

LIFE CYCLE AND ADAPTIVE COLOURATION IN *MICROMATA VIRESCENS* (CLERCK, 1757) (HETEROPODIDAE)

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Abstract. According to observations of *Micromata virescens* in its specific habitats, all in central Germany, the stenochronous species has a biennial life cycle in that region. In consequence two generations of different age are present throughout. Juvenils are subject to reversible colour changes in relation to seasonally conditioned alterations of herbage appearances. Particular environmental influences on the spider colouring are probably temperature and photoperiod. Juvenil colouring either overall green or light brown, blends well with habitat backgrounds and is supposed to serve camouflage functions.

INTRODUCTION

The European heteropodid *Micromata virescens*, an attractive but not a rare species, is locally abundant in open spaces of woodland that offer grass and lower bush vegetation. Due to their vivid green or pale brownish colouring individuals are seldom noticed when sitting on substrates with corresponding colour appearance. So far only some pieces of information are present on the colouring matter (pigment chemistry) of the spider (Holl & Rüdiger, 1975), the dimorphism of sexes (Homann, 1946; Holl, 1987a) and on the colour changes of juvenils (Lux & Holl, 1992). However, life cycle phases, life span and the occurrence of green or non-green stages along with seasonally changing conditions of the biotope had not been clarified, so far. Our findings by field observations refer to those open questions. Yet, only *Micromata* populations of central Germany with its variable temperate climate were the subject of studies.

MATERIALS AND METHODS

Field observations were directed to populations of *Micromata virescens* living in locations within Hessian woodlands (central Germany). For detailed inspections six places (each around 1500 m²) with low but dense vegetation and apart from heavy tree shadows were selected. Searches for spiders and observations of their colour appearance were practiced from the end of 1989 to summer 1993 in terms of one or two weeks. For instance along 1991 and 1992 we collected and observed more than 450 individuals from instar 3 up to the penultimate moult. Most of the spiders were set free after photographing and measuring their standard length. Some 50 juvenils of all stages along seasons (1991–1993) were kept separately in plastic boxes in order to control their further moults for a determination of the stage. Complete series of moults for males and females could be recognized by the breeding of specimens. No catching was needed for identification of the numerous instars 2 in summer. Their numbers were not listed. Furthermore, colour appearance of the *Micromata* habitats along seasons was recorded by photo and video equipment. The rates of green substrates at certain terms had to be estimated.

RESULTS

Life cycle and life span

We have evidence that *Micromata* prefers sunny places of woodland stocked with dense grass and shrubs amongst bushes and low trees. However, when low herbage areas become overgrown the local spider population disappears. For that reason the habitats selected for observations were open places for years. In all the places the populations of the spider persisted throughout.

In principal, young spiderlings and advanced juvenils live between the grass shoots at different levels depending on weather conditions. But adults may also reside on low branches of bushes or trees. In particular, mature females (post copula) pass over to certain substrates (rashberry, blackberry, young oak) in order to find broad leaves for attaching their large brooding sack below. In any case detection of all the spider stages and of egg sacks is rather intricate.

Instar stages of all-sized juvenils taken from the field could be determined through a survey of their further moults. By that we succeeded in correlating sizes and their stages. The length data indicate the persistence of distinct size classes throughout the years. According to the average size data of large and small specimens at all terms (1991–1992) there is a gap of at least 3 mm in length (Fig. 1). Yet, we may have overlooked quite a few individuals of intermediate size. Nevertheless, different size classes are obviously valid representing parallel generations. Beyond that, in summer even three generations are present: adults, their outcoming spiderlings and the advanced juvenils from the former year, as well (Figs 1–2).

When spring was warm, and somehow dry, first adults were noticed already towards the beginning of June. In contrast, maturation is delayed in case of rainy or cold spring weather and the final moult is not processed until the end of June. As a rule, mature

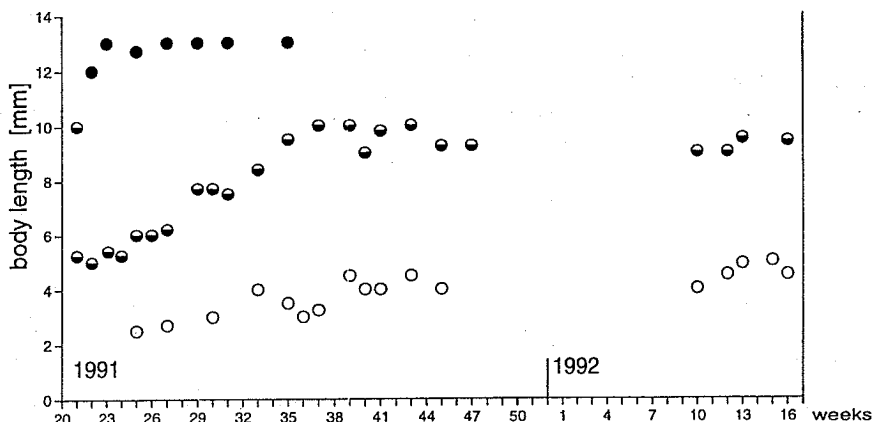


Fig. 1. Occurrence of size classes as indicated by individuals observed from May 1991 to April 1992. Each marking represents the average length of small- or large-sized juvenils and of adults found at a certain term on all of the places. Single finds are not listed. ○ small juvenils; ◐ large juvenils; ● adults.

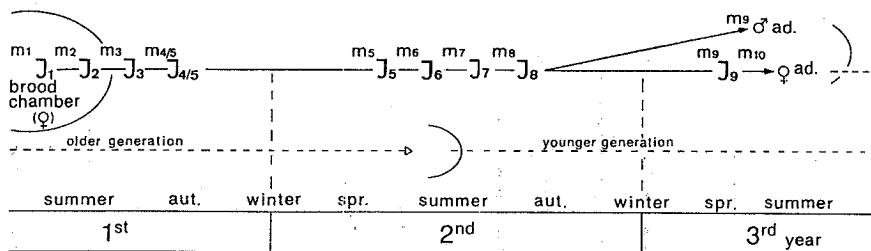


Fig. 2. Developmental stages throughout the biennial life cycle of the stenochronous spider. I_{1-9} instars, m_{1-10} moults. Parallel generations are indicated below (dotted line).

males can be detected one or two weeks earlier than females. Relying on our observations in the described region, the generation of adults comes to an end in late August. Brooding chambers with females guarding their green eggs are not present later.

Since the very first moult is performed as an incomplete stage, spiderlings leave the brooding chamber only a week after their second moult. Many of those instars 2 being all pale green can be found in July and even in August. They are abundant together with instars 3 from early hatches. Some of the latter become yellowish green with red dots. Only one or two more moults are then proceeded until autumn before the young spiders of 4–5 mm in length overwinter a first time as instars 4 or 5 (Fig. 2).

In their second year juvenils carry on moulting in April or May (depending on environmental conditions) and pass through four additional stages thereby growing up to an average length of around 10 mm until September. They do not reach the adult stage but rather a second overwintering and another one or two moults are essential for reaching maturity in June of their third year. As we found in breded specimens, complete number of moults is nine in males and ten in females.

Seasonally conditioned colouring

Not only the continuous presence of two spider generations is remarkable but also is the occurrence of variably coloured individuals. According to our inspections when juvenils were measured, colour variation is characteristic for each size class at the same time. Juvenil spiders were found to be either overall green, haycoloured or of intermediate appearance resulting from colour changes somewhat along with seasonally altering background colours of habitats. Since definite evaluation of background colours is almost impossible we had to rely on estimations for rates of green substrates at certain terms. For instance in 1991 data of spider colouring types and rates of green backgrounds were collected every two weeks from May to November. Those summarized data (habitats and spiders in parallel) reveal considerable correspondence of the prevailing colouring types of the spider to rates of green backgrounds during seasons (Fig. 3).

In particular, young spiderlings of instar 2 are always green in midsummer until their third moult. Instars 3 and 4 then turn out to a yellowish or pale brown with red dots when greenish backgrounds decrease during late summer to autumn. A search for

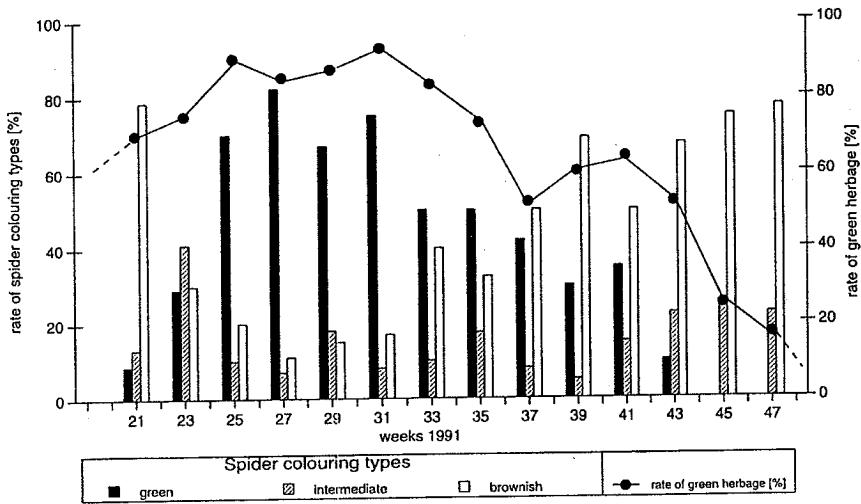


Fig. 3. Occurrence of colouring types of juvenils and estimated rates of green herbage along May to November in 1991 (summarized data collected in three places).

such instars needs patience since they are well hidden amongst the dry blades of grass. The diapause for the young juvenils lasts until April, only then successive moulting is continued. In early summer the dull colouring—leaving a few red dots—turns to a conspicuous green. Those green juvenils reside on the freshly emerged grass. Colour change to an overall green is performed in the course of one or two intermoult through transitional colour phases (intermediates). Therefore in May and June variably coloured individuals, mostly instars 5, are abundant, whereas in midsummer instars 6 and 7 are overall green. But again a colour change to pale fawn is preceded by instars 8 in autumn before their second overwintering (Fig. 3).

Finally in their third year but not until late May, the large preadults absolve the penultimate moult and then take the mature colouring: females become overall emerald green whereas males evolve a yellow opithosoma ornamented by 3 longitudinal, scarlet bands. Above all, the emerald females match perfectly with their seat on green herbage when lurking or basking in the sun.

Colour changes could be well observed in bred specimens and in juvenils from the field, as well, when substrates adverse to the actual spider colouring were offered. In principal there are no differences in colouring types that occur in the habitats. Turnover of spider colouring to background appearance is mostly completed along two intermoult. However, incomplete colour changes or none at all are due to reduced light periods and temperatures below 16°C.

DISCUSSION

Former mentions concerning life span and reproduction period of *Micromata virescens* are rather imprecise (e.g. Locket & Millidge, 1951; Bristowe, 1958; Heimer & Nentwig, 1991) and do not consider the complete life cycle. Besides, there has been no regard to phenomena of life cycle divergence and a possibly different life span in far distant populations of the species with ranges from Italy to southern Scandinavia. For all that, in several European species (e.g. Lycosids, Linyphiids, Theridiids) such differences are common (Schaefer, 1987). As an onset towards clarification of those open questions our studies were directed to *Micromata* populations living in between warmer and colder latitudes.

According to our observations in a number of habitats of the spider, the occurrence of distinct size classes is of remarkable consistence. In consequence, the presence of two parallel generations seems to be valid for the particular region and its climate. Since comprehensive data of juvenil stages and their growth along several years reveal twice an overwintering for either generation the spiders become mature only in their third year. To that extent, the stenochronous species reproducing in summer is biennial in the named region.

Yet, a pervading separation of generations is unlikely. Rather it is supposed that some single males of early hatches may well become adult already in summer of their second year thus being ready to mate with late females of the pregeneration. After all, spiderlings reared under optimum conditions (temperature, light, moisture, food) became mature within seven to nine months exhibiting shorter developmental times for the smaller males. In respect to that, individuals of *Micromata* populations living in warmer latitudes may have an enhanced life cycle pattern with annual or annual-biennial achievement (Schaefer, 1987). On the contrary, a somehow delayed development should be expected in individuals of northern distribution.

As to the variable colouring outfit of *Micromata* specimens, one has to distinguish between the juvenil and the adult phase. Different from the reversible morphological colour changes of juvenils, colouring of adults is definite for all means. According to the definition of Bückmann (1974) the conversion from the premature to the mature appearance in *Micromata virescens* is an ontogenetic colour change.

Colour changes of juvenils are never abrupt but rather transition needs a few weeks. Intervals of transition are somewhat related to certain seasonal phases, that is either spring to summer and summer to autumn. On the other hand the occurrence of overall green individuals is restricted to the verdure period of summer, whereas haycoloured spiders are abundant from September to May when substrates are faded (Fig. 3). On the first view and to that extent, colouring proceedings in juvenils are seemingly responses to backgrounds. Yet, direct influences on spiders exclusively by herbage colours are improbable since additional environmental events are involved, e.g. temperature, light or day length and moisture. In this respect we refer to our observations in specimens kept under different light and temperature conditions: colour changes failed or were incomplete when light exposition and temperature were reduced.

Colouring types of juvenil *Micromata* along seasons were found to be equal in all of the six habitats. Furthermore, adults did not differ in appearance. For that reason the mode of colour variation in *Micromata* is not polymorphic as for instance in *Enoplognatha ovata* (Oxford, 1976; Holl, 1987b).

Colour changes in juvenils of *Micromata virescens* and resulting colourings are suggestively of adaptive significance serving as a life cycle strategy in the course of varying backgrounds of habitats. With regards to crypsis colouration of the species may well serve camouflage functions as is reported for the green lynx spider *Peucetia viridans* (Neck, 1978). Yet, so far we have no information on that subject in *Micromata*. Involved roles of effective camouflage may be directed towards predators such as birds or sphecid wasps and on potential prey, as well. Further studies (field observations, experimental work) are required towards an approach to that question.

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