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Activity-density data reveal community structure of Lycosidae at a Mediterranean shrubland

Igor Armiach, Iris Bernstein, Yaya Tang, Tamar Dayan & Efrat Gavish-Regev

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Abstract. The structure of an ecological community is shaped by diverse factors and processes, including competition for resources between species with similar ecological niches. Species coexistence in the face of competition is achieved by various mechanisms, such as niche partitioning, e.g. division of resources in space and time. We studied the effect of environmental variables on activity-density of the four lycosid species found in a Mediterranean shrubland in Israel, in the spring of 2012. We tested if spatial and temporal niche partitioning enables coexistence among the four ecologically similar lycosid spiders, using multivariate analyses (RDA, Species Response Curves and Trait Analysis (RLQ)) of vegetation structure, habitat characteristics and land use, as well as time in the season. Activity-density was significantly affected by time in the season and the interaction of time and geophyte density. These findings provide first insights into the life cycles of lycosid species in Mediterranean shrublands in Israel, with spider species of the same size-group reaching their activity peaks at different times.

Keywords: *Alopecosa*, coexistence, *Hogna*, Israel, *Lycosa*, niche partitioning, *Pardosa*, seasonality, species assemblage, wolf spiders

Community structure is determined by a combination of factors such as regional species pool, biotic and abiotic environmental variables, and ecological and evolutionary processes (Zobel 1997). Within a community, species that use the same type of resources in a similar way, i.e. – having similar ecological niches, are considered as members of the same guild (Root 1967, Simberloff & Dayan 1991, Wilson 1999). One example of an ecological process, that may occur among species with similar ecological niches (i.e. within guilds), is competition, that can result in either species competitive coexistence or exclusion of species (Wilson 1999, Amarasekare 2003).

In order to coexist, two species' niches have to differ in their position on at least one of the four life-history related axes: resources, predation, space and time (Amarasekare 2003). Identical niches would often result in the exclusion of the species that is less able to maintain positive per capita growth under lowest resource level or highest predation (Amarasekare 2003). Resource partitioning between competitors co-occurring in a given habitat may take place through microhabitat partitioning and prey specialization and define the species' realized niche, i.e. the part of the ecological niche occupied by an organism given pressures from other species (Hutchinson 1957). This way, the abundance of microhabitats and prey types may influence the number of species of a given guild coexisting in a habitat. Temporal partitioning (actual activity time: night/day or seasonality) is another important manner of resource partitioning, which may allow coexistence of species in a given habitat or microhabitat (Kronfeld-Schor & Dayan 2003).

The species-rich spider family Lycosidae comprises over 2000 described species (World Spider Catalog 2016) that are relatively uniform in body structure. Most lycosid species belong to a single ecological guild of cursorial predators (Hatley & MacMahon 1980). Several lycosid species are usually found in a given habitat and cases of resource partitioning between them at the temporal or spatial scales have previously been documented. For example, two lycosid species, *Hogna carolinensis* (Walckenaer, 1805) and *Rabidosa rabida* (Walckenaer, 1837), native to temperate forests in North America, are generalist predators and avoid competition by habitat partitioning; *Rabidosa rabida* is active on the ground, while *Hogna carolinensis* is mostly active under the surface (Kuenzler 1958). Many spiders have an annual or perennial life cycle, in which adults are only present during part of the year (Enders 1976). There also may be a period of dormancy, in which the species is not active at all, allowing for other species of the same guild to utilize the unused resources, with no direct competition (Framenau & Elgar 2005). This type of species turnover has been demonstrated in the prairies of Colorado, where adults of one species of *Gnaphosa* (Gnaphosidae) were shown to be active during May-June, while adults of a sympatric species are active during July-August (Weeks & Holtzer 2000). It is possible that both species were active during May-June, but in that case, they had different maturation times, leading to possible size-related trophic partitioning.

Developmental-stage-related partitioning may occur if an individual's requirements, including prey preferences, change during its lifetime. These changes may affect the habitat preference, time of activity and additional life-history traits. An example of developmental stage related partitioning can be seen in the lycosid species *Schizocosa mccooki* (Montgomery, 1904), as juveniles were found to prefer habitats of mixed shrubs and grasses, while the adults preferred shrubless grassy patches (Weeks & Holtzer 2000), thus partitioning microhabitats between them.

The habitat preferences of Lycosidae in Israel were studied only as part of spider faunal surveys (Mansour & Whitecomb 1986, Pluess et al. 2008) and as of yet we have very little information about the biology, ecology and taxonomy of Israel's lycosids. In particular, studies of the lycosid fauna of one of Israel's most abundant habitats, the Batha shrubland, were never carried out. The Batha shrubland is a characteristic habitat of the Mediterranean part of Israel, suggested to support a high biodiversity, due to its patchy structure, allowing for a high variation in microhabitats (Naveh & Whittaker 1980, Tews et al. 2004, van der Aart 1972).

A recent study (Bernstein 2014, Gavish-Regev unpubl. data) examined the impact of alternative urban development scenarios on species richness and abundance of plants, beetles and spiders in an ecological corridor, which comprises sub-

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Igor ARMIACH, Iris BERNSTEIN, Department of Zoology, Tel-Aviv University;
E-mail: bomtombadil@gmail.com; irisb07@gmail.com
Yaya TANG, Department of Ecology, Evolution and Behavior, The Hebrew University of Jerusalem; E-mail: zhao.tang@mail.huji.ac.il
Tamar DAYAN, The Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, Tel-Aviv University; E-mail: DayanT@tauex.tau.ac.il
Efrat GAVISH-REGEV, The Arachnid National Natural History Collection, The Hebrew University of Jerusalem; E-mail: efrat.gavish-regev@mail.huji.ac.il

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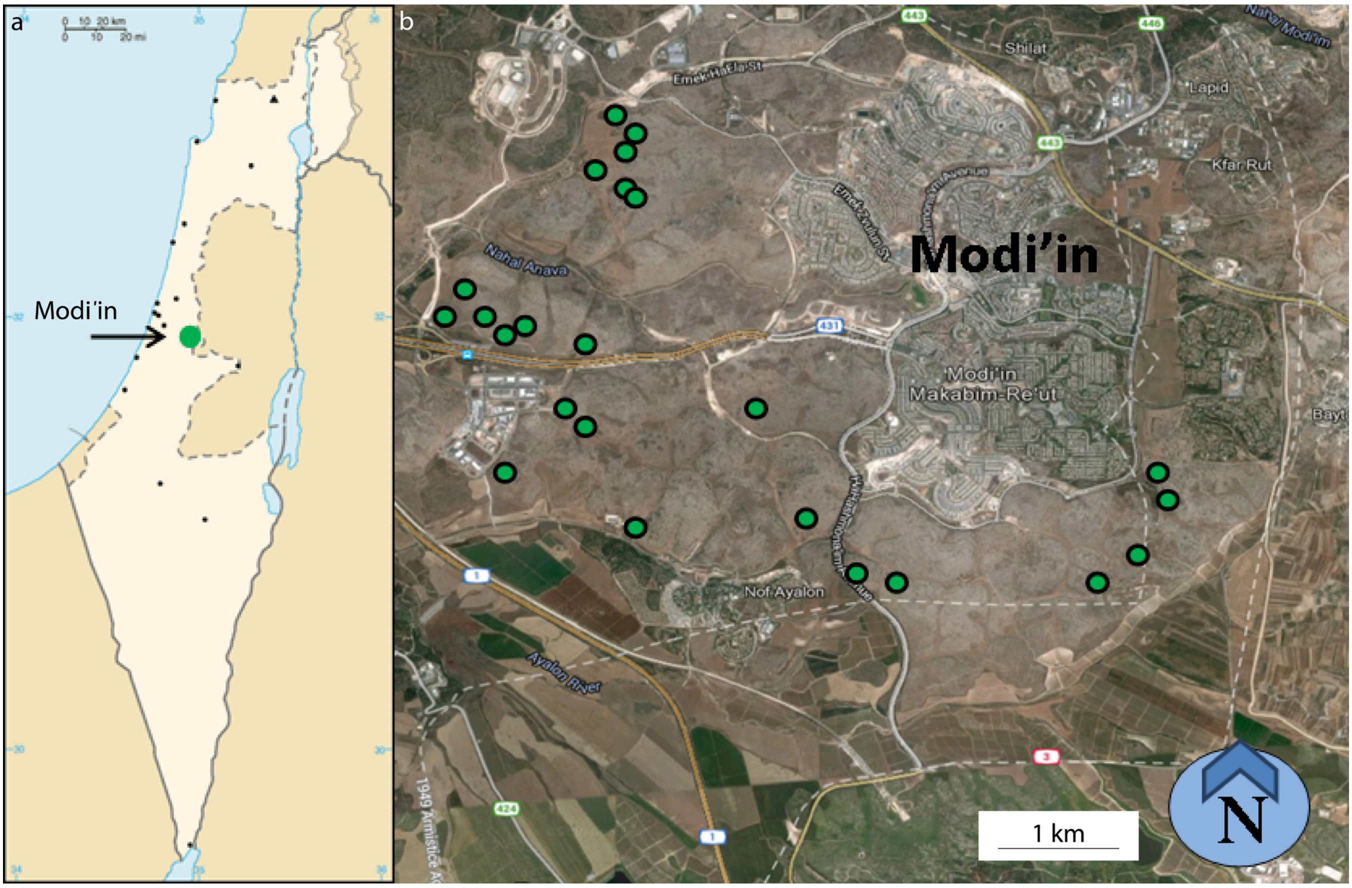

Fig. 1: The study area: **a.** Map of Israel, study area indicated with black arrow (based on Nagy Piroska, 2009); **b.** Map of study area, sampling locations (24 samples) marked with green dots (based on Imagery © 2015 DigitalGlobe, Map data © 2015, Mapa GIsrael)

stantial areas of Batha shrublands. The study found lower activity-densities of lycosids (as a group) in patches with higher shrub densities, and higher activity-densities of lycosids in patches with a higher cover of small stones and in patches at a distance from agriculture (Gavish-Regev unpubl. data).

Using the dataset from Bernstein's study, we studied the effect of environmental variables, such as density of plant life-forms (bushes, dwarf shrubs and grasses), habitat characteristics and land use, as well as time in the season, on the activity-density of lycosid species, sex and developmental stages in spring of 2012. Our hypothesis was that lycosids are represented in the Batha shrubland of the Judean foothills by several species that can coexist due to microhabitat partitioning (spatial resource partitioning), and that coexistence of the different species of lycosids is facilitated by differences in microhabitat preferences that vary between sex and developmental stages. This is the first attempt to look at community structure of Lycosidae (i.e., species distribution in space and time) at the Mediterranean Batha shrubland.

Study area, material and methods

Study area. The study area includes four sites and is located around the city of Modi'in, in the Northern Judean foothills (Figs. 1, 2), at an elevation of 200-300 meters. Each site is an alternative urban development plan for Modi'in (Bernstein 2014). The study area is characterized by a Mediterranean climate (Csa) with average annual rainfall of 550 mm. The rock in the study area is mostly Cretaceous chalk with chert, and the soil is brown rendzina (Sneh 1998). The plant communities are characteristic of disturbed Mediterranean habitats, and are influenced by grazing and fires. The most common plant community in the study area is the Batha shrubland dominated by dwarf shrubs, in particular Prickly Burnet (*Sarcopoterium spinosum* (L.) Spach). Yet, there are two additional plant communities: the Batha grassland (annual grasses) and bush patches (Garrigue) dominated by *Rhamnus lycioides* L. and *Pistacia lenticus* L. (Alon 1993). The climax community, Maquis of *Rhamnus lycioides* L., *Ceratonia siliqua* L. and *Pistacia lenticus* L. (Alon 1993), is very rare in the study area and therefore was not sampled in this study. The habitats in this study were sorted by General Habitat Category (GHC) (Bernstein 2014), the standard evaluation method in the BIOHAB system, which classifies natural habitats into categories based on the dominant plant life-forms (in this study, bushes, dwarf shrubs and grasses), regardless of local factors.

Fig. 2: Mediterranean Batha shrubland and grassland in the study area, May 2012

Spider sampling, measurements and environmental variables. Spiders were collected using pitfall traps with preservative liquid (20 % ethanol, 20 % acetic acid, 60 % glycerol), and moved to 75 % ethanol after sorting and identifying each specimen to the best taxonomic resolution possible (species or genus level) and sex according to its developmental stage (adult, sub-adult, juvenile). Each pitfall trap was made of two plastic cups (one inside the other; diameter 11.3 cm, height 13 cm) buried in the ground such that the rim was level with the ground surface.

The study area included four sites (the alternative urban development plans), that were sampled using the pitfall traps in three periods: 21-29.iii.2012, 11-20.iv.2012 and 9-17.v.2012. In each site three habitats were sampled (with two repeats per habitat) according to the dominant plant life-form: bushes, dwarf shrubs and grasses, a total of six samples (traps location) per site (Fig.1, samples are marked as green dots). Each sample included 13 pitfall traps, in fixed locations for all three sampling dates, a total of 936 pitfall traps for the entire sampling period (due to trampling by livestock, only 902 traps were retrieved).

Environmental variables, including habitat characteristics (% exposed ground, small stones for one square meter, large stones for one square meter), land use (% monthly grazing, % yearly grazing) and plant life-form (density of annual grasses, density of geophytes, density of dwarf shrubs, density of bushes) were measured once in all locations, prior to the collection period and used to test microhabitat preference (coexistence due to resource partitioning).

In order to test coexistence of size-groups we assigned each spider to one of three size categories: carapace length under 3 mm (juveniles only), 3-4.7 mm (adults and sub-adults of small species and juveniles of large species), over 4.7 mm (juveniles, sub-adults and adults of large species) (see Tab. 1 for the results of size groups). Carapace length was measured in Stereomicroscope Nikon SMZ using NIS-Elements D (Nikon 2015, version 420).

As few or no adult specimens of *H.* cf. *graeca* and *L. piochardi* were collected, all measures of adults of *H.* cf. *graeca* and most adults of *L. piochardi* were taken from material collected in other localities in Israel.

Statistical analysis. We used ordination methods (multivariate analysis - gradient analysis) with the program Canoco (Ter Braak & Šmilauer 2002) to test the effect of the environmental variables on lycosid activity-density, using activity-density as a measure of habitat use. We first performed DCA (detrended correspondence analysis) to determine the length of the gradient. As the first axis gradient was shorter than three we used linear methods for the rest of the analysis (Leps & Šmilauer 2003). Redundancy analysis (RDA) with unrestricted Monte-Carlo permutations (4999 permutations) was performed testing ten variables (time in the season, and the nine environmental variables listed above). Partial RDA with unrestricted Monte-Carlo permutations (4999 permutations) was performed testing density of geophytes and time as separate main effects while the other variables served as co-variables. We used CanoDraw (Ter Braak & Šmilauer 2002), to create Species Response Curves, in order to examine the response of each species, sex and developmental stage to the significant variables found in the partial RDA. Response curves were fitted using, for the y-axis, the scores of the first axis obtained in the partial RDA plotted against each significant variable or interaction. The response variable is thus a measure of the activity-density of the species, sex and developmental stage that were affected significantly by the variable or interaction (Leps & Šmilauer 2003, Gavish-Regev et al. 2008). The curves were fitted using GAM (Generalised Additive Model: smooth term complexity with 3 d.f.). A Poisson distribution was assumed for the response variable, and Log was used as the link function. Curve selection was based on the Akaike information criterion (AIC) (Leps & Šmilauer 2003). For all ordinations, all spiders collected from the 13 traps of each sample were grouped due to a low number of captures and high variances between individual traps, i.e. a total of six samples per site and 24 samples in the study area each month (overall 72 samples). All analyses were performed at two levels: species level (undivided) and species divided by sex and developmental stage (males, females and, free-roving juveniles\ sub-adults).

In order to investigate the relationship between species traits and environmental variables, we used RLQ analysis (Doledec et al. 1996, Mouillot et al. 2013) with eight environmental variables (habitat characteristics and plant life-forms (as listed above)) (R table) and three species trait attributes (average size, burrow use and month of activity peak) (Q table), and the relative abundance of each sex and developmental stage of the four species (Total of nine species categories in table L). For the RLQ analysis, the R- and Q-tables first underwent principle component analysis (both tables using the Hill and Smith method (Hill & Smith 1976) for mixing quantitative variables and factors) and the L-table underwent correspondence analysis. RLQ analysis was conducted using the ade4 package in R (Chessel et al. 2004).

Results

From the 72 samples, only 67 samples were used for the analyses. Five samples were omitted due to zero catches of lycosid spiders: two from April and three from May.

Tab. 1: Average carapace length of Lycosidae collected around Modi'in in the spring of 2012, by species, sex and developmental stage. Adults of *L. piochardi* and *H.* cf. *graeca* were collected separately, adjacent to the study area

Sex/developmental stage	***Alopecosa albofasciata* (Brullé, 1832)**	***Pardosa subsordidatula* (Strand, 1915)**	***Hogna* cf. *graeca***	***Lycosa piochardi* Simon, 1876**
Males	4.1 mm (n=20) SD=0.238	3.3 mm (n=1)	7 mm (n=3) SD=0.231	9.5 mm (n=7) SD=1.833
Females	4.5 mm (n=23) SD=0.336	4.1 mm (n=22) SD=0.232	7 mm (n=6) SD=0.849	8.5 mm (n=8) SD=1.533
Juveniles	1.1 mm (n=2) SD=0.151	1.9 mm (n=25) SD=0.280	3.3 mm (n=27) SD=0.916	5.4 mm (n=25) SD=1.560
			March: 1.9 mm (n=2) SD=0.397	
			April: 2.6 mm (n=11) SD=0.369	April: 4.9 mm (n=8) SD=1.272
			May: 4.1 mm (n=14) SD=0.550	May:5.6 mm (n=17) SD=1.662

Fig. 3: The lycosid species found in the current study (live females): **a.** *Alopecosa albofasciata* (Brullé, 1832); **b.** *Pardosa subsordidatula* (Strand, 1915); **c.** *Hogna* cf. *graeca*; **d.** *Lycosa piochardi* Simon, 1876

From all spiders collected (March, April, May), we identified a total of 385 lycosids, of which 302 were adults and 83 were either sub-adult or free-roving juveniles. Hatchlings were not counted. The lycosids were identified to four species (here listed in decreasing order of relative abundance): *Alopecosa albofasciata* (Brullé, 1832) (201 males, 58 females, 4 subadults; Fig. 3a), *Pardosa subsordidatula* (Strand, 1915) (2 males, 40 females, 27 subadults; Fig. 3b), *Hogna* cf. *graeca* (Roewer, 1951) (28 subadults; Fig. 3c) and *Lycosa piochardi* Simon, 1876 (1 female, 24 subadults; Fig. 3d).

Gradient analyses

Environmental variables and time. Habitat characteristics (exposed ground, small stones and large stones), land use (grazing) and plant life-forms (bushes, dwarf shrubs and grasses) did not affect the activity-density of the four lycosid species in this study, yet time in the season and, to some extent, density of geophytes had a significant effect on the activity-density of the four lycosid species.

The four species (undivided). Ordination analyses indicate that two significant variables: time in the season and geophyte density, explained 41.8 % of the variance of species activity-density (Tab. 2, Figs. 4a, 4b). In Partial RDA only time in the season and the interaction between time and geophyte density were found to affect species activity-density significantly (Tab. 3), while time was the only variable in the study to affect all four species significantly (Tab. 4, Fig. 5a), the interaction

Tab. 2: The effect of variables on the activity- density of Lycosidae species in the Batha shrubland: Ordination results. Monte-Carlo permutation tests (4999 runs) of redundancy analysis (RDA). Out of ten variables, three were included in the model, two were significant (time, Geophytes density), the third (Yearly grazing) was marginally significant.

Environmental variables	% explained variance	F-ratio	P-value
Time	38	40,3	0,0002
Geophyte density	4	3,8	0,04
Yearly grazing	3	3,4	0,055

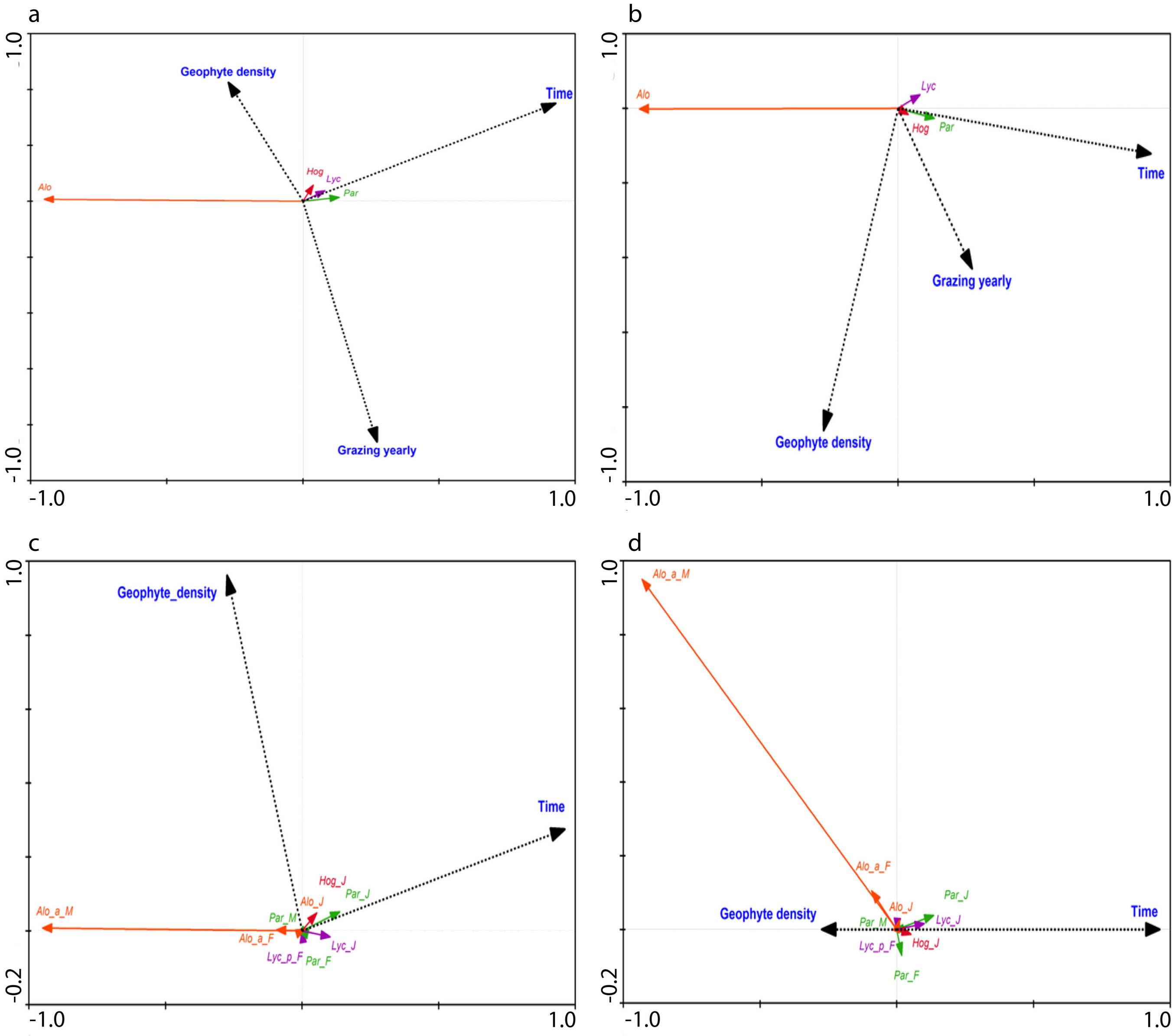

Fig. 4: Lycosid species, sex and developmental stage composition and activity-density based on three sampling dates, in the Mediterranean Batha shrubland, in the spring months of 2012. Ordination diagrams from a redundancy analysis (RDA) of 67 samples from Modi'in area; **a.** biplot (species – environment) of the first and second axes; **b.** biplot (species – environment) of the first and third axes; **c.** biplot (species, sex and developmental stage – environment) of the first and second axes; **d.** biplot (species, sex and developmental stage – environment) of the first and third axes. The quantitative variables are geophyte density, percent of yearly grazing and time; the arrow color of each family (and abbreviated species name) as follows: *Alopecosa albofasciata*: orange (Alo), *Pardosa subsordidatula*: green (Par), *Lycosa piochardi*: violet (Lyc), and *Hogna* cf. *graeca*: red (Hog); Sex and developmental stage are indicated as M: male, F: female, J: juvenile

between time and geophyte density was found to affect only *A. albofasciata* significantly and to affect *H.* cf. *graeca* and *L. piochardi* with marginal significance (Tab. 4, Fig. 5b).

Tab. 3: Partial RDA: The effect of variables on the activity- density of Lycosidae in the Batha shrubland: Ordination results. Monte-Carlo permutation tests (4999 runs). Out of ten variables, two (time and geophyte density) were included in the while the other variables served as co-variables.

Environmental variables	**The four species undivided**		**The four species, divided by sex and developmental stage**	
	F-ratio	**P-value**	**F- ratio**	**P-value**
Time	42	0,002	39	0,0002
Interaction between time and geophyte density	2	0,004	2,74	0,05

The four species, divided by sex and developmental stage. Ordination analyses indicate that two significant variables: time in the season and geophyte density, explained 42 % of the variance of species, sex and age groups activity-density (Tab. 5, Figs. 4c, 4d). In Partial RDA only time and the interaction between time and geophyte density, were found to affect species activity-density significantly (Tab. 3), while time was the only variable to affect all species, sex and developmental stages significantly (Tabs. 6a-c, Fig. 5c), the interaction between time and geophyte density was found to affect all groups of *A. albofasciata* significantly (Tab. 6a) and to affect juveniles of *H.* cf. *graeca* with marginal significance (Tab. 6c, Fig. 5d).

Trait analysis

For the four species, divided by sex and developmental stage,

Tab. 4: Partial RDA: The effect of time and the interaction between time and geophyte density on the four species of Lycosidae. Only variables with significant influence are presented.

Environmental variables	*H. cf. graeca*		*L. piochardi*		*P. subsordidatula*		*A. albofasciata*	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
Time	5,17	0,003	10,98	0,0001	11,88	0,001	30,95	< 1.0e-6
Interaction between time and geophyte density	3,18	0,031	2,75	0,05	Not significant	Not significant	9,71	0,00003

no significant effects were found in the RLQ analysis for the eight environmental variables and the three traits.

Discussion

We found that time in the season affected significantly the activity-density of all four species, sexes and developmental stages, while the interaction between time and geophyte density affected all species but *P. subsordidatula* . At this early stage of lycosid research in Israel, data is insufficient for any clear-cut conclusion, but we suggest a possible temporal partitioning that may contribute towards separation between similar-sized species in this Batha shrubland. The response in activity to the interaction between time and geophyte density might reflect different microhabitat preferences of males, females and juveniles and changes in their levels of activity over the sampling period.

Gradient analyses

Temporal partitioning. In the absence of habitat spatial segregation, coexistence of competitors can rely on separation in time (Carothers & Jaksić 1984, Kronfeld-Schor & Dayan 2003). Possible evidence for separation in time of the Batha lycosid guild may be differences in the activity-density of the different species along the sampling season. A possible mechanism may be separation by prey sizes, as reflected by the predator sizes. It has been demonstrated in lycosids (*Pardosa*, *Alopecosa*) and other non-web-hunting spiders that the preferred prey size is around 50-80 % of the spider's length (Nentwig & Wissel 1986). Maturation of the species in the guild at different times (see Tab. 1) may create different size-groups of spiders and thus reduce interspecific competition (Fig. 6). For example, in April, the juveniles of *H.* cf. *graeca* were in the lower size group (under 3 mm carapace length). In May they reach the middle size group (3.0-4.7 mm carapace length), when the adults of the smaller species (*P. subsordidatula, A. albofasciata*) are at low activity-density. The juveniles of *P. subsordidatula* that were collected in the traps during May all belong to the small size group (under 3 mm), when the juveniles of *H.* cf. *graeca*, collected in the same time, all belong to the larger size group (over 4.7 mm). Temporal trophic separation has been shown previously between the North American species *Lycosa antelucana* and *Pardosa milvina* and between developmental stages within *Lycosa antelucana* (Hayes & Lockley 1990). For these groups different daily activity times were observed. This mechanism is left unexplored by us. However, *Pardosa subsordidatula, H.* cf. *graeca* and *L. piochardi* were observed by us to be nocturnally active, while *A. albofasciata* was mostly observed to be active in daytime.

Partitioning may also be driven by intraguild predation. Lycosids have been shown to feed on conspecifics and lycosids of other species (Rypstra & Samu 2005). If we assume that the preferred prey size is 50-80 % of the predator's body length, the observed seasonal partitioning may be due to predator avoidance by the smaller species. The activity of juvenile *P. subsordidatula* rises at the time of spring with the lowest activity density of adult *A. albofasciata* and *P. subsordidatula*. The activity of adult *A. albofasciata* and *P. subsordidatula* drops in May, when the large juveniles of *L. piochardi* become active.

Geophyte density. Geophyte density was the only habitat characteristic found to significantly affect activity-density of the lycosid species in this study (see below), but this effect was also related to time in the season. This single significant result is unexpected, as Lycosidae in other studies were found to have habitat and microhabitat preferences related to environmental variables such as vegetation structure (Cady 1983, Eason & Whitcomb 1965, Greenstone 1984, Workman 1977). In a former study (Gavish-Regev unpubl.) ordination analysis of the same dataset, analysed at the family level, revealed three

Tab. 5: The effect of variables on the activity-density of Lycosidae species divided by species, sex and developmental stage in the Batha shrubland. Ordination results Monte-Carlo permutation tests (4999 runs) of redundancy analysis (RDA). Out of ten variables, three were included in the model (time and geophyte density were significant, Yearly grazing, is shown for comparison with Tab. 2).

Environmental variables	% explained variance	F-ratio	P-value
Time	38	40,6	0,0002
Geophyte density	4	3,7	0,032
Yearly grazing	2	2,4	0,085

Tab. 6: Partial RDA: The effect of time and the interaction between time and geophyte density (time x density) on the four species of Lycosidae, divided by sex and developmental stage (n. s. not significant).

Environmental variables	*A. albofasciata* J		*A. albofasciata* F		*A. albofasciata* M	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
Time	2,8	0,049	5,09	0,0092	49,4	< 1.0e-6
Time x density	7,74	0,00018	4,07	0,0107	7,8	0,00016

Environmental variables	*P. subsordidatula* J		*P. subsordidatula* F		*P. subsordidatula* M	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
Time	38,67	< 1.0e-6	4,89	0,0042	0,56	0,05
Time x density	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.

Environmental variables	*H.* cf. *graeca* J		*L. piochardi* J		*L. piochardi* F	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
Time	5,17	0,00319	10,27	0,00017	1,82	0,053
Time x density	3,18	0,031	n. s.	n. s.	3,04	0,0025

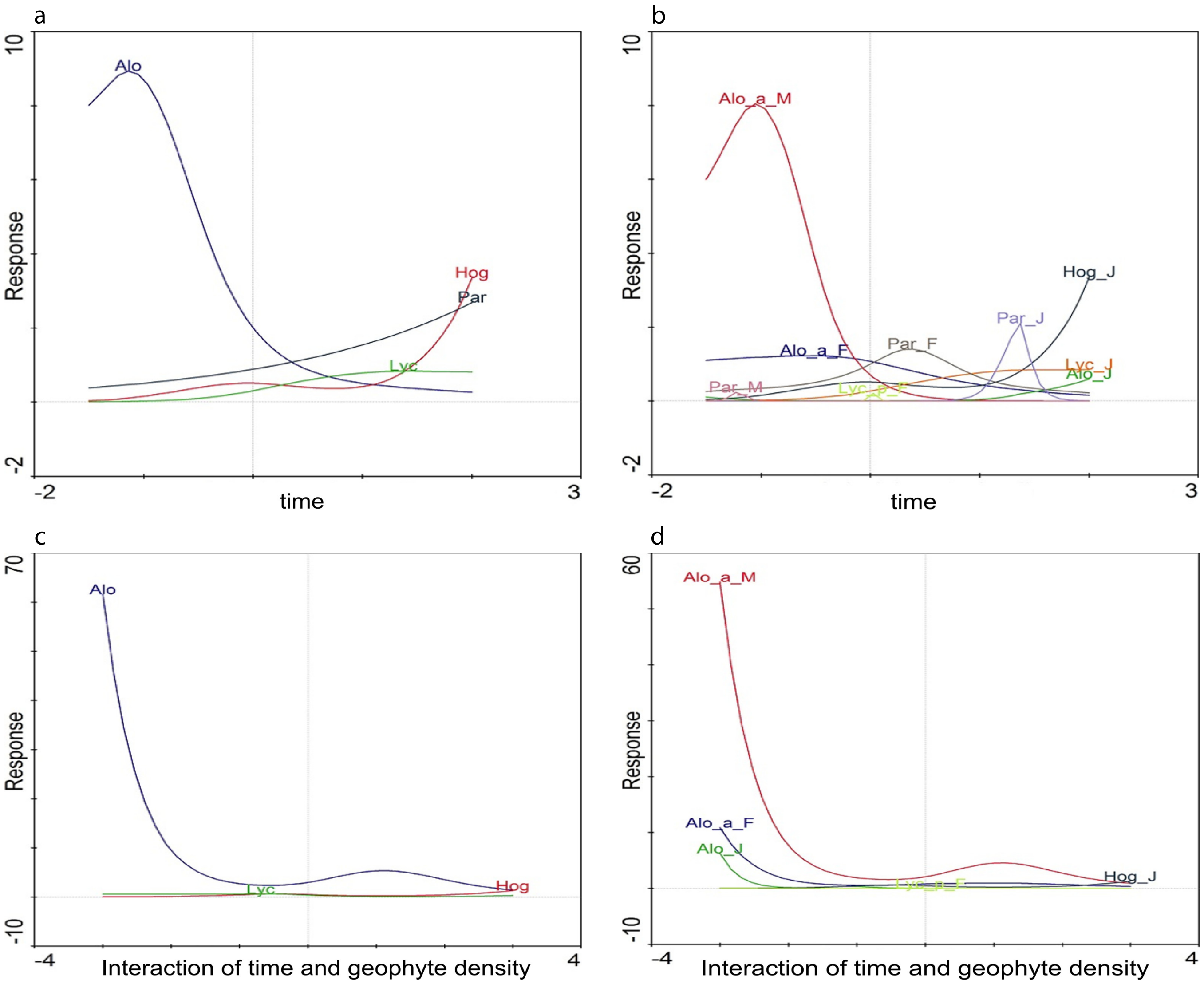

Fig. 5: Species Response Curves of four lycosid species, sex and developmental stage to the first axis of Partial RDA. Only curves of species showing significant response were included and fitted to generalized additive models (GAM). Species abbreviations as follows: *Alopecosa albofasciata*: (Alo/Alo_a); *Pardosa subsordidatula*: (Par); *Lycosa piochardi*: (Lyc/Lyc_p) ; *Hogna* cf. *graeca*: Hog; Sex and developmental stage are indicated as M: male, F: female, J: juvenile. **a.** response curve of species for time; **b.** response curve of species for the interaction of time and geophyte density; **c.** response curve of species, sex and developmental stage for time; **d.** response curve of species, sex and developmental stage for the interaction of time and geophyte density

significant environmental variables affecting activity-density of Lycosidae as a family: Shrub density (negative effect), cover by Small Stones (positive effect) and Distance from Agriculture (positive effect). It is possible that given larger sample sizes, similar effects may yet be found in lycosid species, sexes and developmental stages.

The activity-density *of A. albofasciata* was found to be significantly affected by the interaction between time in the season and geophyte density (Figs. 5b, 5d). The change is negative and implies a magnitude of response diminishing along the season (i.e., spiders respond less to geophyte density as the season progresses). It is possible that the observed trend is due to the seasonal change in vegetation structure (drying up) or a change in the nature of activity of the species along the season.

Geophyte density corresponds with relatively short, grazed vegetation, and with certain rock types (Noy-Meir & Oron 2001). Such conditions may be preferable for lycosid males' reproductive behaviours, maximizing their visibility during display and courtship (similar to the use of display spaces by *Schizocosa ocreata* (Hentz, 1844), Cady 1983).

Trait analysis. This type of analysis potentially connects discrete traits found in different species to the effect of environmental variables on the species, yet, it failed to find any significant effect in the current study. We suggest that lack of significant results in this analysis stems from the scarcity of data. Moreover, the number of traits examined was low, due to insufficient knowledge of the life histories of the Lycosidae in Israel. Using larger datasets and more traits may improve the analysis.

Lycosidae species assemblage. In this study, a similar number of individuals were collected from two ground-dwelling spider families: Lycosidae (385) and Gnaphosidae (346), however only four species of lycosids were found, while 32 species of

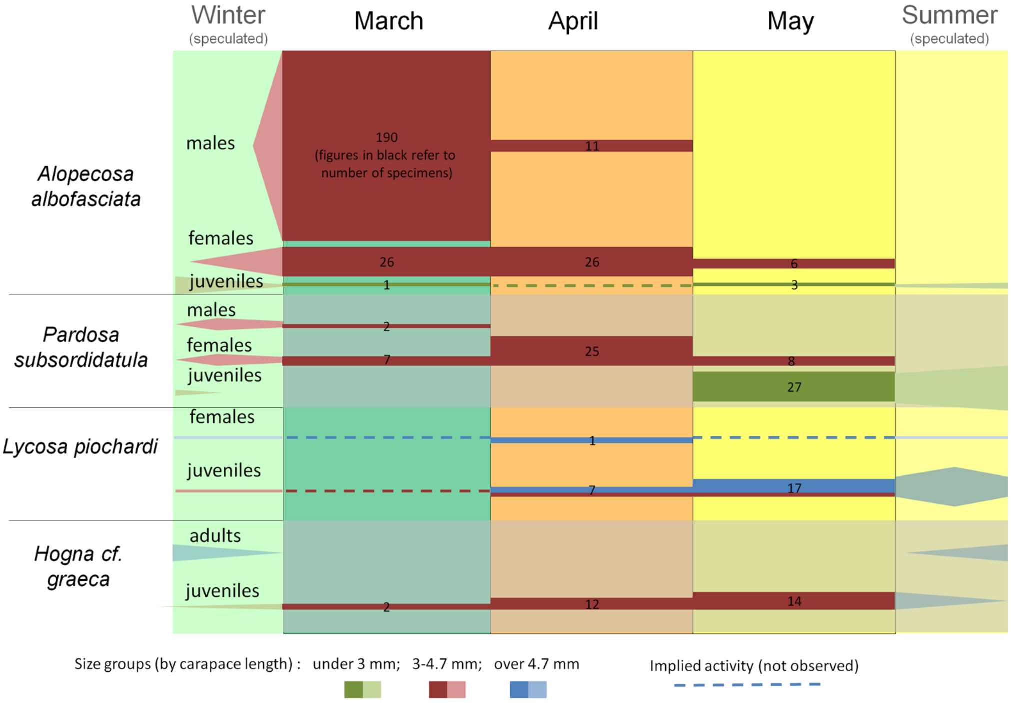

Fig. 6: Observed and implied lycosid activity in the study area (with implied trends in the summer and winter). Figures in black (and line width) denote number of specimens in study.

gnaphosids were found (Gavish-Regev unpubl. data). A possible explanation to the observed low lycosid species richness could be low activity-density of additional species or a poor regional species pool, which would result in lower number of species filtering (Zobel 1997), i.e., less lycosid species that are suitable for living in the Batha: 126 species of gnaphosids are recorded from Israel, compared to 30 species of lycosids (Levy 2009, Zonstein & Marusik 2013). If we assume that for each family's regional pool there is a certain percentage of species that are suitable to colonize the Batha shrubland (filtering), we expect to find more species from the family with a species-rich regional pool in comparison with the family with species-poor regional pool, but a similar magnitude. Indeed, the magnitude of the regional species pool that was found in this study is similar for the two families (25 % of gnaphosid species and 13 % of lycosid species).

It's important to note that all the spiders in this study were collected with pitfall traps and only a few direct observations were made in the field during the spring of 2012 and onwards. Pitfall trapping is a method biased towards more mobile individuals (Lang 2000). Adult males are expected to be more mobile, relative to females and juveniles and are less likely to remain in one habitat (as demonstrated in the North American *Schizocosa ocreata* (Cady 1983)). Indeed, more than half the lycosid specimens were adult males of *A. albofasciata*. Supplementing the collection techniques, enlarging the sample size and lengthening the sampling period to include more than one season will give us a more comprehensive understanding of the biology and ecology of Lycosidae in the Mediterannean Batha shrubland.

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