Activity patterns in different developmental stages and sexes of *Larinioides sclopetarius* (Clerck) (Araneae, Araneidae)

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Summary

The activity patterns in different developmental stages and sexes of the nocturnal orb-web spider *Larinioides sclopetarius* (Clerck) (Araneidae) in Vienna, Austria have been studied. The spiders concentrate around light sources in urban habitats, such as along bridge railings which are equipped with light tubes. The density of spiders belonging to various size classes and sexes throughout the entire nocturnal foraging period (sunset until sunrise) was measured. Despite the high density of individuals, spiders did not cooperate in web construction or prey capture. Behavioural patterns such as web building, actively hunting (hanging head downwards in the hub), and feeding on prey were considered. At the same time, prey availability was sampled using insect traps. The results show the close relationship between activity patterns of the spiders and prey abundance. Furthermore, size-related differences in the nocturnal activity patterns were found and interpreted as a result of age-specific foraging patterns.

Introduction

The foraging behaviour in web building spiders involves: (1) placing the web in the habitat, (2) constructing the web, (3) attacking prey entangled in the web, and (4) ingesting prey (Leborgne *et al.*, 1991). Foraging theory suggests that organisms should exhibit foraging behaviour that optimizes the relationship between benefits and costs (Schoener, 1971; Pyke *et al.*, 1977). The two major benefits of foraging are a decreased risk of starvation and an increased ability to reproduce or grow (Abrams, 1991). While the material invested in each web may represent a majority of the spider's daily energetic cost (Peakall & Witt, 1976; Prestwich, 1977), further potential costs of foraging are the risk of predation, stress from adverse physical conditions, and reduced time available for other fitness-enhancing activities (Abrams, 1982). Furthermore, the relative costs and benefits of foraging may vary according to the development and the sex of the individual (Higgins, 1995), and therefore one might expect different foraging strategies to be employed by individuals of different ages and sexes.

Various studies have found differences in activity patterns of spiders in regard to sex (e.g. Alderweireldt, 1994) or stage of development (Hayes & Lockley, 1990; Bayram, 1996), but they do not provide an explanation for these differences. Similarly, studies have also pointed out relationships between prey availability and the seasonal activity patterns of spiders (e.g. Bradley, 1993). However, the optimization of the time spent foraging, which may vary with prey density, has rarely been studied in terms of optimal foraging theory (but see Caraco, 1980; Abrams, 1982).

Our study aimed to address these issues by describing activity patterns with regard to the developmental stage, sex, and prey abundance in the nocturnal orb-web weaving spider *Larinioides sclopetarius* (Clerck). The spiders can occur in populations with very high densities consisting of individuals of various developmental stages and sexes. They live in permanent, functional independent aggregations in habitats

with high prey abundance. Apart from the males, which live kleptoparasitically on females' webs, the spiders construct, maintain, and defend their own webs against potential intruders (pers. obs.).

Methods

The study site is a footbridge across the Danubian Channel in Vienna, Austria. Spiders of the species *Larinioides sclopetarius* exclusively construct orb webs on the four bridge railings (length = 59 m; height = 1.31 m), two of them equipped with artificial lights.

Spider survey

Visual surveys were conducted during five nocturnal foraging periods in August, 1996. Spiders were surveyed every two hours from 7 p.m. until 7 a.m. Immature spiders were classified into two size categories (< 3 mm body length and > 3 mm body length) and adults were sexed (it was not possible to determine the sex accurately in immature spiders). The spiders were counted and the following behavioural patterns were considered: web building, actively hunting (hanging head downwards in the hub), and feeding on prey items.

Prey abundance

Potential prey abundance was assessed using sticky traps. The traps consisted of wooden frames attached with an adhesive synthetic mesh (18.5 cm height and 13.3 cm width, the quadrat meshes spaced 1.5 mm apart). At the beginning of each two hour period, five traps were exposed at random locations attached to the top of the bridge railings that were equipped with light. They were exposed for one hour and then collected. Captured prey was removed and fixed in alcohol (76%).

Statistical analyses

Two-factor ANOVA was performed to test differences in activity patterns of the four spider categories using the relative numbers of spiders in each category (relative number = number of individuals within each category at time x, divided by the estimated total number of individuals within each category). The normally
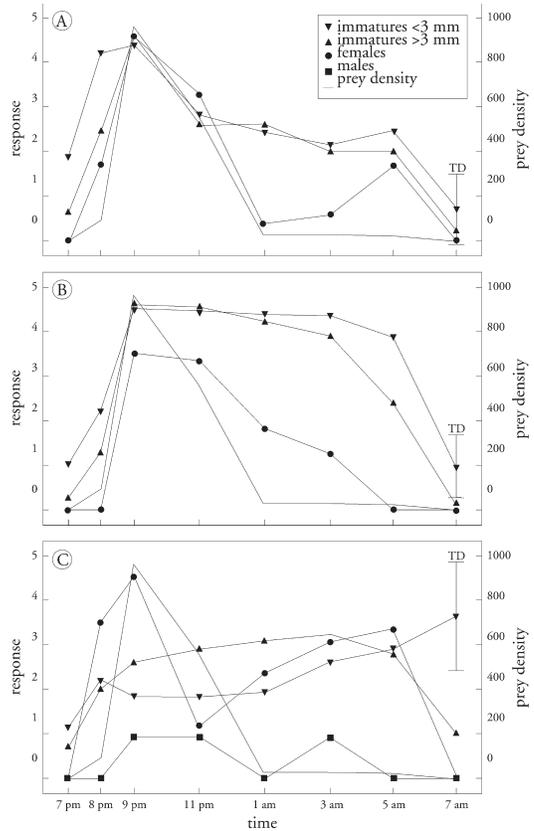
Fig. 1: Interactions between the relative density of four categories of spiders (immatures < 3 mm body length, immatures > 3 mm body length, females and males) in regard to their behaviour (**A** web building, **B** hunting activity, or **C** feeding on prey). The plots show the l_n-transformed relative densities (median, left hand y-axis) of immatures < 3 mm (inverted, filled triangles), immatures > 3 mm (filled triangles), females (filled circles), and males (filled squares). Only one Tukey distance (TD) per plot is drawn to simplify the graphs, because all TDs in each of the three plots are equally long. Thereby overlapping Tukey distances indicate no significant differences. Median prey density (right hand y-axis) is drawn to illustrate the prey dispersion during the night ($n = 5$).

distributed data sets were l_n-transformed to homogenize the variances. As all data sets were equally sized, Tukey-tests were performed for multiple range analyses. Correlation analyses were conducted to compare temporal variation in the prey density to spider census data using

Spearman Rank correlation (R_S) as data sets were not normally distributed.

Results

Temporal activity patterns

The two-factor ANOVA (factors: size and sex categories of spiders; time), showed a significant effect on spider density in each behavioural category: (A) web building ($F_{14,119} = 2.90$, $P < 0.01$); (B) hunting activity ($F_{14,119} = 2.50$, $P < 0.01$); and (C) feeding on prey ($F_{21,128} = 2.03$, $P < 0.01$).

Tukey distances in the interaction plots reveal the significant differences in spider density in regard to the behaviour (Fig. 1). Significantly more immatures < 3 mm body length were building webs in the early evening, compared with females (Fig. 1, Plot A). Similarly, more immatures < 3 mm body length were actively hunting in the early evening and significantly more immatures of both size classes remained in their webs all night long, compared with females (Fig. 1, Plot B). Not surprisingly, males did not engage in web building and more immatures and females were observed feeding on prey during the night. Significantly more small spiders (immatures < 3 mm) were feeding on prey items even after sunrise compared with spiders of any other category (Fig. 1, Plot C).

There was a peak of prey activity at 9 p.m. (Fig. 1) and the density of the various spider categories related to prey abundance differently. While the number of females (all behavioural categories pooled) correlated highly with prey abundance ($R_S = 0.86$, $n = 40$), the number of immatures < 3 mm body length, > 3 mm body length, and males did not correlate as strongly ($R_S = 0.49$, $R_S = 0.65$, and $R_S = 0.59$, respectively, $n = 40$).

Discussion

The spiders studied have different activity patterns with regard to size and sex. The density of small immatures is higher in the early evening and in the morning, indicating that their foraging period is longer compared with that of females and males. Extension of the foraging period may, however, carry certain costs for the individual. The spider is exposed to first, potential predators and/or antagonistic intraspecific individuals, and second, to unfavourable climatic conditions, such as strong winds, that may even dislodge it from the web (pers. obs.). Most spider species, including *L. sclopetarius*, are solitary, potentially cannibalistic predators (Hodge & Uetz, 1995), and defend their webs or even the areas beyond them against conspecifics (Buskirk, 1975; Riechert, 1978, 1982; Christenson, 1984), and high spider abundances lead to a higher degree of agonistic interactions between conspecifics (Smallwood, 1993). Therefore, the advantage of remaining in the hub may be the possibility of defending the web against potential intruders, a strategy that may be profitable, especially for small immatures in habitats with high spider densities, such as in our case, where space is scarce. Furthermore, adult females may occupy the prime positions in the habitat that ensure sufficient prey capture throughout the night. In contrast, the immatures may have to inhabit less favourable web sites and are thus forced to extend their foraging period. A third possible reason for the differences in the foraging period extensions may be that adults construct larger, possibly more stable, webs than immatures (Heiling & Herberstein, submitted). Higher web stability and web size will increase the possibility of entangling and retaining prey (Craig, 1987) and decrease the probability of being destroyed by wind or prey impact (Craig, 1989). Therefore, the larger and more stable webs of adults may enable them to leave their webs during the night, to bring in the web and the prey entangled in it at the end of the foraging period, while the foraging success of immatures depends on their presence in their webs as they need to subdue prey immediately to ensure capture success (Riechert & Łuczak, 1982).

Although the studies concluded that spiders are unable to adjust their behaviour to fluctuations in prey availability (e.g. Bradley, 1996), Sebrier & Kraft (1993) pointed out that memory of information on prey capture enables spiders to monitor prey availability in the habitat. Our results show a close relationship between spider activity patterns and prey availability, particularly for the adult females, indicating that spiders may be able to optimize time spent foraging.

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