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Factors influencing aeronautic behaviour of spiders

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Introduction

By "aeronautic behaviour" of spiders we mean both dispersal through the air by means of silk threads and the preparations for becoming airborne. Many authors (Duffey, 1956, 1963, Kajak, 1959, Meyer, 1971, Nishiki, 1966, Richter, 1971) have published on this behaviour, the relevant meteorological conditions and the spider species involved. The most extensive study on aeronautic behaviour was performed by Duffey (1956). During the period of observation, he studied the spider population and measured certain microclimatic factors. Other authors, however, did not study biotic and abiotic factors in the field simultaneously. Because meteorological factors as well as population and species characteristics play a role in determining aeronautic behaviour, the present authors have started an integrated investigation by measuring the quantitative effects of these factors and their interrelationships. This investigation is a part of an extensive study on the population dynamics of *Erigone arctica* (White), in which dispersal may play an important role.

The study area

The study area is an enclosed part of the beach of the Frisian island Schiermonnikoog (The Netherlands). This area, bordered by a broken row of high dunes and a man-made sand-dike, consists of a mosaic pattern of small dunes and flat, lower parts. Floods over the mudflats have repeatedly inundated the lower parts and have covered them with a thin layer of silt, on which compact vegetational units of *Agrostis stolonifera* L., *Festuca rubra* L. and *Juncus gerardii* Loisl. alternate with an open vegetation of *Glaux maritima* L., *Suaeda maritima* [L.] Dum. and *Salicornia europaea* L. These parts are salty and rather moist.

Methods

The population densities of spiders were measured by taking 40 samples of 625 cm^2 each out of a sampling-area of 100 x 25 m^2, at least once a month. The spiders in these samples were captured by hand-sorting and by drying out the topsoil in a platform temperature-gradient apparatus.

Spiders showing aeronautic behaviour were sampled by two methods:

1) Aspirator captures during five minutes from the upper parts of the vegetation. Spiders captured by this method were presumed to be preparing to become airborne.

2) Captures from 2 iron wires (2 x 24 m) arranged in a cross and stretched on stakes at a height of 170 cm. Spiders whose silk threads became attached to the iron wire were captured with an aspirator; as the stakes were covered with a gum layer, spiders captured from the wire were assumed to have been in the air already.

The meteorological observations during this investigation consisted of measurements of temperature and wind velocity. In a vegetation of about 25 cm height the temperature was continuously measured at four different levels, namely 0, 4, 10, and 20 cm above the soil. The temperature sensor was an NTC-resistance connected to a recorder.

The temperature sensors were protected as much as possible against radiation influences. The accuracy of the temperature measurements was about 0.2°C. The temperature profile was completed by a thermograph recording at a height of 100 cm in a Stevenson screen. The wind velocity was measured continuously with a Lambrecht cup anemometer at a level of 200 cm above the soil. The so-called "roughness parameter" of the soil surrounding the anemometer was 0.2 cm. Finally spot readings were made from two cup-counter anemometers placed at heights of 200 and 40 cm, respectively.

Results

This paper contains the results of the first period of investigation (13 April – 31 October 1972). For

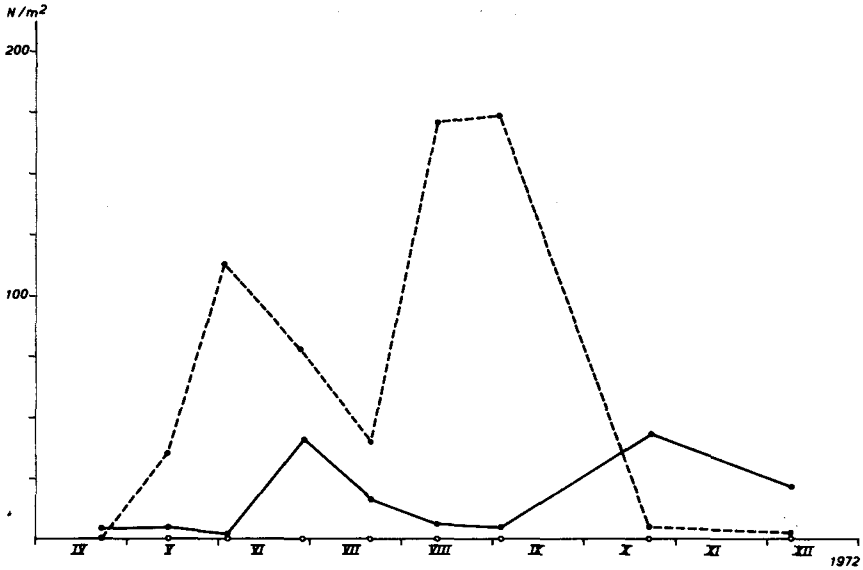

Fig. 1: Density of *Erigone arctica* (White). Full line: adults; dashed line: juveniles (N/m^2 = number per square metre).

the analysis of the biotic events only facts concerning the most abundant spider species in the study area, *Erigone arctica* (White), are given. The density numbers are presented in Fig. 1. This graph shows that *Erigone arctica* has two generations a year. During the period of investigation spiders showing aeronautic behaviour were captured on 30 days. On 24 days individuals of *Erigone arctica* were captured. For each day with aeronautic behaviour the mean number of individuals of *Erigone arctica* per capture has been calculated (Fig. 2). Fig. 2 shows that *Erigone arctica* had a period of aeronautic behaviour in both generations: (a) the period from the beginning of June to mid-July, and (b) the period from the end of August until mid-October.

(a) First period: In the captures from the iron wire individuals of *Erigone arctica* appeared a few days after the population had reached its highest density (first week of June: $114/m^2$). The highest numbers were captured three weeks later (26 June). After the capture of 13 July no more individuals of *Erigone arctica* born from the first generation were captured.

(b) Second period: The first individuals of *Erigone arctica* were captured about two weeks after the population had reached its highest density (second week of August: $191/m^2$). The maximum was reached a few days after the first capture.

The captures in the vegetation showed much variation, probably because sampling during five minutes is not a fully unbiased method. The individuals from both capture methods have been summed per instar over the whole investigation period in order to study the instar distribution (Table 1). It is clear that the numbers of individuals of the third and fourth (= subadult) instars outnumber by far the other instar numbers.

As an example of the results of the meteorological measurements during a period with aeronautic behaviour we consider the measurements of 14 October 1972 (Table 2). In this table the numbers of spiders of all species captured from the iron wire and from the vegetation are given. Some remarkable features, which are representative for most of the measurements, can be noticed.

With $\frac{dT}{dz} < 0$ (T denotes temperature, z denotes height) defining instability and $\frac{dT}{dz} > 0$ defining stability of the air, it is possible to divide the temperature profile into three layers; (a) an unstable part close to the ground from 0 to about 4 cm, (b) a

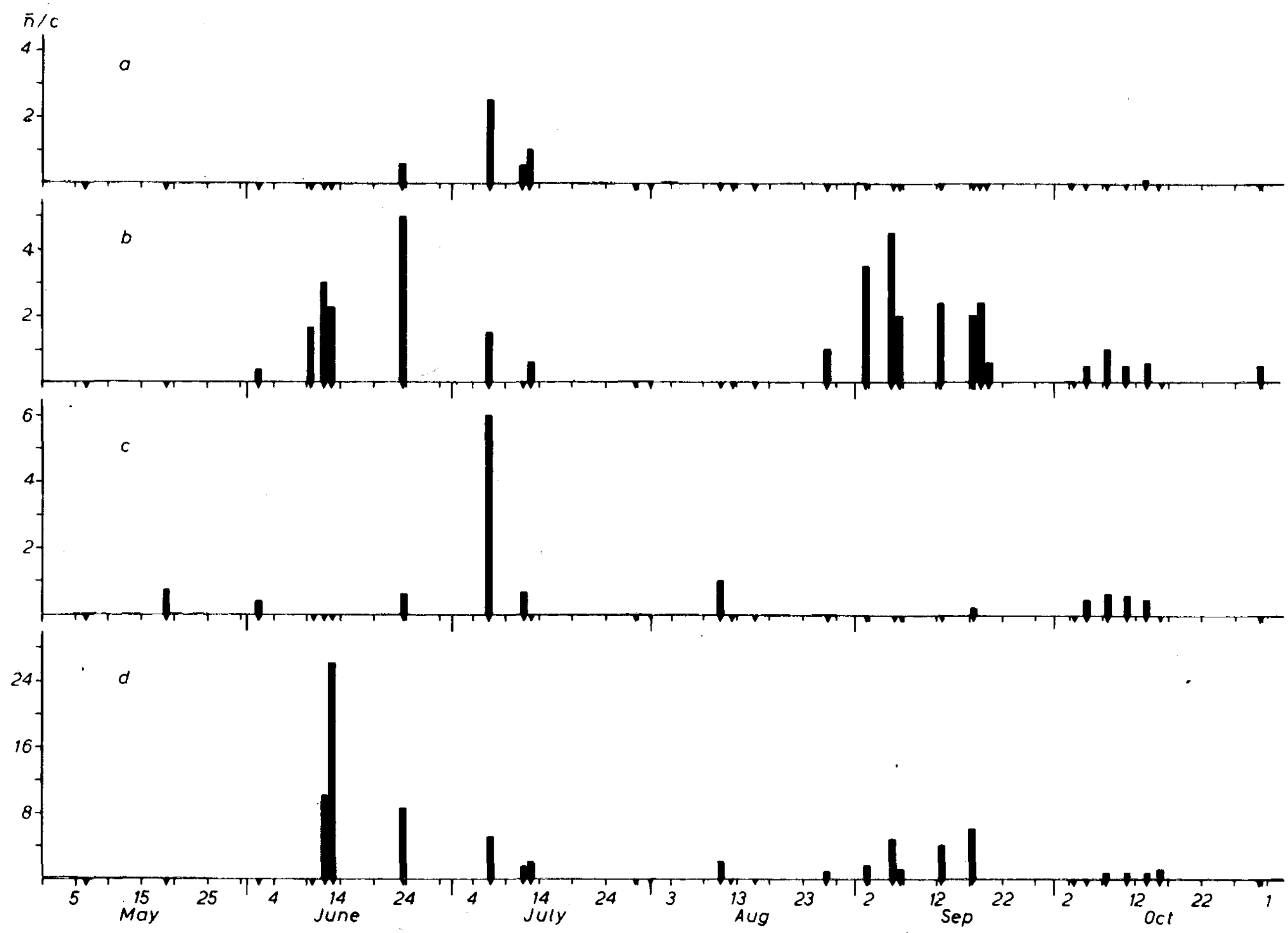

Fig. 2: Captures of individuals of *Erigone arctica* showing aeronautic behaviour, in mean numbers per capture ($\bar{n}$/c). a: captures of adults from the iron wire; b: idem, juveniles; c: captures of adults from the vegetation; d: idem, juveniles. The triangles under the axis represent days on which captures of aeronauts were made.

stable part half-way up the vegetation, from about 4 cm to 10 cm, (c) an unstable part from 10 cm to above the vegetation.

For understanding the varying numbers of spiders captured from the iron wire all measurements of September 1972 are presented in Fig. 3. This graph shows the influences of wind velocity and temperature difference between the vegetation and the air above. It shows that wind velocity and temperature difference interact in determining the numbers captured from the iron wire.

Conclusion and Discussion

From this study it is clear that aeronautic behaviour of *Erigone arctica* takes place in all instars, but that there is a maximum in the third and fourth instars. So it seems justified to accept the working of a biotic factor, too, which stimulates aeronautic behaviour, especially in the third and fourth instars. This is opposed to the views of Braendegaard (1937), Bristowe (1939) and Nielsen (1932), who explain aeronautic behaviour as a result of unfavourable

1a	date	19	2	10	12	13	24	7	12	13	11	27	2	6	7	13	18	19	20	5	8	11	14	16	31	Total
	month	5	6	6	6	6	6	7	7	7	8	8	9	9	9	9	9	9	9	10	10	10	10	10	10	
instar	I													2		1										3
	II			3	1	3							1	5		1	1	1								16
	III		1	2	7	5	15	1		1			2	7	2	12	2	13				2	2			74
	IV				3	1	21	3				1	4	15	6	14	3	12	3	1	2		1		1	91
adult							4	5	1	2													1			13
1b																										
instar	I																									0
	II													7												7
	III				4	37	16		2	1	1	1	3	10	1		8						1			85
	IV				6	15	26	4	2					8		4	12				1	2	2	1		83
adult		2	1				3	6	2		1						1			1	2	2	2			23

Table 1. Instar distribution of individuals of *Erigone arctica* over the period 19 May until 31 October 1972. Table 1a: iron wire captures; Table 1b: vegetation captures.

time	0 cm °C	4 cm °C	10 cm °C	20 cm °C	100 cm °C	wind vel. m/s	$T_{20} - T_{100}$ °C	iron wire captures	veget. captures
10.55	18.4	15.3	22.2	19.4	11.7	2.2	7.7	7	16
11.10	19.0	16.2	23.0	20.1	12.2	2.6	7.9	5	17
11.25	18.0	16.0	23.0	19.9	11.6	2.7	8.3	3	22
11.40	18.2	16.6	21.4	17.5	11.4	2.7	6.1	4	17
11.50	17.7	16.9	19.0	15.3	11.0	2.6	4.3	7	11
12.10	17.0	15.2	19.0	17.1	11.4	2.6	5.7	3	9
12.25	17.4	16.4	23.0	17.9	11.4	2.6	6.5	4	13
12.40	17.4	16.6	22.3	16.0	11.1	2.5	4.9	3	8

Table 2. Meteorological measurements and capture numbers of aeronauts on 14 October 1972. Temperatures at different heights, wind velocity in meters/second, temperature difference between 20 cm and 100 cm and numbers of spiders of all species.

changes in microclimatic conditions only.

Probably the meteorological factors play a role in two ways, namely:

1) Aeronautic behaviour is only possible when wind velocity is low (< 3 m/s at 200 cm), and the air is unstable near the upper parts of the vegetation.

2) An unstable air layer near the ground can be an extra stimulus when the spiders tend to disperse, due to biotic processes in the population.

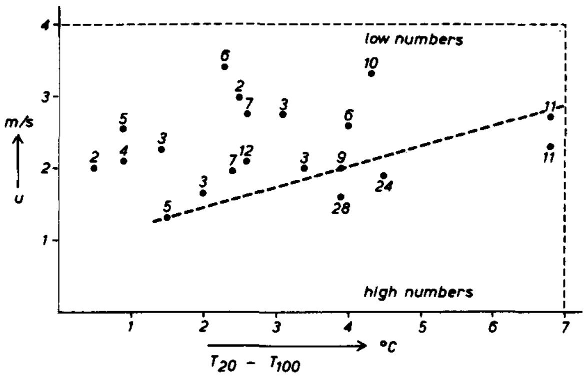

Fig. 3: Iron wire capture numbers from 2 until 18 September 1972, related to wind velocity (u) (vertical axis) and temperature difference between heights of 20 cm and 100 cm (T_{20}-T_{100}) (horizontal axis).

Duffey (1956) distinguishes between aeronautic behaviour of juvenile spiders of different families in summer and that of spiders of the family Linyphiidae shown in autumn and winter. In the latter period nearly all aeronauts are adults. Concerning adult spiders Duffey (1956, 1963) states that aeronautic behaviour is considered to be a normal event in a definite phase of the breeding cycle, which is neither connected with stimuli in the habitat, nor with processes in the population; it is associated in some way with breeding activity, and possibly in some cases with population density. As for juveniles, aeronautic behaviour may be caused by cannibalistic tendencies of the individuals in high-density situations. The simultaneous aeronautic activity of juveniles and adults of *Erigone arctica* in June and July 1972 suggests that in this period individuals of both categories are stimulated by the same factor.

From the results presented in Figs. 1 and 2 it follows that aeronautic activity of *Erigone arctica* coincides with a strong decrease of the field density. It seems reasonable to suppose that aeronautic activity contributes to the lowering of the population density, together with predation and cannibalism.

As the two generations of *Erigone arctica* which were studied showed nearly similar patterns, it is not yet possible to indicate internal processes in the population which determine the numbers of spiders tending to aeronautic behaviour.

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