2018. Journal of Arachnology 46:31–34

Changing oviposition times of the crab spider *Misumena vatia* (Thomisidae) correlate with climate change

Douglass H. Morse: Department of Ecology & Evolutionary Biology, Box G-W, Brown University, Providence, RI 02912 USA. E-mail: d_morse@brown.edu

Abstract. The crab spider *Misumena vatia* (Clerck, 1757) (Thomisidae) is an important sit-and-wait predator at flowers visited by nectar or pollen-seeking insects. Typically, female *M. vatia* molt into their adult stage when many insect-attracting flowers come into bloom, and the spiders quickly gain weight leading up to oviposition. Between 1979 and 2010, the first spider ovipositions shifted one month earlier, from late July to late June, at my study site in coastal Maine, USA, in accordance with a concurrent temperature increase of ca. 0.44°C and a lengthening growing season. Flowering times of the spiders' most important hunting site, common milkweed *Asclepias syriaca*, as well as recruitment dates of their most important prey, bumblebees *Bombus* spp., to flowering milkweed, advanced as well. The shift in spider oviposition times increased the feasibility of second broods, though I found no successful second broods in the field, and the success of such broods would be problematic because of heavy overwintering losses. Differing rates of change of spider, milkweed and bumblebee activity indicated decreasing synchrony among these species; in particular, lessening future hunting opportunities for the spiders.

Keywords: Global warming, egg-laying, growing season, seasonal change, sit-and-wait predator

Recent years have seen increased interest and concern about the effects of climate change on the phenology of animals and plants (Parmesan 2006; Thackeray et al. 2010; Bewick et al. 2016). Changes in seasonality may produce shifts in life cycles that conflict with the currently existing environmental regime, and if they do not match those of interacting species, further problems may arise (Memmott et al. 2007; Johansson et al. 2015). Mean temperature changes may also play a dominant role in shifting habitat ranges and geographic distributions of populations (Primack et al. 2009; Mason et al. 2015), though I will focus here on changes within a site.

In spite of the currently perceived importance of documented climatic change and much anecdotal information for many groups of organisms, rather few long-term measures of organismal response to yearly change currently exist over multiple trophic levels (Clark & May 2002; LeRoy et al. 2013). To the best of my knowledge no such information exists for spiders. However, in the process of a long-term study of the crab spider *Misumena vatia* (Clerck, 1757) (Thomisidae) in coastal Maine, USA (Morse 1979, 2007, 2014), I maintained large populations of adult females over a 32-year period (1979–2010) that allowed me to record initial dates of oviposition for each year. For 16 of these years, I also obtained initial flowering dates of their most important hunting site, inflorescences of common milkweed *Asclepias syriaca*, which attract great numbers of large insects that provide the main resources for *Misumena* reproduction (Morse 1982a; Morse & Fritz 1982). For most of the flowering years I also recorded the dates at which bumblebees, the spiders' most important prey, first recruited to the milkweed flowers. This body of information allowed me to establish whether the activity patterns of these three species shifted in accordance with the changing seasons and whether any such changes affected their relationship to each other. In turn, the results allowed me to assess the effects of climate change on these species over the period of study, as well as to project likely future consequences for their relationships.

METHODS

Misumena vatia is a small sit-and-wait predator that typically hunts on flowers. Females weigh from 35–55 mg upon reaching adulthood, usually in the early summer following hatching in late summer two years earlier. They average 220 mg at laying their single clutch of eggs, with a range of 115 mg to over 400 mg. Their single clutch weighs approximately 65% of their mass immediately prior to egg laying (Morse 2007).

Each year, I maintained 50 or more field-collected adult females in order to gather various life history variables on the population and to obtain young for a wide range of experiments reported elsewhere. I collected the spiders in fields and roadsides at and near the Darling Marine Center, South Bristol, Lincoln County, Maine, U.S.A. (43°57′N, 69°33′W), mostly from common milkweed and pasture rose *Rosa carolina*, with smaller numbers from ox-eye daisy *Leucanthemum vulgare*, common buttercup *Ranunculus acris*, cow vetch *Vicia cracca* and red clover *Trifolium pratense*. I sampled these adults independently of mass, but the sample size ensured that they included individuals likely to become among the earliest ovipositers. I maintained them in 7-dram vials (5 cm long, 3 cm diameter) at ambient temperature and natural day length in an unheated laboratory and fed them moths or large flies every other day. Generally these spiders will not take large prey on successive days (Morse 2007), so the feeding regime resembled that obtained at a high-quality hunting site like that of common milkweed.

The spiders typically refuse to feed one to two days before laying. At that point, I placed them on a milkweed leaf in the field, which resembled a natural nest site, and enclosed the plant with a loosely fitting nylon tricot bag. Most individuals laid either the following night or one night later. I resorted to the field regime because these spiders appeared reluctant to lay in the vials where they could not construct a normal nest. The bags themselves do not significantly affect the temperature within (Morse 1994a). I checked the spiders daily to ensure an accurate laying date.

Additionally, I recorded first observations of egg masses while conducting unrelated fieldwork between 1980 and 1994. They provided a comparison between laying dates in the field and those in the standardized routine described above.

I also recorded the initial flowering dates of milkweed, the most important hunting site for *Misumena* in my study area, during the 16 years (1979–1994) for which I possessed data on the spiders' oviposition date. A perennial, common milkweed grows in clones that vary greatly in size, but that routinely attract large numbers of bees, moths and butterflies when in bloom (Morse 1982a, 2007). Milkweed stems vary from 80–120 cm in height and bear multiple round inflorescences (umbels) that bloom sequentially (Morse 1985). A large clone may remain in flower for three weeks or more.

For 11 of these years (1979–1991, data missing for 1989 and 1990) I also recorded the dates at which bumblebees first recruited to milkweed. Bumblebees, mostly *Bombus terricola* and *B. vagans*, were the most common large diurnal insects that visited milkweed flowers and made up by far the spiders' most important prey (Morse & Fritz 1982).

The vicinity of the study site has undergone measurable climatic change over the 32-year period of data gathering. Using the estimate of Jacobson et al. (2009) of a 0.25° F/decade increase in temperature for coastal Maine in 1975–2009, a period similar to that of this 1979–2010 study, I estimated that the mean temperature of the study area increased 0.44°C between 1979 and 2010, a rate that considerably exceeds the estimated global rate for the entire twentieth century of 0.6°C (Houghton et al. 2001). Precipitation also increased by 6.50 cm during this time (Jacobson et al. 2009). Fernandez et al. (2015) also noted that the warm season in this area (defined as days with a mean daily temperature above 0° C) increased by two weeks over the past century, with both earlier spring and later fall seasons. Increase in winter temperatures exceeded the increase in summer temperatures.

Initially I ran one-way ANOVAs between each one of the three variables (oviposition of spiders, flowering of milkweeds, and recruitment of bumblebees) against the ongoing years to search for whether these variables exhibited systematic change over the period of the study. I first ran these variables separately because of the different lengths of data runs for each of them. In addition to the three separate analyses, I ran a three-way ANOVA that incorporated data from the 11 years (1979 through 1991) for which I possessed data sets for crab spiders, milkweeds, and bumblebees. Analyses were carried out in R Version 2.13.0 (R Development Core Team 2011).

RESULTS

The initial date of oviposition shifted earlier by approximately one month over the 32-year period from 1979 to 2010 (Fig. 1). Although exhibiting considerable year-to-year differences, the highly significant slope moved consistently toward earlier laying dates ($R^2 = 0.524$, $F_{1,30} = 35.05$, $P < 0.0001$ in a one-way ANOVA), as did dates of the egg masses found in the field ($R^2 = 0.828$, $F_{1,13} = 62.56$, $P < 0.0001$ in a one-way ANOVA: Fig. 2). Flowering dates of the milkweed from 1979 to 1994 generally resembled the oviposition pattern of the spiders ($R^2 = 0.334$, $F_{1,14} = 7.03$, $P = 0.019$ in a one-way ANOVA, although considerably weaker. Similarly, recruitment dates of the bumblebees to the milkweed flowers shifted earlier over the period of 1979 to 1991 ($R^2 = 0.485$, $F_{1,9} = 8.46$, $P = 0.017$ in a one-way ANOVA.

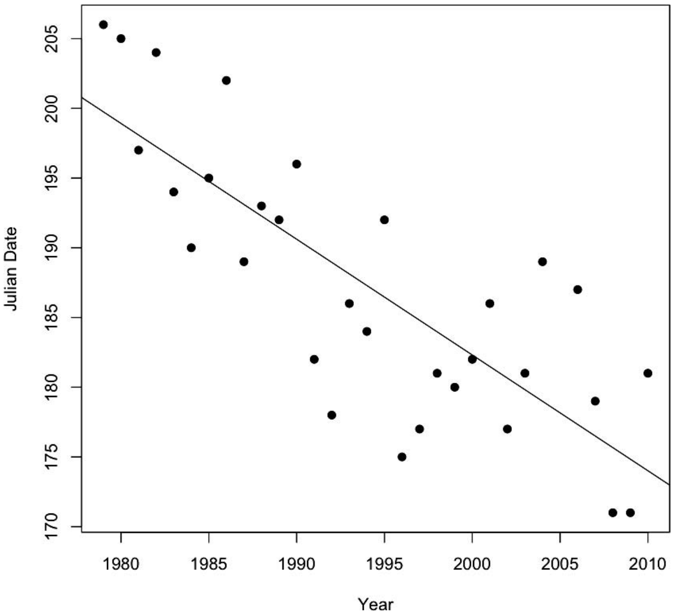

Figure 1.—Change in first oviposition date of field-collected crab spiders *Misumena vatia* from 1979 through 2010. Julian date 170 = 20 June; Julian date 205 = 25 July.

During 1979–1991, when I obtained data on oviposition times of spiders, flowering times of milkweed, and recruitment times of bumblebees (Table 1), the overall relationship among these variables was significant ($R^2 = 0.945$, $F_{3,7} = 25.51$, $P = 0.011$ in a three-way ANOVA), with significant contributions of both oviposition time and flowering time. Recruitment date was not significant, but interactions between oviposition time and flowering time and between flowering time and recruitment time suggested further differences among the three variables (Table 1). The slope of oviposition date over the 1979–1991 period ($R^2 = 0.534$) closely resembled that measure for the entire 32-year period.

DISCUSSION

The initial laying date of crab spiders shifted nearly a month earlier (from late July to late June) during this 32-year analysis. The field-laid broods exhibited an even stronger change during the 15 years in which I recorded them, although a likely outlier contributed to this difference. The procedures used in the two measures also differed significantly, preventing a direct comparison. However, results of the field-laid sample resemble the primary analysis in showing a strong shift toward earlier initial laying dates over time.

This shift to earlier laying dates should enhance overwintering survival of the resulting offspring. Middle and late instars overwinter more successfully than early instars (Morse 2007, 2012). However, the factor most important to the spiders, namely the recruitment of bees to milkweed flowers, should depend to some degree on flowering time, though not in the simplest way, because bumblebees do not recruit to the very earliest milkweed flowers, perhaps because the bees at that time are foraging for pollen to supply the colony's brood

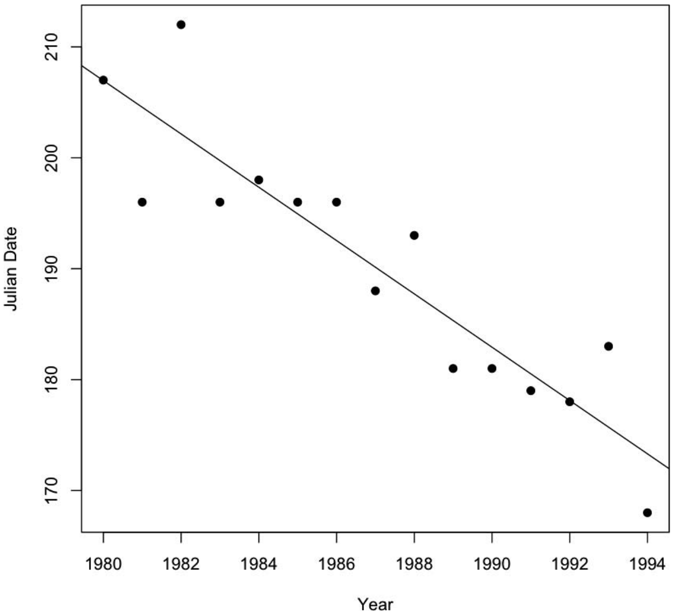

Figure 2.—Change in date of the first crab spider *Misumena vatia* egg masses found in the field from 1980 through 1994. Note the differences in x and y labels in Figure 1 and Figure 2.

(Morse 1982a, 2007). They cannot obtain pollen from milkweeds, because milkweed encapsulates its pollen in pollinia that pollinators can transmit, but cannot exploit (Woodson 1954; Morse 1985). Nevertheless, the bumblebees' recruitment time was significantly related to flowering time, though the significant lag in recruitment to milkweed deprives them of a considerable amount of nectar (Morse 1982b). This lag deprives the spiders as well, since it curtails their time to forage profitably at a highly attractive hunting site (Morse & Fritz 1982).

In the initial years of this census, spiders had little opportunity to produce a second brood due to time limitations, but by the end of the census period oviposition had moved earlier enough to provide the opportunity for a second brood. Indeed, the appearance of several second nests subsequent to rearing a successful first brood suggests the ability to rear a second brood at the study site. Rapid weight gains of females following removal from their first brood followed by supplementary feeding demonstrated that these spiders can produce a second brood if time allows (Morse 1994b), although over the study period I did not find a successful second brood in the field.

Possible advantages of a second brood are open to question because of the stage at which a brood would reach overwintering. A second brood that emerged just before the end of summer would experience a greater overwintering loss than members of first broods, since even members of the latest first broods experience a much lower overwintering success than older juveniles (Morse 1993, 2012). In an analogous situation, Neff & Simpson (1992) found that occasional second broods of the anthophorid bee *Diadasia rinconis* usually failed because of the lack of an adequate flower source. The timing might thus lead second *Misumena* broods into a developmental trap, in which a vulnerable instar reaches the season's end in a stage unfavorable for or fatal to survival (Fielding 2006; Van Dyck et al. 2015).

Table 1.—Results from three-way ANOVA of year vs. oviposition date*flowering date*recruitment date over 1979–1991 period.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Oviposition date	1	86.340	86.340	117.3094	0.001684 **
Flowering date	1	9.352	9.352	12.7071	0.037694 *
Recruitment date	1	3.525	3.525	4.7898	0.116412
Oviposition date: flowering date	1	2.921	2.921	3.9693	0.140368
Oviposition date: recruitment date	1	8.495	8.495	11.5418	0.042545 *
Flowering date: recruitment date	1	19.209	19.209	26.0999	0.014509 *
Oviposition date: flowering date: recruitment date	1	1.585	1.585	2.1540	0.238493
Residuals	3	2.208	0.736		

The lengthened season might appear to provide the opportunity for the spiders to reproduce a year earlier; that is, rather than overwintering a second time, to reproduce the season following their birth. Such offspring, however, would face the problem of immediately encountering the winter, which brings with it low survival rates, especially to the earlier instars conventionally produced (from 3rd year females). Any possible survivors should, however, enhance the fitness of their parents, although producing a second brood might entail countering costs for them, such as increased predation on their first broods resulting from a decreased period of guarding.

The relationship of the ongoing years with spider oviposition, milkweed flowering, and bumblebee recruitment suggests that changing conditions over the study period have affected all of these factors. Regressions for the three species were roughly similar, but if played out over longer periods, their synchrony would decline significantly (Bale et al. 2002). Oviposition date was weakly affected by recruitment date, a reflection of the bumblebees' importance as a food source for the spiders, in spite of the lack of a significant interaction between oviposition and flowering dates. This pattern reflects the response of the spiders directly to their prey, rather than to the flowers themselves, as reported earlier (Morse & Fritz 1982). The one-way analyses confirmed this difference: oviposition and flowering regressions were 0.524 and 0.334, respectively. If continued, this trend would progressively force the spiders to find sites other than milkweed for hunting. Flowering date significantly affected recruitment date; thus the two factors remained relatively in step, perhaps because the bumblebees' nectar sources became available earlier as well. These results all indicate ongoing changes, some of which will continue to decrease the synchrony of these species (Barton et al. 2009; Laws & Joern 2013).

Over the period presented here I have also kept less extended phenological data for several other species in the study area that are minimally related or unrelated to the spider-milkweed-bumblebee system, but show similar trends: emergence dates of adult Japanese beetles *Popilia japonica*, flight dates of Harris' checkerspot butterfly *Chlosyne harrisii*, and eclosion dates of the fern moth *Herpetogramma theseusalis* (Crambidae), the moth's common parasitoid wasp

Alabagrus texanus (Braconidae), and its hyperparasitoid *Aprostocetus* sp. (Eulophidae) (D.H. Morse unpubl. data). Thus, although *Misumena*, milkweed, and bumblebees have demonstrated striking shifts in phenology, they do not appear unusual in their pattern of change.

In conclusion, I have demonstrated long-term shifts in the oviposition times of crab spiders *Misumena vatia* that parallel patterns of climate change. The lengthening of the season increases the feasibility of becoming double-brooded, although such a second brood would face extreme difficulties. This change in oviposition time parallels changes of other species upon which the spiders depend, but the differences in rate of change among these species suggests that the spiders' relationship with them will shift over time and result in future dependence on other species.

ACKNOWLEDGMENTS

A generation of Brown University undergraduates assisted in the collection and care of the spiders. Several US National Science Foundation grants supported this work. I thank the Darling Marine Center of the University of Maine for use of the study site and K.J. Eckelbarger, T.E. Miller, L. Healy, and other staff members for facilitating fieldwork on the premises.

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Manuscript received 3 June 2017, revised 10 October 2017.