Medical and Veterinary Entomology (2007) **21**, 350–357

Population dynamics of pest mosquitoes and potential malaria and West Nile virus vectors in relation to climatic factors and human activities in the Camargue, France

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Abstract. The Camargue is an extensive wetland in the southeast of France, which is highly influenced by human activities. Large ponds, marshes and irrigated fields provide abundant potential breeding sites for mosquitoes. Mosquitoes, which are important in terms of the nuisance they cause to people and animals, the limitations they impose on tourism and their potential threat to human health. Several of the mosquito species present are potential vectors of malaria and West Nile virus. Therefore, the population dynamics of these species were monitored over an entire breeding season during March–October 2005. Mosquito populations were sampled in two study areas once every 2 weeks, using CDC light traps baited with CO_2. Sixteen species were collected. The majority (98.7%) of the catch were *Aedes caspius* (Pallas) (Diptera: Culicidae), *Culex modestus* (Ficalbi), *Culex pipiens* L. and *Anopheles hyrcanus* (Pallas). The population dynamics of these species varied considerably in relation to the species' biology, climatic conditions (rainfall, temperature and season), water management, implementation of mosquito control campaigns and landscape use.

Key words. *Aedes caspius*, *Anopheles hyrcanus*, *Culex modestus*, *Culex pipiens*, irrigation, population dynamics, France.

Introduction

The Camargue is an extensive wetland in the Rhone river delta, located in southern France. Most of its surface is covered by large ponds, marshes and irrigated fields. It is very famous for its beautiful landscapes, but also for an abundance of mosquitoes, which limits tourism in the area. In September 2005, for example, large populations of mosquitoes caused such a nuisance that tourists left the Camargue and schools were closed. Moreover, the potential impact of mosquitoes on human and animal health needs to be considered. Malaria was endemic in the Camargue until World War II, and, although there is currently no autochthonous transmission, potential vectors are still present in the Camargue, leading to an 'anophelism without malaria' situation (Rodhain & Charmot, 1982; Ponçon *et al.*, 2007a). Moreover, three suspected autochthonous malaria cases were described recently in southern France, supporting the supposition that the region remains suitable for malaria transmission (Armengaud *et al.*, 2006; Doudier *et al.*, 2007). Several, although limited, West Nile virus (WNV) outbreaks have been reported since 1960 in this area, and associated vectors were reported recently in the Camargue (Zeller & Schuffenecker, 2004; Balenghien *et al.*, 2006).

The abundance of potential vectors in the Camargue has varied greatly over the last 70 years. Environmental changes, mainly caused by anthropogenic practices, have had an impact on inter-annual variations in the abundance of mosquitoes (Ponçon *et al.*, 2007b). The study presented here was undertaken

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to investigate the impact of environmental factors on the population dynamics of nuisance mosquito species and potential malaria and WNV vectors in the Camargue.

Materials and methods

Study area and location

The Camargue has a Mediterranean climate, characterized by warm, dry summers and mild, wet winters. Total annual rainfall range is usually 500–700 mm, with a maximum during October. The annual mean temperature is 14°C. Mean daily minimum and maximum temperatures range from 0°C to 10°C in winter and 15°C to 30°C in summer. The population dynamics of mosquitoes were investigated in two areas, representative of the main habitat types in the Camargue, Carbonnière and Marais du Vigueirat, which are ~ 45 km apart (Fig. 1). In these areas, marshes are flooded either naturally by rain or artificially by irrigation. The salinity and dryness of the soil have a strong influence on natural vegetation type within the marshes (Dervieux *et al.*, 2002).

'Carbonnière' (4°13′E, 43°35′N) consists of different types of marshes and some arable paddies. Human presence is clearly evident, both in the residential areas and in the extensive activities that take place, which include tourism, agriculture (including wine growing and cultivated reedbeds) and animal husbandry (cattle and horse breeding) and hunting, etc. Mosquito control is practised in Carbonnière, mainly against *Aedes caspius* (Pallas), an extreme nuisance species because of its aggressive daytime biting activity, using *Bacillus thuringiensis* serovar *israelensis* and temephos.

'Marais du Vigueirat' (4°46′E, 43°30′N) is a nature reserve, which consists of similar biotopes to Carbonnière. However, on the western border there is a large area of cultivated rice paddies, which provide a greater area of wetland than would occur naturally, especially in the summer months. Human activities and impacts in the reserve are limited and no mosquito control is conducted.

Mosquito sampling

Adult mosquitoes were captured during March–October 2005. Miniature CDC (Centers for Disease Control) light traps (John W. Hock Co., Gainesville, FL, U.S.A.) (Sudia & Chamberlain, 1962) baited with CO_2 dry ice, in eight locations in each of the two areas, overnight (19.00−10.00 hours) for two consecutive nights, once every 2 weeks. Locations for the CDC light traps were chosen with the aim of sampling the range of biotopes that were accessible.

Processing of mosquitoes

Mosquitoes were identified using morphological characteristics (Schaffner *et al.*, 2001). When more than 100 females were captured per light trap, a random sample of 100 mosquitoes was identified, and the number of mosquitoes per species was extrapolated. Specimens belonging to the *Anopheles maculipennis* Meigen complex were identified to species level using species-specific multiplex polymerase chain reaction (PCR) (Proft *et al.*, 1999). For each night, the numbers of mosquitoes per species, caught from the eight traps, were added together, and an average was calculated based on the two consecutive nights. Hence, the results show the mean number of mosquitoes collected in the area from the eight traps per night.

Environmental data

Climatic data, including daily mean temperature and rainfall, were provided by Météo France, the French national meteorological centre, and were recorded at two different stations: Aigues Mortes (4°12′E, 43°32′N), located 7 km from the Carbonnière site, and Tour du Vallat (4°41′ E, 43°30′N), located 9 km from Marais du Vigueirat. Data concerning artificial or natural flooding, in rice fields or marshes, were recorded during mosquito collection periods and completed by surveys among local people.

Statistical analysis

Median abundance (the date dividing the first half of the total number of collected mosquitoes from the second half) has been calculated for every species in both location. Pearson correlations (linear correlation) were tested between the mean number of mosquitoes collected per species per night and climate data (the mean temperature and cumulative rainfall registered for the period 14−28 days before the date of mosquito sampling).

Results

A total of 670 614 mosquitoes belonging to 16 species were caught in both areas. Numbers of mosquitoes caught per study area and per species are reported in Table 1. Only two species from the *Anopheles maculipennis* complex were identified: *Anopheles melanoon* Hackett and *Anopheles atropravus* Van Thiel. Of these, *Anopheles atroparvus* had been the main malaria vector in the past when malaria was endemic in the Camargue. Only four specimens were caught because the species is currently rare, indicating that its potential future role as a malaria vector is insignificant (Rioux, 1958; Ponçon *et al.*, 2007a). *Anopheles hyrcanus* (Pallas), which is currently the main potential malaria vector (Ponçon *et al.*, 2007a), was the third most abundant species. *Culex pipiens* L. and *Culex modestus* Ficalbi, the fourth and second most abundant species, respectively, are considered to be the main WNV vectors (Balenghien *et al.*, 2007). *Aedes caspius*, *Cx modestus*, *Cx pipiens* and *An. hyrcanus* were the main species collected, representing 98.7% of all mosquitoes collected.

The mean number of mosquitoes caught per night and the median abundance of *Cx modestus*, *Cx pipiens*, *An. hyrcanus*

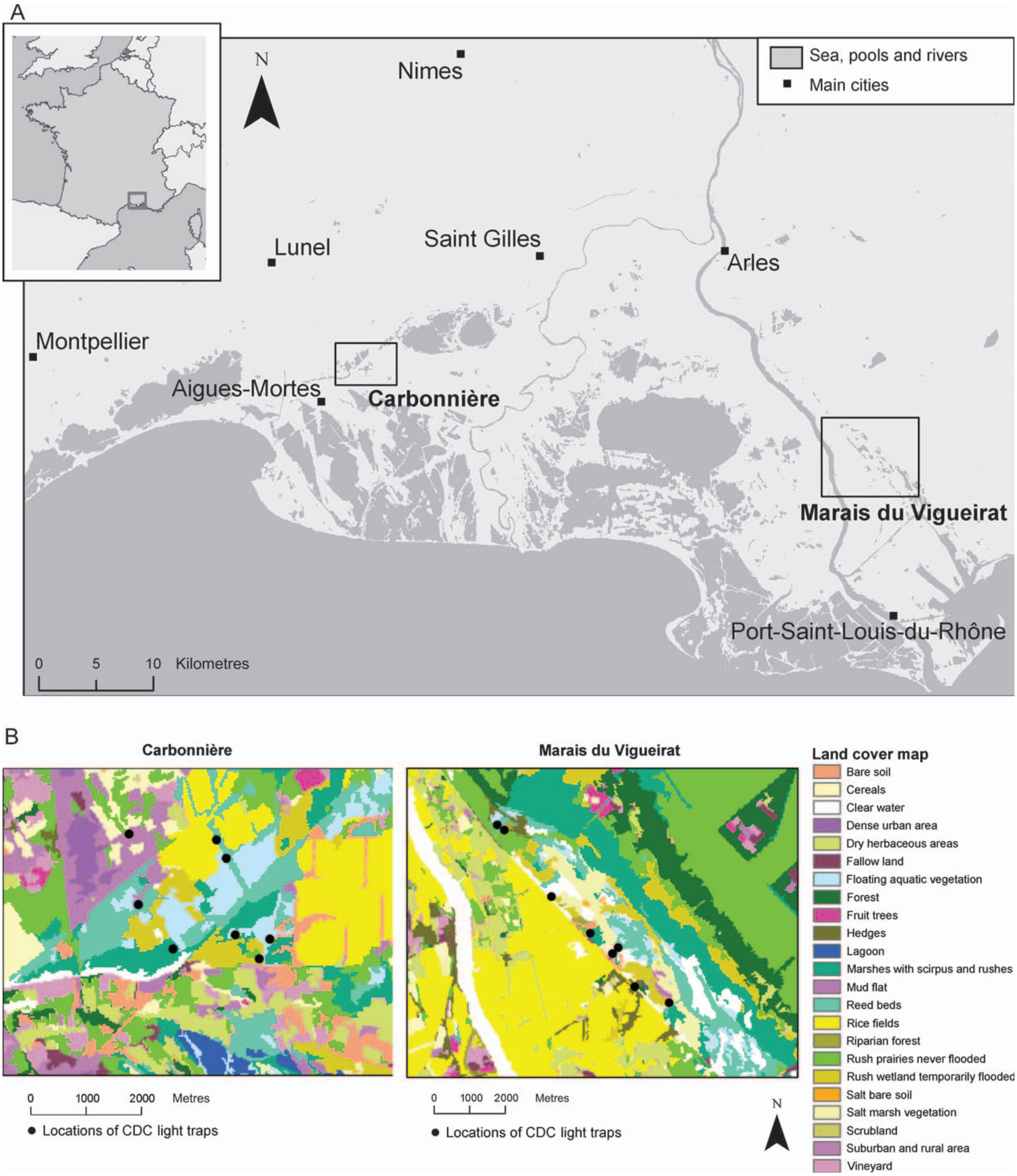

Fig. 1. Locations of (A) the Camargue and field study areas, and (B) CDC light traps in both field study areas, with descriptions of land cover.

and *Ae. caspius*, cumulative rainfall and mean temperature for the 2 weeks preceding the sampling day for each area are presented in Figs 2 and 3. Ponçon *et al.* (2007a) previously reported a detailed study of the population dynamics and biology of *Anopheles* populations in the Camargue. In the present study, the population dynamics of a range of species are presented to highlight differences between the patterns of catches of the main mosquito species and the impact of different environmental factors.

The mean temperature and the mean catch size of *An. hyrcanus* were significantly correlated at Carbonnière ($P < 0.05$) (Fig. 2A). At Marais du Vigueirat, the mean catch size of *An. hyrcanus*, and *Cx pipiens* were significantly correlated with the mean temperature ($P < 0.001$; $P < 0.05$, respectively) (Fig. 2B)

Table 1. Total number of mosquitoes collected per species and area.

	Carbonnière (243 trap nights)	Marais du Vigueirat (239 trap nights)	Total
An. (Ano.) algeriensis Theobald	0	170	170
An. (Ano.) atroparvus Van Thiel	4	0	4
An. (Ano.) hyrcanus (Pallas)	5551	111 931	117 482
An. (Ano.) melanoon Hackett	232	1806	2038
Ae. (Och.) caspius (Pallas)	42 432	221 740	264 172
*Ae. (Och.) detritus** (Haliday)	44	3936	3980
Ae. (Fin.) geniculatus (Olivier)	44	50	94
Ae. (Rus.) rusticus (Rossi)	0	21	21
Ae. (Adm.) vexans (Meigen)	45	1189	1234
Cq. (Coq.) richiardii (Ficalbi)	30	872	902
Cs. (Cus.) subochrea (Edwards)	0	51	51
Cs. (Cus.) annulata (Schrank)	5	42	47
Cx (Bar.) modestus Ficalbi	25 480	163 921	189 401
Cx (Cux) pipiens L.	29 739	60 975	90 714
Cx (Cux) theileri Theobald	0	3	3
Ur. (Psc.) unguiculata Edwards	8	293	301
Total	103 614	567 000	670 614

*and/or Ae. *(Och.) coluzzii*.

and the catch size of *Ae. caspius* and cumulative rainfall were significantly correlated at Marais du Vigueirat ($P < 0.01$) (Fig. 3B).

Some species were found only during a short period: *Aedes vexans* (Meigen) was present only during September–October, *Aedes detritus s.l.* (*Ae. detritus* (Haliday) and/or *Aedes coluzzii* Rioux, Guilvard & Pasteur) only in October, and *Coquillettidia richiardii* (Ficalbi) only at the beginning of the summer.

Discussion

Although the total numbers of mosquitoes collected in each area were very different, the four most abundant of the 16 species present were the same in both areas. The proportions of each species differed, however, depending on biotopes and human activities. The 12 remaining species represented only 1.3% of the total catches, which may be related to the rareness of particular breeding sites in the Camargue in 2005, or possibly to the species-specific efficacy of CDC light traps baited with CO_2 for sampling.

In general, the reproduction strategies of a particular genus of mosquitoes interacts differentially with environmental variables, such as short-term rainfall patterns and seasonal weather patterns. For example, the eggs of *Anopheles* and *Culex* cannot withstand desiccation, hence exceptionally dry periods depress the population until the availability of free-standing water enables surviving adult females to lay eggs successfully again, and populations slowly increase. In these genera, females overwinter in a state of diapause and the few surviving females lay eggs in spring when leaving the diapause state, which begin the next generation. By contrast, *Aedes* species lay eggs which resist desiccation and hatch whenever flooding occurs if eggs are not in a winter diapause state (Kettle, 1995). Consequently, the population density of *Aedes* responds more quickly to successive periods of artificial or natural flooding and dryness.

Anopheles hyrcanus has recently been found to be increasing in abundance in the Camargue and to have relatively high human biting rates, which suggest that it is currently the only mosquito likely to play a role in malaria transmission (Ponçon *et al.*, 2007a,b). Moreover, it is currently responsible for malaria transmission in the north of Afghanistan (Onori *et al.*, 1975; Faulde *et al.*, 2007). During this study, the population dynamics of *An. hyrcanus* were similar at the two sites. Both populations increased in the middle of June, reached a peak near the middle of August and decreased dramatically from the middle of September. This pattern was related to the condition of the rice fields, as these are the main breeding sites for this species, especially from mid-June to the end of August (Rioux, 1958; Ponçon *et al.*, 2007a). During this period rice fields were continuously flooded and rice plants covered the surface of the water. Moreover, the increase in mean temperature throughout the summer increased the rate of larval development and hence the rate of population growth (Jetten & Takken, 1994). Before mid-June, the rice fields, which had been flooded since May, were drained two or three times and rice plants no longer covered the surface, thereby reducing the survivorship of *Anopheles* mosquitoes. None of the following factors − wind, temperature, humidity, intensity of moonlight, modification of *Anopheles* breeding sites or larviciding − were associated with the drop in *An. hyrcanus* density at the end of July in either area. Finally, water was removed from the paddies at the end of August, and, consequently, *An. hyrcanus* populations began decreasing soon afterwards.

Culex modestus is considered to be the main WNV vector, based on abundance, feeding behaviour (Mouchet *et al.*, 1970; Balenghien *et al.*, 2006), previous WNV isolations (Hannoun *et al.*, 1964) and recent experimental transmission (Balenghien *et al.*, 2007). It presented a similar pattern in both areas, being

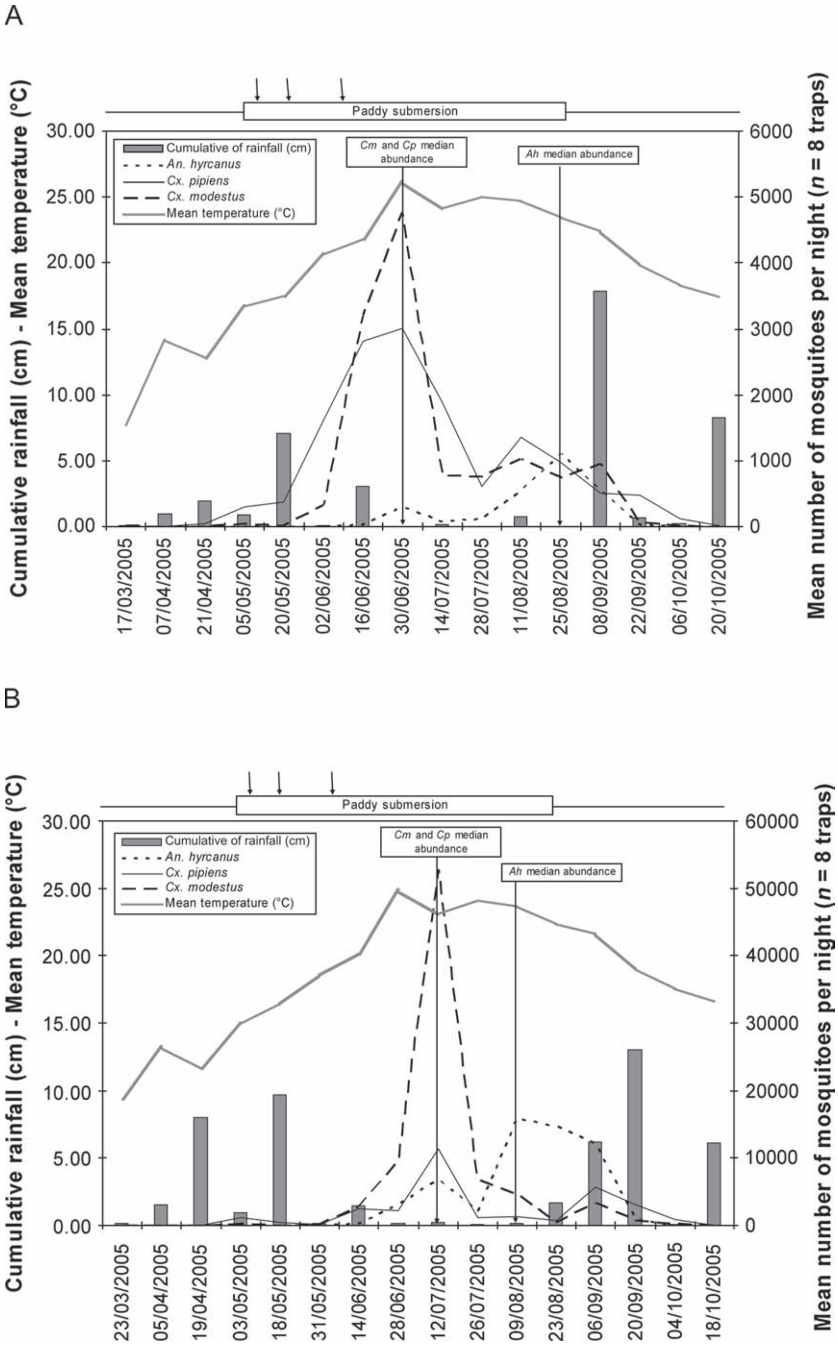

Fig. 2. Seasonal changes in trap catches of *Anopheles hyrcanus*, *Culex modestus* and *Culex pipiens*, and rainfall and temperatures at (A) Carbonnière and (B) Marais du Vigueirat during March–October 2005. Paddy submersion is indicated at the top of each figure, and arrows indicate periods when water was drained from the paddies. Mean number of mosquitoes collected from the eight traps per night is shown. Climate data represent cumulative rainfall and mean temperatures for the two weeks before the samples were collected. The median abundance indicates the date dividing the first half of the total number of collected mosquitoes from the second half. *Cm*, *Culex modestus*; *Cp*, *Culex pipiens*; *Ah*, *Anopheles hyrcanus*.

most abundant near the beginning of the summer. Reed marshes constituted the main natural breeding site for *Cx modestus* in spring and early summer 2005, when these areas were naturally flooded. Post-overwintering females initiated population growth in the spring, which rose with increasing air temperatures (Mouchet *et al.*, 1970; Ludwig *et al.*, 2005). In both areas, natural breeding sites dried up during the course of the summer, with little rainfall from late May to early September, which might explain the spectacular drop in *Cx modestus* catch sizes at the end of July and maintenance at a low level throughout August. Although this species has been described as highly prolific in paddies in the Camargue (Mouchet *et al.*, 1970), the catch size was low in the late summer, especially compared with that of *An. hyrcanus*, the main paddy breeder. This may be related, at least in part, to the shorter distance over which *Cx modestus* adults could disperse from paddies to be captured by the CDC traps, which were located ~ 400 m from the paddies. Although September rains filled the reed marshes, unfavourable climatic autumn conditions did not allow huge populations to develop and females went into over-wintering diapause in October

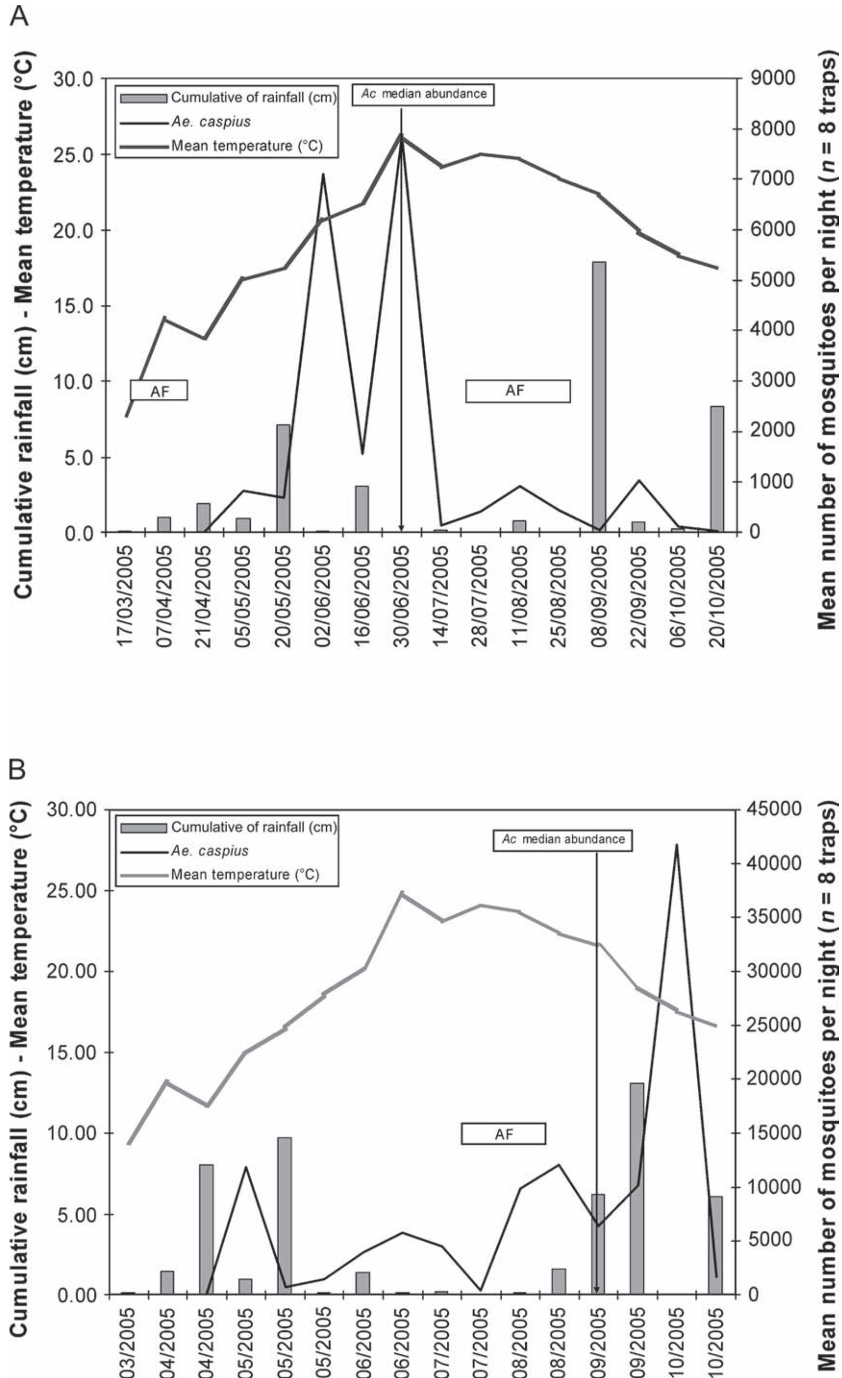

Fig. 3. Seasonal changes in trap catches of *Aedes caspius*, rainfall and temperatures at (A) Carbonnière and (B) Marais du Vigueirat during March–October 2005. Mean number of mosquitoes collected from the eight traps per night is shown for each day of capture. Climate data represent cumulative rainfall and mean temperatures for the two weeks before the samples were collected. AF, artificial flooding conducted in marshes. The median abundance indicates the date dividing the first half of the total number of collected mosquitoes from the second half. *Ac*, *Aedes caspius*.

(Mouchet *et al.*, 1970), and hence mosquito populations decreased.

Culex pipiens is also considered to be a WNV vector in the Camargue, based on abundance and feeding behaviour (Balenghien *et al.*, 2006). Moreover, although no WNV isolation has been reported from *Cx pipiens* in the Camargue, it has been found to be naturally infected with WNV in the Czech Republic (Hubalek *et al.*, 1998), Portugal (Esteves *et al.*, 2005), Romania (Savage *et al.*, 1999) and Russia (Fyodorova *et al.*, 2006). The ability of this species to transmit WNV by blood-feeding has been established in several countries (Tahori *et al.*, 1955; Hurlbut, 1956; Turell *et al.*, 2000; Goddard *et al.*, 2002; Tiawsirisup *et al.*, 2005). In the present study, it presented nearly the same pattern as *Cx modestus*, although it has been reported to breed in every type of fresh-water breeding site, including marshes, natural and artificial pools, flooded pastures and rice fields, and also in salt marshes (Rioux, 1958; Schaffner *et al.*, 2001).

The three main factors that appear to have determined the abundance of *Ae. caspius* in both areas in the Camargue in 2005 were: the characteristics of the breeding sites; the degree and repetition of flooding, and the extent of larvicide treatments. Previous studies have shown that *Ae. caspius* females lay eggs predominantly in the marshes in the Camargue, unlike in Italy, where rice cultivation is responsible for high populations of this nuisance species (Gabinaud *et al.*, 1975; Bellini *et al.*, 1994). It has been reported that during January–October, *Ae. caspius* females appear within 2 weeks following the natural or artificial flooding of breeding sites, corresponding to the time required to complete development from egg through all larval instars (Gabinaud *et al.*, 1975). In the study reported here, an increase in rainfall induced massive natural flooding in May and October and appears to have been responsible for the sharp increase in abundance of *Ae. caspius* at Marais du Vigueirat. Moreover, artificial flooding conducted near Marais du Vigueirat for human activities (e.g. hunting and nature conservation) was responsible for catches of *Ae. caspius* during August, as has been previously observed in the Camargue (Balenghien *et al.*, 2006).

Larviciding against *Ae. caspius* reduced catches dramatically. Catches of *Ae. caspius* at Carbonnière were low after artificial flooding conducted at the beginning of April, at the end of July and at the beginning of August. When significant amounts of rain occurred at Carbonnière in May and June, large flooded areas were successfully treated with larvicides by aircraft application. However, smaller breeding sites, which are less accessible but very abundant and productive, were not treated with larvicides. This resulted in significant local increases in the populations in June (F. Schaffner, personal communication). However, flooding of breeding sites following heavy rains in September did not result in increased numbers of *Ae. caspius*, even though no larviciding took place. It is likely that larvae were washed out by the inundations of water produced by heavy rain. Finally, the overall pattern of catches for *Ae. caspius*, as reflected by median abundance, differed between the two areas as a result of differences in the timing and impact of flooding and larvicidal treatments.

The population dynamics of nuisance mosquitoes and potential vectors of malaria and WNV in the Camargue clearly depend on many climatic factors (e.g. temperature, rainfall and season) and anthropogenic factors (e.g. water management in relation to landscape use and mosquito control activities). A clearer understanding of these dynamics is needed to enable us to model and predict changes in the entomological risk factors contributing to malaria or WNV disease transmission.

Acknowledgements

We thank Michel Babinot, Olivier Bardin, Didier Caire, Dominique Gindre, Nathalie Barras, Christophe Lagneau, Claire Duchet, Alexandre Carron, Charles Jeannin, Cécile Ivanes and Nicolas Sidos from Entente Interdépartementale pour la Démoustication for information and support; Annelise Tran from Cirad for geographic support; Jérémiah Petit from the Syndicat Mixte pour la Protection et la Gestion de la Camargue Gardoise; Jean Laurent Lucchesi, Nathalie Hecker, Grégoire Massez, Jean Baptiste Nogues and Mathieu Chambouleyron from the Marais du Vigueirat Association for hospitality and information; Cyrille Thomas from the French Rice Centre for information on paddies, and Alain Dervieux for his knowledge of the Camargue. This work was supported by the Institut de Recherche pour le Développement and was partially funded by the French Ministry of Agriculture and EU grant GOCE-2003-010284 EDEN (the paper is catalogued by the EDEN Steering Committee as EDEN0061 [http://www.eden-fp6project.net/]). The contents of this publication are the sole responsibility of the authors and can in no way be taken to reflect the views of the EU.

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Accepted 14 September 2007