FEEDING PATTERNS OF MOSQUITOES COLLECTED IN THE SENEGAL RIVER BASIN

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ABSTRACT. Mosquitoes were collected with light traps baited with dry ice at 16 locations in Senegal during the rainy season of 1988. Of 62,055 mosquitoes identified, 1,384 (2.2%), representing 25 species in 4 genera, were bloodfed. Mosquito bloodmeals were screened by enzyme-linked immunosorbent assay against antisera to humans, bovines, goats, sheep and chickens. Overall, 88% of the bloodmeals tested were identified. Bloodmeals from 5 species of *Culex* mosquitoes comprised 82% of the number tested. *Culex antennatus* (36.6%) and *Cx. tritaeniorhyncus* (33.5%) were the most abundant. All *Culex* except those of the *Cx. univittatus* group fed most often on humans. *Aedes* species fed almost equally on all mammals tested, while species of *Anopheles* preferred cattle over humans, goats and sheep.

INTRODUCTION

During October 1987, a major epizootic and epidemic of Rift Valley fever (RVF) was documented in the Senegal River basin, centered around the town of Rosso in southern Mauritania. Two hundred eighty-four human cases were identified by virus isolation and serology, and estimates of total human involvement exceeded 1,000 cases (Jouan et al. 1988). Antibody prevalence among domestic animals in the Rosso area was as high as 85% (Ksiazek et al. 1989). The magnitude of this outbreak generated intense interest for follow-up studies during the rainy season of 1988 to assess the potential for continued RVF viral activity in the region.

During August and September 1988, an arbovirus survey was conducted in the Senegal River basin to look for evidence of RVF viral activity in mosquitoes. In conjunction with this survey, all blood-engorged mosquitoes collected were examined by enzyme-linked immunosorbent assay (ELISA) to determine the source of the bloodmeal. Identification of arthropod bloodmeals is an important aspect in the determination of vector potential and the study of arboviral ecology. By determining mosquito host selection patterns (Boreham and Garrett-Jones 1973) in the Senegal River basin, we hoped to understand better the ecology of RVF viral transmission in the area.

MATERIALS AND METHODS

Study area: The majority of mosquitoes examined were collected in Senegal from 12 locations in the Senegal River basin (Fig. 1). Four additional sites, Dahra and Yonofere (Fig. 2) in the Ferlo region, Dakar on the Atlantic coast, and Kedougou in southeastern Senegal, yielded small numbers of specimens. The vegetative pattern in the Senegal River basin can be categorized as Sahelian to Sudano-Sahelian savannah, dominated by annual grasses and widely dispersed trees, particularly *Acacia* spp. and *Combretacae* spp. (Tucker et al. 1985). The Ferlo region is classified as a shrub pseudo-steppe to shrub savannah and is primarily used for raising livestock (Stanicioff et al. 1986). In this area there is little to no ground cover in the dry season (Fig. 3A); however, heavy rains during relatively wet years can produce ephemeral vegetation reaching more than 1 m in height as shown in Figs. 3B, C. Rainfall occurs primarily during the months of July through October and ranges from 200 to 600 mm annually. The average length of the rainy season varies from 5.5 months for Kedougou to 2 months in the lower Senegal River (Dakar Bango, Ndialene, Rhor). The domestic animals most frequently encountered at the collection sites included cattle, sheep, goats and chickens. Few wild vertebrates were observed in the area with the exception of birds, hares, lizards and rodents.

Mosquito collections: Mosquitoes were collected between August 1 and September 23, 1988, with solid-state U.S. Army miniature light traps (John W. Hock, Co., Gainesville, FL) baited with 0.5 kg dry ice. Five to 7 light traps were set at each collection site and generally placed near dwellings, livestock corrals and possible mosquito emergence sites. Traps were suspended 1–2 m above ground in trees or from metal standards. Mosquitoes were frozen in liquid nitrogen in the field and stored at −70°C prior to identification in the laboratory. After identification, blooded abdomens were removed with a scalpel, placed in round-bottom, 96-well polystyrene plates and stored at −70°C for the ELISA.

Preparation of mosquito samples: A modification of the method of Beier et al. (1988) was

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used. Blooded abdomens were triturated individually in 50 μl of 0.01 M phosphate-buffered saline (PBS), pH 7.4, in U-shaped, 96-well polystyrene plates. After trituration, an additional 50 μl of PBS was added to each well (1:2 dilution), bringing the total volume to 100 μl. The plates were covered with cellophane and stored at −70°C until tested.

ELISA reagents: Species-specific, horseradish peroxidase-labeled antibody conjugates (anti IgG, H+L) were purchased from Kirkegaard and Perry Laboratories, Inc., Gaithersburg, MD (human, bovine, goat and chicken) and Zymed Laboratories, Inc., Burlingame, CA (sheep). Optimal dilutions of the conjugates were determined in preliminary experiments by checkerboard titration with normal sera as positive controls. Dilutions of the conjugates ranged from 1:800 for the sheep to 1:2,000 for the human. Abdomens from unfed *Culex pipiens* Linn. (El Gabal strain, colony maintained at USAMRIID) served as negative controls. Optimal specificity of the conjugates was achieved by the addition of a mixture of varying dilutions (1:500 to 1:2,000) of heterologous sera to the conjugate solutions prior to application to the plate.

Direct ELISA: Mosquito bloodmeal samples were diluted 1:50 in PBS, and 50 μl volumes were added to wells of U-shaped, polyvinyl chloride, 96-well microtiter plates (Dynatech Laboratories, Inc., Alexandria, VA); plates were incubated at room temperature (22°C) for 3 h. After incubation, the plates were washed 3 times with PBS containing 0.5% Tween 20 (PBS/TW-20). Fifty μl of host-specific conjugate, diluted in blocking buffer (PBS containing 0.5% boiled casein, 0.025% Tween 20, 0.01% thimerosal, and 0.002% phenol red), was then added. Each specimen was tested against a battery of the following antibody conjugates: human, bovine, sheep, goat and chicken. After a 1-h incubation at 22°C, the plates were washed 5 times with PBS/TW-20, and 100 μl of ABTS (2,2; pp -azino-di [3-ethyl benzothiazoline sulfonate]) peroxidase substrate (Kirkegaard and Perry Laboratories, Inc.) was applied. After a final incubation of 30 min at 22°C, the plates were read spectrophotometrically (MR600 microplate reader, Dynatech Laboratories, Inc.) at 410 nm. Positive and negative controls were incorporated on every plate. A sample was considered positive if its absorbance value exceeded the mean plus 3 times the standard deviation of the negative controls.

RESULTS

Of 62,055 mosquitoes identified, 1,384 (2.2%) representing 25 species, had evidence of blood in the abdomen. Ten species comprising 1,317 specimens (95% of the total) were selected for inclusion in Table 1 and further analysis. The remaining 67 (5% of the total) blood-fed speci-

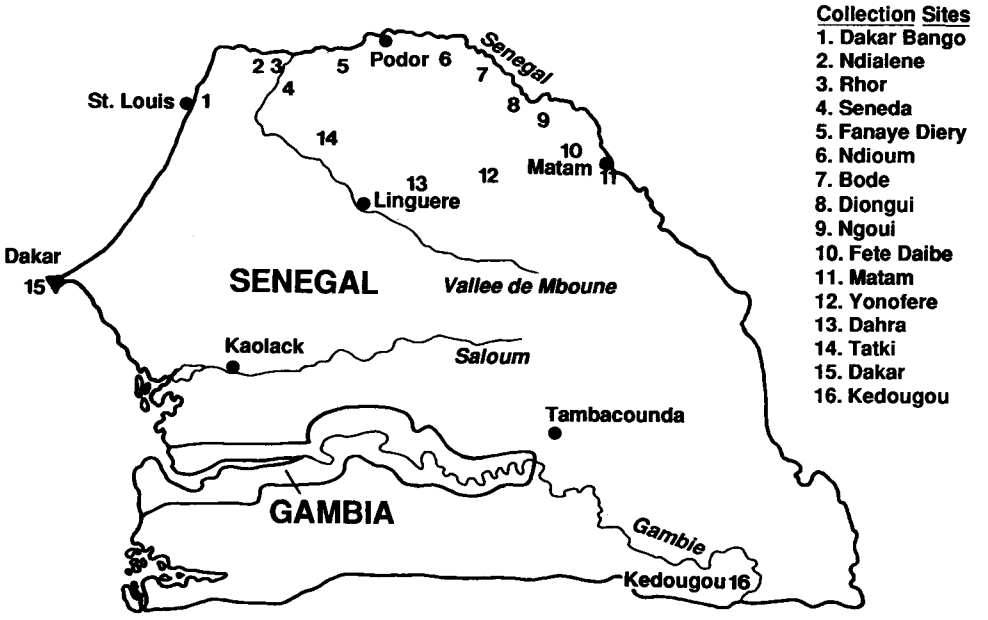

Fig. 1. Map of Senegal with mosquito collection sites.

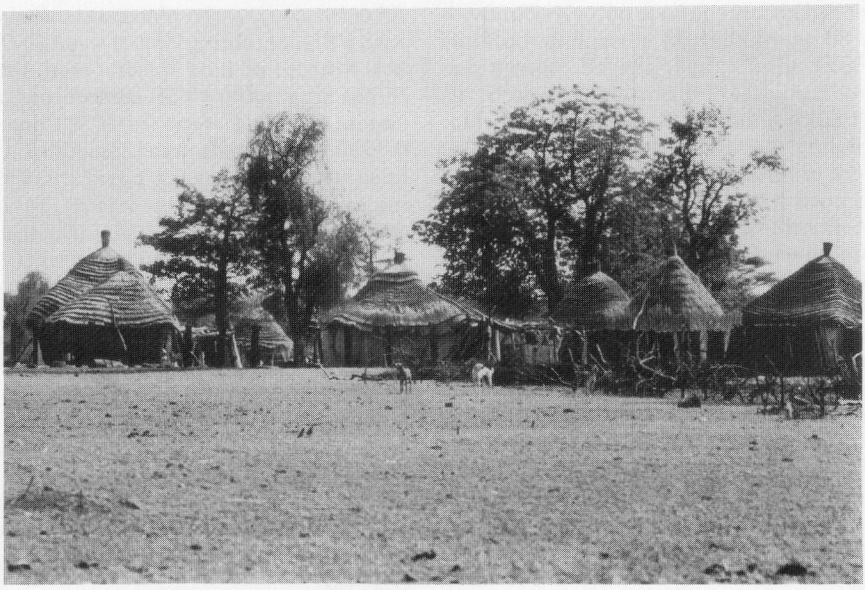

Fig. 2. Village of Yonofere, Ferlo region, Senegal in September 1988 where mosquitoes were collected.

mens that were tested included 15 species in 4 genera.

Overall, 88% of the bloodmeals tested were identified. Five species of *Culex* mosquitoes accounted for 82% of the bloodmeals tested [*Cx. antennatus* (Becker) (36.6%), *Cx. tritaeniorhynchus* Giles (33.5%), *Cx. poicilipes* (Theobald) (6.6%), *Cx. univittatus* Theobald group (3.8%) and *Cx. thalassius* Theobald (1.7%)]. The 3 most abundant *Aedes* [*Ae. hirsutus* (Theobald), *Ae. sudanensis* (Theobald) and *Ae. ochraceus* (Theobald)] made up 9.4% of the sample, while *Anopheles gambiae* Giles *s.l.* and *An. pharoensis* Theobald accounted for 3.5%.

Culex antennatus, *Cx. tritaeniorhynchus* and *Cx. poicilipes* all showed similar feeding patterns. Each species had bloodmeals that reacted with all 5 antibody conjugates. Human and bovine bloodmeals were most common, and goats were fed upon more often than sheep. Multiple feedings were detected in 10 *Cx. tritaeniorhynchus*, 8 *Cx. antennatus* and 2 each of *Cx. poicilipes* and *Cx. thalassius* (Table 1).

We observed great variation in host selection by both *Cx. antennatus* and *Cx. tritaeniorhynchus* collected from different locations. Of 199 bloodfed *Cx. antennatus* collected in Rhor, 85% fed on humans and 3.5% on bovines. In contrast, of 52 collected in Diongui, 82.6% were from bovines and 11.5% from humans (Fig. 4). *Culex tritaeniorhynchus* collected in Rhor (n = 118) also preferred humans (77.1%) over bovines (12.7%); while in Dakar-Bango (n = 59) the opposite pattern occurred (59.3% bovine, 16.9% human) (Fig. 5). A third pattern was observed in Fanaye Diery (n = 164) where *Cx. tritaeniorhynchus* fed more often on goats or sheep (68.2%) than on either humans (15.2%) or bovines (10.9%) (Fig. 5).

All *Culex*, with the exception of the *Cx. univittatus* group, fed to a greater extent on humans than any of the other hosts examined (Table 1). The high percentage of unidentified feeds in *Cx. univittatus* (53%) suggests that a preferred host was not included in our tests. *Culex thalassius* had the highest percent of both human and chicken meals (57% and 22%, respectively).

Aedes sudanensis and *Ae. ochraceus* fed almost equally on all mammals tested; however, undetermined bloodmeals accounted for approximately 30% of the samples in both species. *Aedes hirsutus* showed a slight preference for bovines (34%) over humans (22%) and sheep or goats (18%). Six specimens of *Ae. hirsutus* contained multiple feeds (5 bovine/human and 1 bovine/goat) (Table 1).

Both *Anopheles gambiae s.l.* and *An. pharoensis* fed most frequently on bovines (54% and 31%, respectively), but feeding on humans was also common (23% and 14%, respectively). Nearly 45% of *An. pharoensis* bloodmeals were not identified (Table 1).

DISCUSSION

To establish the natural host(s) of a species, the collection of bloodmeals should be fully representative (indoor vs outdoor, baited traps vs

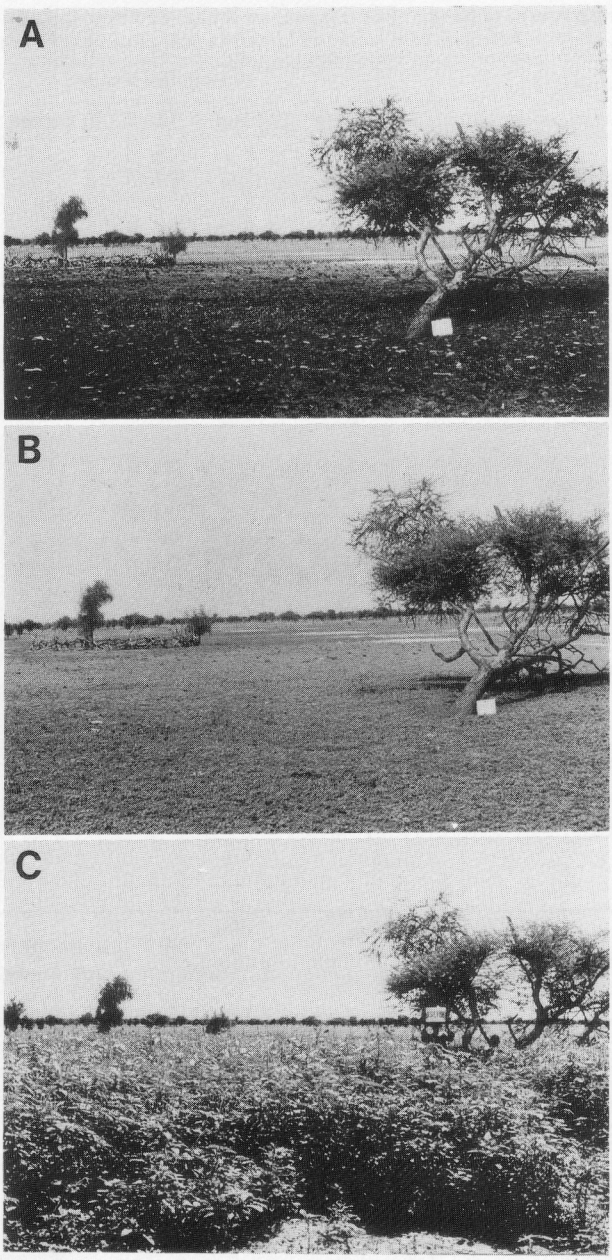

Fig. 3. Collection site at Dahra, Ferlo region, Senegal on A) August 4, 1988, B) August 11, 1988, and C) September 1, 1988, demonstrating the vegetation development following heavy rainfall.

resting collections and daytime vs night). Because all specimens tested in the present study were collected with light traps, this may have introduced a strong bias toward exophilic species. Indoor sampling with aspirators or light traps would undoubtedly have yielded larger numbers of human-positive specimens.

Culex antennatus was the most frequently collected mosquito in this study and also accounted for the most blood-engorged specimens. Overall, 53% (268/507) showed evidence of human blood although we noted considerable variation among collection sites. Bovine-positive bloodmeals were most numerous in 9 locations, human pos-

Table 1. Bloodfeeding patterns of the 10 most common mosquitoes collected in CO_2-baited U.S. Army miniature light traps in Senegal, 1988 (number in parenthesis is percent of samples tested).

Species	Total tested	Bloodmeal source						
		Human	Bovine	Sheep	Goat	Chicken	Mult[a]	ND[b]
Aedes hirsutus	90	20 (22.2)	31 (34.4)	7 (7.8)	9 (10)	—	6 (6.7)	17 (18.9)
Ae. ochraceus	14	3 (21.4)	3 (21.4)	2 (14.3)	2 (14.3)	—	—	4 (28.6)
Ae. sudanensis	26	5 (19.2)	6 (23.1)	—	6 (23.1)	—	1 (3.8)	8 (30.8)
Anopheles gambiae s.l.	13	3 (23.1)	7 (53.8)	—	1 (7.7)	1 (7.7)	—	1 (7.7)
An. pharoensis	36	5 (13.9)	11 (30.6)	2 (5.5)	2 (5.5)	—	1 (2.8)	15 (41.7)
Culex antennatus	507	268 (52.8)	149 (29.4)	14 (2.8)	33 (6.5)	3 (.6)	8 (1.6)	32 (6.3)
Cx. poicilipes	91	27 (29.6)	16 (17.6)	6 (6.6)	12 (13.2)	4 (4.4)	2 (2.2)	24 (26.4)
Cx. thalassius	23	13 (56.5)	1 (4.3)	—	1 (4.3)	5 (21.7)	2 (8.7)	1 (4.3)
Cx. tritaeniorhynchus	464	173 (37.3)	121 (26.1)	38 (8.2)	88 (19)	1 (.2)	10 (2.1)	33 (7.1)
Cx. univittatus group	53	3 (5.7)	13 (24.5)	—	6 (11.3)	3 (5.7)	—	28 (52.8)

[a] Multiple feed.
[b] Bloodmeal not determined.

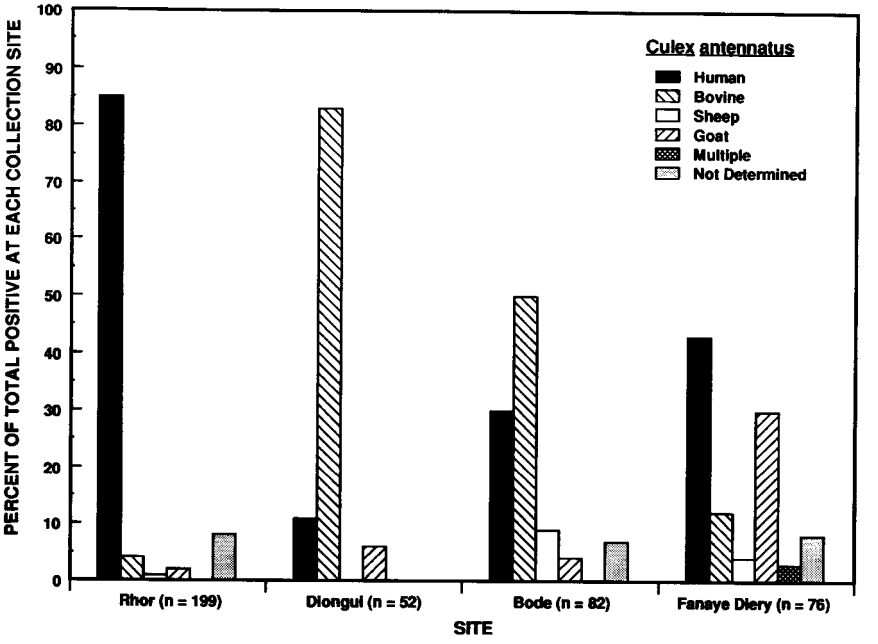

Fig. 4. Feeding preferences of *Culex antennatus* at 4 collection sites where it was most commonly collected.

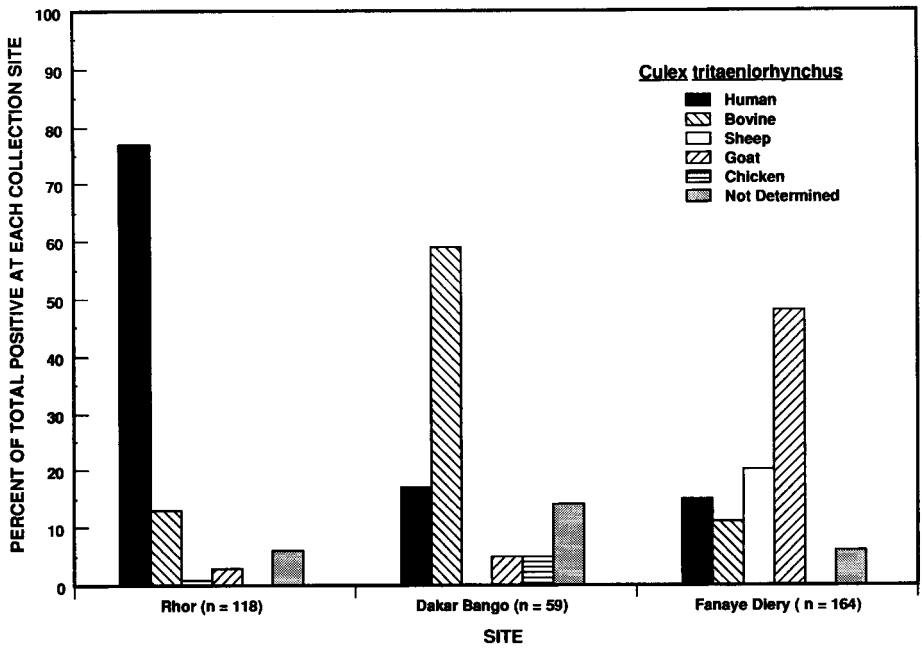

Fig. 5. Feeding preferences of *Culex tritaeniorhynchus* at 3 collection sites where it was most commonly collected.

itives in 3 and sheep positives in one location. In Kenya, Chandler et al. (1975, 1976) found that *Cx. antennatus* collected indoors fed mainly on human blood, and outdoors mainly on cattle. Eight multiple feeds were recorded, 5 human/bovine, 2 bovine/goat and 1 human/goat.

Culex tritaeniorhynchus, the second most common species, was found to feed more frequently on humans (37.3%) than on cattle (26.1%), or sheep or goats (27.2%). This is in contrast to studies in Pakistan where cattle accounted for 84% (Reisen and Boreham 1976) and 93.4% (Reisen and Boreham 1979) of identified *Cx. tritaeniorhynchus* bloodmeals. Similar results were reported from India by Christopher and Reuben (1971). In Okinawa, Pennington and Phelps (1968) found pigs to be the preferred host, and despite the abundant availability of humans in the area, only 4/20,522 *Cx. tritaeniorhynchus* tested positive for human blood. Colless (1958) noted that in Singapore, *Cx. tritaeniorhynchus* was attracted to humans in the absence of cattle, but was slow to feed. In The Gambia, Snow and Boreham (1973) found that 88.2% of the specimens had fed on cattle and concluded that there was no difference in the feeding habits of *Cx. tritaeniorhynchus* in West Africa and the eastern part of its range. In Senegal, feeding patterns of *Cx. tritaeniorhynchus* show considerable variation from location to location and appear to be closely related to host abundance and availability in a particular area. Of the 11 sites where bloodfed *Cx. tritaeniorhynchus* were collected, bloodmeals from cattle were most prevalent at 6 sites, human at 3, and sheep or goats at 2 sites.

Culex poicilipes fed most frequently on humans (29.6%), then on cattle (17.6%) and goats (13.2%). However, 26% of *Cx. poicilipes* bloodmeals could not be identified. In Kenya, Chandler et al. (1976) found this species to feed on birds to a great extent and secondarily on cattle and dogs. It is possible that the chicken conjugate used in this study did not react with the more common wild birds in the area, thus explaining the large number of unidentified feeds. Some may also have fed on local small mammals.

Small numbers of both *Cx. univittatus* group and *Cx. thalassius* were also examined. *Culex thalassius* fed predominately on humans (56.5%) and birds (21.7%). *Culex univittatus* group fed most often on bovines (24.5%) and goats (11.3%); however, over 50% of bloodmeals could not be identified. In The Gambia, *Cx. thalassius* was found to be non-specific in host selection, feeding on mammals (59.5%), avians (38.1%) and reptiles (2.4%) (Snow and Boreham 1973). Hamon et al. (1971) found *Cx. thalassius* to be ornithophilic in southwestern Senegal, but it was often a pest of humans outdoors when populations were high. *Culex thalassius* has not been

implicated in the transmission of pathogens to humans, but several arboviruses have been isolated in Senegal from this species (Bres et al. 1969, Institut Pasteur 1989). Because it feeds readily on both man and birds, it would appear to be a good candidate vector.

The *Cx. univittatus* group is most likely represented in Senegal by either *Cx. neavei* Theobald or *Cx. perexiguus* Theobald (Harbach 1988). In outdoor collections from Kenya (Chandler et al. 1976) and South Africa (Anderson 1967), *Cx. univittatus* was found to be primarily ornithophilic. In southern Senegal, Abonnenc (1956) noted that *Cx. univittatus* occasionally fed on humans outdoors but never indoors.

All 3 species of *Aedes* fed almost equally on humans, cattle and sheep or goats. In Kenya, bloodmeals from 95% of *Ae. hirsutus* and *Ae. ochraceus* (Chandler et al. 1975) and 92% of *Ae. sudanensis* (Linthicum et al. 1985b) tested positive for cattle. Hamon et al. (1964) found *Ae. hirsutus* to be moderately anthropophilic in Burkina Faso (Upper Volta).

Anopheles pharoensis showed a preference for cattle (30.6%) over humans (13.9%), and sheep or goats (11%); however, 41.7% of the bloodmeals were not identified with the screening battery used. In a 1987 survey in the Senegal River basin, *An. pharoensis* was the most common man-biting anopheline collected in bednets in houses (Carrara et al. 1990). More than 90% of these *An. pharoensis* were positive for human blood. In Tanzania, White (1971) found that 90% of *An. pharoensis* examined had fed on cattle and only 2% on humans. In Egypt, where *An. pharoensis* is recognized as a vector of malaria (Halawani and Shawarby 1957), Kenawy et al. (1987) found that 62% of bloodfed specimens collected inside houses and 50% of outdoor collections had fed on humans. *Anopheles pharoensis* has also been identified as an important human pest species in irrigated areas of Sudan (El Safi and Haridi 1986).

The small numbers of *An. gambiae s.l.* tested showed bovines (53.8%) and humans (23.1%) to be the most common hosts. No attempt was made to separate the various members of the *An. gambiae* complex; however, a recent study by Petrarca et al. (1987) indicates that both *An. gambiae* and *An. arabiensis* Patton occur inland along the Senegal River.

Undetermined bloodmeals were probably the result of either the narrow host range selected for testing or the advanced digestion of the bloodmeal. The efficacy of the ELISA used in this study declines rapidly with bloodmeals older than 24 h due to degradation of IgG antibody (Beier et al. 1988).

Multiple feeding, defined as 2 or more bloodmeals from different vertebrate hosts, the last of which has been taken before the first has been digested, has been reported previously (Boreham and Garrett-Jones 1973). Including species not listed in Table 1, 32 (2.3%) mosquitoes tested in this study had evidence of multiple feeding. The most common combination was human/bovine (20), followed by human/goat and bovine/goat (5 each), and human/sheep (2). Rates of multiple feeding in individual species ranged from 1.6% in *Cx. antennatus* to 8.7% in *Cx. thalassius*. Edman and Downe (1964) reported the incidence of multiple feeding to range from 9.7 to 61.8% in 17 culicine species in Kansas.

Over the past 28 years, the Institut Pasteur de Dakar (Centre Collaborateur OMS de Reference et de Recherche pour les Arbovirus) has accumulated extensive records on virus isolations from mosquitoes in Senegal (Institut Pasteur 1989). However, only a few studies have attempted to relate mosquito host selection patterns to the ecology of arboviruses (Bres et al. 1969, Hamon et al., 1971). Of the 10 most common mosquitoes collected in this study, only *Cx. antennatus* and *An. pharoensis* have been found naturally infected with RVF virus (Linthicum et al. 1985a); and a third, *Cx. univittatus* from South Africa, has been shown experimentally to transmit the virus (Meegan and Bailey 1989). Vector competence with RVF virus should be studied in *Cx. tritaeniorhynchus*, *Cx. poicilipes* and *Cx. thalassius*, as all 3 species were abundant and fed on humans and domestic animals to a high degree.

While no evidence of RVF viral activity was detected in this study, the potential for future outbreaks of the disease throughout the Senegal River basin still exists. Flood-induced ecological changes in the delta region resulting from the implementation of a water development program may have contributed to the 1987 epidemic (Linthicum et al. 1990). No epidemics of RVF had been reported in this area prior to the construction of the dams on the Senegal River (Walsh 1988). The establishment of new irrigation agriculture programs, like those of the Nile and Senegal rivers, which preceded RVF outbreaks, may also create conditions favorable to increases in mosquito populations and incidence of mosquito-borne disease (Digoutte and Peters 1989).

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