**Fig. 4.** Percentage of boodmeals taken on different sources for *An. gambiae* and *An. arabiensis* captured by pyrethrum spray in bedrooms during the rainy seasons (July–October) in Barkedji.

and *P. ovale* was detected. A mixed infection of both *P. falciparum* and *P. malariae* was found in 1 *An. gambiae* captured on human bait in August 1995.

**Entomological Inoculation Rates.** The annual entomological inoculation rate was 128 during 1994 and 100 during 1995 (Table 4). Transmission took place mainly from August to December (Fig. 5). In 1994 *An. gambiae* was responsible for 53% of *P. falciparum* transmission, but only for 15% in 1995. However, *An. gambiae* was the major vector during the 1st mo of transmission during both years, and was responsible for 70% of transmission in September 1994 and 82% in August 1995. In 1994, transmission reached its peak in October with 40 infecting bites per human during the first 15 d of the month. In 1995 this peak was reached at the end of September with 37 infecting bites per human during the last 15 d.

## Discussion

Although *An. funestus* is a mosquito that may be found in certain regions with a Sahelian climate, none were captured in Barkedji. High peripheral vegetation, which is favorable for oviposition by this species, does not grow in the temporary pools around Barkedji.

During 1995–1996, anophelines were captured until March 1996, whereas in 1994–1995 none were found after January 1995 (Fig. 2). The explanation for this could be the extended duration of temporary pools after the rains in December 1995. However, only *An. arabiensis* was found after December. The fact that no anophelines were captured during the dry season raised the question of how these mosquitoes survive from one rainy season to another. Did some females remain in hibernation or did recolonization take place at the beginning of each rainy season? Omer and Cloudsley-Thompson (1970) demonstrated that a few autochtonous females remained during the dry season. Taylor et al. (1993), studying gene frequencies of *An. arabiensis* in various villages in Mali and Burkina Faso, suggested that populations were maintained continuously, but with seasonal variation.

During 1994 the number of resting anophelines varied greatly among the 16 bedrooms studied. However, the maximum and minimum number of

**Table 3. Circumsporozoite protein rates with confidence interval (in brackets) determined by ELISA from head-thoraces of mosquitoes captured on human bait (Barkedji July 1994 to March 1996)**

| Mosquito species | 1st yr | | | | 2nd yr | | | |
|---|---|---|---|---|---|---|---|---|
| | No. tested | P.f. | P.m. | P.o. | No tested | P.f. | P.m. | P.o. |
| *An. gambiae* | 1,065 | 4.5 (3.5–5.9) | 0.09 (0.5–0) | 0 | 327 | 2.8 (1.3–5.1) | 0.3 (1.7–0) | 0.3 (1.7–0) |
| *An. arabiensis* | 2,998 | 1.3 (0.9–1.8) | 0.03 (0.18–0) | 0 | 3,302 | 1.3 (0.9–1.8) | 0.03 (0.17–0) | 0 |

P.f., Infection rate for *P. falciparum*; P.m., Infection rate for *P. malariae*; P.o., Infection rate for *P. ovale*.

**Table 4. Annual entomological inoculation rates estimated by ELISA, for the 3 *Plasmodium* species, for each vector species (Barkedji July 1994 to March 1996)**

| Species | 1st yr | | | 2nd yr | | |
|---|---|---|---|---|---|---|
| | P.f. | P.m. | P.o. | P.f. | P.m. | P.o. |
| *An. gambiae* | 66.7 | 1.25 | 0 | 14.6 | 1.4 | 1.4 |
| *An. arabiensis* | 58.7 | 1.90 | 0 | 82.1 | 2.0 | 0 |
| Total | 125.4 | 3.15 | 0 | 96.8 | 3.4 | 1.4 |

P.f., *P. falciparum*; P.m., *P. malariae*; P.o., *P. ovale*. One *An. gambiae* specimen captured in August 1995 was positive for *P. falciparum* and *P. malariae*.

specimens always were captured in the same bedrooms. We were unable to explain this disparity by factors such as distance from breeding sites, number of persons per bedroom, and number of animals in the surroundings. Significant differences also were observed within the same compound, where all other parameters were equal. The type of housing construction did not affect the results, contrary to what was observed elsewhere (Gamage-Mendis et al. 1991, Lindsay et al. 1995), because the 16 houses selected were identical.

The ratio of *An. gambiae* to *An. arabiensis* was higher among resting than among host-seeking collections. *An. gambiae* therefore seemed to have a higher degree of endophily than *An. arabiensis*. However, the rate of endophagy was not statistically different, and the night biting cycles were similar for *An. gambiae* and *An. arabiensis*.

The study of vector blood feeding behavior should be approached cautiously. Comparisons between *An. gambiae* and *An. arabiensis* should only be made during the rainy season when the 2 species were present simultaneously. From November onward, *An. arabiensis* became significantly more abundant than *An. gambiae*, and at the same time there was a change in host accessibility and in the proportion of bloodmeals on humans and animals. During the rainy season, all animals spend the night around the houses, except some of the horses and donkeys, which remained outside the village in the farming camps (i.e., the most accessible hosts were humans and cattle). However, at the end of the rainy season cattle also were moved to surrounding pasture, and the farmers returned to the village with their horses and donkeys. This explained the increase in human and equine bloodmeals, and the decrease in cattle bloodmeals for *An. arabiensis* after the rainy season. Comparison between human and bovine blood indices calculated during the same time did not show any significant differences between *An. gambiae* and *An. arabiensis*, contrary to what was observed in Nigeria (White and Rosen 1973) and Kenya (Petrarca et al. 1991).

The frequency of mixed bloodmeals in this region was at least 17.8%, but probably much higher, because it was not possible to detect the number of bloodmeals taken on 2 different hosts of the same vertebrate species using ELISA. Feeding patterns also were opportunistic, depending on host availability. Likewise, the rate of patent mixed bloodmeals, mainly human–cattle, was the same for *An. gambiae* and *An. arabiensis*.

To our knowledge, a high percentage of mixed bloodmeals rarely has been observed for malaria vectors (Burkot et al. 1988). Beier et al. (1988) showed that it was possible to identify host blood

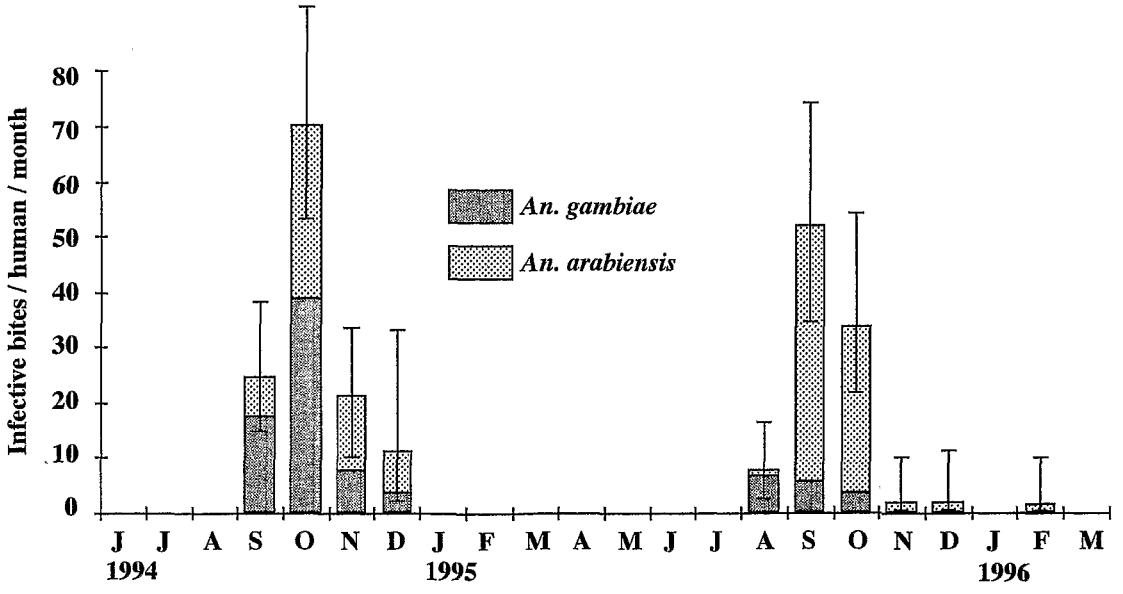


**Fig. 5.** Monthly entomological inoculation rate for *An. gambiae* and *An. arabiensis* in Barkedji from June 1994 to March 1996.

by ELISA up to 30 h after blood feeding. In Barkedji it was not possible to know if mixed bloodmeals were caused by the interrupted bloodmeals during the same night or multiple feeding on several nights during a single gonotrophic cycle. It was shown experimentally that *An. gambiae* females may take >1 bloodmeals within 6–24 h (Briegel and Hörler 1993). Such multiple feedings also were observed in the field (Beier 1996).

Despite a lower circumsporozoite protein rate, *An. arabiensis* was responsible for 63% of malaria transmission, because it was more abundant than *An. gambiae* and remained active within the village for a long time. To explain the higher circumsporozoite protein rate of *An. gambiae*, the following 3 hypothesis are proposed: (1) *An. gambiae* has a higher parity rate than *An. arabiensis* as observed during 1994–1995. However, data collected during 1995–1996 showed that the parity rate of *An. gambiae* was significantly lower than *An. arabiensis*, but there was no difference in the circumsporozoite protein rate, (2) The feeding frequency differed between the 2 species. If *An. gambiae* fed more frequently than *An. arabiensis*, its circumsporozoite protein rate might be elevated because of more host contacts, (3) Genetic susceptibility to *Plasmodium* differed. Differences may exist between genetically characterized populations within the *An. gambiae* complex, as reported in Kenya by Petrarca and Beier (1992). Differences in genetic susceptibility to *Plasmodium* may account for the higher circumsporozoite protein rate in *An. gambiae* than *An. arabiensis*.

## Acknowledgments

We thank Mamoudou Diallo, Henri Manga, and Sadjo Sow for their technical assistance, Frank Collins (Centers for Disease Control and Prevention) for providing the *Plasmodium* monoclonal antibodies and for advice on PCR, Pauline Roussilhon for help in the English translation, Andre Spiegel, Christophe Rogier, and 2 anonymous reviewers for very helpful suggestions, and the villagers in Barkedji for their cooperation throughout the survey. This work was supported by the Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM).

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*Received for publication 10 June 1996; accepted 3 January 1997.*