Spatial and temporal distribution patterns of Agelena labyrinthica (Clerck, 1757) webs (Agelenidae) in an unfertilized, calcareous grassland in the Swiss Jura mountains

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Spatial and temporal distribution patterns of *Agelena labyrinthica* (Clerck, 1757) webs (Agelenidae) in an unfertilized, calcareous grassland in the Swiss Jura mountains

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The spatial distribution, density and size of sheet-funnel webs of the spider *Agelena labyrinthica* (Clerck, 1757) were examined in a nutrient-poor, calcareous grassland in the Northwestern Swiss Jura mountains over a period of four years (1993–1996). Individuals of *A. labyrinthica* are known for their high web-site tenacity. Webs of *A. labyrinthica* showed an aggregated dispersion pattern. Web density was significantly higher in 1993 (0.23 webs/m^2) than in the three succeeding years (0.06, 0.07 and 0.05 webs/m^2). In each year there was a pronounced spatial heterogeneity of web density in the grassland examined. There was also a considerable variability in web size (area of the horizontal sheet) within and between years (range of yearly mean values: 50.2–96.8 cm^2). However, web size was not affected by web density. After successful hibernation spiderlings frequently chose the same positions for web construction as did spiders of the parent generation in the preceding year. This indicates that certain spots in the grassland might be particularly suitable for webs of *A. labyrinthica*.

Keywords: Araneae, *Agelena labyrinthica* (Clerck, 1757), density, spatial distribution, web, Jura mountains

INTRODUCTION

Microhabitat, substrate structure and prey availability are important determinants of the distribution of spiders (e.g. Uetz, 1975; Hatley & MacMahon, 1980; Lubin *et al.*, 1993). Grassland vegetation provides varying types of substrates and microhabitats which are differentially suitable for spiders (Nyffeler & Benz, 1987). In web-building spiders, random spacing of webs may signify independence of individuals and/or uniformity of the vegetation structure. Regular spacing of webs in more sedentary web spiders may indicate competition for food and space, while aggregated webs may indicate heterogeneity of the vegetation structure and prey availability and/or attraction between individuals. The spacing of webs in more sedentary spiders has important implications for the growth, survival and reproduction of individuals, but field data addressing this topic are scant (see Riechert & Tracy, 1975; Riechert, 1976; Hodge & Storfer-Isser, 1997). Analysis of spatial pattern is an essential basis for understanding scales at which organisms interact with one another or with their environments (Underwood & Chapman, 1996).

The spider *Agelena labyrinthica* (Clerck, 1757) (Agelenidae) lives in ruderal areas, fens, nutrient-poor grasslands and heather (Hänggi *et al.*, 1995). Individuals of both sexes build a sheet-funnel web near the ground or in low vegetation. Website tenacity is high in *A. labyrinthica*; new webs are built only exceptionally (Schlott, 1931).

The aim of the present study was to examine the between-year variation in web density of *A. labyrinthica* in an unfertilized, calcareous grassland. In particu-

lar, the following questions were addressed: (1) How are the webs spatially distributed in the grassland? (2) Does the density of A. *labyrinthica* webs change during the season and vary between years? (3) Do spiders from consecutive generations use the same spots to build their webs?

MATERIAL AND METHODS

Study species

Agelena labyrinthica has an annual life cycle. Individuals reach sexual maturity in July or August. The males visit females in their webs where they mate. Four to six weeks after copulation, females lay their eggs into cocoons between dead leaves, under stones or in holes in the soil. Females die after reproduction in October. Newly-hatched spiderlings stay in their cocoon during winter. In spring, spiderlings leave the cocoon, disperse and search for suitable sites to build their own webs (SCHLOTT, 1931). The web of A. *labyrinthica* has an attached funnel that extends under a piece of stone or a grass clump. Flying and jumping insects such as bumblebees, butterflies, Diptera and grasshoppers are caught in the labyrinth of thin filaments streched over the horizontal web sheet (NYFFELER & BENZ, 1978). A. *labyrinthica* is hiding most of the time in the protected part of the funnel. Individuals leave their hiding place to repair the web or to enlarge the web sheet, to secure prey and to defend the web against intruders.

Study site

The study was conducted in a nutrient-poor, dry calcareous grassland (belonging to the *Teucrio-Mesobrometum* type; ELLENBERG, 1988), located near Vicques (6 km E of Delémont) in the Northwestern Swiss Jura mountains. Detailed descriptions of the plant and invertebrate communities are given in BAUR *et al.* (1996). The investigation site is located on a SE-facing slope (inclination 15–27°) at an altitude of 570 m a.s.l. The humus layer is thin and there is mixed beech forest at the SW-border of the site. The pasture was grazed by cattle until 1993. From 1993 onwards the entire grassland was mown once per year at the end of October.

Spatial distribution, density and size of webs

The spatial distribution, density and size of A. *labyrinthica* webs were examined in four patches (hereafter referred to as patch A-D) each measuring 32 m x 32 m. The patches were situated 10–50 m apart.

The spatial distribution of A. *labyrinthica* webs was recorded in four plots measuring 10 m x 10 m (one plot per patch). A grid consisting of four units (each 25 m² in area) was set up in each plot by marking the corners of the units with a stake. The position of the centre of each A. *labyrinthica* web was recorded at monthly intervals from May to August by measuring the distances to the nearest two stakes in the grid. On the basis of these data Cartesian coordinates were calculated for the web positions. Patterns of spatial web distribution were analysed using the distance-to-nearest-neighbour method of CLARK & EVANS (1954).

Web density was assessed in six permanently marked small plots of 4.5 m x 4.5 m in each patch in 1993–1996 (only five plots were used in 1993). Webs were counted at monthly intervals from May to August (in 1993 from June to August). Each web was permanently marked with a stake.

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Web size was assessed by measuring the largest (a) and smallest (b) diameter of the horizontal web sheet. Web area (in cm²) was approximated by the formula abπ/4.

Coincidence of web positions

To examine whether spiderlings use the same spots for web construction as did spiders of the preceding generation, we determined the percentage of webs, whose positions in the year y+1 overlapped with the positions of webs in the year y (accuracy 20 cm). The null hypothesis that web positions in a given year were independent of web positions from the previous year was tested by assigning the number of webs observed in the year y+1 to random positions and comparing them with actual web positions from the year y. This step was repeated 1000 times for each comparison of years.

Decay of webs

Without repair the permanent web of *A. labyrinthica* may decay in the course of the season. We performed an experiment to examine the rate of decay of webs in which any repair was prohibited. This experiment was run in an area adjacent to the study site. Webs of 48 *A. labyrinthica* females were randomly assigned to one of three treatments: (I) the spider was removed, but the web was not disturbed, (II) the horizontal sheet of the web was mechanically destroyed, but the funnel and the spider were not disturbed, and (III) neither the web nor the spider were disturbed (control). The area of the horizontal sheet was determined in each web at intervals of 3–5 days over a period of 33 days as described above. Mean web size was equal in all three groups at the beginning of the experiment.

RESULTS

Spatial distribution, density and size of webs

In 1993, webs of *A. labyrinthica* were aggregated in all plots examined as indicated by the distance-to-nearest-neighbour method (Tab. 1). In patch A, webs were also aggregated in 1994, but not in 1995 and 1996. Fig. 1 shows the spatial distribution of *A. labyrinthica* webs in the years 1993–1996. Too few webs occurred in

Tab. 1. Distance-to-nearest-neighbour analysis of the spatial distribution of *A. labyrinthica* webs in four plots measuring 10 m x 10 m. R-values (ratio of observed to expected mean distances to nearest neighbour), number of webs (n) and p-values are given for plots which contained more than 10 webs. R-values < 1 indicate a tendency towards aggregation.

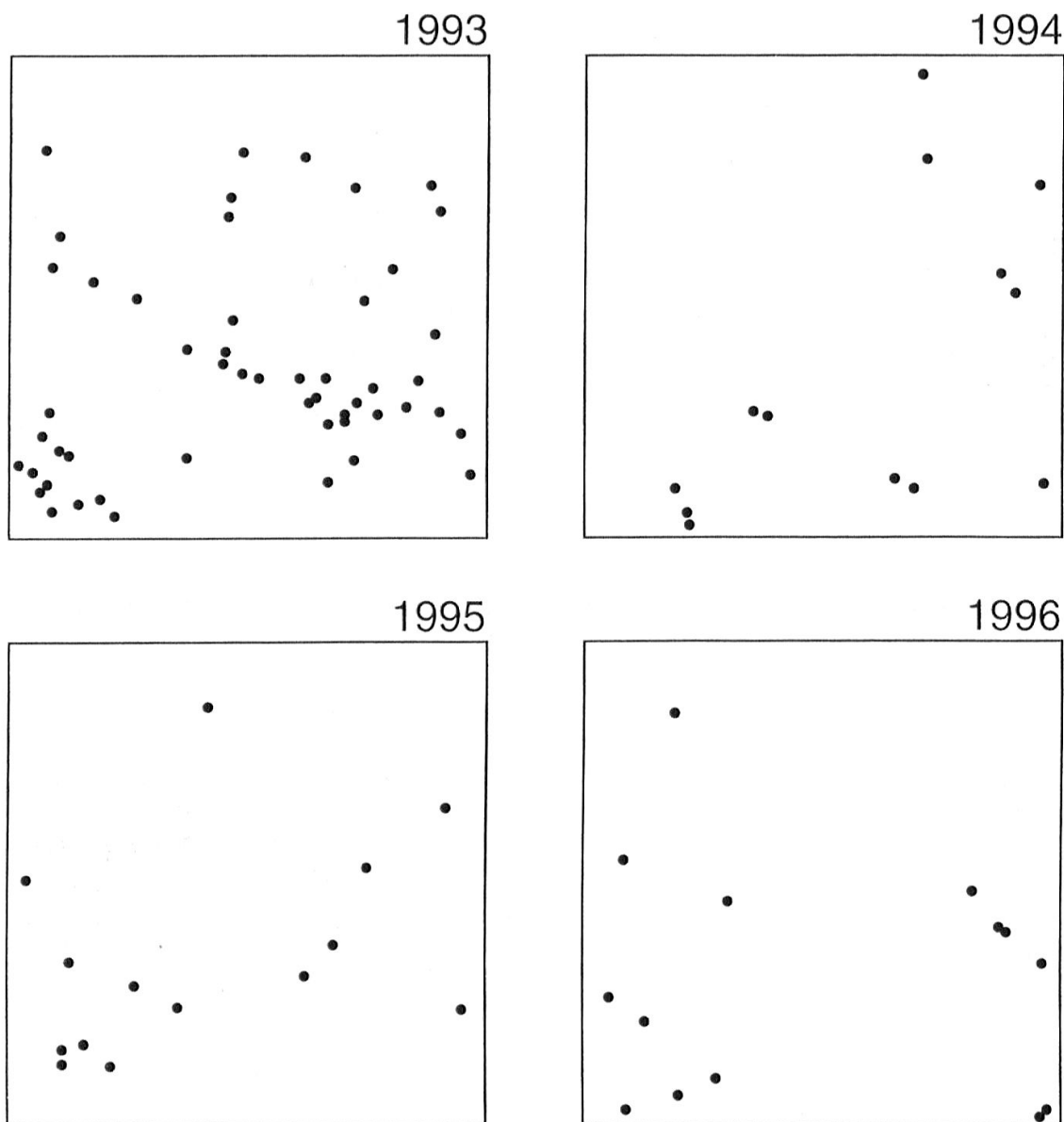| Year	Plot A			Plot B			Plot C			Plot D		
	R	n	p	R	n	p	R	n	p	R	n	p
1993	0.85	51	0.043	0.82	50	0.018	0.72	13	0.050	0.69	22	0.006
1994	0.58	13	0.004	–	8	–	–	2	–	–	0	–
1995	0.88	14	>0.300	–	7	–	–	1	–	–	0	–
1996	0.82	14	>0.190	–	9	–	–	4	–	–	0	–

Fig. 1. Spatial distribution of *A. labyrinthica* webs in an area of 10 m x 10 m (patch A) in 1993–1996. In all years web positions were recorded in June.

the patches B, C and D in the years 1994–1996 to apply the distance-to-nearest-neighbour analysis.

In June 1993, the density of *A. labyrinthica* webs was high (0.40 ± 0.11 webs/m²; mean $\pm$ S.E.), but decreased to 0.14 ± 0.02 webs/m² in August (ANOVA, $F_{2,9} = 5.55$, $p = 0.03$; Fig. 2). No seasonal decrease in web density was observed in the years 1994–1996 (ANOVA; $p > 0.9$ in all three years; Fig. 2). Mean web density in June 1993 was significantly higher than in the corresponding month of the years 1994–1996 (ANOVA, $F_{3,12} = 6.57$, $p = 0.01$; Sheffé's test, $p < 0.04$ in all three comparisons; Fig. 2). Considering only data from July and August, mean web
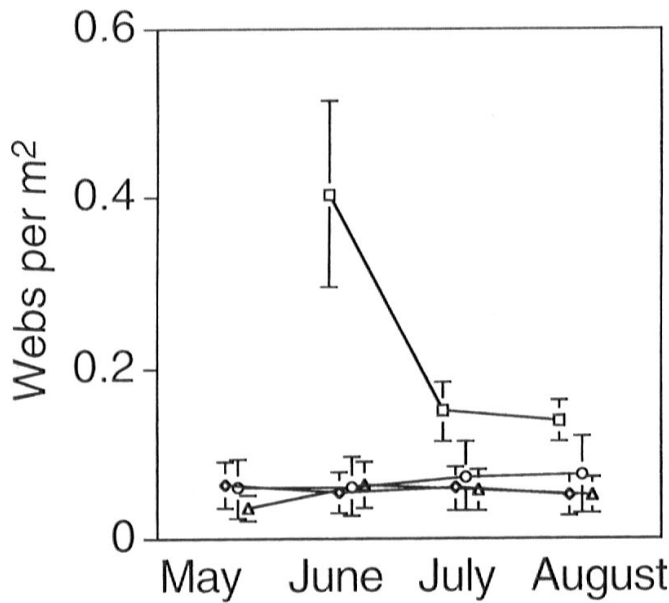
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Fig. 2. Mean web density (± S.E., n = 4 patches with each 6 plots measuring 4.5 x 4.5 m) from May to August in the years 1993 (□), 1994 (◇), 1995 (○), and 1996 (△).

density did not differ among years (ANOVA, July: $F_{3,12} = 1.39$, p = 0.29; August: $F_{3,12} = 1.49$, p = 0.27; Fig. 2).

In all years, web density varied among patches (ANOVA; June 1993: $F_{3,16} = 3.08$, p = 0.06; June 1994: $F_{3,20} = 3.82$, p = 0.03; June 1995: $F_{3,20} = 5.63$, p = 0.01; June 1996: $F_{3,20} = 3.79$, p = 0.03; Fig. 3). In the years 1994–1996, web density was highest in patch A, followed in order of decreasing density by patch B, C and D.
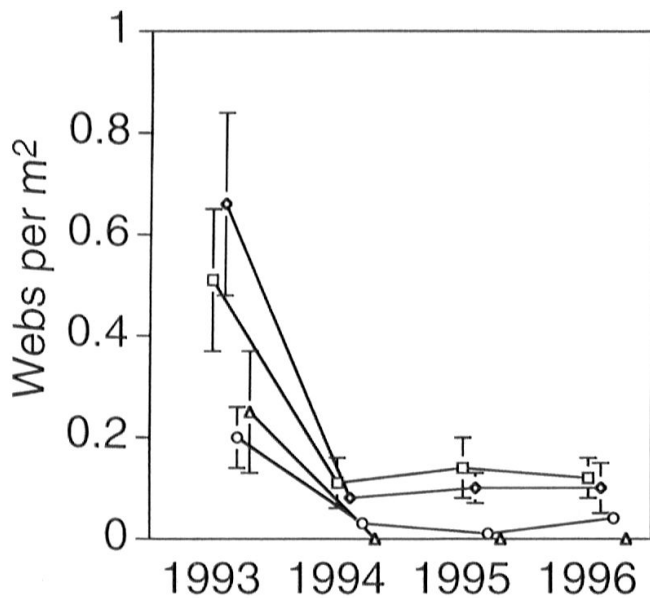

Fig. 3. Among-year variation in web density (mean ± S.E.) in June (1993–1996). Data are presented for the patches A (□), B (◇), C (○), and D (△).

Tab. 2. Size of horizontal web sheets (mean ± S.E., in cm²) of *A. labyrinthica* in patch A. Figures in parentheses indicate the number of webs.

Year	May	June	July	August
1993	–	70.8 ± 14.5 (52)	93.0 ± 27.3 (19)	109.2 ± 27.7 (17)
1994	84.0 ± 28.7 (14)	78.0 ± 30.1 (13)	131.3 ± 41.3 (14)	92.5 ± 30.6 (14)
1995	137.4 ± 18.7 (17)	111.7 ± 28.8 (17)	68.9 ± 36.2 (15)	52.5 ± 36.6 (14)
1996	96.0 ± 25.1 (8)	50.5 ± 19.7 (14)	60.0 ± 27.6 (12)	9.3 ± 4.7 (12)

The frequency of web relocation, indicated by the appearance of new webs during the season, was relatively low in 1993 (9.4%; 17 out of 181 webs), but high in the following years (1994: 40.0% of 50 webs; 1995: 34.1% of 44 webs; 1996: 48.4% of 31 webs).

Data on web size (area of the horizontal web sheet) are presented in Tab. 2. There was a considerable variability in web size within and between years. In the years 1993 and 1994, webs were relatively large towards the end of summer (August), whereas in the years 1995 and 1996 there was a continuous decrease in web size from May to August. The small mean web size in August 1996 was due to a high proportion of decaying webs. Web size was not correlated with web density in small plots measuring 4.5 m x 4.5 m (Spearman rank correlation with data from June: in all years $p > 0.14$).

Coincidence of web positions

Data from patch A were used to examine whether spiderlings chose the same spots to build their webs as did spiderlings of the preceding generation. In 1994, 62% of the webs were built in the same spots as in 1993. In 1995, 21% of the webs were built in the same spots as in the previous year. The corresponding value for 1996 was 21%.

The hypothesis that the observed coincidence of web positions between succeeding years could be obtained by chance was tested using the simulation program described in the methods. The probability that the 13 webs observed in 1994 coincide in 62% of the cases with the actual web positions in 1993, when the webs from 1994 were randomly distributed, was 2.7% (based on 1000 simulations). Corresponding values were 8.5% for the 1994/1995 comparison and 7.0% for the 1995/1996 comparison. This indicates that many spiderlings chose the same or nearly the same positions to build their webs as did spiders of the parent generation one year before.

Decay of webs

An experiment was performed to examine the decay rate of *A. labyrinthica* webs in the field. Webs which were partly destroyed at the beginning of the experiment (treatment II) were repaired within three days and the new web sheets did not differ in size from the original web sheets (paired t-test, $t = 1.46$, d.f. = 14, $p = 0.17$). Overall, web size decreased over the period of 33 days. However, webs from which the spiders were removed (treatment I) showed a more pronounced size decrease than webs from the treatment groups II (web sheet mechanically destroyed) and III (control). After 14 days, the difference in web size was significant (treatment I:

34.8 ± 8.6 cm^2 (mean ± S.E.); treatment II: 171.4 ± 43.2 cm^2; treatment III: 142.9 ± 30.8 cm^2; ANOVA; $F_{2,36}$ = 5.42, p = 0.009; Scheffé's test: I vs. II, p = 0.028; I vs. III, p = 0.021; treatment II vs. III, p = 0.99). This indicates that individuals of *A. labyrinthica* make a substantial effort to maintain and repair their webs.

DISCUSSION

The present study revealed a considerable spatial and temporal variation in web density of *A. labyrinthica* in a nutrient-poor, dry calcareous grassland. Web density may represent a good estimate of population density because *A. labyrinthica* builds a permanent funnel-web.

The between-year variation in web density could be a result of variable female fecundity, differential winter survival of spiderlings, differences in the spiderlings' dispersal behaviour and/or yearly variation in prey availability and weather conditions. However, our data do not allow to distinguish among these factors. A similar between-year variation in web density was observed in the area adjacent to our investigation site (S. LEDERGERBER, unpubl. data). It seems therefore unlikely that our measurements affected the natural web density.

The seasonal decrease in web density observed in 1993 could be a result of an increased predation rate and/or a decrease in food availability. RIECHERT & HEDRICK (1990) found that *Agelenopsis aperta* (GERTSCH, 1934) (Agelenidae) living in a riparian woodland was heavily affected by bird predation. In single patches average losses of 40 % of the spiders were recorded per week during bird-nesting periods. Similar information is not available for *A. labyrinthica*. There is some experimental evidence that spider populations are regulated by the level of food supply (e.g. WISE, 1975), but structural features of the habitat may be more important (COLEBOURN, 1974; RIECHERT, 1974; ROBINSON, 1981). For example, the availability of suitable sites for the construction of webs appears to be the most important factor limiting the population size of *Floronica bucculenta* (CLERCK, 1757) (Linyphiidae) (SCHAEFER, 1978). A seasonal decrease in web density could also result from sexually-mature males leaving their webs to mate with females in July and August.

Spatial segregation is one way in which spiders may partition habitat resources (ENDERS, 1974). This may take the form of horizontal or vertical separation, or it may be the result of differential preferences for habitat structures (e.g. ROBINSON, 1981). Funnel-web spiders actively select their web sites on the basis of specific web-site characteristics (RIECHERT, 1974, 1976). RIECHERT & TRACY (1975) evaluated the effects of the thermal environment and prey availability on the reproductive success of *Agelenopsis aperta* occupying various web-site types. They found that more energy for reproduction is to be gained from selection of a favourable thermal environment than from a site offering a higher density of prey. The presence of flowers at web sites increases the probability of high prey density, whereas litter and habitat features providing shade (woody plants and depressions) allow increased spider activity.

The specific web-site characteristics of *A. labyrinthica* are not known in detail. However, different factors such as structural properties of the vegetation, availability of prey, thermal environment and soil surface structure (e.g. fissures) may contribute to the suitability of web sites of *A. labyrinthica*. The significant coincidence of web positions between successive years suggests that *A. labyrinthica* spiderlings are able to recognise the set of specific web-site characteristics.

TANAKA (1989) estimated the energy cost of web construction and rate of web relocation in *Agelena limbata* THOMAS, 1897. This spider constructs a sheet-funnel web consisting of a tight mesh of silk threads. The web of *A. limbata* is costly in terms of the energy needed for construction, which ranges from 9 to 19 times the daily maintenance energy. As other sheet-funnel weavers, *A. limbata* showed a high web-site tenacity. The energy cost of web construction may be important in determining the frequency of web relocation.

ZUSAMMENFASSUNG

Bei der Trichternetzspinne *Agelena labyrinthica* (CLERCK, 1757) wurden die kleinräumige Verteilung sowie Dichte und Grösse der Netze auf einer Juramagerwiese in der Nordwestschweiz während vier Jahren (1993–1996) erfasst. *A. labyrinthica* ist für ihre Ortstreue beim Netzbau bekannt; ein vollständig ausgebautes Trichternetz wird selten aufgegeben. Netze von *A. labyrinthica* zeigten auf der Magerwiese eine geklumpte räumliche Verteilung. Die Netzdichte war 1993 signifikant höher (0.23 Netze/m²) als in den drei nachfolgenden Jahren (0.06, 0.07 und 0.05 Netze/m²). In allen vier Jahren variierte die Netzdichte kleinräumig auf der untersuchten Fläche. Auch die Netzgrösse (horizontale Fläche des Trichters) variierte beträchtlich sowohl innerhalb wie auch zwischen den Jahren (Spannbreite der jährlichen Mittelwerte: 50.2–96.8 cm²). Die Netzgrösse wurde jedoch durch die Netzdichte in den Untersuchungsflächen nicht beeinflusst. Für den Netzbau benutzten Jungspinnen nach Überwinterung häufig die genau gleichen Stellen, die auch im Vorjahr von den Spinnen der Elterngeneration verwendet wurden. Dies deutet darauf hin, dass gewisse Stellen der Magerwiese für den Netzbau von *A. labyrinthica* besonders geeignet sind.

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