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Life history of *Bathyphantes simillimus* (Araneae: Linyphiidae) in Stołowe Mountains, Poland

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Abstract. The density, reproduction and life-cycle of *Bathyphantes simillimus* (L. KOCH 1879) were studied in the Stołowe Mountains (Poland) where this species inhabits deep, sandstone rock crevices. Constant observations indicate that studied species has exceptional triennial life cycle where new individuals join the population in summer, survive the following winter, grow, mature and breed throughout the next year, live through the next winter then breed again and die in the year following their second winter. The prolonged life cycle may be the result of adaptation to cooler environmental conditions.

Key words: Linyphiidae, *Bathyphantes simillimus*, density, life cycle, Stołowe Mountains.

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I. INTRODUCTION

The exact life-span of spiders is known only in few dozen species (FOELIX 1996). It is commonly thought that spiders living in temperate zones have annual life-cycles (GERTSCH 1979; FOELIX 1996), however species studied from high altitudes, northern latitudes and under cooler conditions require more than one year to complete their development (BUDDLE 2000; LEECH 1966). Moreover, spider's life history may change from annual to biennial depending on geographical location (PUTMAN 1967; DONDALE 1961; DONDALE & BINNS 1977). Individuals of the same population may also extend their life cycle under particular circumstances (EDGAR 1972). Thus, as traditional life-history theory assumes, growth rates vary in response to the environment (ROFF 1980; GEBHARDT & STEARNS 1988). Spiders may respond differently to various types of nutritional stress (starvation, toxicity of prey, deterrency, nutritional insuffiency). Some findings show that growth rates may change even under similar conditions (GOTTHARD 2000). Such observations demonstrate the plasticity of spiders life history.

Linnyphiids are the second most diverse spider family, they dominate especially northern spider faunas (BUDDLE & DRANEY 2004). Members of the family display different patterns where biennial and mixed annual-biennial strategies (in which some members of a population are annual and some are biennial) become common (AICHISON 1984; SHAEFER 1977; DE KEER et al. 1987; TOFT 1976, 1978; VAN HELSDINGEN 1965). Different species overwinter as juveniles, adults or, more rarely, eggs (SHAEFER 1976, 1977) and some species actively feed and even reproduce during the northern winter (HUTHA & VIRAMO 1979; AICHISON 1978, 1984). But, the absence of identifiable juveniles from this family makes it difficult to determine the exact duration of their life cycles (AICHISON 1984). Such knowledge is crucial for understanding population dynamics and community ecology of particular family members.

Bathyphantes simillimus (L. KOCH 1879) is a very rare species. It is distributed in the northern areas of Eurasia and America, between 40ş and 70ş N (MARUSIK et al. 1993). In Central Europe it is restricted to a few regions with low temperatures all year round. It has been found in stony debris and among rocks in the Czech Republic, Slovakia, Germany, France and Belgium (RŮ IČKA 1988, 1994; BLICK 1991; BLICK & MOLENDA 1997). In northern areas the species has been found in stone belts and on cliffs (KOPONEN 1974). *B. simillimus* is believed to be a relict of periglacial or early postglacial times in Central Europe (WO NY & CZAJKA 1985; RŮ IČKA 1988; BLICK & MOLENDA 1997). In Poland, *B. simillimus* is known to exist only in the Stołowe Mountains, where it inhabits the central parts of the sandstone boulder area (the "Stone Town"). At these localities there are rock fissures, which are usually tens of meters deep and only tens of centimeters wide. The species is abundant in dark, moist and cold crevices.

As low temperatures depress growth and consequently prolong the length of spider life in cold climate (EDGAR 1972), the objective of this study was to describe the life cycle of *B. simillimus.*

II. METHODS

L o c a l i t i e s o f s t u d y. The site of field studies and collection of specimens was the Błędne Skały (850 m a.s.l., 50º29' N, 16º17' E) the part of the Stołowe Mountains National Park in the central part of the Sudety Mountains.

D e n s i t y e s t i m a t e s. The spider population was observed for at least 24 hours per week from March to November 2000-2001 under natural conditions.
Density of *B. simillimus* was estimated by counting the individuals on the rock surface where 10 square areas (1×1 m) were selected (in the places where spiders were the most abundant), then some of alive individuals were collected (the web was tapped opposite the spider causing the spider to drop down into container held below) and brought to the laboratory. The procedure was repeated 106 times during 2 seasons between 29 March 2000 and 30 October 2001.

R e p r o d u c t i o n. Density of cocoons was estimated by counting egg sacs on the rock surface (56 samplings). Females staying near egg sacs, or those appearing to be gravid (with swollen abdomens) were collected during the spring 2000 and 2001. Data about reproduction were collected for 43 females. Many females produced egg sacs in captivity. Eggs were counted under natural conditions (46 times).

In laboratory adults were kept in jars (various sizes) singly, in twos, or in groups, while juveniles were held in Petri dishes (5 cm diameter) singly, in twos, or in groups, too. The total number of spiders kept in the laboratory: 17 juveniles and 56 adults. L/D 16:8 (16 hrs of light/8 hrs of darkness), with humidity varying from 90 to 100% (cotton wool soaked with water) and temperature maintained at 5-10 C. Prey: 30 springtails per week (per jar and dish) from family Isotomidae, regarded as a high-quality food (MARCUSSEN et al. 1999), collected with an aspirator in a nearby park.

M e a s u r e m e n t s. As carapace width (CW) is the most useful measurement to distinguish life history stages (HAGSTRUM 1971; DONDALE 1961; BUDDLE 2000; PICKAVANCE 2001). In this study CW of juveniles, subadults and adults species was measured in a plastic Petri dish to the nearest 0.01 mm using an ocular micrometer. Juveniles were either very small newly hatched spiderlings or smaller specimens showing no differences that would indicate their future sex, or larger specimens with males showing at most a slight thickening of the palpal tarsi and females having no sign of any palpal swelling.

L i f e c y c l e. Samples were taken after snow melt on sand stones (end of March -early April).The crucial information for that species was whether adults survived the winter and what does the general structure of the population look like after overwintering. Thus, samples were taken and counted in the early spring (March) at each site. Some of them were put into the plastic containers and carried to the laboratory either for further observation or placed directly into 70% ethanol for storage and later examination. Specimens with fully developed functional palps or epigyne were regarded as mature. Specimens before last moult were defined as nymphs (subadults). Additionally, total number of moults was counted (under laboratory conditions).

Additionally, on 19.IV.2002 ten mature specimens (five females and five males) were labeled on the carapace according to Buddle's method (2000). A small hole was drilled in a Petri dish placed over the spider gently held on a piece of foam; specimens were maneuvered on the foam so that their carapace was directly below the hole and a stick dipped in paint was inserted through the hole to place paint on the carapace. Data about life span of *B. simillimus* in captivity were obtained through the constant observation of juveniles hatched in laboratory (17 specimens) during three subsequent years (2000-2003).

S t a t i s t i c a l a n a l y s i s. Data presented as mean ± SE (*n*). Density estimates were tested with Mann-Whitney U test.

III. RESULTS

D e n s i t y e s t i m a t e s. A total number of *B. simillimus* specimens was counted during 106 density estimate samplings. At the beginning of the year the population began with low numbers of adults and subadults. The highest density occurred between August and September (Fig. 1) and decreased in the final sampling period. Males were encountered less frequently during the survey and their density estimates were half as low as females (Fig. 2, U test P=0.001). The species predominated on the rock surface.

R e p r o d u c t i o n. Egg-sacs were produced after 28.51 ± 0.94 (n=43) days from the moment of copulation. A total number of *B. simillimus* cocoons was counted (n=56). The highest density occurred between July and August (Fig. 3) and decreased constantly until the end of September. The mean number of eggs in one cocoon was 11.41 ± 0.9 (n=46). Females produced up to 3 egg sacs during the whole season.

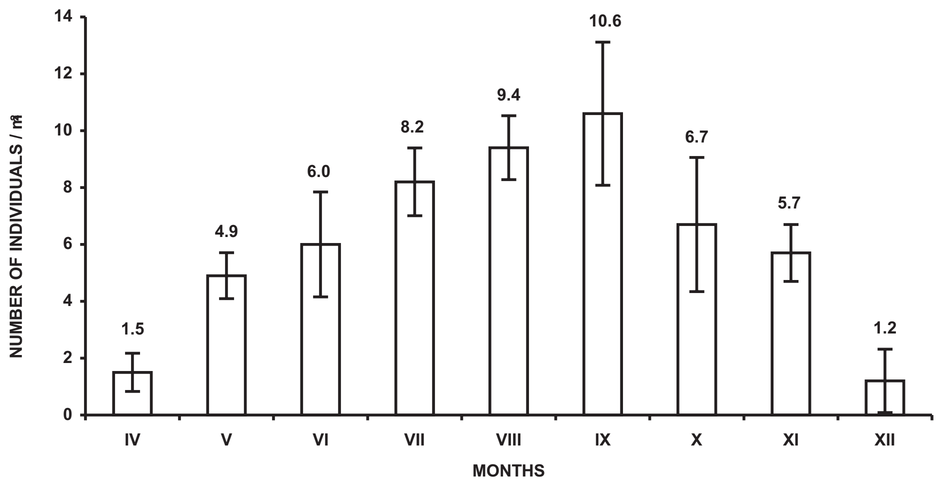

Fig. 1. Density estimates (per m^2) for *B. simillimus* from April to December (n=106, error bars=SE).

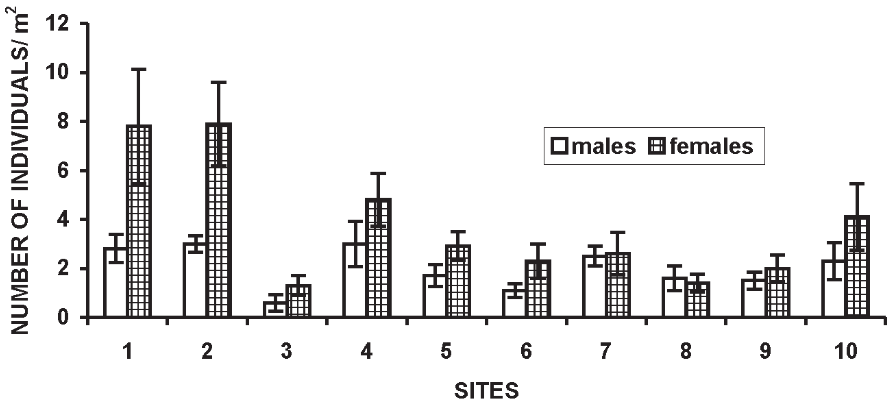

Fig. 2. Density estimates of males (empty bars) and females (checked bars) in 10 sites in September 2001 (*n*=10, error bars=SE).

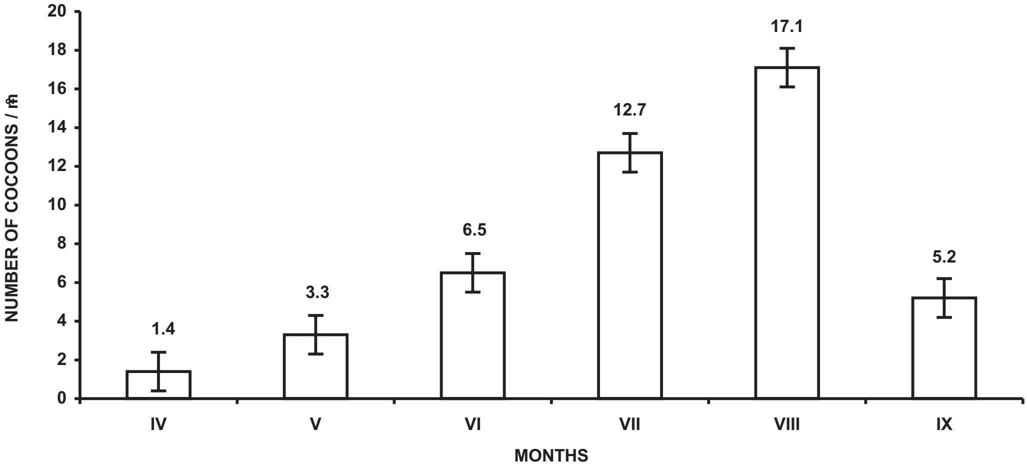

Fig. 3. Comparison of the mean density of *B. simillimus* cocoons 10 sites (from April to September) (*n*=56, error bars=SE).

Parental care was never observed in the population of *B. simillimus*. Females stayed near their cocoons, but after hatching process they were not interested in newly emerged juveniles.

Hatching took place usually after 36.34 ± 1.23 days (*n*=43) (data obtained in the warmest period). The total number of juvenile molts (*n*=17) until the spider reaches the sexual maturity was 6 ± 1. Males had one molt less than females. Spiderlings were active from late spring until autumn months. The first overwintering often took place in the larval stage, the only exception were specimens hatching at the beginning of summer (June). They might reach sexual maturity before the first overwintering.

M e a s u r e m e n t s. The carapace width of adult *B. simillimus* was 1.08 ± 0.03 (*n*=56) The mean CW of subadult specimens (just before the expected molt to maturity) was 0.82 ± 0.13 (*n*=17). The mean CW of immature spiders was 0.22 ± 0.02 (*n*=31) for newly hatched spiderlings, 0.41 ± 0.03 (*n*=17) for smaller juveniles and 0.67 ± 0.07 (*n*=17) for larger specimens.

L i f e c y c l e. The scheme of life-cycle is presented in Fig. 4. In each season four cohorts *of B. simmilimus* were observed:

1. Juveniles in the first year of their life, directly after hatching. They were observed in the field from the beginning of June, and overwintered as nymphs.

2. Juveniles in the second year of their life hatched in the previous season, before overwintering. They were active in the field from the beginning of April and reached their maturity in the late spring (from April to June).

3. Adults in the second year of their life. They produced cocoons and laid eggs (the first breeding season).

4. Adults, after overwintering they laid eggs (the second breeding season), and died before the winter.

Under the laboratory conditions spiders survived for three years. Female life span was 906.4 days ± 29.85 (n=10) and males lived for 961.9 days ± 39.27 (n=7). Marked spiders were released on 26.IV.2002 and individuals of either sex were re-captured on 23.IX.2002 (4 females and 3 males), showing that spiders live at least 172 days in field after being collected and marked. Next year (2003) only two females were re-captured on 6 VI. Males were not found in the field.

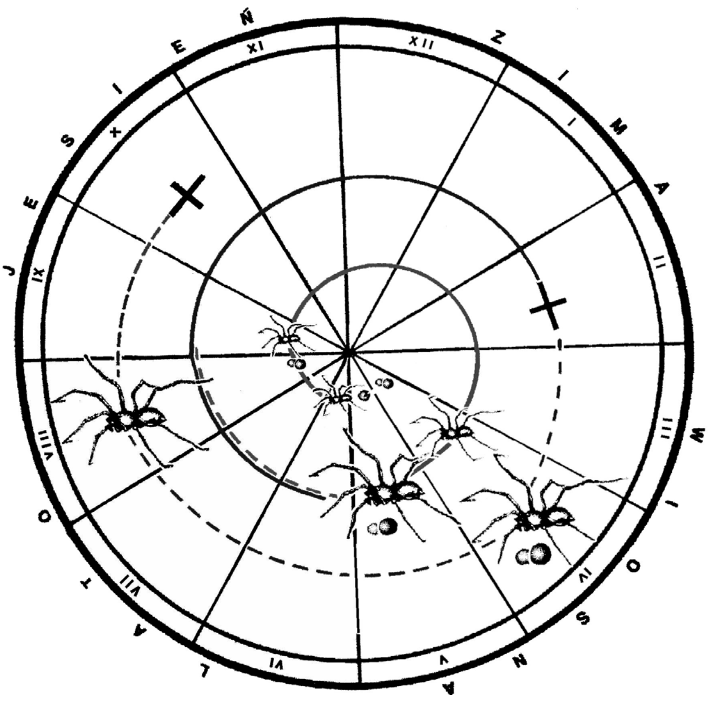

Fig. 4. The life-cycle model of *B. simillimus*. Legend: spherical symbols- cocoons produced by females; crosses – the moment of spider's death; dashed lines- potential prolonged life of some individuals (spiders kept under laboratory conditions).

IV. DISCUSSION

D e n s i t y e s t i m a t e s. The maximum number of *B. simillimus* specimens per m^2 was 26 which seems high although comparable data does not exists for this species. Densities of other studied linyphiids differed significantly depending on the environment (THORNHILL 1983; TOPPING & LÖVEI 1997; TOPPING & SUNDERLAND 1998). TURNBULL (1973) estimated that average density of all spiders inhabiting meadow, a much more fertile environment, was 130.8 specimens per square meter. Such data may suggest that sandstone crevices provide favorable life conditions for the population of *B. simillimus* as it is relatively frequent in this environment (personal observations). This may be due to the presence of Collembola, a major component of the prey of linyphiids (NENTWIG 1983, 1987), which are abundant in these cool crevices (RYBAK 2007). On the other hand, linyphiids are the most ubiquitous group of spiders in the world.

R e p r o d u c t i o n. The period between copulation and egg laying as well as the hatching process took a little longer in *B. simillimus* than in other linyphiids e.g. *Lepthyphantes leprosus* (OHLERT 1895) laid eggs after 7-14 days and hatchlings emerged after 3 weeks (VAN HELSDINGEN 1965). These differences can be attributed to climate. A significant impact of temperature on egg and larval development was already observed (BUCHE 1966; VAN PRAET & KINDT 1979; DE KEER et al. 1987; TOPPING & SUNDERLAND 1998) for some other linyphiids (*Erigone atra* (BLACKWALL, 1833), *Oedothorax fuscus* (BLACKWALL, 1834), *Centromerus sylvaticus* (BLACKWALL, 1841), *Lepthyphantes tenuis* (BLACKWALL, 1852).

In comparison to other linyphiids, *B. simillimus* produced smaller number of eggs. In *L. leprosus* the number of eggs in one egg-sac varied from 15 to 25 (VAN HELSDINGEN 1965), in *E. atra* – from 4 to 16 depending on the diet (MARCUSSEN et al. 1999) and from 10 to 24 eggs depending on the temperature (DE KEER et al. 1987). The number of eggs depends on various factors such as food quality and availability (MARCUSSEN et al. 1999; MAYTNZ et al. 2003; MAYTNZ et al. 2005). Only some Collembola are a high quality food and may support numerical increase of predator population. However, in sandstone crevices where *B. simillimus* lives, various species of Collembola were widely available and abundant (RYBAK 2007). According to some other authors the number of eggs depends on female size (BUDDLE 2000). The bigger the female, the more eggs it produces. On the other hand, the number of eggs is lesser in species in which the parental care is observed (PETERSEN 1950; TURNBULLL 1962; KESSLER 1971). No trace on parental care was observed in studied species. It seems probable that the smaller number of eggs of *B. simillimus* results from low temperature impact and the small body size of spider.

M o u l t s. BONNET (1930) claimed that the total number of moults depends mainly on spider size. Small species undergo usually only few moults (on average 5) less than the big ones (on average 10). The number of moults in *B. simillimus* (on average 6) fits well the above proportion. The pace of moults depends also on the food availability (FOELIX 1996). According to HIGGINS & RANKIN (1996) and JESPERSEN & TOFT (2003), the total development time is rather a function of instar duration than of the number of instars. In *L. tenuis* fed by aphid *Rhopalosiphum padi* L. (poor quality food) until the first moult the total development time increased only slightly. The number of instars to maturity did not change, only the instar duration increased (BECK & TOFT 2000). On general, different spiders species could respond differently to various types of stress.

L i f e c y c l e. In the temperate zone the reproductive period usually starts in May (TRETZEL 1954) and spiderlings hatch in summer time. Some species could reach their sexual maturity in autumn, but the majority overwinter as nymphs. Such scheme of seasonal activity exists in *B. simillimus*.

The majority of temperate zone linyphiid spiders exhibit annual and biennial life cycle (FOELIX 1996; NENTWIG 1987; AICHISON 1984; SHAEFER 1977; DE KEER et al. 1987; TOFT 1976, 1978; VAN HELSDINGEN 1965). The triennial life cycle of *B. simillimus* is an exception among the well-known cycles of other linyphiids and stenochronic species (reproducing once a year). The development of linyphiid juveniles takes also longer (DE KEER et al. 1987). The difference in life cycle of *B. simillimus* is attributed to cooler conditions in "Błędne Skały". The majority of females live longer than males which die shortly after copulation (FOELIX 1996). *B. simillimus* shows different pattern: males and females survive up to three years. Males usually outlived females in captivity, however in nature males were half as abundant as females which suggest their higher mortality. The laboratory conditions could considerably modify spider lifespan. It was observed repeatedly that males lived longer in captivity than in nature (FOELIX 1996; BARTOS 2000). Such observations demonstrate the flexibility of linyphiids life history. This flexibility may be a factor explaining their dominance in many terrestrial ecosystems.

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