

Population fluctuations in Costa Rican golden silk orbweavers (*Trichonephila clavipes*)

Emma Reder^{1,2}, Chloe Lesh¹, Gabriela Ochoa¹, Sabrina Wu¹ and Elise Ferree^{1,3}: ¹Keck Science Department of Scripps and Pitzer Colleges, 925 N. Mills Ave, Claremont, CA 91711; E-mail: eferree@kecksci.claremont.edu; ²Wake Forest University, Winston-Salem, NC 27109; ³Pitzer College, Claremont, CA 91711

Abstract. Globally, arthropod populations are declining at alarming rates, but the causes are rarely understood. Our research details and examines possible causes for fluctuations in the size of a Costa Rican population of golden silk orbweaver spiders (*Trichonephila clavipes* (Linnaeus, 1767)). Over a seven-year period from 2013–2019, we noted a sharp decline and then partial recovery of the study population during the wet season (June, July), but then failed to locate any spiders during a brief survey in June 2022 when they would otherwise be abundant. We monitored webs daily during 2013–2019 to test whether variation in prey capture, competitors, female size, male availability, predation, temperature, or rainfall related to population fluctuations. We were unable to explain *T. clavipes* population trends with the collected data. Future studies are needed to determine whether the extremely low population densities we witnessed in 2017 and 2022 can be interpreted as the lowest values of this species' normal population fluctuation cycle or whether these extremes are part of a long-term spider decline.

Keywords: Tropical rainforest, low abundance, orb spiders, arthropod demographics, life cycles
<https://doi.org/10.1636/JoA-S-22-046>

Species are currently going extinct faster than their ecological roles can be filled, and terrestrial arthropods are among the species in decline (Schuch et al. 2012; Lister & Garcia 2018; Møller 2019; Seibold et al. 2019; Wepprich et al. 2019; Hallmann et al. 2020; Nyffeler & Bonte 2020; Janzen & Hallwachs 2021). These declines are alarming given the essential role of insects and other arthropods in nutrient cycling, pollination, pest control, and as food sources for higher trophic levels (Öckinger & Smith 2007; Ollerton et al. 2011; Norma-Rashid et al. 2014; Yang & Gratton 2014). Spiders are one group of arthropods subject to decline. For example, the current population densities of adult female garden spiders (*Araneus diadematus* Clerck, 1757) (Araneidae) in the Swiss midland are less than 1% of the densities 40 years ago (Nyffeler & Bonte 2020). Factors negatively affecting spider populations include habitat alteration, climate change, biological factors (predators and parasites) and pollutants (Shochat et al. 2004; Jocque et al. 2005; Shrewsbury & Raupp 2006; Meineke et al. 2017; Seibold et al. 2019; Nyffeler & Bonte 2020). Spider populations, like those of other organisms, can also cycle up and down over time, responding in a density-dependent way to fluctuations in food, predation, and competitors (Hunter & Price 1998). Over small time-scales, it can be challenging to distinguish cycles from declines, and even with robust data, population cycles are complex to model (Barraquand et al. 2017). Finally, the timing of reproduction in some spider populations varies among years, which can alter spider abundance patterns within a year (Higgins 1992a). Given the urgency of understanding and conserving arthropod populations, it is important to make data on population trends widely available.

The purpose of our study was to document and investigate correlates of population fluctuations of golden silk orbweaver spiders, *Trichonephila clavipes* (Linnaeus, 1767) (Araneidae), in a secondary growth tropical rainforest on the Pacific slope of Costa Rica. We studied the trade-offs of facultative clustering in *T. clavipes* in detail from 2013–2019 (Ferree et al. 2018) and noted population fluctuations during this time, which extended into years after our primary study ended. Despite the tropics being species-rich, long-term studies of tropical populations are relatively rare (Sánchez-Bayo & Wyckhuys 2019), and spiders are important parts of these ecosystems (Branco & Cardoso 2020).

Furthermore, it has been predicted that insect populations living in mid- and high-latitudes might expand as the climate warms, while declines are expected in the tropics (Deutsch et al. 2008). It is essential to develop a better understanding of the responses of tropical spider species to a changing climate, either direct or indirect, so that more effective actions can be taken to mitigate negative impacts.

We report on fluctuations in the number of individuals in a Costa Rican population of *T. clavipes* across seven years. Using daily monitoring data taken during the rainy season each year, we then examined how the biological factors of prey capture, competition, spider size, the availability of mates, and predation rate, as well as the abiotic factors of temperature and rainfall, could relate to these fluctuations. We expected less favorable conditions in the year leading up to the initial population decline, namely, fewer prey, more competitors, smaller female size, fewer mates, higher predation, extremely high or low rainfall, and high temperatures, compared to prior years when population size was stable. We also noted observations of dark color morphs and parasitoids in the population.

METHODS

Study system.—We collected data on golden silk orbweaver spiders *Trichonephila clavipes* over a seven-year period from 2013–2019 during the months of June and July and briefly in June 2022. We did not conduct research in 2020 and 2021 due to the global coronavirus pandemic. Our study took place at Pitzer College's Firestone Center for Restoration Ecology in Barú, Costa Rica (9° 18' N latitude, 83° 54' W longitude). The 60-hectare reserve and research station consists of mostly secondary growth rainforest and is adjacent to the 330 hectare Refugio Nacional de Vida Silvestre Barú. We also briefly looked for *T. clavipes* at the Alturas Wildlife Sanctuary 10 km away near Dominical, Costa Rica in 2019 and 2022, which is similar habitat. The wet season in this area of Costa Rica extends from May through September–November of one calendar year, and the dry season from December until April of the following year (Agnarsson 2003). Similar to the seasonal and tropical populations of *T. clavipes* in Panama, we assume that breeding happens at the end

of both the wet and dry seasons (Higgins 1992a, 2000), although we have not directly observed breeding in our study population. In temperate regions, the population can be univoltine, breeding at the end of the summer season, or facultatively bivoltine in subtropical areas (Moore 1977; Higgins 1992a, 2000). Females undergo six to ten molts of increasing size (Moore 1977; Higgins 2000). Males are primarily found on the webs of larger, mature females (Fincke et al. 1990). Asynchrony in reproduction and plasticity in female growth rate based on food intake can create populations with individuals of varying size classes (Moore 1977; Higgins 1992a, 2000; Higgins & Rankin 2001), which exist in our study population. The lifespan of *T. clavipes* is approximately one year in North America and probably longer in tropical regions (Moore 1977; Higgins & Rankin 2001).

Trichonephila clavipes females build their large orb webs in open forest or edge habitats of the tropical and subtropical Americas (Moore 1977; Fitzgerald & Ives 2017), either solitarily or in a cluster of 2–11 spiders (Ferree et al. 2018). The web serves primarily as a food capturing device with prey mostly consisting of flying insects, such as flies, moths, bees, and beetles. The smaller males cease to spin webs after maturation and then move onto the webs of mature females for courtship and mating (Moore 1977; Christenson & Goist 1979; Vollrath 1980). Several families of araneophagic spiders (Mimetidae, Oxyopidae, Salticidae) are potential predators of *T. clavipes* (Moore 1977; Vollrath 1980; Higgins 1992b), and we have observed jumping spiders (Salticidae) and kleptoparasites of unknown species consuming them. Kleptoparasites are also potential competitors, living on and consuming prey captured in females' webs (Agnarsson 2003). Birds and spider-hunting wasps are other predators (Higgins 1992b; Hodge & Uetz 1992; Rogers et al. 2012; pers. obs.), and parasitoid wasps kill females as well (Fincke et al. 1990; Durkin et al. 2021).

Data collection.—For six weeks each year, we added webs to the study as we encountered them along a 2 km dirt road ranging in elevation from 60 to 280 m, bordered by secondary growth forest. We monitored each web daily for three weeks or until the web was no longer in use, whichever came first. Upon initial discovery of a web, we measured female cephalothorax width in mm using digital calipers and the width of the web in m using a tape measure. Each morning between 0730 and 1200, we recorded the number of prey, kleptoparasites, and males within the webs. Larger prey items could be used as food for several days, while small prey items were eaten on the day of capture, and we counted both as an estimate of the relative amount of food available to a female on a given day (Rittschof & Ruggles 2010; Blackledge 2011; pers. obs.). In addition to recording the number of prey found within the web, we used sticky traps to attain an estimate of the number of flying insects in the study site in 2013, 2014, 2017, 2018 and 2019. We coated 20 semi-translucent, plastic, 6 oz drinking cups with Stickem Special (Seabright Laboratories, Emeryville, CA) and hung them at web height, 1–2 m from the ground, dispersed along the transect in the general vicinity of webs. After 24 hours, we counted the number of insect prey captured.

Webs could persist through the three-week observation period or become inactive for one of three reasons: depredation of the resident spider, relocation, or death in the web. If spiders were not present, but their webs remained, we assumed they had been depredated (Higgins 1992b; Hodge & Uetz 1992). We calculated

a 3-week predation rate for each year as the percent of spiders estimated to be depredated during their three weeks of observation. If a spider was gone and no web remained, we assumed it had consumed the web and moved away (Tanaka 1989; Higgins 1992b; Nakata & Ushimaru 1999). In a few cases, a female was found dead in the web. Furthermore, in several cases, we noted females turning into a dark color morph as well as the presence of parasitoid larvae on the spider; these observations were collected as anecdotes. Daily minimum and maximum temperatures were collected from a local weather station in Hacienda Barú, Dominical. Average monthly precipitation from within the Barú reserve was also obtained for the years 2013–2019. We also conducted brief, informal surveys of *T. clavipes* at Alturas Wildlife Sanctuary in 2019 and 2022 to assess relative abundance there compared to our main study site.

Statistical analysis.—All statistical analyses were conducted in R version 4.1.0 (R Core Team 2021). To examine the fluctuations in spider numbers, we first used a chi-square test to compare population size among years. To address our main question of what might account for the population fluctuations, we then compared the median number of prey, kleptoparasites, and males in webs among the years (Table 1). We calculated medians for each web, which were the average number of prey, kleptoparasites, and males in a web across the three-week observation period. We used medians to describe the average for each web rather than means, because the data within each web were not normally distributed. We compared the proportion of webs that had the following median prey: 0,1,2, or 3+, kleptoparasites: 0,1,2, or 3+, and males: 0,1, or 2+ among years with a separate contingency table analysis for each variable. Most of the variation in these data stemmed from whether there were on average any prey, etc. in a web, and so we then compared the proportion of webs that had a daily average of zero or one or more prey, kleptoparasites, and males (0, 1+) among years. Following significant overall results, further post-hoc contingency table analyses tested whether the proportion of webs with prey, kleptoparasites, and males (0,1+) differed in 2013–2015 compared to 2016 (the year before the population decline) and whether 2016 differed from 2017 (Table 1).

The sticky trap data, recorded as the number of prey per trap per day, met the assumption of equal variances but not normality. We applied a square root transformation and then conducted an ANOVA followed by Tukey HSD tests. The female cephalothorax width data were non-normal and could not successfully be transformed, so we used a Kruskal Wallis test followed by a post hoc multiple comparisons test with R package *pgirmess* (Giraudoux 2022). Finally, within each year we calculated the proportion of webs that were depredated or not and compared these proportions among years using a contingency table analysis.

We examined the temperature and rainfall data in relation to fluctuations in *T. clavipes* numbers. For temperature, we calculated the mean average daily temperature in Celsius from recorded daily maximum and minimum temperatures. The temperature data (minimum, maximum, and average) were assessed for normality and equal variances within the wet and dry seasons, and then six Kruskal Wallis tests (for each of three variables and two time periods) were conducted followed by post hoc multiple comparisons tests using the R package *pgirmess* (Giraudoux 2022). The rainfall data were recorded as total rainfall in mm for each month. Because the rainfall data were normally distributed with equal variances, we used ANOVA to compare average monthly rainfall among years.

Table 1.—Summary of predictions and results for comparisons of the median number (0 vs 1+) of prey, kleptoparasites, and males in *Trichonephila clavipes* webs among years.

	General prediction	2013–2015 vs 2016	2016 vs 2017
Prey	Least prey in 2016 and 2017	Not significant $\chi^2_1 = 0.27, P = 0.60$	More in 2017 $\chi^2_1 = 12.43, P = 0.0004$
Kleptoparasites	More kleptoparasites in 2016 and 2017	Less in 2016 $\chi^2_1 = 47.10, P < 0.0001$	Not significant $\chi^2_1 = 0.63, P = 0.42$
Males	Fewest males in 2016 and 2017	Not significant $\chi^2_1 = 0.49, P = 0.48$	Not significant $\chi^2_1 = 2.59, P = 0.11$

RESULTS

The number of spiders found on our study transect at the Firestone Center for Restoration Ecology differed significantly among years ($\chi^2_6 = 386.89, P < 0.00001$; Fig. 1). We encountered around 350 spiders on the transect in 2013–2015, with almost 450 in 2016. In 2017 there were fewer than 40 spiders, which then increased to around 250 spiders in 2018 and 2019. We did not collect data in 2020 and 2021 due to the global coronavirus pandemic. During a brief surveillance of the study site in 2022, we could not find any *T. clavipes* webs along the transect. At Alturas Wildlife Sanctuary 10 km away *Trichonephila clavipes* was relatively abundant in both 2019 and 2022.

Did biological factors relate to the population decline in 2017?—The proportion of webs with varying amounts of prey differed significantly among years (contingency table $\chi^2_6 = 252.22, P < 0.00001$; Fig. 2a), but prey were not scarcer in the year before (2016) the decline of 2017 or in 2017 itself (Table 1; Fig. 2a). The mean number of prey caught in sticky traps also varied significantly across years ($F_{4,95} = 7.214, P < 0.00001$; Fig. 2b), however, 2017 did not have fewer prey than other years. We did not use sticky traps in 2016. The presence of kleptoparasites differed significantly among years ($\chi^2_6 = 137.39, P < 0.00001$; Fig. 2c). Kleptoparasites were relatively rare in females’ webs in 2016 compared to earlier years but not compared to 2017 (Table 1).

Median female size varied significantly across years ($\chi^2_6 = 287.83, P < 0.00001$). In 2016, spiders were on average larger than in the two preceding years (2015 and 2014),

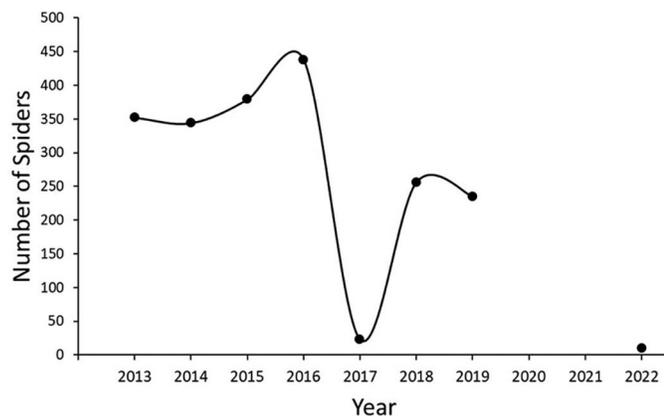


Figure 1.—The number of *Trichonephila clavipes* webs in each year. No data were collected in 2020 and 2021 (see Methods).

smaller than in 2013 (Kruskal-Wallis multiple comparison tests, $P < 0.05$), and did not differ from the average spider size in 2017 ($P > 0.05$; Fig. 3). The proportion of females that had, on average, zero males on their webs differed significantly among years ($\chi^2_6 = 47.91, P < 0.00001$; Fig. 2d), however, in 2016 males were not scarcer than in preceding years or in 2017 (Table 1).

Predation rates differed significantly across years ($\chi^2_6 = 148.71, P < 0.00001$), but the proportion of webs depredated during our observation period was not higher in 2016 compared to earlier years or compared to 2017 (2016 vs. 2013–2015: contingency table $\chi^2_1 = 0.16, P = 0.69$; 2016 vs. 2017: contingency table $\chi^2_1 = 0.013, P = 0.91$; Fig. 4).

A single dark-colored morph of female *T. clavipes* was first observed in 2016, the year before the population decline. Typically, a dark morph female made a small web, remained inactive, and then disappeared after a few days (Supplemental Fig. 1, Online at <https://doi.org/10.1636/JoA-S-22-046.s1>). Another dark *T. clavipes* color morph was observed in 2017, four in 2018 and three in 2019 within our study population. An ectoparasitoid larva was first noted on a *T. clavipes* female in 2014. Two spiders in 2018 and five spiders in 2019 were affected by what was presumed to be an ichneumoid wasp larvae (Supplemental Fig. 1; Fincke et al. 1990).

Did environmental factors relate to the population decline?—The average, minimum, and maximum temperatures in the dry season varied significantly across years (average: $\chi^2_6 = 127.30, P < 0.0001$; minimum: $\chi^2_6 = 129.07, P < 0.0001$; maximum: $\chi^2_6 = 185.68, P < 0.0001$). The average temperature in the dry season was significantly greater in 2015–16 than in all other years (Kruskal-Wallis multiple comparison tests, all $P < 0.05$; Fig. 5a), as was the minimum temperature (Kruskal-Wallis multiple comparison tests, $P < 0.05$). The dry season maximum temperature was also significantly higher in 2015–2016 than in 2013–14, 2014–15, 2016–17 and 2017–18 (Kruskal-Wallis multiple comparison tests, all $P < 0.05$).

The average temperatures in the wet season differed significantly across the years ($\chi^2_6 = 196.48, P < 0.0001$), but not with a consistent pattern ($P < 0.05$; Fig. 5b). The wet season minimum temperatures also varied significantly across the years ($\chi^2_6 = 125.25, P < 0.00001$), with the wet season of 2013 having a significantly lower minimum temperature than all other years except 2018 (Kruskal-Wallis multiple comparison tests, $P < 0.05$). The minimum temperature in the wet season was higher in 2015 and 2016 than in most years, before going down in 2017 and 2018 ($P < 0.05$). Lastly, the mean wet season maximum temperature differed significantly across the years ($\chi^2_6 = 259.70, P < 0.00001$), again with no consistent patterns. The max temperature in the wet

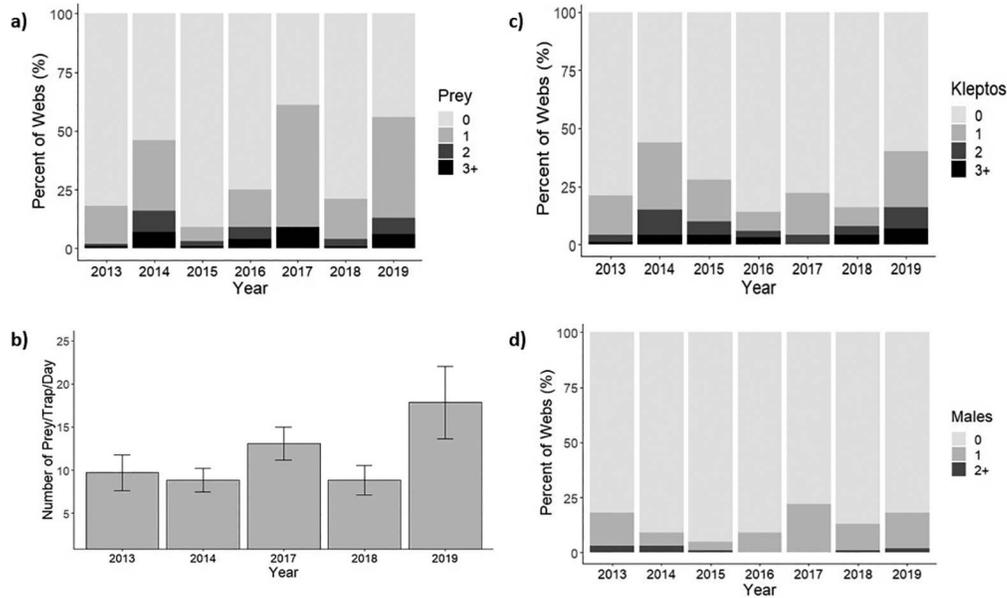


Figure 2.—(a) The percent of *Trichonephila clavipes* webs that had a given number of prey in each study year. (b) The number of prey caught in sticky traps in years in which those data were collected (mean \pm 95% CI; $n = 20$). The y-axis values were back-transformed. (c) The percent of *T. clavipes* webs that had a given number of kleptoparasites (kleptos) and (d) males in each study year.

season of 2016 and 2017 did not differ significantly, while 2015 was significantly warmer than both of those years. Mean monthly rainfall did not vary significantly across years ($F_{1,81} = 0.008$, $P = 0.93$; Fig. 6).

DISCUSSION

The purpose of our study was to investigate potential drivers of the observed population fluctuations in a Costa Rican population of golden silk orbweavers *Trichonephila clavipes* over more than seven years in the rainy season. The population declined from around 500 spiders one year (2016) to fewer than 40 the next (2017), and during a brief visit to the study site in

2022, researchers could not find any *T. clavipes* individuals when they would otherwise normally be abundant. Contrary to what we have observed at our study site, *T. clavipes* in a similar habitat 10 km away remained abundant. Based on the analysis of data from our study location, none of the measured biological or environmental factors relate to the 2017 decline of the study population. The relative abundance of prey, kleptoparasites, and males along with the average size of females did not indicate that the population would experience high mortality or low reproduction in either 2016, the year before the decline, or 2017 itself compared to previous years when the population was higher. We also expected increased predation before the decline, but the 3-week predation rate was not significantly higher before

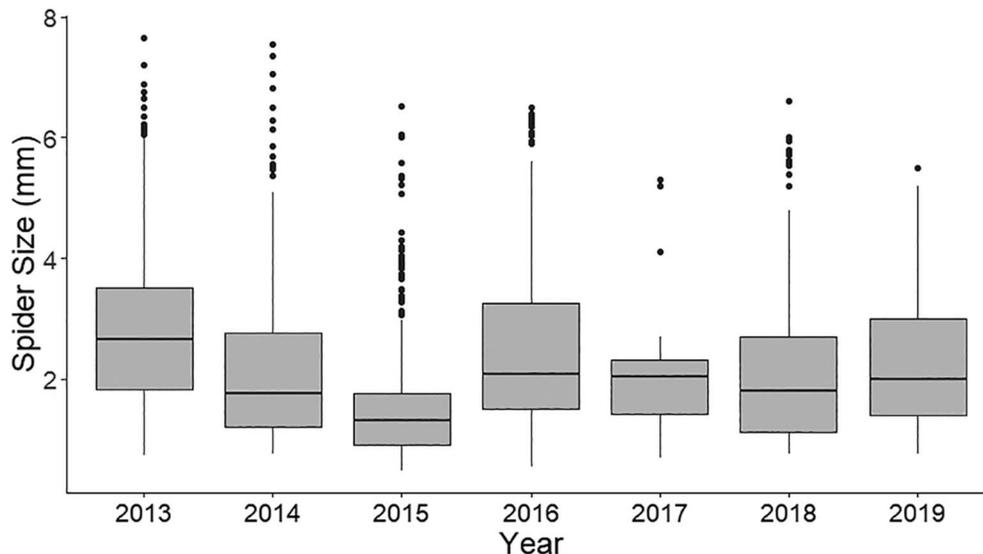


Figure 3.—Median female spider size (cephalothorax width in mm) with inter-quartile ranges across the study years (see Fig. 1 for sample sizes).

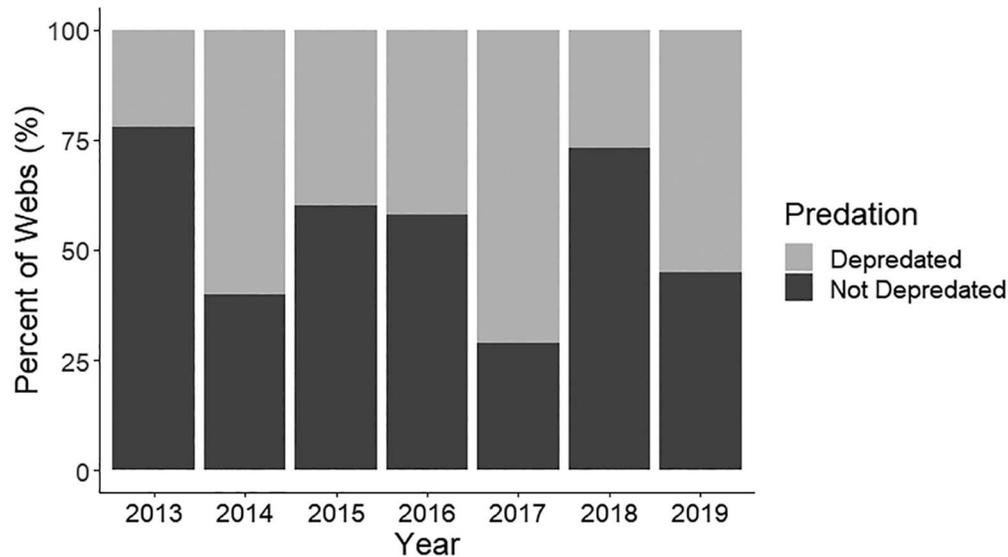


Figure 4.—The proportion of *Trichonephila clavipes* webs each year in which females were depredated or not during a 3-week observation period of each web.

or during the decline than in previous years with more robust populations. Cycles in populations are often driven by predators, parasites and food (Huntington 1931), but our estimates did not link predators and food to population dynamics in the studied population. Climatic variables, namely temperature and rainfall, likewise did not appear to relate to fluctuations in the population.

We predicted that having relatively few males and small females in 2016, both indicative of lower reproductive potential (Higgins 1992a), could have led to a low population size in 2017. Instead, the presence of males was similar across years, and females were comparatively large in 2016 and 2017, indicating that reproductive potential was likely not reduced in association with the population decline. Variation in food availability within and among years, as well as asynchrony in breeding cycles are likely causes of variation in female size (Higgins 1995, 2000), but in our population, prey abundance was not clearly related to variation in female size.

Two biological phenomena of interest include the observation of color morphing in our study population and the presence of parasitoid larvae on female *T. clavipes*. Dark color morphs of *T. clavipes* in the population were first observed in 2016, the year before the decline, and seen again in 2017–2019. When females darkened, they built small webs that failed to capture prey, before the females themselves disappeared. In related species, *Nephila pilipes* (Fabricius, 1793), dark morphs also exist, and in this morphology, females catch, on average, half as many prey as the typical, more colorful morph (Tso et al. 2002, citing specimens as *Nephila maculata*). The lower capture rates seemed more likely to be due to differences in UV-reflectance than to differences in web size, and in *N. pilipes*, dark morphs existed at stable frequencies, making up about 20% of the population. DNA analysis showed minimum genetic differentiation, but genetic changes could underlie the color morphing itself (Tso et al. 2002). Melanic morphs were rare in our study population (<1%) and seemed almost diseased in their behavior. Although worthy of further investigation, it is unlikely that their existence had a large impact on the overall population size of *T. clavipes*.

We observed ectoparasitoids affecting several *T. clavipes* individuals starting in 2014 and most noticeably in 2018 and 2019. An ectoparasitoid wasp was found in much higher numbers in a Panama population in 1984 and 1985, where it led to the rapid death of infected females and reduced the normal abundance of mature females prior to breeding (Fincke et al. 1990). Given the apparent rarity of parasitoids found here, it is unlikely that they had a huge effect on our study population. Additional research should examine the spiders for parasites and pathogens such as viruses, bacteria, mites, nematodes, and fungi, which are relatively understudied in arachnids (Durkin et al. 2021), as well as track the presence of ectoparasitoids.

In relation to climatic factors, we predicted that there would be uncharacteristically high temperatures in 2016 or 2017. Various studies have shown negative effects of climate warming on arthropod populations (Deutsch et al. 2008; Lister & Garcia 2018), and the critical thermal maximum is negatively related to female weight in *T. clavipes* (Krakauer 1972). The dry season was significantly warmer on average in 2015–16 than in all other years by about 1°C. It is unclear, however, how a warm, dry season in 2015–16 would not affect the population in the following wet season (2016) but have a negative impact a year later in 2017. The observed average temperatures (around 28°C) were not near the maximum critical temperature for most spiders, 40°C (Ferreira-Sousa et al. 2021), and variation in maximum temperatures at the study site did not relate to population patterns. Rainfall also did not clearly relate to variation in the *T. clavipes* population, but rather average monthly rainfall was relatively consistent among years.

Rather than our study population being in decline, an alternative explanation is that the timing of breeding and, therefore, female abundance shift among years. The peak abundance of *T. clavipes* females depends on the number and timing of breeding periods in the population (Higgins 1992a). In Barro Colorado Island, Panama, breeding occurs at the start of both the rainy and dry seasons, and females are most abundant during those periods (Lubin 1978; Higgins 1988). Females in Houston, Texas, USA,

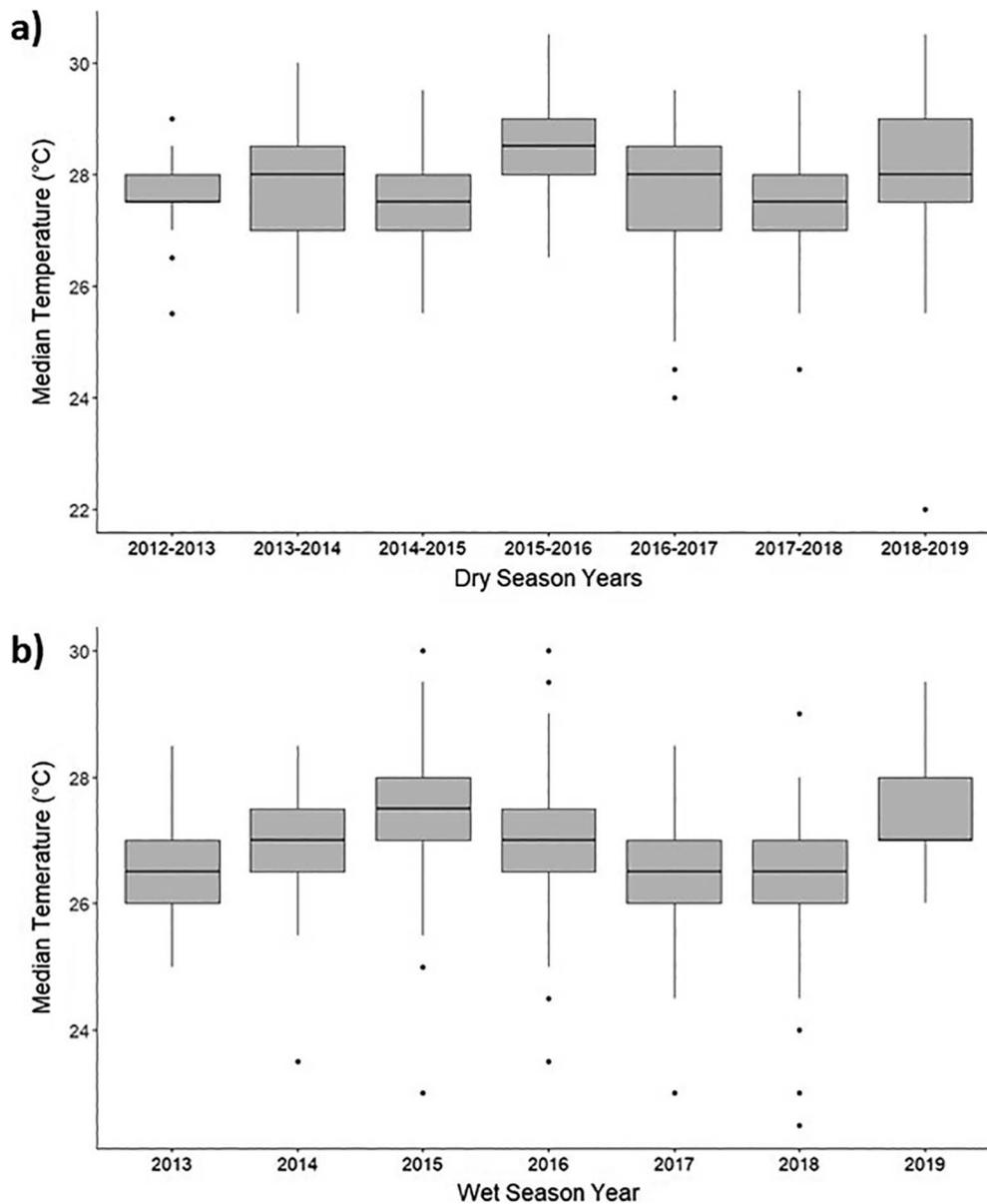


Figure 5.—(a) The median temperature in the dry season was greater in 2015–16 than in all other years ($n = \sim 180$ days per year). (b) The median temperature in the wet season went up from 2013 to 2015 and then down until 2018 before increasing again ($n = \sim 180$ days per year).

are univoltine and most abundant in August and September (Higgins 1988). Between these two extremes, in Los Tuxtlas, Veracruz, Mexico, females typically breed and are most abundant in August-September, but under certain conditions, breeding and high female density also occur in May when rains begin (Higgins 1992a). It could be that spiders in this Costa Rican population reflect patterns seen in the Mexican population of *T. clavipes*, where breeding and female abundance at the start of the wet season varies among years (Higgins 1992a). The fact that by 2022 spiders were still rare in the early rainy period is consistent with a temporal shift in breeding and, therefore, female abundance, or with a permanent decline. However, because *T. clavipes* have apparently remained abundant at a location only 10 km away from our study site, it appears that regional climatic conditions are not responsible for our localized population trends. The

comparison between locations, while intriguing, necessitates rigorous data collection contemporaneously at both sites.

What else could be affecting the study population on a local level? A factor not accounted for in our study is changes in forest structure that might influence web location and spider success. *Trichonephila clavipes* builds its web typically in light shade to mostly sunny conditions (Moore 1977). As the secondary forest along the study transect grows, it will provide increasing amounts of shade, which could negatively impact the spiders. Herbivores can also impact forest structure through their diet, which in turn, directly and indirectly, influences spider abundance and diversity (Landsman & Bowman 2017). It is unlikely that the forest in our study site changed quickly enough to cause a sudden population decline in 2017. Still, GIS modeling of forest structure would be useful for determining the long-term suitability of the study site

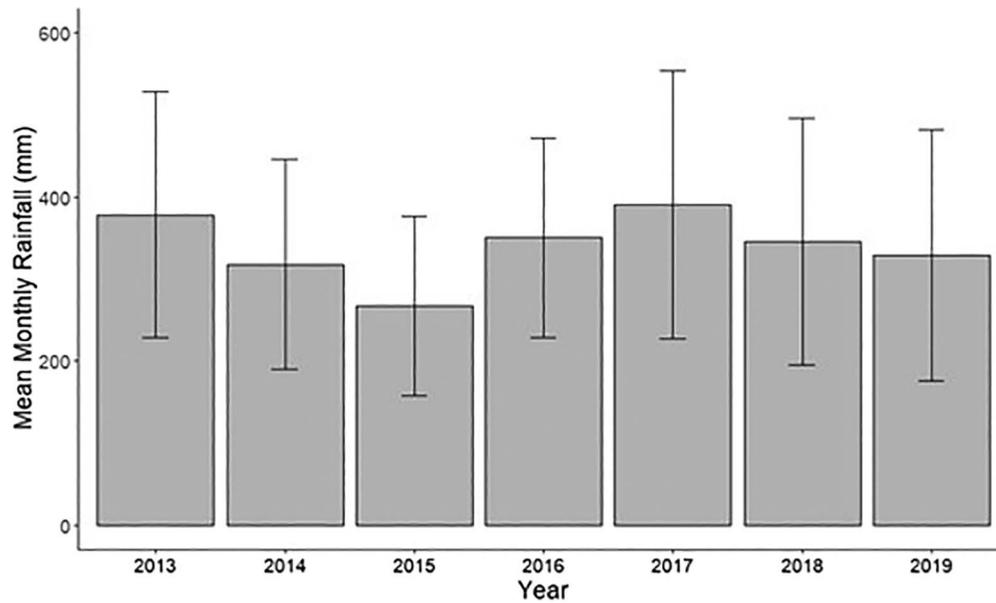


Figure 6.—Mean monthly rainfall (mm) across the study years (\pm 95% CI; $n = 12$).

for *T. clavipes*. Lastly, other spider species might be outcompeting *T. clavipes* and becoming dominant in the study site. Contrary to this idea, we have noticed a general decline in all spider species. For example, the yellow garden spider (*Argiope aurantia* Lucas, 1833) (Araneidae) was once common, but now hardly seen at our study site (pers. obs.).

While documenting relatively dramatic fluctuations in the population of golden silk orbweavers *T. clavipes* in Costa Rica over seven plus years, we are unsure whether these fluctuations represent an ongoing decline, periodic cycles, or shifts in the timing of reproduction. The biological and environmental data that we collected through daily monitoring at our study site do not correlate with the fluctuations. It is interesting to compare our spider population sizes to those in Europe, where long-term declines have been documented. In the time period from 2013–2019 (excluding 2017), we found about 100–200 *Trichonephila clavipes* spiders per 1000 m of walking distance, comparable to the average densities of large orbweavers (*Araneus diadematus*) in Western and Central Europe 40–50 years ago (Martin Nyffeler, pers. comm.; Nyffeler & Bonte 2020). In recent times, however, densities of only 1 spider per 1000 m of walking distance were recorded for *A. diadematus* in Switzerland and similar landscapes of Germany and France (Martin Nyffeler, pers. comm.; Nyffeler & Bonte 2020). The comparatively high orbweaver densities recorded at our study site in an average year could indicate that the tremendous arthropod die-off occurring in parts of Europe has probably not yet occurred in southwestern Costa Rica. That said, researchers documenting insect populations in a conservation area in northwestern Costa Rica (Area de Conservación Guanacaste) have seen insect species richness and density decline since 1970s, suggesting that the sixth mass extinction has arrived in at least some parts of Costa Rica (Janzen & Hallwachs 2021). Only future studies will indicate whether the extremely low population densities at our study site in 2017 and 2022 are part of a larger, global spider decline.

ACKNOWLEDGMENTS

We acknowledge the following individuals who collected data in the field: Daniella Barraza, Sophie Boerboom, Emma Crabo, Jenna Florio, Charlotte Garner, Haley Godtfredsen, Kennedy Holland, Kanyarat Jitmana, Stephen Johnson, River Joo, Kaya Mark, and Jiravit Moontep. We also thank Don McFarlane, Juan Carlos Araya, Greddy Arias, Giovanni Montoya, Marianela Fernández, and Warren Roberts for logistical support, Jack Ewing of Hacienda Barú for temperature and rainfall data, Matthew Faldyn for help with statistical analyses, and the editor and reviewers who helped improve the manuscript. We thank Pitzer College for access to the Firestone Center for Restoration Ecology. This work was supported by the Eaton Ecological Research Fellowship, the W.M. Keck Fund; the Norris Foundation; the Rose Hill Foundation; and Pitzer College.

SUPPLEMENTAL MATERIALS

Supplemental Figure 1.—Dark color morph of a female *Trichonephila clavipes* and parasitoid (most likely an ichneumonoid wasp ectoparasitoid) on a female *T. clavipes*' abdomen. Online at <https://doi.org/10.1636/JoA-S-22-046.s1>

LITERATURE CITED

- Agnarsson I. 2003. Spider webs as habitat patches: the distribution of kleptoparasites (Argyrodidae, Theridiidae) among host webs (*Nephila*, Tetragnathidae). *Journal of Arachnology* 31:344–349.
- Barraquand F, Louca S, Abbott KC, Cobbold CA, Cordoleani F, DeAngelis DL, et al. 2017. Moving forward in circles: Challenges and opportunities in modelling population cycles. *Ecology Letters* 20: 1074–1092.
- Blackledge TA. 2011. Prey capture in orb weaving spiders: are we using the best metric? *Journal of Arachnology* 39:205–210.

- Branco VV, Cardoso P. 2020. An expert-based assessment of global threats and conservation measures for spiders. *Global Ecology and Conservation* 24:e01290.
- Christenson TE, Goist KC. 1979. Costs and benefits of male-male competition in the orbweaving spider, *Nephila clavipes*. *Behavioral Ecology and Sociobiology* 5:87–92.
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105:6668–6672.
- Durkin ES, Cassidy ST, Gilbert R, Richardson E, Roth AM, Shablin S, et al. 2021. Parasites of spiders: their impacts on host behavior and ecology. *Journal of Arachnology* 49:281–298.
- Ferree E, Johnson S, Barraza D, Crabo E, Florio J, Godtfredsen H, et al. 2018. Size-dependent variability in the formation and trade-offs of facultative aggregations in golden orb-web spiders (*Nephila clavipes*). *Behavioral Ecology and Sociobiology* 72:157.
- Ferreira-Sousa L, Zepp P, Motta P, Gawryszewski F. 2021. Shaped by the Sun: the effect of exposure to sunlight on the evolution of spider bodies. *Biology Letters* 17.
- Fincke OM, Higgins L, Rojas E. 1990. Parasitism of *Nephila clavipes* (Araneae, Tetragnathidae) by an ichneumonid (Hymenoptera, Polysphinctini) in Panama. *Journal of Arachnology* 18:321–329.
- Fitzgerald MR, Ives AR. 2017. Conspecific attraction drives intraspecific aggregations by *Nephila clavipes* spiders. *Ethology* 123:51–60.
- Giraudoux P. 2022. pgirmess: Spatial analysis and data mining for field ecologists. R package version 2.0.0. <https://CRAN.R-project.org/package=pgirmess>
- Hallmann CA, Zeegers T, van Klink R, Vermeulen R, van Wielink P, Spijkers H, et al. 2020. Declining abundance of beetles, moths and caddisflies in the Netherlands. *Insect Conservation and Diversity* 13:127–139.
- Higgins LE. 1988. Variation in web structure in the orb-weaving spider *Nephila clavipes* and correlated changes in life history. Ph. D. Dissertation. University of Texas at Austin.
- Higgins LE. 1992a. Developmental plasticity and fecundity in the orb-weaving spider *Nephila clavipes*. *Journal of Arachnology* 20:94–106.
- Higgins LE. 1992b. Developmental changes in the barrier web under different levels of predation risk. *Journal of Insect Behavior* 5:635–655.
- Higgins LE. 1995. Direct evidence for trade-offs between foraging and growth in a juvenile spider. *Journal of Arachnology* 23:37–43.
- Higgins LE. 2000. The interaction of season length and development time alters size at maturity. *Oecologia* 122:51–59.
- Higgins LE, Rankin MA 2001. Mortality risk of rapid growth in the spider *Nephila clavipes*. *Functional Ecology* 15:24–28.
- Hodge MA, Uetz GW. 1992. Antipredator benefits of single- and mixed-species grouping by *Nephila clavipes* (L.) (Araneae, Tetragnathidae). *Journal of Arachnology* 20:212–216.
- Hunter MD, Price PW. 1998. Cycles in insect populations: Delayed density dependence or exogenous driving variables? *Ecological Entomology* 23:216–222.
- Huntington E. 1931. The Matamek conference on biological cycles. *Science* 74:229–235.
- Janzen DH, Hallwachs W. 2021. To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. *Proceedings of the National Academy of Sciences* 118:e2002546117.
- Jocque R, Samu F, Bird T. 2005. Density of spiders (Araneae: Ctenidae) in Ivory Coast rainforests. *Journal of Zoology* 266:105–110.
- Krakauer T. 1972. Thermal response of the orb-weaving spider *Nephila clavipes*. *American Midland Naturalist* 88:246–250.
- Landsman AP, Bowman JL. 2017. Discordant response of spider communities to forests disturbed by deer herbivory and changes in prey availability. *Ecosphere* 8:e01703.
- Lister BC, Garcia A. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences* 115:E10397–E10406.
- Lubin YD. 1978. Seasonal abundance and diversity of web-building spiders in relation to habitat structure on Barro Colorado Island. *Journal of Arachnology* 6:31–35.
- Meineke E, Holmquist AJ, Wimp GM, Frank SD. 2017. Changes in spider community composition are associated with urban temperature, not herbivore abundance. *Journal of Urban Ecology* 3:juw010.
- Møller AP. 2019. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution* 9:6581–6587.
- Moore CW. 1977. The life cycle, habitat and variation in selected web parameters in the spider, *Nephila clavipes* Koch (Araneidae). *The American Midland Naturalist* 98:95–108.
- Nakata K, Ushimaru A. 1999. Feeding experience affects web relocation and investment in web threads in an orb-web spider, *Cyclosa argenteoalba*. *Animal Behaviour* 57:1251–1255.
- Norma-Rashid Y, Zainudin WMAW, Dzulhelmi MN, Masduki N. 2014. Spiders as potential ecofriendly predators against pests. Pp. 245–254. In Basic and Applied Aspects of Biopesticides. (K Sahayaraj, ed). Springer-India, New Delhi.
- Nyffeler M, Bonte D. 2020. Where have all the spiders gone? Observations of a dramatic population density decline in the once very abundant garden spider, *Araneus diadematus* (Araneae: Araneidae), in the Swiss Midland. *Insects* 11:248.
- Öckinger E, Smith HG. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology* 44:50–59.
- Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rittschof C, Ruggles K. 2010. The complexity of site quality: Multiple factors affect web tenure in an orb-web spider. *Animal Behaviour* 79: 1147–1155.
- Rogers H, Lambers JHR, Miller R, Tewksbury JJ. 2012. 'Natural experiment' demonstrates top-down control of spiders by birds on a landscape level. *PLOS ONE* 7:e43446.
- Sánchez-Bayo F, Wyckhuys KAG. 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* 232:8–27.
- Schuch S, Wesche K, Schaefer M. 2012. Long-term decline in the abundance of leafhoppers and planthoppers (*Auchenorrhyncha*) in Central European protected dry grasslands. *Biological Conservation* 149:75–83.
- Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D, et al. 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574: 671–674.
- Shochat E, Stefanov WL, Whitehouse MEA, Faeth SH. 2004. Urbanization and spider diversity: influences of human modification of habitat structure and productivity. *Ecological Applications* 14:268–280.
- Shrewsbury P, Raupp M. 2006. Do top-down or bottom-up forces determine *Stephanitis pyrioides* abundance in urban landscapes? *Ecological Applications* 16:262–272.
- Tanaka K. 1989. Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*. *Oecologia* 81: 459–464.
- Tso IM, Tai PL, Ku TH, Kuo CH, Yang EC. 2002. Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Animal Behavior* 63:175–182.
- Vollrath F. 1980. Male body size and fitness in the web-building spider *Nephila clavipes*. *Zeitschrift Für Tierpsychologie* 53:61–78.
- Wepprich T, Adrion JR, Ries L, Wiedmann J, Haddad NM. 2019. Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLOS ONE* 14:e0216270.
- Yang LH, Gratton C. 2014. Insects as drivers of ecosystem processes. *Current Opinion in Insect Science* 2:26–32.