Kris Decleer
Laboratorium voor Ecologie der Dieren, Zoögeografie en Natuurbehoud, K.L. Ledeganckstraat 35, 9000 Gent, België

TEMPORARY INUNDATION AS A DETERMINING FACTOR FOR THE SPIDER COMMUNITIES OF MARSHLAND HABITATS.

INTRODUCTION

What happens to the invertebrate creatures of marshy grounds, when suddenly their habitat becomes flooded ? How are they able to survive, what are the losses and what are the final consequences for the local communities ? These are some questions which will be discussed in this paper with respect to spiders. Data are based on both field and laboratory observations.

DIFFERENT APECTS OF FLOODING

Natural inundations are mainly due to periodically high amounts of precipitation which cause overall rising of the ground water level and swelling of lakes, rivers or dikes. Obviously, in wetlands the risks of flooding are higher as the soil level becomes lower. Water level fluctuations can differ in seasonality, frequency, amplitude and duration. Furthermore the quality of the water may influence the survival proportion of spiders in a flooded habitat for it influences the oxygen concentration of the water. Temperature also plays such a role, and in addition determines spider activity, and thus their escape possibilities. Finally, the speed of flooding may be very crucial.

Clearly, several different main types of flooding scenario are possible in nature and each of them probably has different consequences for the spider community in situ. It should require many years of both field and laboratory research to enable discussion of each of these flooding scenario's. Moreover, the effects of the same flooding conditions most probably differ between oligotrophic and eutrophic habitats. This article is therefore restricted to some generalities on the behaviour of spiders, especially from reedmarshes, and the importance of flooding for the composition of spider communities.

SURVIVAL STRATEGIES

Without considering any specific situation of flooding, four survival strategies were observed in the field and the laboratory :

1. Climbing in the vegetation

During the first hours of a winter flooding of a sedge rich meadow it was observed how hundreds of spiders had climbed up to every structure that was above the water level. However, due to wind activity, by the next day most of the spiders seemed to have fallen into the water. If they can not get a strong hold by building a silk construction or find shelter in protective plant structures, it seems that this survival strategy is only of short-term importance. TABLE 1 illustrates how hollow stalks, leaf sheaths and seed panicles, i.e. protective structures of dead Phragmites australis, indeed can be very important for the survival of spiders during flooding.

	A	A	A	A	B	B	C	D	E	F'	F'	F	F
	l	s	p	t	s	p	p	s	s	s	p	s	p
Pirata piraticus	-	2	-	3	-	-	-	-	-	-	-	-	-
Clubiona phragmites	17	14	80	8	-	3	5	11	10	6	2	6	2
lutescens	-	-	-	1	-	-	-	-	-	-	-	-	-
juvenis	-	-	-	-	-	-	-	-	1	12	2	2	-
Larinioides cornutus	-	-	115	-	-	-	25	-	-	-	-	-	2
Pachygnatha clercki	-	-	-	9	-	-	-	-	-	-	-	-	-
Tetragnatha striata	-	-	2	1	-	-	-	-	-	-	-	-	-
montana	-	-	-	1	-	-	-	-	-	-	-	-	-
Tmeticus affinis	1	1	1	-	-	-	-	-	-	-	-	-	-
Gnathonarium dentatum	8	4	3	-	-	-	-	-	-	-	-	-	-
Donacochara speciosa	3	7	4	-	2	-	-	3	-	10	-	-	-
Hypomma fulvum	6	5	81	7	-	-	-	-	4	-	-	-	-
bituberculatum	-	1	61	13	-	-	-	-	-	-	-	-	-
Bathyphantes approximatus	-	-	1	2	-	-	-	-	-	-	-	-	-
Baryphyma pratensis	-	-	2	5	-	-	-	-	-	-	-	-	-
Gongylidium rufipes	-	-	2	-	-	-	-	-	-	-	-	-	-
Unidentified juveniles	1	-	2	3	-	-	-	-	-	-	-	-	-

Table 1. Number of spiders found in dead vertical plant structures at the end of February and the beginning of March 1988 in six reedmarsh areas (A-F). Area A was sampled just after an, up to 1,5 m high, one month long flooding period. The other areas (B-F) are not subjected to such a pronounced flooding. F' is a reedbelt with submerged soil, contrary to F. Distinction is made between different dead Phragmites structures : broken, vertical stalks (s), leaf sheaths(l) and seed panicles (p) and, in addition, dead Typha stalks and leaf sheaths (t). Each time 100 specimens were sampled, except for Typha (20 specimens).

2. Walking or floating on the water surface

With the rising of the water, some species were found to be specially adapted for active walking on the water surface. Commonly known in this respect are the Pirata species, but also several smaller spiders were found to be perfectly able to perform this 'striding' behaviour : e.g. Antistea elegans, Donacochara speciosa, Lophomma punctatum, Oedothorax gibbosus, Gnathonarium dentatum, Tmeticus affinis, Silometopus elegans. The hydrophobic action of a dense coat of tiny hairs on the ventral side of carapace and abdomen, in combination with well developed tarsal claw tufts enables these species to stand high on their legs and to make walking movements. Theoretically, it thus is possible for these species to search actively for higher ground or safer places above the water surface. This is in contrast with other species which have no such water walking capacity. In the laboratory, the latter was found to be the case for the vegetation inhabiting Larinioides cornutus and Xysticus ulmi, and non-wetland spiders such as Ceratinella brevis, Diplostyla concolor, Lepthyphantes tenuis and Micronete viaria. They are totally helpless floating on the surface. Many intermediate forms occur with limited active walking capacity, never performing it as markedly as the first listed species. Females, with their larger abdomen, often had more difficulties here to avoid the surface tension forces than the smaller males. Temperature plays an important role too : in the laboratory it was found that many species remain more or less passive on the water surface at 4°C, while at 20°C a larger proportion performed striding behaviour. Furthermore, the duration of this behaviour is limited, even for the best water striders. After a while the spider body gets wet and finally makes contact with the water, the legs thereby stretching down through the water surface. In the case of lycosid spiders this is a matter of days (Pirata hygrophilus : 10 days; Pardosa amentata : 6 days, both at 4°C), while for other species (mainly Linyphiidae) it is a matter of fewer days or only hours or minutes. For sure, before sinking, all spider species spend some time walking or floating on the water surface and there they are subjected to wind activity. Wind may blow them to obstacles onto which they can climb or to higher ground or borders. It was witnessed how a striding Tmeticus affinis even elevated his abdomen to an almost vertical position to act as a sail in order to catch the wind and to be blown away.

3. Drifting in litter masses

When the flooding starts, little twigs and other dead plant material begin to float, together with the animals living in them. By attaching themselves, the animals do not sink and due to wind action, huge quantities of this litter may drift ashore or against obstacles. However, as time passes, litter and spiders do sink, so the drifting possibilities are time dependent. In a sedge rich meadow site, for instance, which was flooded in February 1988, 30 grams dry weight were sampled from a large surface of litter, which had drifted together in a sheltered corner. 119 spider individuals belonging to 24 species were found in it. Five days later, a comparable volume of litter was sampled but spiders were no longer recorded in it.

4. Survival under water

More than 50 spider species (mostly Linyphiidae) were briefly tested in the laboratory in order to have an idea of their behaviour with respect to submersion. All of them were in fact perfectly able to walk under water. Many of them succeeded in getting back above the water surface by climbing stalks of plants, although females, with their larger abdomen, often had visibly more difficulties to overcome the surface tension. Specimens which kept a sufficiently large air bubble around the body reached the surface without problem, simply by loosing contact with the substratum. If the spider remained submerged, underwater activity slowed down after a while and finally almost stopped. In this lethargic condition the spiders were able to survive for a certain period. ROVNER (1986) already indicated the importance of low activity and spider hairiness with respect to flooding survival, the latter being responsable for the holding of an air store. However, this air store disappeared after one to a few days, and as the respiratory openings finally get wet, the capacity for cutaneous respiration possibly may be the limiting factor for underwater survival. Some interspecific differences in flooding survival are illustrated in TABLE 2. Clearly, true wetland spiders, living in the ground layer, are more adapted to survive flooding than others.

Although for some species, the underwater survival chances may already seem considerably large, they probably are still insufficient to allow survival during long periods of winter inundation which frequently occur in nature. Other strategies must thus be involved. The function of silk constructions as a physical gill has been pointed out by ROVNER (1987). Indeed, could be observed in the laboratory that the nests of Clubiona

ALIVE / DEAD	5	10	20
CLUBIONIDAE			
Clubiona phragmites°	2/3	-/5	-/5
reclusa	-/5	-/5	-/5
stagnatilis°	-/5	*	*
LYCOSIDAE			
Pardosa amentata	-/10	1/9	-/10
Pirata piraticus°	4/6	-/10	-/10
Hygrolycosa rubrofasciata°	-/5	*	*
THOMISIDAE			
Xysticus ulmi°	-/5	-/5	-/5
AGELENIDAE			
Antistea elegans°	4/1	2/3	*
TETRAGNATHIDAE			
Pachygnatha clercki°	5/5	-/10	*
ARANEIDAE			
Larinioides cornutus°	2/8	-/10	-/10
LINYPHIIDAE			
Agyneta decora	*	*	-/5
Bathyphantes approximatus°	*	6/4	4/6
gracilis	*	-/5	-/5
Carorita paludosa°°	10/-	5/5	3/7
Centromerus incultus°°	*	*	1/4
Ceratinella brevipes°	6/4	1/9	-/10
brevis	*	*	-/10
Diplocephalus permixtus°	8/2	2/8	*
Diplostyla concolor	-/5	*	-/10
Donacochara speciosa°°	*	3/7	2/8
Erigonella ignobilis°°	2/3	-/5	*
Gnathonarium dentatum°	7/3	2/8	-/10
Hypomma bituberculatum°	5/5	1/9	-/10
Linyphia clathrata	-/5	*	*
Lophomma punctatum°	*	-/10	*
Oedothorax fuscus	-/10	-/10	-/10
gibbosus°	6/4	4/6	1/4
Pocadicnemis juncea	9/1	2/8	-/10
Porrhomma pygmaeum°	*	*	-/10
Walckenaeria unicornis°	*	-/5	*

TABLE 2. Laboratory survival of different spider species after 5, 10 and 20 days of submersion with aerated tap-water at 4°C, and without permitting the occurrence of any silk construction. Each time 5 or 10 specimens were tested, except for the combinations indicated with '*'. ('°°' indicates a rare wetland species; '°' a more widespread wetland species.)

	1	2	3	4	5	6	TOTAL
Clubiona phragmites	1	-	1	1	-	-	3
spec.	-	1	1	-	1	-	3
Pirata piraticus	1	-	-	-	-	-	1
Pachygnatha clercki	-	-	-	1	-	-	1
Allomengea vidua	2	-	6	15	6	8	37
Baryphyma pratensis	2	2	2	1	1	4	12
Bathyphantes gracilis	-	1	-	-	-	1	2
Carorita paludosa	1	1	2	-	-	-	4
Ceratinella brevipes	1	1	-	-	-	2	10
Donacochara speciosa	2	-	-	-	-	-	2
Erigone atra	3	2	1	1	1	2	10
dentipalpis	-	-	-	-	1	-	1
vagans	-	-	1	-	-	-	1
Gnathonarium dentatum	3	1	1	1	1	-	7
Hypomma bituberculatum	5	4	5	3	-	1	18
fulvum	4	2	3	-	3	1	13
Porrhomma oblitum	-	-	-	1	-	-	1
pygmaeum	-	1	-	2	1	2	6
Savignyia frontata	-	-	-	1	-	1	2
Tmeticus affinis	-	-	-	1	1	-	2
Walckenaeria unicornis	-	1	1	1	-	2	5

TABLE 3. Yields after three months of sampling with six pitfall traps, each placed inside a hermetically covered enclosure of 40x40 cm in reedmarsh litter, just after a high, one month long February flooding in 1988. (Also including juveniles; total area sampled = 0,96 m^2.)

phragmitis, a common species in reedmarshes, could hold an air bubble and so enhance the animals survival. However, the construction of such a nest is an exception among wetland spiders. It is therefore hypothesized that long period survival for the others is only possible when the spider is enclosed by a persistent air store such as we find inside tussocks of grasses and sedges, in dead, hollow stalks of *Phragmites*, *Filipendula*, *Angelica* or *Urtica*, between leaf sheaths of *Typha* or in interstitial spaces in a dense litter layer. Some evidence for this has already been given in TABLE 1. This is also illustrated in TABLE 3 where the results are presented of post-flood sampling of reedmarsh litter, consisting of numerous old, broken reed stalks and dead leaves. Here, many spiders clearly survived the inundation, contrary to the drowning experiments in the laboratory (in which no air reserves were available) which indicated that they could hardly persist so long under water. Also, in another experiment, it was witnessed how, during the initial phase of submersion, several species (with a small air bubble around their abdomen) were perfectly able of active fusion with artificial air stores they accidentally encountered during their wandering under water.

	A 84/85	B 84/85	C 84/85	D 84/85	TOTAL 84/85
SPECIES CAUGHT IN LOWER NUMBERS					
Ceratinella brevipes°	72/1**	57/2**	93/4**	66/-**	288/7
Halorates distinctus°°	182/20**	21/3	2/-	2/-	207/23
Hypomma bituberculatum°	111/57*	27/6*	179/6**	73/4**	390/73
fulvum°°	232/61**	43/6**	48/8**	27/2**	350/77
Lophomma punctatum°$^{(2)}$	97/47*	14/2	40/13**	18/5*	169/67
Carorita paludosa°°	23/1**	4/-	20/1**	-/2	47/4
Tallusia experta	6/-*	3/-	5/-	-/-	14/-
Clubiona lutescens	-/-	-/-	13/2	1/1	14/3
Diplostyla concolor	-/5	-/-	43/21*	6/3	49/29
Antistea elegans°	9/13	9/10	54/31*	20/6*	92/60
Robertus lividus	-/-	-/-	12/4	-/-	12/4
Pachygnatha clercki°	13/14	105/28**	3/8	22/33	143/83
Tetragnatha montana	7/7	4/3	125/11	56/2	192/23
Larionioides cornutus°	111/14	53/19	64/9	24/1	252/43
SPECIES CAUGHT IN HIGHER NUMBERS					
Erigone atra^{2}	4/355**	150/263**	15/67**	6/66**	175/751
vagans^{2}	-/3	18/75**	-/2	-/19**	18/99
Allomengea vidua°°	142/914**	2/16**	100/130	104/75	348/1135
Porrhomma pygmaeum°^{2}	9/25**	32/48	1/24**	10/134**	52/231
Pardosa amentata	12/17	9/19*	71/212**	33/45	125/293
Bathyphantes gracilis^{2}	42/116**	113/96	35/66**	49/94	239/372
Lepthyphantes tenuis^{2}	7/28*	16/21	4/5	14/19	41/73
Oedothorax fuscus^{2}	4/12	164/184	13/94**	15/25*	196/315
SPECIES WITH LESS CLEAR TENDENCY					
Clubiona phragmitis°	6/11	3/5	10/8	8/3	27/27
Pirata hygrophilus°	-/-	-/2	249/224	143/49**	392/275
Pirata piraticus°	93/190*	522/419	91/49	210/229	916/887
Bathyphantes approximatus°^{2}	101/184*	66/30**	119/101	44/55	330/370
Gnathonarium dentatum°^{2}	149/118	112/187*	171/83**	111/66*	543/454
Savignya frontata°°	4/6	28/4**	3/10	3/4	38/24

TABLE 4. Some results of pitfall trapping during the same period (April-September) in four sites (A-D) in the year before (1984) and after (1985) extreme flooding of 'De Blankaart' reedmarsh. The reedbelts in site C and D are much narrower; B is cut in summer and D in winter, while A and C are untreated with presence of a thick litter layer. Significantly different numbers between the two years are indicated : * = 0,05>p>0,01; ** = p<0,01 (Mann-Whitney U Test).
(For *T.montana* and *L.cornutus* results of repeated sweep-netting are listed (including juvenile specimens); consequently no levels of significance could be indicated.)
('°°' indicates a rare wetland species, '°' a more widespread wetland species, '^{2}' means two reproductive periods/year.)

A CASE STUDY : Changes in the spider community after an extreme period of inundation.

In "De Blankaart" reedmarsh (Woumen, Belgium) different sites were sampled by pitfall trapping in 1984 and 1985. The sampling period was abruptly interrupted by an extreme flooding with eutrophic water from the middle of September 1984 until the end of February 1985, with water level peaks up to 70 cm above soil level, followed by some smaller peaks until the beginning of April. For the same period (April-September) of both years, the total numbers of some abundant species were statistically compared. The results are presented in TABLE 4. The variation between the sites is largely due to differences in location and differences in vegetation structure as a result of different cutting treatments. It is striking how after the flooding some species known as good aeronauts, having in addition two reproduction periods each year, were caught far more numerous after the flooding. The most successful colonizer undoubtedly was Erigone atra, although reed marshes can by no means be called its favourite habitat. Only one non-ubiquitous species, Allomengea vidua, increased. This is the only species hibernating as an egg in a waterproof silk cocoon which makes it very well adapted to winter inundation. On the contrary, the numbers of several other species significantly decreased after flooding, including some typical and rare wetland spiders, or ruderal species from the border zone of the narrower reedbelt C. Recruitment from outside the area seemed not to have been important here. Moreover, nearly all of the decreasing species have only one reproduction period per year, mostly restricted to the spring. Finally some common species are listed which show a less clear pattern of increase or decrease. Both intersite differences, due to location and cutting management of the reedmarsh, and the influence of extreme flooding, will each be discussed in more detail in forthcoming papers.

CONCLUDING REMARKS

Still very little is known of the exact consequences of temporal inundations, in all their different aspects, on local spider communities. The preliminary data presented here, indicate that this kind of dynamics may indeed be very important and, taking the interspecific differences in flooding tolerance in account, possibly forms one of the major explanations of the presence or absence of a specific species in a specific wetland area. In nature conservation the importance of water level management with respect to plants or birds has already been recognized a long time. Especially to improve the ornithological value of a wetland area, the water level is often artificially elevated during winter. Thus conflicts may arise with entomological interests, for it was shown in the 'Blankaart' area that ubiquitous species, with great dispersal power, are largely favoured contrary to several more rare and typical species, when a certain limit of flooding intensity is exceeded. From the botanical point of view, cutting management is valuable if executed regularly in fixed periods of the year. In this regard, the necessity for the preservation of sufficient large areas with a developed litter layer and the presence of vertical plant structures, in order to enhance flooding survival chances of invertebrate animals must be stressed.

REFERENCES

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Jocqué: Is it so that the vast majority of spiders surviving on standing reeds belong to species normally living there?
Decleer: Not entirely. Some specimens do indeed belong to reed inhabiting species (e.g. Larinioides cornutus and Clubiona spp.) but others are really escaping from inundation by climbing the reeds (e.g. Hypomma spp.).