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Phenological dynamics of web-building spider populations in alfalfa: implications for biological control

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Abstract. Web-building spiders form a major component of the generalist predator fauna in arable fields. They have been purported to contribute to the biological control of pests such as aphids and leafhoppers. However, their successful contribution to pest suppression is contingent upon their ability to adapt to highly-disturbed agroecosystems. We examined the population dynamics of these important natural enemies to compare phenological patterns in relation to crop cycles among species in an alfalfa agroecosystem using quadrat-based sampling and time-series analysis. Three common species of web-building spiders had generation times similar to the duration of a crop cycle (31 to 44 days), with peak abundances of adult spiders occurring at 15–18 days after harvest. The timing of these peaks corresponds with the critical early phase of the pest population cycle, during which natural enemies can have the maximum impact on pest populations, suggesting that these spiders are capable of contributing to pest suppression as part of an assemblage of natural enemies.

Keywords: Generalist predators, time-series analysis, population dynamics, disturbances, Linyphiidae

Spiders are an important component of the community of arthropods frequenting agroecosystems, often outnumbering most or all other groups of natural enemies (Nyffeler & Sunderland 2003), and feeding on many important pest species, such as aphids and leafhoppers (Nyffeler 1999; Harwood et al. 2004). The potential for generalist predators, such as spiders, to contribute to pest regulation has been an important focus of the biological control literature (Riechert & Lockley 1984; Nyffeler & Sunderland 2003). Generalist predators usually experience loose, diffuse dynamical links with any specific prey item and thus are thought to be less likely to respond heavily to changes in the populations of a specific pest (Hagen & van den Bosch 1968; Symondson et al. 2002). This contrasts with the tightly-coupled relationships of specialist natural enemies with their pest prey, which provide them an advantage in terms of responding to specific prey items. However, such highly synchronized dynamics can place them at a disadvantage in shifting environments (e.g., frequently harvested crops), in which pest population cycles can deviate unexpectedly from the conditions to which the specialist is adapted. In such instances, species with polyphagous habits and multivoltine life cycles have the flexibility to persist even as pest populations fluctuate, or before pest populations have been established (Settle et al. 1996; Scheu 2001), thereby exerting predatory pressure when pest populations are establishing and growing (Landis & van der Werf 1997; Harwood et al. 2004, 2007). This is important because the early, establishment phase of pest population growth is critical in the context of biological control and is the time during which the greatest impact by natural enemies can be realized (Ekbom et al. 1992).

Despite these favorable traits, the ability of generalist predators to contribute to pest regulation through early-season predation is challenged by the disturbances caused by agronomic practices, which impact predators as much as, if not more than, pests. Thus predators are required to adapt to cyclical agronomic disturbances (such as crop harvests), which can potentially neutralize their advantage as natural enemies. Such adaptations become increasingly important as the level of disturbance in crops increases. For example, forage crops, such as alfalfa, *Medicago sativa* L. (Fabales: Fabaceae), are harvested several times during any growing season, presenting spiders with only ephemeral habitats in which to forage for prey and complete development. These conditions are highly disruptive to the synchronized dynamics of specialist predators and their prey, but may be conducive to ruderal, generalist predators with rapid life cycles, such as web-building spiders. Indeed, the cyclical disturbances in these systems may favor spiders with very specific life-cycle characteristics.

Web-building spiders constitute a large portion of the spider fauna in North American alfalfa fields (Birkhofer et al. 2007). The family Linyphiidae, for example, includes a large number of agrobiont species with varying life cycle characteristics, including univoltine, bivoltine and multivoltine species (Wise 1984; Thorbek et al. 2003; Bolduc et al. 2005). In alfalfa systems, a polyphagous diet and a multivoltine life cycle could allow persistence in spite of intensive disturbances.

Herein, we present population data on web-building spiders collected by absolute population sampling in quadrats in a North American alfalfa agroecosystem throughout an entire growing season. The objective of this research is to examine the dynamics of spider populations in a highly disturbed agroecosystem, with the intent of determining life-cycle and phenological patterns in relation to agronomic disturbances. Our hypothesis is that the disturbances of crop management will select for specific life-cycle phenologies. We thus predict that the most common species will display life cycles that closely match the crop cycles in alfalfa.

METHODS

Study site.—This research was performed in two alfalfa fields (total area: 10.8 ha) at the University of Kentucky Spindletop Research Farm, Lexington, KY, USA (GPS coordinates: 38°07′32″N, 84°30′43″W) during the spring and summer of 2009. As a fast-growing forage crop, alfalfa was harvested repeatedly at approximately five-week intervals throughout the growing season (April–October), making it an excellent model system for studying disturbance-mediated population dynamics of generalist predators. In central Kentucky, important pests of alfalfa that are captured by web-building spiders include the pea aphid, *Acyrthosiphon pisum* (Harris) (Sternorrhyncha: Aphididae) (Romero and Harwood 2010), and the potato leafhopper, *Empoasca fabae* (Harris) (Auchenorrhyncha: Cicadellidae) (Harwood and Obrycki 2007). *A. pisum* populations are high early and late in the season, but drop during the middle of the season (Harper et al. 1990). In contrast, *E. fabae* population densities in alfalfa are high throughout the middle of the season (Emmen et al. 2004).

Field sampling.—To collect spiders, the alfalfa fields were divided into a total of 50 grid squares (approximately 2160 m^2/grid). On five days each week, a 0.25-m^2 quadrat was placed within approximately 10 randomly selected grids, such that all 50 grids were sampled once each week. This quadrat-based technique was favored over trapping techniques in order to provide a direct measure of absolute population densities (spiders per unit area), as opposed to activity-densities, to enable reliable analysis of population data. Within each quadrat, spiders were collected from webs by hand and preserved in 95% ethanol for identification.

The period of time analyzed here encompasses two complete alfalfa growth cycles, beginning after the first harvest of the season (18–19 May). Two additional harvests occurred on 26–27 June and 7–8 August. Alfalfa was cut early in the morning and allowed to dry in situ for approximately 24 h before raking and baling, at which point it was removed from the field. No pesticides were sprayed in these fields or adjacent crop fields during the study period.

Species identifications.—Genus-level identifications were based on Ubick et al. (2005), and species-level identifications were based on Hormiga & Döbel (1990) and Crosby & Bishop (1928). Three species of spiders were used in this study: *Tennesseellum formicum* (Emerton 1882) (Araneae: Linyphiidae: Linyphiinae), *Erigone autumnalis* Emerton 1882 (Araneae: Linyphiidae: Erigoninae), and *Glenognatha foxi* (McCook 1894) (Araneae: Tetragnathidae). These three species combined comprised approximately 80% of the web-building spider community in collections. Immature *T. formicum* and *G. foxi* could be identified by comparison to laboratory-reared specimens, using the following protocols. *T. formicum* is distinguished from other linyphiid spiders in our system by the spiracle, which is separated from the spinnerets. This character is visible in immature spiders, as well. *G. foxi* is distinguished from the only other tetragnathid spider in our system, *Tetragnatha laboriosa* Hentz 1850, by habitus, having a subspherical abdomen as opposed to the elongate, oval abdomen of *T. laboriosa*. Immature *E. autumnalis* could not be reliably distinguished from other erigonine spiders found in the system–*Grammonota inornata* Emerton 1882 and *Mermessus* (three species)–and are thus excluded from this study. Voucher specimens of all species were deposited in the University of Kentucky Insect Collection.

Data analysis.—Population density data for adult spiders of all three species were analyzed using sample autocorrelation. Density (spiders/m^2) of each species was calculated for each sampling day. Sampling data were not collected uniformly, and since autocorrelation analysis requires uniformly distributed time series, the seven-day moving average of each date was calculated. A seven-day moving average was chosen because seven days corresponds to the largest gap between sampling dates (see Rasmussen et al. [2001] for discussion of time series analysis.) Each uniform time series was analyzed using the autocorrelation function in MATLAB version 7.10.0.499 R2010a (function *autocorr*, The MathWorks, Inc., Natick, Massachusetts, USA). This technique can qualitatively determine the stationarity and periodicity in time-series data (Turchin and Taylor 1992), and can identify regions in a time series that are significantly correlated with one another. In effect, it estimates the lag time between successive peaks (a positive correlation) or between an adjacent trough and peak (a negative correlation) over a time series. In the present study, positive correlations were interpreted as generation times in alfalfa, while negative correlations were interpreted as establishment times; i.e., the time between a density trough (which occurred at each harvest) and a subsequent density peak.

In addition, a similar analysis was run on two life stages (immatures versus adults) of *T. formicum* and of *G. foxi* (*E. autumnalis* was omitted because immatures could not be reliably identified). Protocols were identical to those used to analyze the adult data sets, except that the crosscorrelation function in MATLAB (function *crosscorr*) was used. This function works similarly to the autocorrelation function, except it compares a pair of time series to one another instead of comparing different regions of the same time series. In this case, a positive correlation corresponds to the lag between the peak of one time series and the peak of the other, while a negative correlation corresponds to the lag between the peak of one time series and the trough of the other. For species with discrete generations, positive correlations estimate the duration of the final instar. Negative correlations, while producing significant signals in analyses, can be regarded as an artifact of the analysis, and do not carry any biological meaning for this data.

RESULTS

Collection data show two peaks in density of adult females for each species (Fig. 1), indicating that two generations were completed within the 75-day study. Each of the three spider species had unique time lags (generation times) between successive peaks in adult densities (Fig. 2): *T. formicum* had a significant positive autocorrelation at a 44-day lag, *E. autumnalis* had a significant positive autocorrelation at a 40-day lag, and *G. foxi* had a significant positive autocorrelation at a 31-day lag. Significant negative autocorrelations occurred at a lag (establishment time) of 15 days for *T. formicum*, 18 days for *E. autumnalis*, and 17 days for *G. foxi*.

In the life-stage analysis for *T. formicum* (Fig. 3), the positive crosscorrelation at −4 days suggests that the final instar for *T. formicum* lasts only 4 days, and indicates that this species undergoes a cyclical pattern of discrete generations. For *G. foxi* (Fig. 4), a pattern of discrete generations was also uncovered, and the final instar lasts 9 days; however, strong crosscorrelation values were also present at other lag times, suggesting *G. foxi* populations experience additional periodic fluctuations that *T. formicum* populations do not experience. These results suggest other periodic factors, such as seasonal effects (as opposed to crop cycle), influence the life-stage distribution of this species.

DISCUSSION

This research has provided evidence that web-building spider population dynamics closely match the cyclical

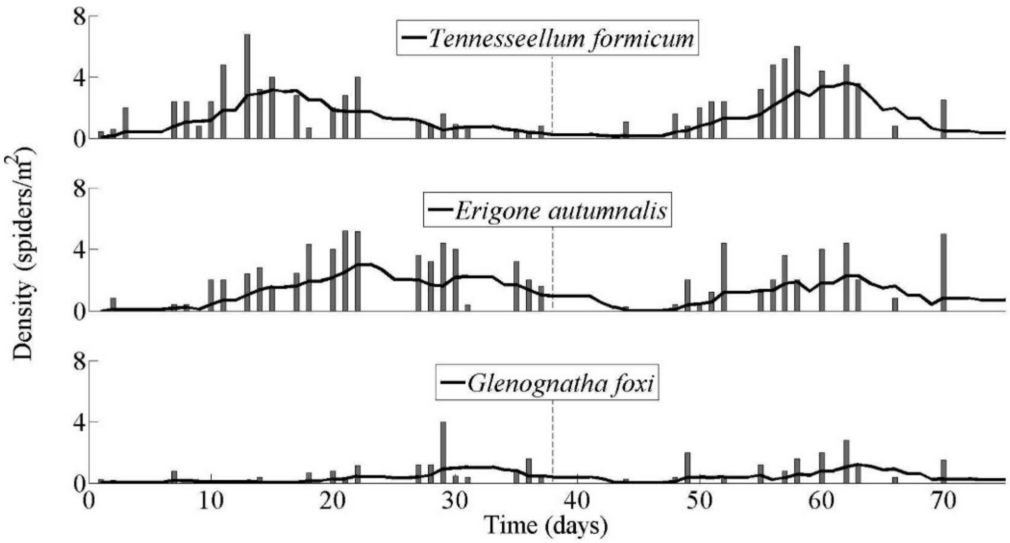

Figure 1.—Seven-day moving average density (solid lines) of three spider species during two alfalfa crop cycles. Raw density data are shown as bars on the day of collection. Harvests occurred at day 0 (19 May), day 37 (26 June; vertical dotted line), and day 75 (7 August; end of sampling period).

disturbance patterns in an alfalfa agroecosystem. Harvests occurred approximately 40 days apart, and spider generation times closely matched this. In addition, the lowest densities of active life stages for these spiders occurred very close to harvest, while peak densities occurred within 2.5 wk of harvest for all three species. This has important implications for the pest suppression activity of these spiders. Emmen et al. (2004) showed that potato leafhopper immigration into Pennsylvania alfalfa reaches its highest rates 2–3 wk after the alfalfa is harvested, indicating that adult spiders are at their highest densities during the critical establishment phase in the leafhopper population cycle, thereby suggesting that these spiders can play an important role in leafhopper suppression early in the growth cycle. However, Birkhofer et al. (2007) showed that pea aphid populations in Kentucky alfalfa can return to pre-harvest densities within 2 wk after harvest, and similar results were found in Canadian alfalfa (Harper et al. 1990). This indicates that web-building spider dynamics are not optimized for suppression of aphids by adult spiders; however, immature spiders are present and accumulating in the habitat during the critical establishment phase of the aphid population cycle and thus may still contribute to aphid suppression to some extent.

Particularly noteworthy is the timing of spider population peaks and troughs. Densities of adults of each species reached their lowest densities very near the time of harvest (Fig. 1). Other authors have previously shown strong negative effects of management disturbances on predator populations (Thorbek & Bilde 2004; Öberg & Ekbom 2006). It is tempting to apply this explanation to the dynamics of *G. foxi*, which appear not to have completed a full population cycle before the end of the first crop cycle and to have declined in density

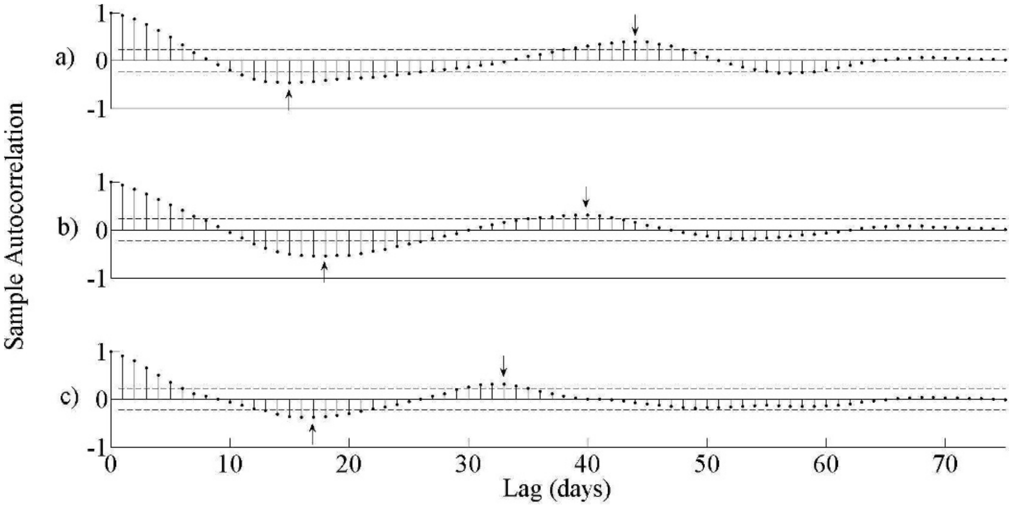

Figure 2.—Autocorrelation functions for each of three species of spider in an alfalfa agroecosystem. In each panel the dashed lines represent 95% confidence intervals and arrows mark the strongest negative and positive autocorrelation. a) *Tennesseellum formicum*; b) *Erigone autumnalis*; c) *Glenognatha foxi*.

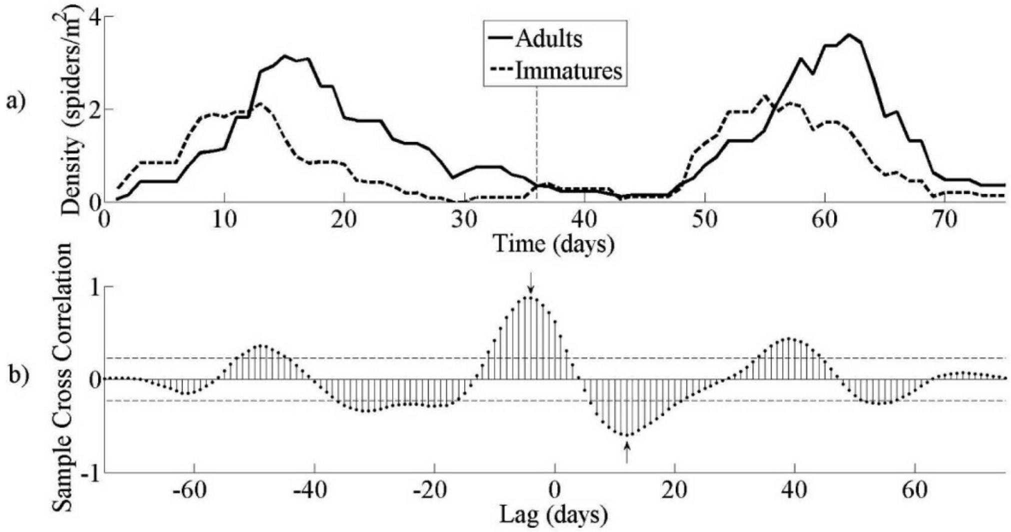

Figure 3.—a) Seven-day moving average density of *Tennesseellum formicum* adults and immatures during an alfalfa growing season. At day 0 and 37, the alfalfa was harvested. b) Crosscorrelation analysis between adult and immature *T. formicum*. Crosscorrelation analysis finds temporal patterns in correlated time series.

after the harvest. However, the density of active stages of *T. formicum* clearly declined steadily throughout the latter half of the crop cycle until reaching its lowest level at harvest. The decline of this species thus does not appear to be related to the disturbance from harvest, but to a pattern of discrete generational phenology in which the egg stage—which was not sampled in this study — coincides with harvest. Thus, the phenology of *T. formicum* may be a pre-adaptation to the crop cycles of alfalfa and allow this spider to persist in high numbers in this agroecosystem. Interestingly, Bolduc et al. (2005) uncovered a bivoltine/trivoltine life cycle for this species in Quebec vineyards, with a time lag between successive generational peaks that closely approximated the time lag we uncovered, indicating that the findings of the present study are not a specific adaptation to the alfalfa system, but a general characteristic of the species. However, the egg stage for *T. formicum* is completed in approximately 10 days under laboratory conditions (K.D. Welch unpublished data). Thus, we should expect the peak density of immatures to occur within 10 days of the prior adult peak. However, in field collections, the gap between the peak density of adults and the subsequent peak density of immatures is approximately 40 days, four times the duration of the laboratory egg stage. This suggests that either 1) the egg stage lasts considerably longer in the field than in the laboratory (although Thorbek et al. (2003) found that linyphiid eggsac development times of 40 days occurred only at temperatures of ≤ 12° C); 2) the subsequent peak of immatures does not derive from eggs laid at peak adult densities, but from eggs laid later in the population cycle; or 3) spider hatchlings undergo a prolonged stage in which they do not utilize webs and thus were not collected by our web-centric sampling protocols.

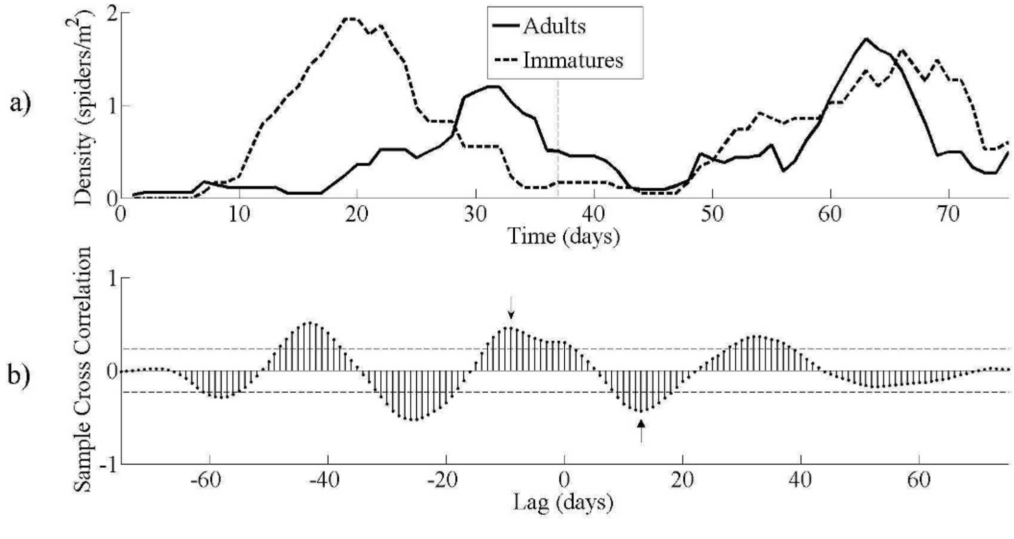

Figure 4.—a) Seven-day moving average density of *Glenognatha foxi* adults and immatures during an alfalfa growing season. b) Crosscorrelation analysis between adult and immature *G. foxi*.

Additionally, a qualitative assessment of the collection data suggests that during the first crop cycle adult density peaks were staggered across species, producing a succession-like dynamic in which each species is associated with a specific phase in the crop cycle (Fig. 1). However, in the second crop cycle, this staggered pattern in density peaks disappeared, and, consequently, the time lags calculated when both cycles are incorporated did not differ substantially. The staggered dynamic may have been simply a coincidence, or it may have been an effect of phenological shifts in the community across crop cycles due to seasonality and the timing of population cycles for different species. For *T. formicum*, peak densities of each life stage were comparable across crop cycles, both in timing (relative to one another and relative to harvest) and in magnitude, which may indicate a stable generational dynamic in which the observed densities represent a maximum enforced by resource limitations or predation/competition pressures and suggest that the four-day estimate of the final instar duration is accurate. However, in the life-stage analysis of *G. foxi*, strong periodic signals were uncovered at time lags longer than the generation time (Fig. 4). This is likely related to a seasonal phenological dynamic: immature *G. foxi* peaked at higher densities than adults during the first crop cycle, while adults peaked at higher densities than immatures during the second crop cycle. It is possible that the adult peaks for this species do not represent two discrete generations at all, but a single generation (or pattern of overlapping or indiscrete generations) interrupted by a harvest, with migration modulating the dynamics following harvest (cf. Thorbek & Bilde 2004; Gavish-Regev et al. 2008). This is supported by the observation that adult *G. foxi* reached peak densities much sooner after the second harvest than they had after the first, and the observation that, during the second crop cycle, the adult density peak occurs before the immature density peak. This may explain why the "generation time" obtained for *G. foxi* was so much shorter than for *T. formicum*: both generation time and final instar duration were likely underestimated for *G. foxi* by assuming that the two peaks in adult density represented two discrete generations. It also suggests that the timing of harvest will impact whether or not these spiders' pattern of occurrence in the latter part of the season will repeat the staggered pattern of the earlier part of the season, and that agronomic disturbances in crop systems have the potential to alter patterns of natural enemy community structure across the growing season.

The phenology of web-building spider life cycles closely matches the phenology of an alfalfa agroecosystem. Spider populations were able to survive agronomic disturbances in the egg stage and build up densities of active stages rapidly thereafter, allowing them to be present in time to contribute to some extent to the suppression of alfalfa pests. However, these data indicate the presence of other factors influencing spider population cycles, including seasonal and developmental dynamics, as well as potential dispersal patterns, and further work will be needed to elucidate these dynamics.

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