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ORIGINAL PAPER

Responses of orb-weaving spider aggregations to spatiotemporal variation in lake-to-land subsidies at Lake Mývatn, Iceland

Jose A. Sanchez-Ruiz[1] · Joseph S. Phillips[2] · Anthony R. Ives[2] · Claudio Gratton[3]

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Abstract Tundra ecosystems are often unproductive, and peaks in resource availability are highly variable in space and time. Therefore, the success of organisms inhabiting these biomes likely depends on their ability to efficiently exploit heterogeneously distributed resources. We assessed how orb-weaving spider (*Larinioides patagiatus*) aggregations near Lake Mývatn, Iceland, respond to large midge (Diptera: Chironomidae) emergences that subsidize ecological communities in the surrounding landscape. The emergences occur for only a few weeks each summer, and the subsidy declines with distance from the lakeshore, producing large spatiotemporal variation in prey availability that might drive orb-weaver foraging behavior. We conducted three surveys during different phases of the summer emergence along a distance gradient to quantify variation in spider aggregation, web size, and habitat use in response to prey abundance. We found that aggregation size increased with the abundance of aerial prey, with the highest orb-weaver densities occurring at peak midge emergence. In contrast, changes in web size did not vary with midge abundance, but rather were determined by physical habitat structure. Our results illustrate how orb-weaver aggregations and web building can respond to spatiotemporal variation in resource subsidies across ecosystem boundaries.

Keywords Allochthonous subsidies · Aquatic insect emergence · Habitat complexity · Spider aggregations · Subsidies · Web size

Introduction

Movement of materials and energy across ecosystem boundaries is widespread and can either directly or indirectly subsidize consumer populations (e.g., herbivores and predators) beyond the levels that local primary production would otherwise support (Polis et al. 1997; Nakano and Murakami 2001; Carpenter et al. 2005; Croll et al. 2005; Baxter et al. 2005). In unproductive landscapes, such as deserts and tundra, aquatic production in adjacent bodies of water can greatly exceed terrestrial production and provide an important subsidy to consumers living along the shore (Polis and Hurd 1995; Sabo and Power 2002; Croll et al. 2005; Gratton et al. 2008; Dreyer et al. 2012). For example, desert islands in the Gulf of California (Polis and Hurd 1995) and subarctic islands in the Aleutian archipelago (Croll et al. 2005) can sustain relatively high densities of arthropods due to marine subsidies, such as algal wrack and seabird guano. However, aquatic-terrestrial subsidies vary dramatically through space and time, and the capacity for consumers to effectively exploit subsidies depends on their ability to track spatiotemporal variation in their resources (Polis et al. 1997; Orr et al. 2005; Yang et al. 2010; Hoekman et al. 2011).

In this study, we explored responses of the orb-weaving spider *Larinioides patagiatus* (Clerck, 1757) (Aranea: Araneidae) to aquatic insect emergences from Lake

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✉ Joseph S. Phillips
jsphillips2@wisc.edu

[1] Department of Biology, Georgia Southern University, Statesboro, GA 30460, USA

[2] Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI 53706, USA

[3] Department of Entomology, University of Wisconsin-Madison, Madison, WI 53706, USA

Mývatn in northern Iceland. Due to its high latitude and location in an actively volcanic region, much of the landscape surrounding the lake consists of barren lava fields that support limited primary production (Einarsson et al. 2004). However, Mývatn itself is naturally eutrophic and supports large midge (Diptera: Chironomidae) emergences that subsidize the terrestrial habitats immediately adjacent to the lakeshore (Einarsson et al. 2004; Gratton et al. 2008; Dreyer et al. 2015). Midge deposition near shore can exceed 100 kg ha^{-1} yr^{-1} (Dreyer et al. 2015) and several studies have demonstrated the importance of this subsidy for arthropod communities surrounding the lake (Dreyer et al. 2012; Hoekman et al. 2012). Mývatn's midge emergences are highly variable through space and time; the two dominant taxa only emerge for a few weeks each summer and fluctuate over four orders of magnitude between years (Einarsson et al. 2002; Ives et al. 2008). Furthermore, the magnitude of midge deposition declines dramatically with distance from the lakeshore (Dreyer et al. 2015). Therefore, we expected that the size of *L. patagiatus* aggregations would vary spatiotemporally in response to the availability of food, as has been observed for aggregations of other orb-weavers (Rypstra 1983, 1985; Gillespie 1987).

Our objective was to assess the responses of *L. patagiatus* to temporal and spatial variability of prey by surveying the size of aggregations and webs at various distances from Mývatn's shore and at three times before and during a midge emergence. We hypothesized that *L. patagiatus* would form larger aggregations near the lake and during peak midge emergence, reflecting a reduction in territoriality associated with competition for food (Riechert and Tracy 1975; Wise 2006; Kasumovic and Jordan 2013). Furthermore, we expected web size to be smallest near shore and during peak emergence, because even small webs would catch enough prey to meet the energetic demands of individual spiders. Variation in physical habitat structure can strongly influence aggregation formation and web size. Therefore, we also quantified variation in substrate type and vertical substrate complexity so that their effects could be accounted for when investigating the effects of prey abundance on web and aggregation size.

Methods

Study site

Lake Mývatn is located in northeast Iceland with a subarctic climate (Björnsson and Jónsson 2004) and is surrounded by a matrix of grassland, heathland, and barren lava fields (Gratton et al. 2008). The lake is moderately large (37 km^2), shallow (mean depth = 2.5 m), and is fed by nutrient rich springs that support high primary and secondary production (Einarsson et al. 2004). *Tanytarsus gracilentus* is the dominant midge and typically has two emergences each season (late spring and mid summer), while the second most abundant species (*Chironomus islandicus*) has a single emergence in late spring (Einarsson et al. 2004). The remaining species ($\sim$40) emerge throughout the summer, although they compose a small portion of the aquatic-terrestrial subsidy. The adult midges move passively and actively across the landscape and decline in abundance from the lakeshore up to 500 m (Dreyer et al. 2015). This study was conducted near the Kálfaströnd peninsula along the southeastern shore of the lake (65°33′58.60″N, 16°56′48.60″W) (Fig. 1), which is characterized by lava formations that provide a substrate for *L. patagiatus* to build their webs.

Study organism

Larinioides patagiatus is a widespread species of orb-weaving spider (family Araneidae) with a holarctic distribution (Levi 1974). The life history of *L. patagiatus* has not been well characterized at Mývatn. However, it likely takes at least one or two years for it to complete, with a single cohort of spiderlings hatching in late spring and early summer of each year (personal observation). In other locations, adult females are active from April to September and males from May to October (Nentwig et al. 2017). However, their period of activity is likely shorter at Mývatn due to its cool climate and late persistence of snow. While it is not clear how synchronized hatching of spiderlings is, we focused our study in late summer when we expected most of the cohort to have hatched. Juvenile and adult *Larinioides* generally build their webs near water on elevated structures such as bushes, trees, and rocky pillars (Šestáková et al. 2014). At Mývatn, *L. patagiatus* primarily inhabit lava pillars, which are topographically prominent and are abundant on the Kálfaströnd peninsula.

Surveys

To assess the responses of *L. patagiatus* to spatiotemporal variability in prey, we measured aggregation and web sizes in 30 2×2 m plots extending from 3 to 417 m from the lakeshore (Fig. 1). The plots were selected haphazardly, while ensuring that each contained lava formations that would provide suitable habitat for *L. patagiatus*. These lava formations are discrete landscape features and the focal points for the formation of *L. patagiatus* aggregations. The plots straddled a highway that passed 200–300 m from the lakeshore. We surveyed each plot three times in the summer of 2015 (30 July, 13 August, and 20 August). The first survey occurred before the midge (primarily *Tanytarsus*)

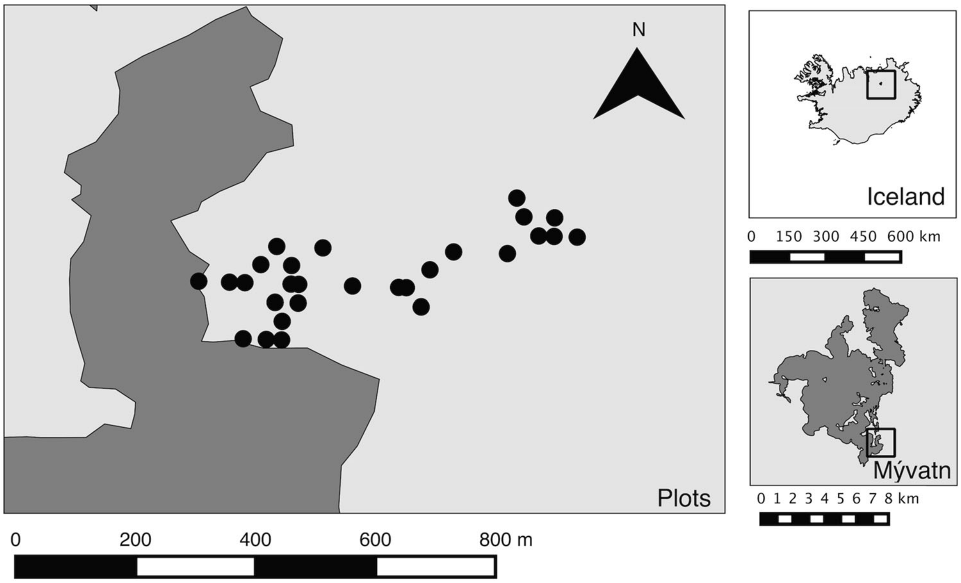

Fig. 1 Maps showing the positions of the plots within our field site, the position of our field site with respect to Lake Mývatn, and Lake Mývatn with respect to Iceland. The map was prepared using QGSIS (QGSIS Development Team 2014). Mývatn is located at 65°40′N 17°00′W, approximately 100 km S of the Arctic Circle

emergence started, and the subsequent two occurred during the emergence.

Larinioides patagiatus is quite cryptic in this landscape and detection of individuals likely varies with different landscape features (e.g., presence of vegetation) that show strong variation with distance from the lake. Therefore, we focused on the number of webs in each plot as a proxy for the number of spiders in each aggregation, which is likely less biased than counts of spiders. In this context, "aggregation" refers to the density of individuals located in a discrete portion of landscape, (e.g., lava pillar located within the plots), rather than the degree to which the distribution of individuals is spatially clumped. There is a single other large orb-weaving species at Mývatn (*Tetragnatha extensa*). However, it is primarily restricted to grassland habitat and was never observed in the plots used in this study, making it unlikely that the webs in our plots could have been made by any species other than *L. patagiatus*. For each survey, we counted the number of webs in each plot (as a proxy of the number of spiders in the aggregation) and measured the vertical (d_v), horizontal (d_h), and hub (d_b) diameters of a random subset of 851 webs across the 30 plots. The web measurements were used to calculate the web areas by approximating the web as an ellipse and subtracting the circular hub area, with the following formula: web area $= \pi\ (d_v d_h - d_b^2)/4$ (Herberstein and Tso 2000). An important limitation of these data is our inability to distinguish juvenile from adult spiders, beyond their differences in web size. Ideally, we would have been able to collect individual spiders from each survey to obtain a direct measure of age distributions and size (as a proxy of fitness). However, to allow repeated surveys of the same plots, we did not disturb the populations in each plot through specimen collection.

To quantify the abundance of aerial prey during each survey, we secured 10 × 12 cm transparent adhesive cards (WindowBugCatcher, Alpha Scents, OR, USA), designed to trap flying insects, to rebar stakes 1 m above the ground. We set the traps nine days prior to the first survey and reset the traps for each subsequent survey immediately after collection. After collection of each trap, we counted the total number of midges and other flying insects on each adhesive card. As the traps were deployed for different numbers of days (9, 13, and 7) for the three surveys, we divided the counts by the number of days each trap was set to calculate the capture rate. Hereafter, "aerial prey" refers to the total number of midges and other flying insects captured per day per card.

Habitat structure

To quantify variation in substrate complexity for each plot, we adapted a method for measuring topographical complexity of corals (McCormick 1994). In the center of each plot, we placed a vertical pole of a fixed height with a rotating arm parallel to the ground that extended 1 m from the center pole. We oriented the arm to the north and measured the vertical distance from the arm to the substrate for every 10 cm along the arm (negative values for points below the arm and positive for points above). For each point, we also categorized the substrate as "rock" or "other" (primarily bare ground or vegetation). This procedure was repeated for every cardinal and intercardinal orientation of the arm (eight directions). We defined "substrate complexity" as the standard deviation in distances from the arm to the substrate (i.e., the total variation in substrate height, closely related to surface roughness) (McCormick 1994; Hoechstetter et al. 2008) and "rockiness" as the proportion of points on the substrate that were classified as rock. Substrate complexity and rockiness were weakly negatively correlated ($r = -0.24$, $p = 0.02$), as the lava formations that contributed to complexity were partially covered by soil and sparse vegetation.

Statistical methods

We fit linear models to quantify variation in rockiness and substrate complexity with distance, and we fit a linear mixed model to quantify variation in aerial prey with distance and (categorical) survey. For the latter, we included the distance × survey interaction and a random intercept by plot to account for repeated measures.

The size of *L. patagiatus* aggregations in a particular location depends on the overall population density, which could be influenced by a variety of factors beyond the scope of this study (e.g., stochastic colonization by ballooning spiderlings or differences in landscape use by juveniles and adults). Furthermore, webs might have persisted for different lengths of time, depending on habitat features and behavioral plasticity of individual spiders. To control this variation, we used the change in the number of webs between consecutive surveys as the response variable in a linear mixed model including rockiness, substrate complexity, aerial prey, and distance from shore. Therefore, our analysis focuses on the factors that determine temporal variation in aggregation size, rather than aggregation size per se. We included all two-way interactions between explanatory variables and a random intercept by plot to account for repeated measures. We performed a parallel analysis on web size (actual, rather than change between surveys), and included terms for (categorical) survey and its two-way interactions.

To reduce skew in the residuals, we log-transformed aerial prey (as a response variable) and web size. We z-transformed (subtracted the mean and divided by the standard deviation) rockiness, substrate complexity, distance from shore, and aerial prey so that we could compare the coefficients as "effect sizes". All analyses were conducted with R version 3.3.1 (R Core Team 2014), using either the 'lm' function or the 'lmer' function from the package 'lme4'. We calculated p values with F tests (using Kenward-Rogers denominator degrees of freedom for mixed-models) and dropped non-significant interactions via backwards selection before calculating p values for the corresponding main effects.

Results

Aerial prey, substrate complexity, and rockiness

The abundance of aerial prey increased across the three surveys ($F_{2,55.12} = 49.5$, $p < 0.0001$), with surveys two and three corresponding with the emergence of summer-generation midges (Fig. 2a). Aerial prey decreased with distance from shore ($F_{1,44.5} = 4.9$, $p = 0.0328$), and the rate of this decline increased through time ($F_{2,55.0} = 13.9$, $p < 0.0001$) as it was primarily due to the midges that emerged from the lake. Rockiness increased with distance from shore ($F_{1,28} = 31.1$, $p < 0.0001$; Fig. 2c) as the landscape transitioned from grassland and mixed heathland to barren lava fields. In contrast, substrate complexity displayed no consistent trend with distance ($F_{1,28} = 0.8$, $p = 0.3757$; Fig. 2b).

Aggregation size

Average aggregation size increased between consecutive surveys (mean change = 4.6 individuals ± 1.3 SE, $n = 59$) and changes in aggregation size were positively related to the abundance of aerial prey (Table 1; Fig. 3). In contrast, aggregation size did not vary with rockiness, substrate complexity, or distance from shore. None of the interaction terms in the model were significant. The variance in the change in aggregation size was substantially larger when the abundance of aerial prey was low. This likely is due in part to the difference in sample size, as the distribution of aerial prey was quite skewed. Repeating this analysis using square-root transformed aerial prey abundance to reduce skew yielded qualitatively identical results (not presented).

Web size

Web size increased with substrate complexity and distance from shore (Table 2). Furthermore, the substrate complexity × distance interaction was significantly positive, such that web size was greatest at high substrate complexity far from shore (Fig. 4). Web size also increased between the three surveys, with mean areas (cm^2) of 119±11.2 SE ($n = 30$), 175.2±14.4 ($n = 30$), and 199±18.6 ($n = 29$) for surveys one, two, and three (Fig. 5). Aerial prey and rockiness had no effect on web size.

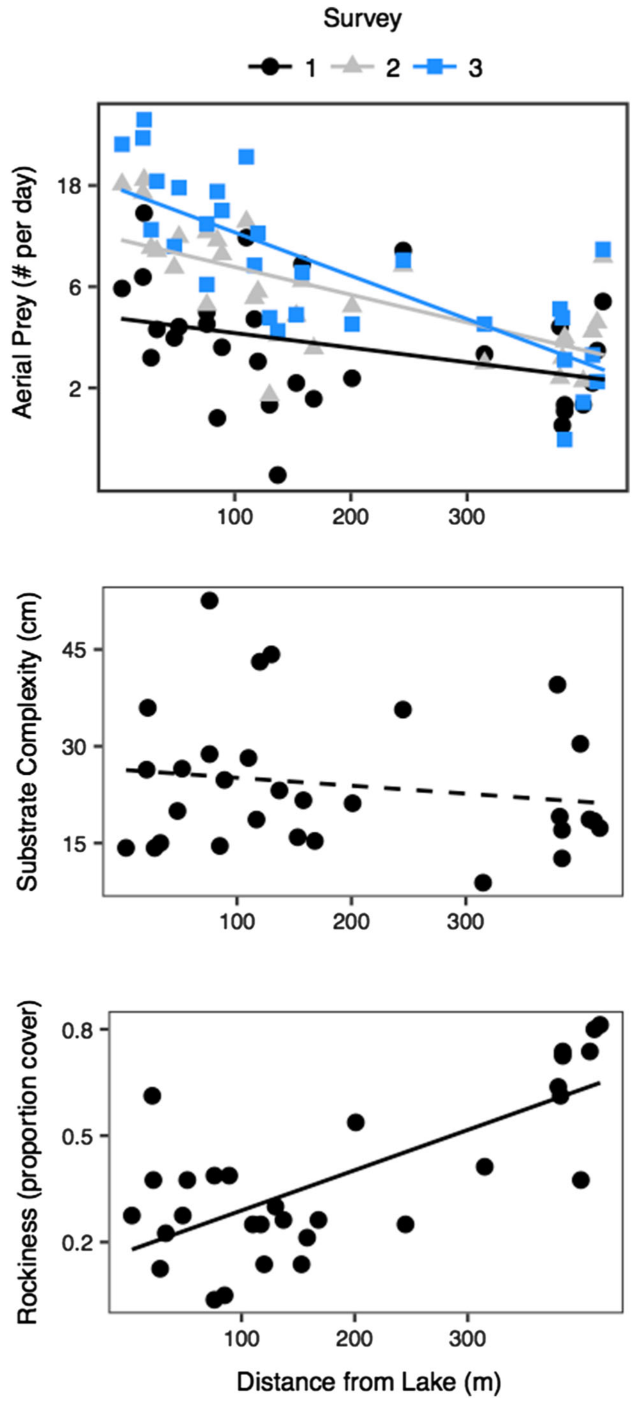

Fig. 2 **a** Aerial prey capture rate (number per day), **b** substrate complexity (cm), and **c** rockiness (proportion) plotted against distance from the lakeshore (m). Panel **a** includes data for the three surveys (*black circles* = survey 1, *gray triangles* = survey 2, *blue squares* = survey 3). The *lines* show model predictions, with *solid lines* indicating statistically significant relationships and the *dashed line* indicating a non-significant relationship. (Color figure online)

Table 1 Results of *F* tests for linear mixed model relating change in aggregation size to explanatory variables, with Kenward–Roger denominator degrees of freedom (ddf)

Parameter	*F*	ddf	*p*
Distance	1.81	33.70	0.187
Aerial prey	4.79	45.70	0.034*
Substrate complexity	1.70	24.80	0.207
Rockiness	0.001	28.10	0.922

Non-significant interactions omitted for clarity

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

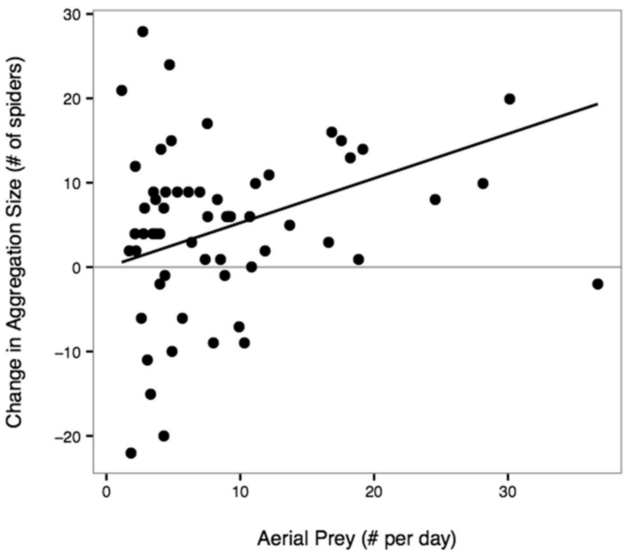

Fig. 3 Change in *Larinioides patagiatus* aggregation size (number of spiders) plotted against distance from the lakeshore (m), with the *line* showing the model prediction. The change in aggregation size was calculated as the differences in size between consecutive surveys

Table 2 Results of *F* tests for linear mixed model relating web size to explanatory variables, with Kenward–Roger denominator degrees of freedom (ddf)

Parameter	*F*	ddf	*p*
Distance	25.80	34.34	<0.0001****
Aerial prey	0.23	61.88	0.631
Substrate complexity	5.50	24.15	0.028*
Rockiness	2.36	26.86	0.136
Survey	13.10	65.64	<0.0001****
Distance × substrate complexity	8.45	23.82	0.008**

Non-significant interactions omitted for clarity

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

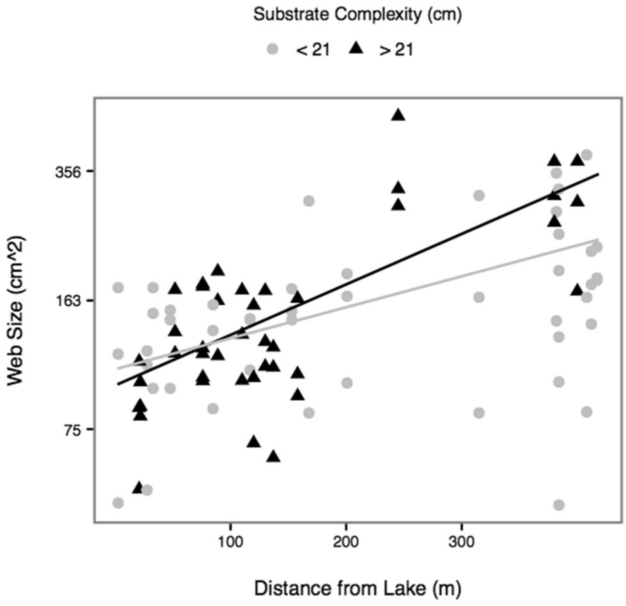

Fig. 4 *Larinioides patagiatus* web size (cm^2) plotted against distance from the lakeshore (m). *Gray circles* show data below the median substrate complexity (21 cm), *while black triangles* show data above the median substrate complexity. The *lines* show model predictions, evaluated for substrate complexities corresponding to quartiles one (16 cm; *gray*) and three (29 cm; *black*)

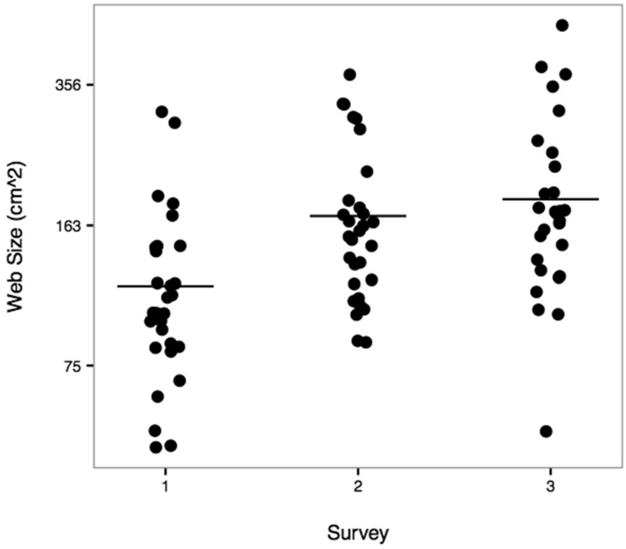

Fig. 5 *Larinioides patagiatus* web size (cm^2) plotted by survey, with *horizontal lines* showing model predictions

Discussion

We investigated spatiotemporal patterns in orb-weaver aggregations and web size in response to prey availability and habitat features. Our results showed that temporal variation in the size of orb-weaver aggregations was influenced by the abundance of aerial prey (Fig. 2). Aggregation size increased by 46% over the course of the midge emergence (between the first and third surveys), and the increases between surveys were greater in locations where the abundance of aerial prey was higher (Fig. 3) This result is consistent with previous studies that have documented increases in orb-weaver aggregation size in response to abundant prey, (Rypstra 1983; Gillespie 1987; Kralj-Fišer and Schneider 2012). By quantifying aggregation and web formation in response to midge emergence at Mývatn, this study links previously known effects of prey variability on spider aggregations with spatiotemporal variation in cross-ecosystem subsidies to an otherwise unproductive landscape.

Contrary to our expectations, orb-weaver web size did not respond to spatiotemporal variation in aerial prey. Nonetheless, web size did vary through space and time due to other factors. The increase in web size through time is likely due to the ontogeny of *L. patagiatus*, as adult spiders build larger webs than juveniles (Herberstein and Tso 2000; Marczak and Richardson 2008). Spatial variation in web size was partly due to an increase in web size with substrate complexity. However, web size also increased with distance, and the effects of distance and substrate complexity interacted; web size was greatest at high substrate complexity far from shore. This could be explained by spatial variation in habitat use between juveniles and adults (Werner and Gilliam 1984); juveniles may be more dependent on chironomids emerging from the lake, making it advantageous for them to aggregate near shore where they would build smaller webs. However, the increase in aggregation size with the abundance of aerial prey was independent of distance from shore, arguing against differences in habitat use by juveniles and adults causing our result that web size increased away from shore. Furthermore, web size may have varied among individuals of similar ages, and distance from shore is associated with a suite of factors (e.g., differences in plant and terrestrial arthropod communities) that could be responsible for such variation (Hoekman et al. 2011; Dreyer et al. 2012; Bultman et al. 2014).

Multiple studies have documented effects of substrate topography on orb-weaver aggregations and web size, typically due to geometric constraints on web construction that limit the total number of webs (and therefore spiders) that can occupy a given area (Rypstra 1983; Sandoval 1994; Halaj et al. 1998; Chan et al. 2009). However, our results suggest that *L. patagiatus* populations were not so constrained during our study period, as aggregation size was independent of variation in substrate. Furthermore, while web size did increase with substrate complexity, both aggregation and web size increased through time, with the mean total web area per plot increasing from 2600 to 6500 cm^2 (150%). Such a dramatic increase in total web area is inconsistent with a strict geometric constraint on the total substrate available for web building, suggesting that substrate complexity is correlated with some other feature of the environment that is important for web building. For example, topographic complexity may provide habitats for additional prey items or collect masses of adult midges, which are weak fliers and can easily become trapped in slightly enclosed spaces.

Cross-ecosystem subsidies are ubiquitous and often important for sustaining consumer populations in barren landscapes (Polis et al. 1997; Nakano and Murakami 2001; Carpenter et al. 2005; Croll et al. 2005; Baxter et al. 2005). However, subsidies are heterogeneously distributed and their impact on consumer populations depends on the ability of consumers to track them through space and time (Polis et al. 1997; Orr et al. 2005; Yang et al. 2010; Hoekman et al. 2011). Our results show how the size of orb-weaver aggregations responds to large, but variable, midge emergences that subsidize the terrestrial landscape, and this may have consequences for the reproductive fitness and the resulting dynamics of the orb-weaver populations.

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References

Baxter CV, Fausch KD, Carl Saunders W (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones: prey subsidies link stream and riparian food webs. Freshw Biol 50:201–220. doi:10.1111/j.1365-2427.2004.01328.x

Björnsson H, Jónsson T (2004) Climate and climatic variability at Lake Myvatn. Aquat Ecol 38:129–144. doi:10.1023/B:AECO.0000032061.51508.e6

Bultman H, Hoekman D, Dreyer J, Gratton C (2014) Terrestrial deposition of aquatic insects increases plant quality for insect herbivores and herbivore density: terrestrial effects of midge deposition. Ecol Entomol 39:419–426. doi:10.1111/een.12118

Carpenter SR, Cole JJ, Pace ML et al (2005) Ecosystem subsidies: terrestrial support of aquatic food webs from 13C addition to contrasting lakes. Ecology 86:2737–2750. doi:10.1890/04-1282

Chan EKW, Zhang Y, Dudgeon D (2009) Substrate availability may be more important than aquatic insect abundance in the distribution of Riparian orb-web spiders in the tropics. Biotropica 41:196–201. doi:10.1111/j.1744-7429.2008.00463.x

Croll DA, Maron JL, Estes JA et al (2005) Introduced predators transform subarctic islands from grassland to tundra. Science 307:1959–1961. doi:10.1126/science.1108485

Dreyer J, Hoekman D, Gratton C (2012) Lake-derived midges increase abundance of shoreline terrestrial arthropods via multiple trophic pathways. Oikos 121:252–258. doi:10.1111/j.1600-0706.2011.19588.x

Dreyer J, Townsend PA, James CH III et al (2015) Quantifying aquatic insect deposition from lake to land. Ecology 96:499–509. doi:10.1890/14-0704.1

Einarsson Á, Gardarsson A, Gíslason GM, Ives AR (2002) Consumer–resource interactions and cyclic population dynamics of Tanytarsus gracilentus (Diptera: Chironomidae). J Anim Ecol 71:832–845. doi:10.1046/j.1365-2656.2002.00648.x

Einarsson Á, Stefánsdóttir G, Jóhannesson H et al (2004) The ecology of Lake Myvatn and the River Laxá: variation in space and time. Aquat Ecol 38:317–348. doi:10.1023/B:AECO.0000032090.72702.a9

Gillespie RG (1987) The role of prey availability in aggregative behaviour of the orb weaving spider Tetragnatha elongata. Anim Behav 35:675–681. doi:10.1016/S0003-3472(87)80103-3

Gratton C, Donaldson J, Zanden MJV (2008) Ecosystem linkages between lakes and the surrounding terrestrial landscape in Northeast Iceland. Ecosystems 11:764–774. doi:10.1007/s10021-008-9158-8

Halaj J, Ross DW, Moldenke AR (1998) Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. J Arachnol 26:203–220

Herberstein ME, Tso I-Min (2000) Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneoidea, Araneae). J Arachnol 28:180–184

Hoechstetter S, Walz U, Dang L, Thinh N (2008) Effects of topography and surface roughness in analyses of landscape structure—a proposal to modify the existing set of landscape metrics. Landsc Online 3:1–14. doi:10.3097/LO.200803

Hoekman D, Dreyer J, Jackson RD et al (2011) Lake to land subsidies: experimental addition of aquatic insects increases terrestrial arthropod densities. Ecology 92:2063–2072. doi:10.1890/11-0160.1

Hoekman D, Bartrons M, Gratton C (2012) Ecosystem linkages revealed by experimental lake-derived isotope signal in heathland food webs. Oecologia 170:735–743. doi:10.1007/s00442-012-2329-5

Ives AR, Einarsson Á, Jansen VAA, Gardarsson A (2008) High-amplitude fluctuations and alternative dynamical states of midges in Lake Myvatn. Nature 452:84–87. doi:10.1038/nature06610

Kasumovic MM, Jordan LA (2013) Social factors driving settlement and relocation decisions in a solitary and aggregative spider. Am Nat 182:532–541. doi:10.1086/671930

Kralj-Fišer S, Schneider JM (2012) Individual behavioural consistency and plasticity in an urban spider. Anim Behav 84:197–204. doi:10.1016/j.anbehav.2012.04.032

Levi HW (1974) The orb-weaver genera *Araniella* and *Nuctenea* (Araneae: Araneidae). Bull Mus Comp Zool 146:291–316

Marczak LB, Richardson JS (2008) Growth and development rates in a riparian spider are altered by asynchrony between the timing and amount of a resource subsidy. Oecologia 156:249–258. doi:10.1007/s00442-008-0989-y

McCormick MI (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Mar Ecol Prog Ser Oldendorf 112:87–96

Nakano S, Murakami M (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc Natl Acad Sci 98:166–170. doi:10.1073/pnas.98.1.166

Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C (2017) *Larinioides patagiatus* (Clerck, 1757). Spiders of Europe. https://araneae.unibe.ch/data/964. Accessed 31 July 2017

Orr M, Zimmer M, Jelinski DE, Mews M (2005) Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86:1496–1507. doi:10.1890/04-1486

Polis GA, Hurd SD (1995) Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. Proc Natl Acad Sci 92:4382–4386

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316

QGIS Development Team (2014) QGIS geographic information system. Open Source Geospatial Foundation. http://qgis.osgeo.org

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Riechert SE, Tracy CR (1975) Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. Ecology 56:265–284

Rypstra AL (1983) The importance of food and space in limiting web-spider densities; a test using field enclosures. Oecologia 59:312–316. doi:10.1007/BF00378855

Rypstra AL (1985) Aggregations of *Nephila clavipes* (L.)(Araneae, Araneidae) in relation to prey availability. J Arachnol 13:71–78

Sabo JL, Power ME (2002) Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology 83:3023–3036

Sandoval CP (1994) Plasticity in Web Design in the Spider *Parawixia bistriata*: a response to variable prey type. Funct Ecol 8:701. doi:10.2307/2390229

Šestáková A, Marusik YM, Omelko MM (2014) A revision of the Holarctic genus *Larinioides* Caporiacco, 1934 (Araneae: Araneidae). Zootaxa 3894:61–82. doi:10.11646/zootaxa.3894.1.6

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Evol Syst 15:393–425

Wise DH (2006) Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. Annu Rev Entomol 51:441–465. doi:10.1146/annurev.ento.51.110104.150947

Yang LH, Edwards KF, Byrnes JE et al (2010) A meta-analysis of resource pulse–consumer interactions. Ecol Monogr 80:125–151. doi:10.1890/08-1996.1