Different phenological strategies in two nemastomatid harvestmen (Arachnida, Opilionida, Nemastomatidae)

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Summary

During eight years of pitfall trapping 16848 adult and juvenile specimens of two nemastomatid harvestmen were caught. Cluster analysis allowed the recognition of six nymphal stages in both species. *Mitostoma chrysomelas* (Hermann) is a bivoltine species (this revokes the conclusion of an earlier paper) with nymphs active throughout the year. *Nemastoma lugubre* (Müller) is a univoltine species with nymphal activity in spring and early summer; a small number of the adults overwinter, and summer diapause may synchronise both generations. The mean number of ripe eggs per female is 15.5 in *M. chrysomelas* and 2.3 in *N. lugubre*.

Introduction

Tauber & Tauber (1978) stated: "Probably the most important and all-encompassing environmental variable that organisms face is seasonality, and thus one of the most basic and unifying components of each species' overall adaptive strategy is its phenological strategy . . . ". In an earlier paper (Meijer, 1972) I presented data on the phenology of *Nemastoma lugubre* (Müller) and *Mitostoma chrysomelas* (Hermann). Data on *M. chrysomelas* are rare and mostly based on just a few observations, e.g. Weiss (1975) reported 18 specimens and the conclusions in my earlier paper were based on the, at that time, considerable number of 76 adult and 13 juvenile specimens. Since then material that has been gathered over 8 years allows a more detailed description of the phenology of these species.

Methods

The catches described here were made by the very same five pitfall traps that provided the material on which the previous paper was based. For a description of the study area and the traps the reader is therefore referred to Meijer (1972). The study area was destroyed in the winter of 1978/79 and as a consequence no exact data on the final stage of the vegetation are available. However, the vegetation did not seem to have changed significantly over the study period, perhaps owing to fires in the early spring of 1972 and 1978. Such fires are quite usual in small uncultivated areas surrounded by arable land and they tend to throw back the development of the vegetation.

Martens (1978: 106 and 145) stated that the specimens reported in my 1972 and 1973 papers were collected in a recently reclaimed polder with little vegetation ("... in frisch geschlossenen Polder mit wenig Krautvegetation"). In fact the traps were used in an uncultivated area in an approximately 100-year-old polder next to the Lauwerszeepolder. The latter was indeed not reclaimed until 1969, and until 1981 the only harvestmen caught in this polder were *Oligolophus tridens* (C. L. Koch) and *Mitopus morio* (Fabricius).

During eight years (1971-1978) a total catch of 14025 adult and 146 juvenile *N. lugubre* and 2257 adult and 420 juvenile *M. chrysomelas* was made. All female specimens caught in 1971, 1972 and 1974 were dissected in order to count the number of ripe eggs per female. Body length and width (between third pair of legs) of all juvenile specimens were measured by means of an eyepiece micrometer at 40x magnification. Juveniles of the two species can easily be identified, since in *M. chrysomelas* the legs are much longer and more slender than in *N. lugubre*. Pfeiffer (1956) published data on larval systematics of some harvestmen including the present species. In later nymphal stages (V and VI) males can be recognised by the small apophysis on the basal joint of the chelicerae. According to Muñoz-Cuevas (1971), in the laniatorid *Pachylus quinamavidensis* Muñoz-Cuevas secondary sexual characteristics are also present in the last two nymphal stages.

The measurements were submitted to cluster analysis (CLUSTAN) that divides the data into groups according to distance (squared euclidian distance) between individuals and/or groups (group average method) (Everitt, 1974). Male nymphs V and VI were treated separately.

Results

A summary of the data (Fig. 1) shows that adult activity in both species starts in spring or summer and decreases during the winter. Only juveniles of *Mitostoma chrysomelas* are active throughout the year. As the traps were emptied once a week (during winter once each fortnight) the results are presented over 13 four-week periods rather than over the usual twelve months.

Closer examination of the data reveals more differences between the two species. The cluster analysis of the measurements of the juvenile stages produced six groups in both species; in juveniles recognised as males (and treated separately) two groups were found. According to Immel (1954) in *Paranemastoma quadripunctatum* (Perty) there are seven juvenile stages, the first of which is very short-lived, up to one hour, and moreover is virtually immobile. The results of the cluster analysis therefore indicate the six mobile stages or nymphs. The measurements of these nymphs are presented in Table 1.

The complete data on *M. chrysomelas* are presented in Fig. 2. Adults were caught throughout the year, except in late winter (February and March). Activity in winter is very low. The diagrams indicate two periods of activity, not always at the same time of year; e.g. peak 2 occurred in month 9 (August/September) in 1974 and in month 11 (October) in 1977. The earliest nymphs I appear in May/June and it is possible that some of these mature in late summer (e.g. 1974, 1976). Nymphs I produced later in the year (October) appear as older nymphs in successive months in the winter and mature in early spring (e.g. 1974/75 and 1975/76).

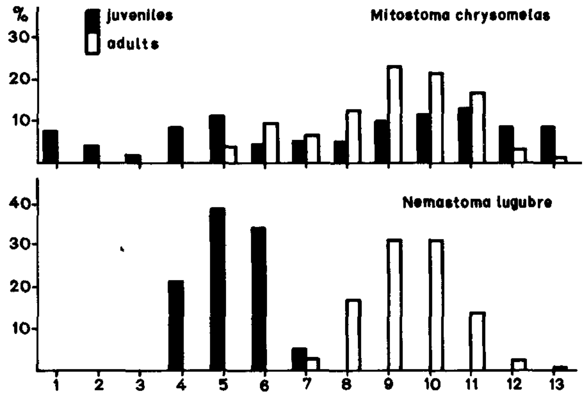

Fig. 1: Seasonal activity of juvenile and adult *Mitostoma chrysomelas* and *Nemastoma lugubre*. Complete data over eight years of trapping.

Table 2 summarises all the catches of nymphs of *M. chrysomelas* over the complete eight year period. Nymph I was never caught during winter and nymph VI only rarely; the low catches in month 3 (see also Fig. 2) suggest that winter takes a heavy toll. However the data in Fig. 2 show that the total catches over a long period may give a wrong impression. In the first five months of 1976 26 nymphs V were caught, half the total number caught in that period over the eight years (Table 2). The number of nymphs caught in the first part of the year seems to bear only a slight relation to the number of adults caught later in the same year, cf. 1976 and 1977. The low numbers of adults caught in 1972 and 1978 were probably caused by the spring fires.

The catches of the six nymphal stages are different.

	N. lugubre			*M. chrysomelas*		
Nymph	*n*	length	width	*n*	length	width
I	14	0.585 ± 0.027	0.391 ± 0.022	54	0.481 ± 0.048	0.302 ± 0.029
II	56	0.716 ± 0.060	0.439 ± 0.031	88	0.664 ± 0.076	0.431 ± 0.045
III	22	0.865 ± 0.048	0.556 ± 0.034	51	0.885 ± 0.062	0.564 ± 0.043
IV	25	1.054 ± 0.047	0.676 ± 0.032	81	1.147 ± 0.113	0.714 ± 0.051
V ♂	11	1.239 ± 0.115	0.794 ± 0.046	56	1.251 ± 0.087	0.804 ± 0.057
♀	12	1.255 ± 0.086	0.765 ± 0.037	40	1.372 ± 0.087	0.879 ± 0.048
VI ♂	2	1.615 ± 0.120	0.980 ± 0.096	23	1.567 ± 0.084	0.918 ± 0.056
♀	4	1.606 ± 0.243	1.003 ± 0.065	27	1.775 ± 0.120	1.043 ± 0.070

Table 1: Overall length and width (between third pair of legs) in mm (mean ± S.D.) of the nymphs of *Nemastoma lugubre* and *Mitostoma chrysomelas*.

It is to be expected that nymph I is more common than nymph II, etc., but, owing to the sampling method used (pitfall trapping is highly dependent on the activity of the animals), differences in density of the nymphal stages are not necessarily reflected in the catches. Moreover the duration of various nymphal stages need not be the same and it is likely to be longer when temperatures are lower. Therefore only catches of one nymphal stage may be compared (e.g. nymph I was more common in 1976 than in 1972).

Adults were uncommon in spring, even in 1975 after such a good year as 1974, and in spite of the winter of 1974/75 being the mildest during the study period: no days with maximum temperatures below 0°C and only 28 days with minimum temperatures below 0°C. The succession of the various nymphs and adults depicted in Fig. 2 seems to indicate that in this species two generations a year occur in the study area. There may even be a continuous succession of generations that is retarded during winter when embryonal and nymphal development is slowed

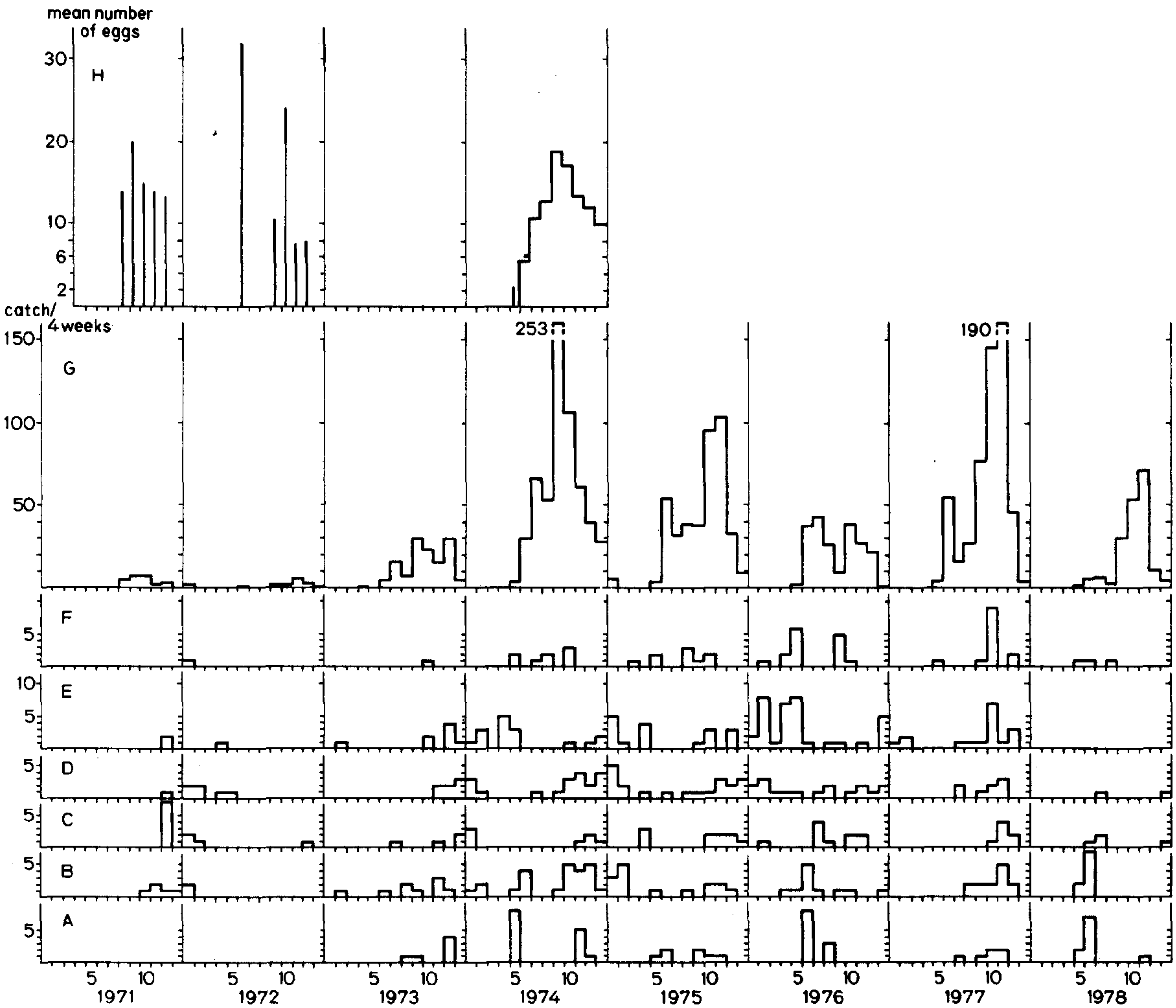

Fig. 2: Seasonal occurrence of *Mitostoma chrysomelas.* A to F = Nymphs I to VI, G = adults, H = mean number of ripe eggs per female; if based on less than 10 females represented by lines instead of bars. (Thirteen four-week months a year.)

down, but adult longevity is not increased (Juberthie, 1964), with the result that two generations a year are produced.

Females of *M. chrysomelas* had a mean number of 15.50 ± 9.65 ripe eggs (n=395); the maximum number of eggs counted was 44. Both very young (light colour and soft integument) and older females without ripe eggs were found. In 1974 the mean number of eggs per female (Fig. 2) seems to reflect the activity pattern of the species. In 1971-72 the low catches do not permit any conclusions.

The data on *Nemastoma lugubre* are presented in Fig. 3. The phenology of this species is much more clearcut: nymphs were caught only in months 4 to 7 inclusive, adults were present throughout the year, if not in each period every year, with a distinct peak of activity in month 10 or 11. Activity of some importance only started after month 7. Over the entire eight year period a mere 1.66% of the total catch was made in months 13 and 1-6 inclusive. The lack of catches in the first part of the year could be caused either by low activity or by low population density. However some adults survive until the time when high catches are made in the following year: three males caught in month 7 in 1978 were so heavily sclerotised that they undoubtedly belonged to the 1977 generation. During periods of low activity males were caught more frequently than females. In the total catch in all months 13 and 1-6 inclusive the male/female ratio was 4.11, but in months 7-12 it was 2.26.

The mean number of ripe eggs per female (n=644) was 2.31 ± 2.44 (maximum number found was 14). The number of eggs per female is seen to decline as activity declines (Fig. 3).

Generally the catches of nymphs are related to the catches of adults in the previous year (561 adults were caught in 1970). However the relatively high catches of nymphs in 1972 and 1978 might have been caused partly by the spring fires in those years. Evidently sufficient eggs survived, but as a result of the fires there may have been less shelter, which may have stimulated increased activity of the nymphs. This, however, may have increased the risks of desiccation (and hence higher mortality), and may have resulted in the disappointing catch of adults in 1978.

Discussion

In an earlier paper (Meijer, 1972), on the basis of a small catch, it was concluded that *Mitostoma chrysomelas* exhibited a type 2 life history (Todd, 1949), i.e. a short period of embryonic development followed by a very extended post-embryonic period from which adults emerge in spring. This conclusion now turns out to be misleading, since in fact both embryonic and post-embryonic development, as well as adult life, are short. From the data presented here it may be concluded that *M. chrysomelas* in the study area is a bivoltine species in contrast to the univoltine *Nemastoma lugubre.* In the first species reproduction and development may occur at any time of the year if circumstances are favourable. Retardation of development in winter could cause bivoltinism instead of multivoltinism and it would also account for some degree of synchronisation. The type of phenology found in *M. chrysomelas* is relatively rare, previously reported in Western and Mid Europe only in the alpine phalangiids *Gyas titanus* Simon, *G. annulatus* (Olivier), *Dicranopalpus gasteinensis* Doleschall and *Leiobunum limbatum* L. Koch (Martens, 1978).

Period		1	2	3	4	5	6	7	8	9	10	11	12	13	Total
Nymph	I	–	–	–	–	11	17	1	4	4	3	9	5	–	54
	II	6	8	–	1	5	17	1	5	5	11	16	10	3	88
	III	5	2	–	1	–	1	7	1	–	5	10	14	5	51
	IV	12	8	1	3	2	1	4	4	3	8	14	8	13	81
	V	9	15	1	17	11	1	1	2	3	13	2	13	8	96
	VI	1	1	1	3	11	1	1	6	7	16	–	2	–	50
All stages		33	34	3	25	40	38	15	22	22	56	51	52	29	420

Table 2: Total catches of the six nymphal stages of *Mitostoma chrysomelas* over eight years (13 four-week periods a year).

The data seem to indicate that in *N. lugubre* diapause occurs in the egg stage (eggs overwinter and hatch during the following spring) and perhaps in some way in the adult, so that the old and new generations are synchroneously active in autumn, some time after the disappearance of nymph VI. A detailed study of *N. lugubre* populations should show whether overwintering specimens contribute significantly to reproduction in their second season. Activity data do not point that way, but some sort of quiescence phase might reduce activity until autumn.

Phillipson (1959) presented data on British *N. bimaculatum* (Fabricius), a species which for a long time was mistaken for *N. lugubre* (Gruber & Martens, 1968). These data are in complete accordance with the present data on *N. lugubre*. He reported survival of adults through the winter, and egg-laying by survivors after the eclosion of eggs laid the previous year. However, he did not indicate the actual number of survivors; the long time he spent in searching for a sufficiently large sample suggests that there were not many. His data indicate that these survivors were not very fit: their fecundity was low, since second-year females laid only 21% of their eggs in contrast to 50% in the first-year females, and they had died out by August when the new generation became active.

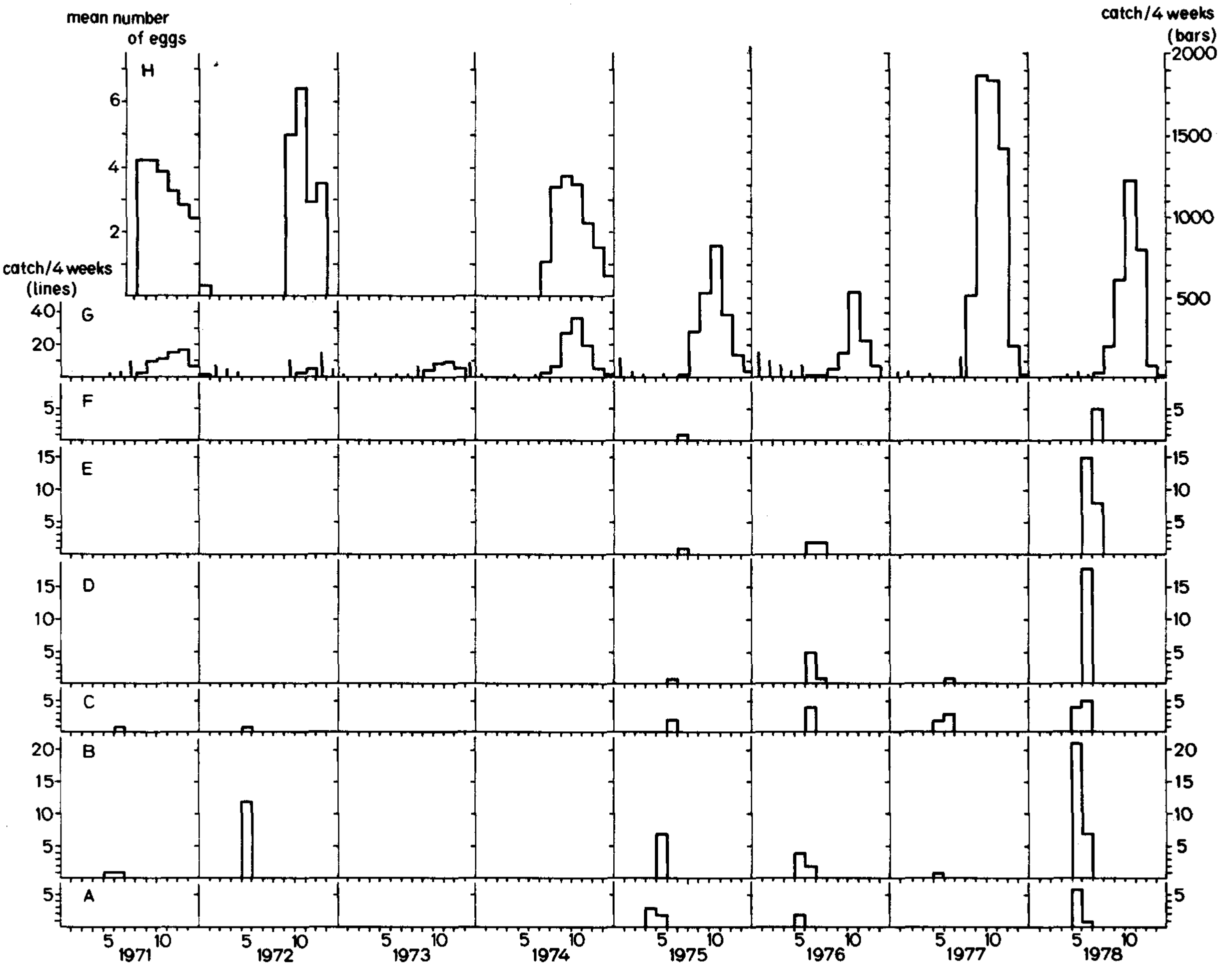

Fig. 3: Seasonal occurrence of *Nemastoma lugubre*. A to F = Nymphs I to VI, G = adults, H = mean number of eggs per female. (Thirteen four-week months a year.)

According to Southwood (1977) species have developed various strategies for coping with heterogeneity in time and space. The nemastomatid species discussed in the present paper would not seem to be able to disperse actively, in fact very little is known about their means of dispersal. In any case they have different ways of overcoming heterogeneity in time. *Mitostoma chrysomelas* has the opportunistic "here and now" approach: reproduction and development whenever conditions permit, resulting in peaks of activity (and probably density) of short-lived adults at different times of the year. In this way it may risk extinction if winter is severe. *Nemastoma lugubre* on the other hand, escapes unfavourable conditions by means of winter diapause in the egg stage, "here but later", resulting in rigorous synchronisation and timing of activity (and probably density). Reproductive success of this species is moreover increased by the overwintering of a (small?) part of the population. Both species have to reproduce in the habitat where they normally live, i.e. "here".

Acknowledgements

I would like to thank Mr A. Aling for his permission to use the study area. Thanks to Mr F. T. Wiersum the series of catches was not interrupted during holidays. Prof. dr L. Vlijm gave invaluable support by his suggestions in many discussions. Mr G. W. H. van den Berg prepared the figures and drs F. Veldkamp and drs G. Veldkamp-Bouma corrected the text.

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