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Exposure of sheep to mosquito bites: possible consequences for the transmission risk of Rift Valley Fever in Senegal

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Abstract. Rift Valley Fever (RVF) is a growing health problem in West Africa. In northern Senegal, the candidate vectors of this arbovirosis are *Aedes* (*Aedimorphus*) *vexans* Meigen and *Culex* (*Culex*) *poicilipes* Theobald (Diptera: Culicidae). Domestic ruminants are the reservoirs of the virus. A study was undertaken during the 2002 rainy season to assess spatial and temporal variations in exposure to mosquito bites in sheep herds, and to evaluate the possible consequences on the risk of RVF transmission to sheep.

Mosquitoes were collected with sheep-baited traps. The number of *Ae. vexans* females (the predominant species during the 2002 rainy season) trapped per trap-night was the dependent variable in statistical analyses. The trapping periods were divided into six series of two to five consecutive days, from July to November 2002. Three temporary ponds were selected according to their ecological features: depth, bank slope, size and vegetation cover. Traps were laid on the pond bank and in the nearest available compound, close to the sheep night pen. Data were analysed using mixed-effects Poisson models. The explanatory variables were the trapping period, the pond, and the capture site.

The exposure to mosquito bites varied according to the pond type, suggesting that the risk of transmission was spatially heterogeneous. However, there was no obvious trend in transmission risk due to the effect of the distance from the compound to the pond. The period with the highest exposure was in October, i.e. when transhumant herds left the Ferlo to relocate to their dry-season settlement. It is thus hypothesized that transhumance, the seasonal movements of herds, plays a significant role in the dissemination of RVF virus in the region.

Key words. *Aedes vexans arabiensis*, Rift Valley Fever, sheep, vector, Senegal.

Introduction

The large extent of the 1987 Rift Valley Fever (RVF) epidemic in southern Mauritania (Jouan *et al.*, 1988), and more recent outbreaks in Mauritania, Senegal and The Gambia (OIE, 2002a,b, 2003) drew the attention of veterinary and public health services to this mosquito-borne disease, which is now considered a major threat in this part of Africa. RVF is caused by a *Phlebovirus* (Bunyaviridae) which infects humans and ruminants. Mass abortion and high mortality in newborn kids and lambs are observed in naive ruminant

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populations. In humans, a flu-like syndrome is often the only clinical manifestation, but haemorrhagic fever, encephalitis or ocular disease may occur in rare cases (Wilson, 1994).

In Sahelian Africa, domestic ruminants are the reservoirs of the virus, which is commonly transmitted by mosquitoes in the genera *Culex* and *Aedes* (House *et al.*, 1992; Fontenille *et al.*, 1998). In Senegal, the main candidate vectors are *Culex* (*Culex*) *poicilipes* Theobald and *Aedes* (*Aedimorphus*) *vexans* Meigen (Fontenille *et al.*, 1998; Diallo *et al.*, 2000). The RVF virus was also isolated from *Aedes* (*Aedimorphus*) *ochraceus* Theobald, but in Senegal, the epidemiological role of this species is probably insignificant because of its low abundance. Vertical transmission was also described for some *Aedes* species (Wilson, 1994). When environmental conditions are suitable, transovarially transmitted virus may be amplified on vertebrate hosts and *Culex*, and lead to an outbreak.

Because low-level circulation of RVF was described in the Ferlo, northern Senegal (Wilson, 1994; Fontenille *et al.*, 1995), a study was undertaken to understand which circumstances might induce the amplification of the virus cycle, and thus RVF epidemics. The goal of this paper is to describe the contact between mosquitoes and their hosts, i.e. how the virus might be transmitted from mosquitoes to domestic ruminants.

Materials and method

The study zone

The rural community of Barkedji (14°52′ W, 15°16′ N) is located in the Ferlo region, in the Sahelian part of Senegal (Fig. 1). The climate is hot and dry with annual rainfall ranging from 300 to 500 mm. The terrain is composed of dunes, either flattened or stabilized by the vegetation (GEMS/FAO, 1988), lying on a lateritic plateau. This plateau is modelled by a large hydrographic basin called the Ferlo valley, corresponding to a former tributary of the Senegal River, which stopped flowing at the end of the last humid Saharan period (Neolithic era).

The Ferlo valley crosses the rural community of Barkedji from east to west with lateral spurs extending to the north and the south. During the rainy season, temporary ponds are flooded by rainfall and constitute a network of surface waters a few kilometres apart.

Rural activities are dominated by low-input farming of Gobra zebu cattle, Peul-Peul sheep and Sahelian goats. The size of ruminant herds is generally high: tens to hundreds of animals. Cattle and small ruminants usually spend the night in pens (fenced with branches of thorny shrubs). The availability of water is the most significant constraint in this pastoral system. During the rainy season (July–October) farmers construct their compounds around the temporary ponds to utilize the free surface waters and the surrounding grasslands.

The maximum size of temporary ponds ranges from a few hundred square meters to several hectares. Their depth is generally shallow (2 m at the most) and varies according to the rainfall frequency and the intensity of evaporation. Because slopes are often very gradual, small variations in depth correspond to large changes in flooded surface areas.

Temporary ponds

Three temporary ponds were selected according to their ecological features. The Barkedji pond which surrounded the eponymous village was large (several hectares) and deep (maximum depth 1.7 m), and located in the main bed of the Ferlo valley. The pond flooded a rather dense stand of trees

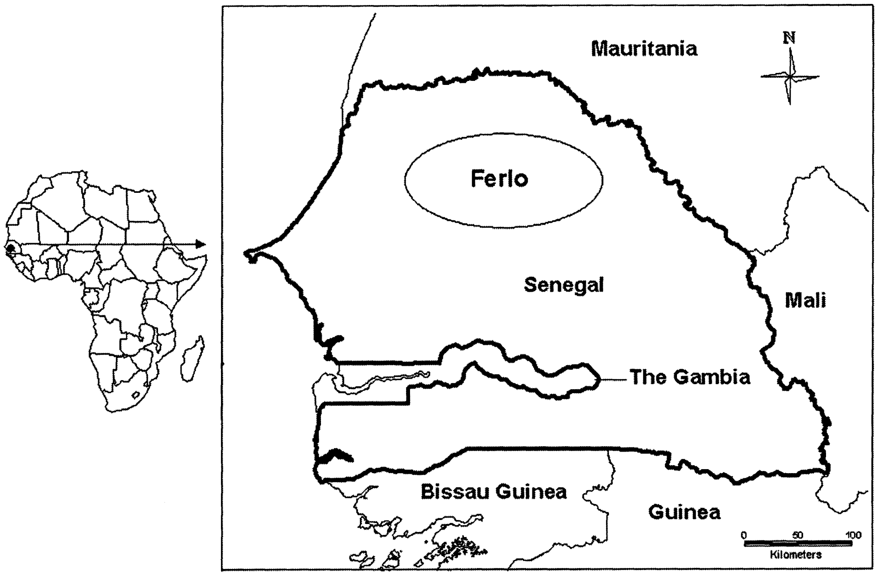

Fig. 1. Location of the Ferlo area (Senegal).

(*Mytragena inermis*, *Piliostigma reticulatum*, *Adansonia digitata*) and supported water lilies (*Cenatotheca sesamoïdes*) during the rainy season. Vegetation surrounding the Barkedji pond included trees (*Diospyros mespiliformis*, *Mytragena inermis*, *Piliostigma reticulatum*, *Balanites aegyptiaca*) and grass species (*Cenchrus prieurii*, *Corchorus* sp.).

The two other ponds were outside the main bed of the Ferlo. The Furdu pond was small and shallow (maximum surface = 1.4 ha, maximum depth = 0.6 m). It was surrounded by thorny trees such as *Balanites aegyptiaca* but poorly covered by herbaceous species: *Mytragena inermis* and *Oryza* sp. (wild rice). The Ngao pond was of intermediate size and depth (maximum surface = 3 ha, maximum depth = 0.8 m). It was densely covered by trees (*Acacia nilotica*, *Acacia radiana*, *Adansonia digitata*), as well as water lilies and other annual grasses during the rainy season. The pond bank was also densely covered by trees (*Balanites aegyptiaca*, *Acacia radiana*, *Acacia ataxacantha*) and grass species (*Cissus quandrangularis*, *Capparis dicidua*).

Exposure to mosquito bites

Mosquito traps were installed in two sites near each of these three ponds. The first trap was located on the pond bank and the second one in the pond's nearest compound, close to the domestic ruminants' night pen. Distances between the pond and the compound were 200 m, 400 m and 1 km for the Barkedji, Furdu and Ngao sites, respectively.

Previous studies on arbovirus vectors carried out in the Ferlo used human baited-traps, which might not be relevant to study mosquito-feeding behaviour towards ruminants. Therefore, it was decided to use a trap adapted from Bown & Bang (1980). It was made of a metal frame covered with a mosquito net, so that mosquitoes could enter the trap at its base. The trap was baited with a sheep. Attracted mosquitoes ascended after biting and were trapped in a removable box set on top of the trap. They were collected before sunrise.

The study was carried out from 15 June to 15 November 2002. Mosquitoes were trapped during six time periods: 18–21 July, 5–7 August, 22–24 August, 17–22 September, 14–19 October and 5–7 November. Rainfall data were supplied by the Direction de la Météorologie Nationale (Dakar, Senegal). They were recorded with a rain gauge located in Barkedji, and were then compared to the 1961–1990 average, taken to be the norm.

Aedes vexans and *Cx. poicilipes* have different diel activity patterns: the former is a crepuscular species, whereas the latter is mostly a night species. Therefore, traps were set between sundown and sunrise, i.e. from 18.00 to 06.00 hours. All the collected mosquitoes were killed in a freezer, identified and counted by species. The exposure to mosquito bites was based on the abundance of female mosquitoes captured in each trap on each trapping occasion. This count was the dependent variable in subsequent statistical analyses.

Data analysis

The goal of the analysis was to assess spatial and temporal variations in exposure to mosquito bites. A Poisson model was used for this purpose (MacCullagh & Nelder, 1989). The explanatory variables were the period (six of them, as described above), the pond (Barkedji, Furdu or Ngao) and the capture site (pond or compound). Main effects, two- and three-way interactions were retained as the fixed effects. To account for time clustering of trapping dates (possibly resulting in correlated residuals caused by unobserved events such as mosquito hatching after rainfall), the date was coded as a discrete variable and included in the model as a random effect. A penalized quasi-likelihood algorithm was used to obtain a first estimate of the parameters, which was subsequently refined by the optimization of the second-order Laplacian approximation to the marginal log-likelihood (Schall, 1991; Breslow & Clayton, 1993; Wolfinger & O'Connell, 1993). Other nested models were fitted to assess the statistical importance of the three-way interaction and the global influence of each main effect and its interactions with other explanatory variables. They were compared using the Akaike information criterion (1):

$$AIC = -2 \text{ maximized likelihood} + 2k, \qquad (1),$$

where k was the number of parameters in the model.

Because the number of parameters in the models was high compared to the number of observations, a small-sample correction of *AIC* (*AICc*) was also used (2):

$$AICc = AIC + \frac{2k(k+1)}{n-k-1}, \qquad (2),$$

where n was the number of observations in the model (number of trapping results). For both of these information criteria, the best model was the one with the lowest criterion. For each criterion, between-model differences >7 indicated that models with higher values for that criterion were highly implausible, given the observed data. Hence, models with the lowest information criteria were the most plausible (Burnham & Anderson, 2002).

Confidence intervals for model parameters were computed with a Monte-Carlo Markov Chain (MCMC) algorithm (Zeger & Karim, 1991; Browne & Draper, 2000). The 2.5% and 97.5% quantiles of each MCMC-simulated parameter were used to form its 95% confidence interval. Two software applications were used for data analysis: MLwiN for MCMC estimations (Rasbash *et al.*, 1999) and R for any other analyses (Bates *et al.*, 2004; R Development Core Team, 2004).

Results and discussion

During the 2002 rainy season, 267 mm of rainfall was recorded in Barkedji, i.e. 131 mm (33%) below the norm (Fig. 2). This deficit was marked in July (58%) and September (54%). Rainfall in August (131 mm) was normal. A rain

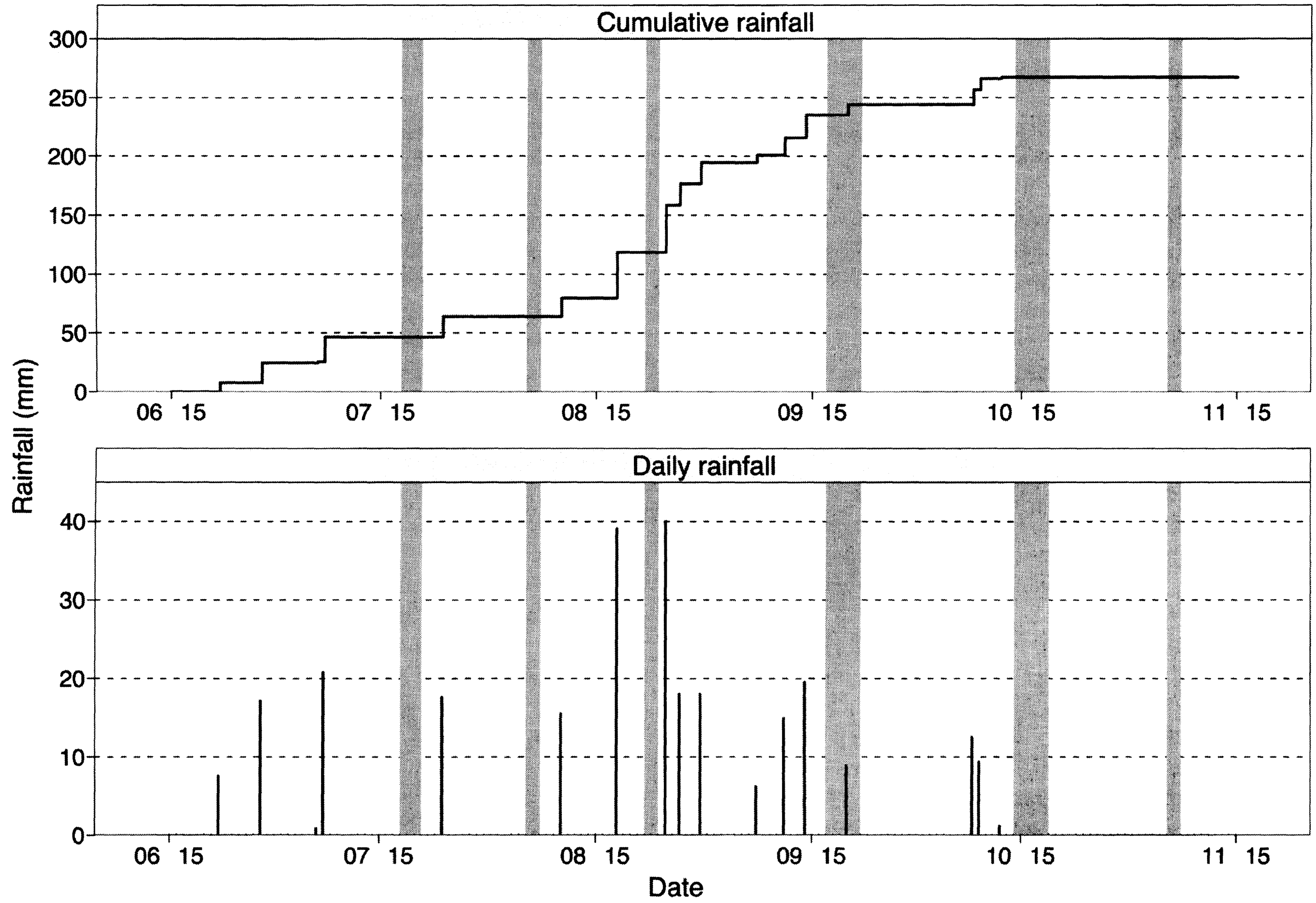

Fig. 2. Rainfall pattern and mosquito-trapping periods from June to November 2002 in Barkedji (Senegal).

pause happened from 8 July to 23 July, i.e. at the beginning of the rainy season. Therefore, transhumant farmers delayed their arrival in Barkedji, and few compounds were settled around the temporary ponds. A second rain pause was observed from 21 September to 7 October, and the last rain occurred on 12 October. Transhumant farmers left Barkedji area to relocate to their dry-season settlement soon after.

A total of 8122 female mosquitoes were collected (Table 1). The three presumed RVF vectors (*Ae. vexans*, *Cx. poicilipes* and *Ae. ochraceus*) represented 94.2% of the trapped mosquitoes. During a 6-year study in Barkedji, Fontenille *et al.* (1998) found that *Cx. poicilipes* was the most abundant species on several occasions. However, in this study, the most abundant species was *Ae. vexans* (88.1% of the captured mosquitoes). Because of this highly predominant abundance, we only considered *Ae. vexans* in the subsequent analyses.

The observed species pattern may have been because of the rather uncommon rainfall pattern encountered during the 2002 rainy season: a regional deficit with two large rain pauses, which probably broke the population dynamics of *Cx. poicilipes*. Free water is necessary for the development cycle of this insect (Beaty & Marquardt, 1996). Usually,

Table 1. Overall frequency of mosquito species captured with six sheep-baited traps in six trapping sites and 25 trapping nights from July to November 2002 in Barkedji rural community (Senegal).

Species	Number	Frequency (%)
Aedes vexans[a]	7138	88.1
Aedes ochraceus[a]	252	3.1
Culex poicilipes[a]	242	3.0
Aedes sudanensis	156	1.9
Aedes fowleri	60	0.7
Anopheles rufipes	42	0.5
Aedes mcintoshi	39	0.5
Other *Anopheles*. sp.[b]	86	0.01
Other *Culex*. sp.[c]	56	0.007
Other *Aedes*. sp.[d]	2	0.003

[a] Presumed Rift Valley fever vector, according to the scientific literature.

[b] *Anopheles* mosquitoes captured with a frequency lower than 0.5%: *An. gr. gambiae*, *An. pharoensis*, *An. constani*, *An. ziemani*, *An. squamosus*, *An. domicola*, *An. pretoriensis*, *Anopheles* sp., *An. nili*.

[c] *Culex* mosquitoes captured with a frequency lower than 0.5%: *Cx. quinquefasciatus*, *Cx. gr. annulioris*, *Cx. sitiens*, *Cx. antennatus*, *Cx. ethiopicus*.

[d] *Aedes* mosquitoes captured with a frequency lower than 0.5%: *Ae. gr. tarsalis*, *Ae. mucidus* sp., *Ae. metallicus*, *Ae. unilineatus*.

Table 2. Comparison of five mixed-effect Poisson models of sheep exposure to *Ae. vexans* bites near the ponds of Barkedji, Furdu and Ngao (Ferlo, Senegal) during the rainy season 2002.

Model[a]	loglik[b]	k[c]	AIC[d]	AICc[e]
1[f]	– 259.0	20	558.0	584.3
2[g]	– 332.9	16	697.8	712.9
3[h]	– 431.2	8	878.5	881.7
4[i]	– 1051.6	8	2119.1	2122.4
5[j]	– 1113.8	11	2249.5	2256.0

[a] In each model, the random effect was associated with the intercept and the grouping factor was the date.
[b] Logarithm of the maximized likelihood.
[c] Number of parameters in the model.
[d] Akaike information criterion.
[e] Corrected Akaike information criterion.
[f] Period + place + site + period*place + period*site + place*site + period*place*site.
[g] Period + place + site + period*place + period*site + place*site.
[h] Place + site + place*site.
[i] Period + site + period*site,
[j] period + place + period*place.

Culex populations peak several weeks after ponds are watered, coinciding with a decline of *Aedes* populations.

No mosquito was trapped in November during three consecutive capture nights. Different factors might explain this situation. Firstly, the rainfall deficit resulted in the premature draining of the temporary ponds. Secondly, hygrometry and night temperature dropped at the end of October 2002, announcing the beginning of the cool, dry season. These climatic conditions were probably unable to ensure the survival of most mosquitoes in Barkedji. November data were discarded from the following analyses.

The provisional trapping design was not perfectly maintained for logistical reasons: no trapping sessions were performed in Barkedji in July and during the second period of August. Rather than using incomplete data, we preferred to run two different analyses. The first involved all three ponds in early August, September and October. The second involved only Furdu and Ngao during five trapping periods (July–October). The results are displayed in Tables 2–5 and Figs 3 and 4.

In each analysis, model comparison (Tables 2 and 4) showed that the best-AICc model was the one with the three-way interaction between the place (Barkedji, Furdu or Ngao), the capture site (pond or compound) and the period (five periods). Because AICc differences were >>7, other models were highly implausible, given the observed data. They were not considered in the rest of the paper. Therefore, each explanatory variable accounted for an important part of the observed variation in the data, but this influence depended on the value of the other variables in the model. The spatial and temporal patterns of exposure to mosquito bites were thus complex.

On average, the exposure increased from Barkedji (lowest) to Ngao (highest) (Fig. 3). It was lower in Furdu than in Ngao (Figs 3 and 4). Although *Ae. vexans* was found everywhere, the exposure to its bites differed from place to place: assuming that the RVF-transmission risk was related to this exposure, this risk was heterogeneous from a spatial viewpoint in the region of Barkedji.

Assuming that some features of the ecology of North-American subspecies are also applicable to Ferlo conditions, entomological knowledge of *Ae. vexans* might provide insights to understand this spatial heterogeneity.

Table 3. MCMC estimates for the coefficients of the best-AICc mixed-effect Poisson model of sheep exposure to *Ae. vexans* bites near the ponds of Barkedji, Furdu and Ngao (Ferlo, Senegal) during the rainy season 2002.

Parameter	Mean	SD[a]	Median	Q 2.5% [b]	Q 97.5% [c]
Intercept	2.431	0.890	2.394	0.724	4.205
Sept.	– 1.539	1.349	– 1.487	– 4.393	0.979
Oct.	0.713	1.343	0.734	– 2.034	3.252
Furdu	– 4.435	1.241	– 4.255	– 7.583	– 2.522
Ngao	1.142	0.167	1.139	0.819	1.473
Compound	– 3.439	0.837	– 3.324	– 5.379	– 2.090
Sept. * Furdu	5.287	1.827	5.191	1.943	9.210
Oct. * Furdu	7.158	1.684	7.102	3.930	10.658
Sept. * Ngao	0.874	1.369	0.827	– 1.728	3.787
Oct. * Ngao	1.493	1.255	1.445	– 0.811	4.195
Sept. * Compound	0.070	1.531	0.166	– 3.285	2.857
Oct. * Compound	1.313	0.873	1.206	– 0.128	3.299
Furdu * Compound	6.266	1.517	6.098	3.719	9.653
Ngao * Compound	2.139	0.857	2.026	0.751	4.126
Sept. * Furdu * Compound	– 4.193	2.028	– 4.166	– 8.251	– 0.165
Oct. * Furdu * Compound	– 6.219	1.538	– 6.061	– 9.622	– 3.637
Sept. * Ngao * Compound	– 0.103	1.558	– 0.186	– 2.942	3.290
Oct. * Ngao * Compound	– 0.061	0.893	0.042	– 2.098	1.421
Variance of the random effect	2.462	1.595	2.046	0.844	6.617

[a] Standard deviation, [b] 2.5% quantile, [c] 97.5% quantile.

Table 4. Comparison of five mixed-effect Poisson models of sheep exposure to *Aedes vexans* bites near the ponds of Furdu and Ngao (Ferlo, Senegal) during the rainy season 2002.

Model[a]	loglik[b]	k[c]	AIC[d]	AICc[e]
1[f]	− 453.5	22	951.1	976.4
2[g]	− 907.1	18	1850.2	1865.7
3[h]	− 1774.8	6	3561.6	3563.1
4[i]	− 1446.0	12	2916.0	2922.2
5[j]	− 1304.4	12	2632.8	2639.0

[a] In each model, the random effect was associated with the intercept and the grouping factor was the date.
[b] Logarithm of the maximized likelihood.
[c] Number of parameters in the model.
[d] Akaike information criterion.
[e] Corrected Akaike information criterion.
[f] Period + place + site + period*place + period*site + place*site + period*place*site.
[g] Period + place + site + period*place + period*site + place*site.
[h] Place + site + place*site.
[i] Period + site + period*site.
[j] Period + place + period*place.

Females usually lay their eggs on the wet soil of temporary ponds. After the mud dries up, eggs may survive for several years in the soil (O'Malley, 1990). When the ponds are flooded again, there is a mass hatching of mosquito eggs, and adult neonates appear 4–8 days later (Harwood & Horsfall, 1959; Mondet *et al.*, 2003). Following this mechanism, ponds with a highly varying water level should be the most favourable for *Ae. vexans*. Assuming that mosquitoes trapped near a pond had emerged from that particular pond, this phenomenon might explain why the lowest exposure to mosquito bites was observed in Barkedji: this pond was large and deep, and its slopes were more steep than in Furdu and Ngao. Therefore, the same amount of rainfall resulted in smaller variations in the flooded surface than in the two other ponds. Furthermore, the exposure was fluctuated more in Furdu than in Ngao (Fig. 4). Furdu was smaller and less deep than Ngao, with less vegetation to offer havens for adult mosquitoes. A moderate amount of rainfall probably induced a large increase in flooded surface, and thus a large hatching of mosquitoes. On the other hand, the small size and depth of the pond caused the draining of Furdu during the first rain pause (July 2002), and most adult mosquitoes either died or moved to more humid areas. Ngao's larger size and depth, as well as its

Table 5. MCMC estimates for the coefficients of the best-AICc mixed-effect Poisson model of sheep exposure to *Aedes vexans* bites near the ponds of Furdu and Ngao (Ferlo, Senegal) during the rainy season 2002.

Parameter	Mean	SD[a]	Median	Q 2.5% [b]	Q 97.5% [c]
Intercept	1.824	0.459	1.834	0.901	2.720
Aug.$_1$	− 3.792	1.525	− 3.604	− 7.328	− 1.341
Aug.$_2$	3.293	0.693	3.294	1.892	4.662
Sept.	− 0.037	0.721	− 0.036	− 1.461	1.371
Oct.	4.089	0.686	4.070	2.819	5.476
Ngao	2.137	0.200	2.132	1.759	2.539
Compound	2.107	0.201	2.102	1.723	2.510
Aug.$_1$ * Ngao	3.461	1.354	3.231	1.461	6.770
Aug.$_2$ * Ngao	− 2.562	0.211	− 2.557	− 2.984	− 2.159
Sept. * Ngao	− 0.976	0.303	− 0.975	− 1.566	− 0.382
Oct. * placeNgao	− 2.226	0.204	− 2.221	− 2.636	− 1.840
Aug.$_1$ * Compound	0.741	1.391	0.529	− 1.378	4.099
Aug.$_2$ * Compound	− 1.728	0.208	− 1.723	− 2.143	− 1.329
Sept. * Compound	− 3.397	0.485	− 3.380	− 4.393	− 2.494
Oct. * Compound	− 4.186	0.217	− 4.183	− 4.620	− 3.767
Ngao * Compound	− 1.978	0.220	− 1.974	− 2.416	− 1.557
Aug.$_1$ * Ngao * Compound	− 2.170	1.403	− 1.963	− 5.549	− 0.009
Aug.$_2$ * Ngao * Compound	1.139	0.242	1.136	0.671	1.621
Sept. * Ngao * Compound	1.934	0.550	1.923	0.888	3.040
Oct. * Ngao * siteCompound	4.009	0.238	4.005	3.548	4.484
Variance of the random effect	0.787	0.427	0.683	0.307	1.880

[a] Standard deviation, [b] 2.5% quantile, [c] 97.5% quantile.

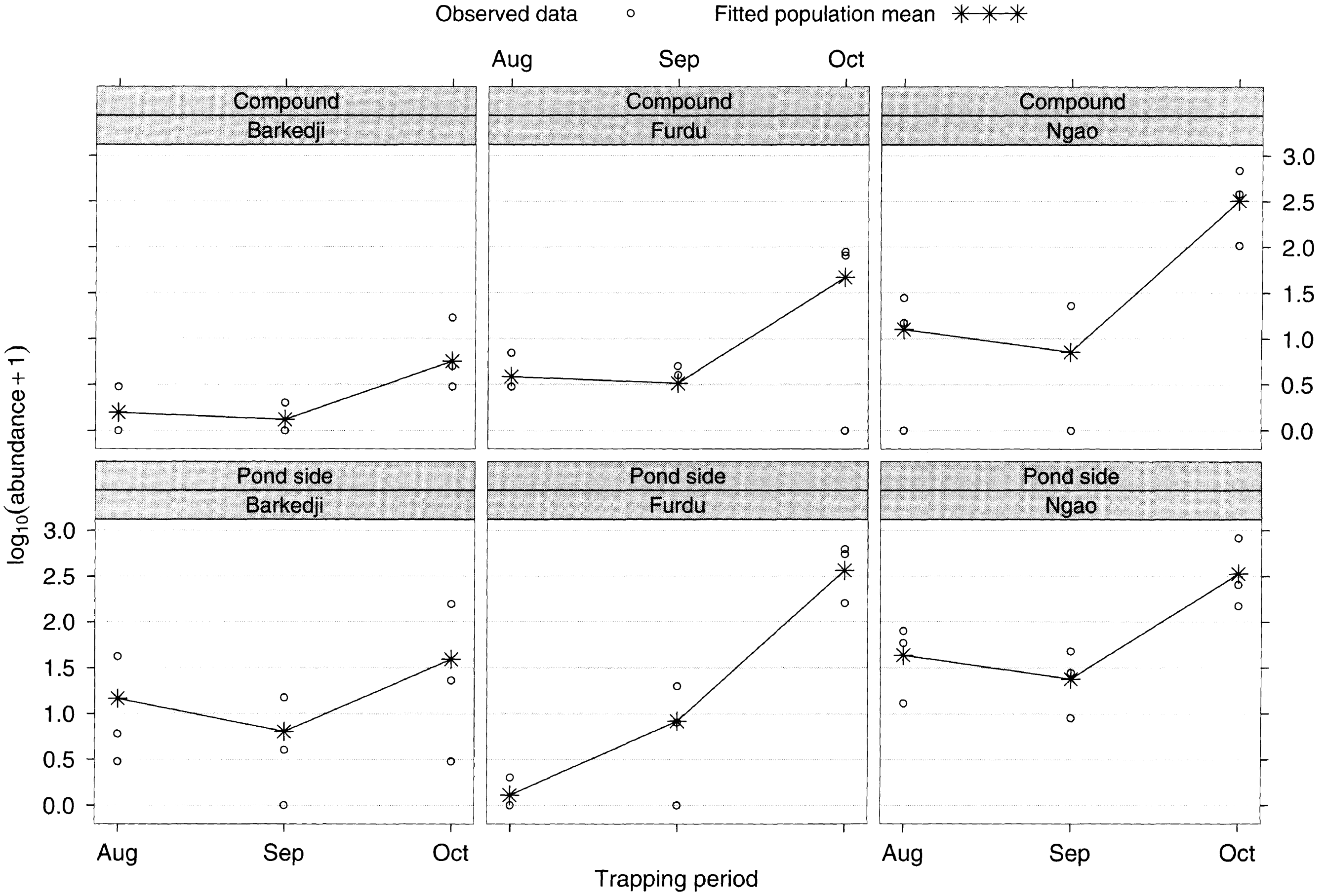

Fig. 3. Abundance of *Aedes vexans* observed in sheep-baited traps near three temporary ponds during the rainy season 2002 in Barkedji (Senegal). Small symbols show the observed data. Large symbols connected with broken lines were drawn at the mean values predicted by the fixed part of the mixed-effect Poisson model (MCMC estimation).

richer vegetation cover, allowed water to remain during the rain pause, and offered more suitable havens for adult mosquitoes than in Furdu. Lastly, these results suggested that the number of *Ae. vexans* emerging from a pond varied according to the pond type.

The study of seasonal variations showed three peaks in exposure to mosquito bites (Fig. 4): firstly, the end of a peak in July (during the first rain pause), probably related to the rainfalls in late June and early July (Fig. 2). The second peak was observed during the third trapping period (22–24 August) and was probably related to the heavy rainfall that occurred on 18 August (39 mm). The third peak was observed during the fifth trapping period (14–19 October). It occurred after two moderate rainfalls (13 mm and 9 mm on 8 and 9 October, respectively), but these rainfalls came after a long rain pause and caused a large increase in pond water levels in Furdu and Ngao. Given the presence of the RVF virus, the transmission risk was probably irregular during the 2002 rainy season. Moreover, the opportunity for older female mosquitoes to acquire and transmit pathogens increases with age (Beaty & Marquardt, 1996). Therefore, the risk of RVF transmission was probably highest at the end of October. This was important from an epidemiological viewpoint because transhumant farmers left the Barkedji region during the second fortnight of October to relocate to their dry-season settlement located in different regions of Senegal and even in The Gambia. The above-described October rainfalls and cattle movements also happened in other parts of the Ferlo and the Senegal River valley. The simultaneous occurrence (November 2002) of several RVF outbreaks in different parts of Mauritania, Senegal and The Gambia (OIE, 2002a,b, 2003) might thus have been triggered by livestock movements, disseminating the virus from the rainy-season foci to permanent-water ecosystems (Senegal and Gambia River valleys), with long-lasting populations of *Culex* spp.

The comparison between the pond bank and the compound gave inconsistent results for the three ponds (Figs 3 and 4). Although the pond was close to the village of Barkedji, the exposure to mosquito bites was constantly higher (by 10-fold) on the pond bank than in the compound. This might be related to the low mosquito production of the Barkedji pond during the 2002 rainy season, and to a dilution effect caused by a small number of mosquitoes among a large concentration of human and animal prey.

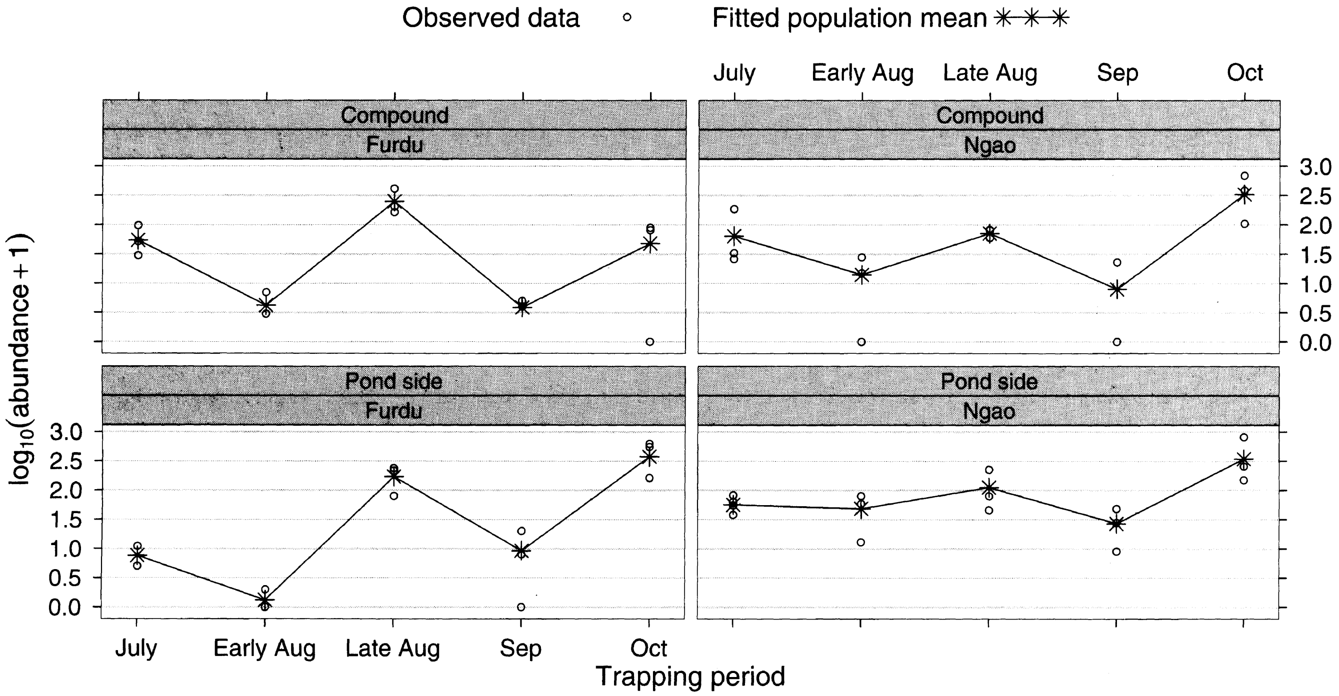

Fig. 4. Abundance of *Aedes vexans* observed in sheep-baited traps near Furdu and Ngao temporary ponds during the rainy season 2002 in Barkedji (Senegal). Small symbols show the observed data. Large symbols connected with broken lines were drawn at the mean values predicted by the fixed part of the mixed-effect Poisson model (MCMC estimation).

The pattern observed for the Ngao pond was similar to Barkedji. The most likely explanation of the greater exposure near the Ngao pond is that the distance between the pond and the compound was large compared to *Ae. vexans* flight capacities, leading them to look for a host near the pond. However, the exposure difference between pond and compound was zero in July (at the beginning of the first rain pause) and in October. In July, this might be related to the progressive draining of the pond and the consecutive dispersion of mosquitoes looking for hosts. In October, the exposure to mosquito bites was higher than in July (by 30-fold). This greater exposure could result in stronger competition for hosts, an increased risk of infection of vectors due to multiple feeds on different hosts, and a wider dispersion of mosquitoes on the outskirts of the pond.

In Furdu, the compound attracted mosquitoes at the beginning of the rainy season. In July, the exposure to mosquito bites was 12-fold higher in the compound than on the pond bank, and three-fold higher in early August. However, it was generally low on these two occasions, and no cattle or sheep were present in the compound. Humans were the only possible hosts and their low number (a few families) did not result in a dilution effect. In late August, exposure was much higher (by 100-fold). The dispersion hypothesis that was advanced for Ngao may also be advanced for Furdu in October. In September and October, the exposure ratio between the pond bank and the compound was reversed: in October, exposure was 100-fold higher on the pond bank than in the compound, and attained the maximum observed in Furdu. Although the exposure to mosquito bites was much higher in Furdu than in Barkedji, a similar explanation might be posited: mosquitoes were attracted by their hosts, but host density was much higher at that time (transhumant herds had joined the compound), probably leading to a dilution effect, thus to a decreased individual transmission risk. This phenomenon was described in other circumstances. During the West-Nile fever outbreak, which occurred in Camargue (France) in 2000, a serological survey on horses showed that the within-herd prevalence was inversely correlated to the herd size (Durand *et al.*, 2002).

This study showed that during the 2002 rainy season in Barkedji, the exposure to mosquito bites varied according to the type of temporary pond and rainfall frequency. The limited sample of ponds and the lack of prior knowledge of the biology and ecology of this mosquito did not allow definitive conclusions on the transmission risk of RVF.

Within the limited range of investigated distances (0.2–1.0 km), this study did not bring any evidence that the distance to the pond had a protective effect against mosquito bites. Further studies are needed to evaluate *Ae. vexans arabiensis* active and passive flight capacities, as well as the influence of environmental factors on these capacities.

Nonetheless, some other hypotheses arose about the important variation factors to consider. To assess these hypotheses, another study is being undertaken on a new sample of ponds selected according to their three-dimensional shape (surface, depth, bank slope) and vegetation cover (trees, water lily and other water grasses). A more thorough understanding of the relationship between exposure to mosquito bites, rainfall, water level, flooded surface (estimated from simulations of mathematical terrain models) and pond ecosystem is expected from this ongoing study. This would allow the implementation of a spatial and temporal model for the transmission risk of RVF in the Ferlo.

Further studies are also needed to describe the mosquito patterns emerging from different rainfall patterns, and to understand the population dynamics of other important species. Higher rainfall would probably induce a more abundant *Cx. poicilipes* population, and consequently a different spatial and temporal risk pattern.

Beyond the understanding of exposure to mosquito bites, a serological incidence survey was also implemented for a direct assessment of RVF transmission risk. Thus, we should soon be able to know whether it is reasonable to expect useful and practical results from a modelling approach of RVF occurrence and spread in the Ferlo, such as the prediction of high-risk areas or periods, or the assessment of control measures against the vectors (pond arrangement) or the virus (vaccination campaigns on target population during high-risk periods).

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