

## Research

# Climate Change, Succession, and Reproductive Success of a Praying Mantid

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## Abstract

We examined the adult phase of the Chinese praying mantid, *Tenodera aridifolia sinensis* (Saussure) (Mantodea: Mantidae) at the end of five growing seasons spanning two decades (1999–2018) in a successional old field. Sex ratio, which is generally male-biased by the time all members of a cohort are adults, exhibited a steady decline in proportion of males and eventual reversal by 2016, even though the calendar time of the study did not vary among years. Increasing length and warmth of the growing season resulted in earlier maturation, so we were seeing later portions of the adult phase at the same calendar time over successive years. This result is consistent with the earlier-published hypothesis that global warming can reduce fitness by warming and extending the growing season: earlier maturation results in earlier oviposition, which in turn causes eggs to hatch before onset of winter, thereby dying before egg diapause can occur. This may push the latitudinal distribution of this, and of other univoltine semelparous insects, farther north as the climate continues to warm. Reproductive output for the population, measured as total number of eggs produced by a cohort, peaked in 2004 at 8,514 and then fell to 226 by 2018, as did estimated numbers of adults. This decline was probably due to shrinkage of the open field area where prey were more abundant, by more than 2/3 as cedar trees replaced herbaceous vegetation during plant secondary succession. This is consistent with the hypothesis that succession limits the residence time in a habitat for these mantids.

**Key words:** climate change, global warming, mantid population, old-field succession, praying mantid

Animals living in habitats that experience changing environments over time have three basic choices: adjust to new conditions, find another habitat, or face extirpation. Adjustment of populations may be short-term when environments are prone to stochastic variation, involving phenotypic plasticity of individuals or phenotypic polymorphism in which some individuals are preadapted to changing conditions in the environment (Levins 1968). Over longer time, adjustment can be in the form of evolutionary changes in gene structure and niche dimensions. Finding new habitats when local conditions deteriorate can involve metapopulation dynamics and source-to-sink dispersal when regional populations inhabit a number of independent local habitats that have sufficient connectivity among them, an important issue in conservation biology generally (Hanski and Gaggiotti 2004, Hurd et al. 2016).

For relatively predictable, natural, changes such as seasonality, the strategy of finding another place to live rather than going dormant (e.g., diapause over winter) may take the form of regular migration back and forth between seasonally suitable locations for feeding and/or reproduction, sometimes over great geographical distances (Chapman et al. 2015). As global climate change advances and the onset of spring in temperate zones comes earlier, individuals

of some migratory species may have sufficient phenotypic plasticity to adjust their life history phenologies to new seasonal timing in resource availability (e.g., birds: Charmantier et al. 2008).

Most animals are insects, and insect populations are subject to all of the above. Insect metapopulation structure (Thomas and Hanski 2004), seasonal migration (Howard and Davis 2015), and responses to climate change (Kingsolver et al. 2011, Reddy et al. 2015) are becoming increasingly well-represented in the literature. Insects are among the taxa that are declining in diversity and abundance during the Anthropocene (Hallmann et al. 2017, Youngsteadt et al. 2019), so we need to know more about what constitutes reduced habitat quality, and how insects are affected by changes in the environment.

Ecosystem succession is a natural environmental change that has long been known to have profound effects, both on insects and how insects affect plant assemblages (Brown and Southwood 1983, Brown and Gange 1992). The plant assemblage, in turn, and its change over successional time ultimately determines the suitability of the habitat for many species of arthropods (Schaffers et al. 2008). For highly mobile flying insects that exist as metapopulations, movement from a site that has aged out of a suitable place to live to a younger one within its

region would seem to be a simple matter. For many species that are not able to disperse so easily, that option can be problematic. The Chinese praying mantid, *Tenodera aridifolia sinensis* (Saussure) (Mantodea: Mantidae) is an inhabitant of early to middle seral successional old fields where it is a member of the generalist predator guild (Hurd and Eisenberg 1990). Although both adult males and females have functional wings, only males are capable of sustained flight, and therefore, colonization of younger seral habitats not immediately adjacent to those that have developed too far in succession is apt to be very slow or impossible if these insects are left to their own devices. It is therefore doubtful that they fit the metapopulation paradigm, and most probable that their wide geographic range has been achieved by a combination of accidental and purposeful distribution by humans (Hurd 1999). These insects are primarily found in the herbaceous vegetation where arthropod prey are plentiful, so that tree encroachment reduces the useful habitat for them. Rose and Hurd (2016) hypothesized that succession to a tree-dominated site was responsible for population decline in two congeneric mantids occupying an old field in eastern Virginia, *T. a. sinensis* and *Tenodera angustipennis*.

The impact of climate change on the environments of insects is of signal importance to researchers (ESA 2019). Much of the literature on insect responses to climate change involves temperature effects on life history phenology of herbivores (see review by Bale et al. 2002). However, a comparison of the movement capabilities of the predator, *T. a. sinensis*, with rates of latitudinal shifting predicted by models of global warming in the north temperate zone suggests the hypothesis that they cannot move fast enough on their own to escape encroachment of an untenable seasonal environment on their present range (Rooney et al. 1996). The impact of these predators on the prey community can be significant, resulting in trophic cascades down to the primary producer level (Moran et al. 1996, Moran and Hurd 1997). Therefore, whatever alters the demography of these generalist predators can have community-wide effects.

We report on a census of adult praying mantids during their reproductive period, in 5 yr spaced out over two decades, as an exercise in the laboratory portion of a university ecology course. Since both succession and climate change occurred over this period, we were especially interested in how this population may have responded to the challenges imposed by these processes.

## Materials and Methods

### Study Site

The site was a successional old field adjacent to an unmanaged, cedar-dominated wooded area in Rockbridge County, Virginia on the campus of Washington and Lee University in Lexington. This field had a history of annual mowing until 1995, when it was fenced off for use as a study site for a field ecology laboratory. From 1995 to 2018 the field underwent a successional sequence typical of the region, from open field with herbaceous vegetation (chiefly stickweed, goldenrod, asters, and milkweed) replacing grasses, and gradually colonization by trees (mainly red cedar) that grew in height and girth such that the amount of open field diminished over the years. This field was naturally colonized by Chinese mantids (*T. a. sinensis*) sometime between 1995 and 1998, and these were the subject of population biology exercises (described below) at irregular intervals over two decades: 1999, 2004, 2012, 2016, and 2018.

### Sampling Procedure

As adults, *T. a. sinensis* are ideal subjects for this kind of study because they are large enough (7–10 cm length) to be conspicuous,

they are easily captured and marked, and they are not subject to appreciable dispersal to or from the field (Eisenberg et al. 1992). The procedure for sampling was for the students to form a skir-mish line across the field and carefully walk through the vegetation to search for mantids until the entire field area had been traversed. Each mantid was marked on the prothorax with a felt-tipped pen with permanent ink, sex was determined, and then the insect was released. On the following sample date, 1 wk later, the collection contained both marked (recaptured) and unmarked individuals and were recorded as such in order to calculate an estimated population size on the first sample date using the Lincoln Index, as described in Hurd et al. (1994).

During the week prior to the beginning of each sampling procedure, L.E.H. made a brief visual survey of the study site to determine whether the mantid population appeared to have reached the adult stage, and would, therefore, be ready for the planned exercise. Marking mantid nymphs is problematic since they lose the mark when they molt. One or two late instar nymphs were noticed at that time in 1999 and 2004, but not in 2012, 2016, or 2018. No nymphs were found in any sample year by the time of the beginning of the exercise. Although different groups of students were involved in the lab each fall during which the course was taught, sampling procedure did not vary among years, and the first sample was taken at essentially the same time of the calendar each year: 14th in 1999, 13th in 2004, 12th in 2012, 13th in 2016, and 13th in 2018.

At the end of the growing season, frost kills both the adult mantids and most of the open field above-ground vegetation, making it easy to find and collect the oothecae from leafless stalks and tree branches. Females tend to oviposit on the ends of lower tree branches or stalks of forbs, but oothecae are easily spotted on either kind of vegetation. All oothecae in the field site were collected, brought into the laboratory and weighed, after which they were returned to the field and attached to oviposition sites so that the population could continue. Oothecae that were found on cedar branches, which were the majority of them, were replaced by wedging them into the fork of a branch. Those oviposited on forb stalks were attached by tying on with sewing thread run through the dried foam surrounding the eggs. One of the oothecae collected in 2018 hatched in the lab before it could be returned to the field, and several weeks before killing frost.

### Data Collected

For all years, population size was estimated and sex ratio (male N/total N) was determined for the first sample date, and reproductive output was determined following the end of the growing season (i.e., after killing frost). The sex ratio of the adult population changes because, because females attract males and sometimes eat them, which causes disproportionate male mortality (Hurd et al. 1994: see Discussion). Thus, over the course of the adult phase, the later the sample occurs the smaller the proportion of males. Therefore, the sex ratio is an indicator of how late in the adult phase of the life cycle the first sample was taken, even though the calendar date of the sample remained essentially constant. The square roots of the sex ratios of males/total N were log-transformed and subjected to linear regression to test the null hypothesis that there was no significant change over time.

The area of the open field portion of the study site also was measured each year of sampling in order to get an estimate of population density as the open field habitat diminished by virtue of tree encroachment. These mantids are univoltine, hatch early in the spring, and require the relatively high arthropod prey densities in open field

areas to feed and complete their life cycle by the end of the growing season (Hurd 1999). Oothecae were counted and weighed to determine number of eggs according to the regression of ootheca mass on number of eggs provided by Eisenberg and Hurd (1977).

## Results

Over the nearly two decades of this study, the open area of the field declined steadily as cedar trees gradually replaced herbaceous vegetation, such that the open field habitat in 2018 was less than a third of the area in 1999 (Table 1). Both estimated adult population size and density increased from 1999 through 2012, and declined thereafter, reaching the lowest values in 2018. Reproductive success measured as the number of oothecae produced was higher from 1999 to 2012 than during 2016 and 2018. The number of eggs per ootheca was highest in the three middle years, and lowest in the last year. The most important numbers, from the standpoint of population growth, are the total numbers of eggs produced by a cohort at the end of each year ( $\Sigma$  eggs, Table 1), which was highest in 2004, whereas in 2018 it was more than an order of magnitude lower than previous years and the product of only three very small oothecae, with the combined egg total of one moderate-sized ootheca (Eisenberg and Hurd 1977).

Sex ratio at the same calendar time each year, measured as the number of males relative to total estimated adults, declined steadily from 1999 to 2018 (Fig. 1). The ratio remained above 0.5 until 2012, and then dropped well below that value by 2018. The negative relationship was significant in linear regression ( $R^2 = 0.7973$ ;  $P = 0.04$ ).

## Discussion

There are two main conclusions we make from the data in this study. First, decreasing open field habitat area over two decades of old-field succession is largely responsible for the decline in adult population numbers and reproductive output from 2012 to 2018. Second, the life cycle of these mantids has shifted so that maturation occurred successively earlier over the two decades. Therefore, we were actually sampling later during the adult phase each year, which means that each year there was more time for adult mortality to occur, especially among males, before the actual samples were taken. However, the reduction in both number of oothecae produced and in total eggs from 2012 to 2018 (Table 1) argues that the population itself was, in fact, declining during that period.

The reduction in population size as the open field area got smaller is not surprising, and in fact has been suggested previously (Rose and Hurd 2016, Gall et al. 2017), but area was not quantified. The fact that the population increased in both size and density from 1999 to 2012 could simply be because it had so recently colonized the field and was still expanding in response to a relatively large space with abundant prey. The peak year for abundance was 2012, but oothecae from that year were substantially smaller than in 2004 or 2016, which may indicate an effect of intraspecific competition. Both

2004 and 2012 exhibited very high recruitment potential based on total eggs produced. The last 2 yr, 2016 and 2018, showed a sharp decline in abundance and density, but reproductive output remained high in 2016 by virtue of heavier, though fewer, oothecae produced. The 2018 cohort produced only three very small oothecae, and consequently, many fewer eggs.

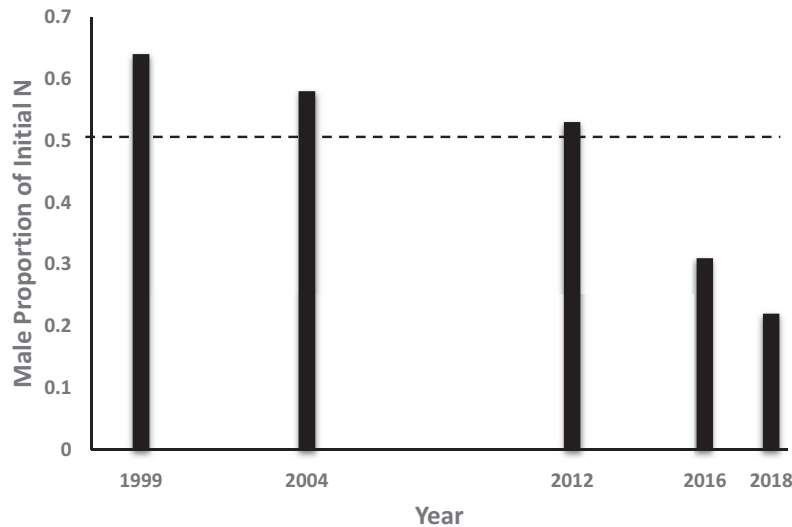
The length of the growing season in the United States, as well as temperature, have steadily increased for almost four decades (Kunkel 2016). This means that the growing season begins earlier and ends later, so that *T. a. sinensis* would have been hatching earlier, developing faster, and therefore reaching maturity earlier at the end of the summer. Added to this is that summers in the North Temperate are getting warmer (Monahan et al. 2016) which, even without the increased season span, increases development rate (Hurd et al. 1989). Thus, egg production would be earlier, and the earlier oothecae are produced the earlier they will hatch (Hurd et al. 2004). Since eggs of this species begin developing as soon as oothecae are produced they will develop until frost brings a halt to the process. The longer the time between oviposition and killing frost, the greater the likelihood that nymphs will hatch during the fall and be killed by frost before winter diapause (Hurd 1999).

Sex ratio of *T. a. sinensis* at the beginning of the adult portion of the life cycle is generally male-biased (Hurd et al. 1994), although at egg hatch the sexes are evenly split (Moran and Hurd 1994), so females must have a lower survival rate as nymphs than males. However, the relative survival advantage that males enjoy during their developmental phase disappears when they are adults, chiefly because males have at least one more predator to contend with than females have: males are frequently eaten by females (ca. 17% per encounter: Hurd et al. 1994) before, during, or after copulation. Male *T. a. sinensis* in the field show no ability to assess risk of cannibalism when approaching a female, unlike the laboratory results of a different species from South America, *Parastagmatoptera tessellata* (Scardamaglia et al. 2015).

Since both males and females can mate more than once, the cumulative probability of being eaten by a female increases with the number of intersexual encounters. The main evidence that climate change in Virginia has altered the phenology of the life cycle of this mantid is that the initial sex ratio of adults was male-biased in 1999, 2004, and 2012, but the bias was successively smaller, and sex ratio was decidedly female-biased in 2016 and 2018. Our record of sampling over the two decades admittedly is sporadic, but the pattern of decline in male proportion of the population over those years mimicked what has been found over the course of any single season. In fact, the pattern shown in Fig. 1 of this article fits the 4-wk decline in mean male proportion for three consecutive years shown by Fig. 1 in Hurd et al. (1994). Accordingly, it is tempting to suggest that maturation occurred 1 mo earlier in 2018 than in 1999, but warmer summers also decrease time in stadium by as much as 1 d for every degree Celsius increase (Hurd et al. 1989), so over the course of seven stadia an average of 1°C could speed up development by a week.

**Table 1.** Population size and reproductive output of mantid cohorts, 1999–2018: Area of open field ( $m^2$ ), marked sample size of first capture (M), estimated initial number of adult mantids from Lincoln index (Est.N), estimated initial population density (Est.N/ $m^2$ ), total number of oothecae, mean  $\pm$  SE eggs per ootheca, and total number of eggs produced by each cohort ( $\Sigma$  eggs)

Year	$m^2$	M	Est.N	Est.N/ $m^2$	Oothecae	Eggs/ootheca	$\Sigma$ eggs
1999	1,101	43	98	0.09	51	90.4 $\pm$ 52.2	4,609
2004	848	56	110	0.13	39	218.3 $\pm$ 55.2	8,514
2012	799	72	288	0.36	44	168.1 $\pm$ 57.7	7,395
2016	402	17	68	0.17	26	225.5 $\pm$ 59.4	5,864
2018	337	9	14	0.04	3	75.4 $\pm$ 54.3	226



**Fig. 1.** Sex ratio of adult *Tenodera aridifolia sinensis* expressed as male proportion of all mantids collected at the beginning (essentially the same calendar date) of the mark-release-recapture exercise on each year of the study.

Two incidental bits of evidence in support of the effect of longer and warmer growing seasons on mantid phenology are: 1) Except for the first 2 yr, 1999 and 2004, no immature individuals were seen in the study field in the week prior to the beginning of the exercise; 2) One of the oothecae collected in 2018 hatched shortly after being collected that fall and well before killing frost. The nymphs from this ootheca would not have survived the onset of winter.

We were, of course, only looking at the adult phase of univoltine mantid cohorts that had been in the field since hatching the previous spring each year, and we have no data on the number of eggs produced by their parental cohorts the previous fall because no 2 yr were sequential. We also lack data on the survival trajectory from egg to imago for all these years. Aside from temperature, food availability exerts a major influence on development and body size. Mantid nymphs will increase in linear size by an order of magnitude from hatching to adult, over which feeding opportunities will vary considerably among members of a cohort, resulting in appreciable asynchrony in phenology of reproduction (Hurd 1999). Although most of their diet will consist of arthropods, a laboratory experiment (Beckman and Hurd 2003) indicates that both nymphs and adults can benefit from pollen feeding as well. Adult female *T. a. sinensis* found on flowers late in the season produce more eggs than those found on flowerless vegetation (Hurd 1989), both because flowers attract prey and possibly because they also provide pollen. We know from stable isotope analysis of field-caught nymphs that as they grow in size they also shift trophic levels, beginning with herbivorous prey and gradually including a higher proportion of carnivores in the diet (Hurd et al. 2015). The relative abundance of food items of different trophic levels is therefore also likely to influence growth, and this is something that could easily vary within and between growing seasons.

According to data from six fields in Maryland and Virginia over a combined total of 12 seasons, survival from egg hatch to imago averaged about 6%, with a range of 0–17% (Hurd et al. 1995, 2004). Using these percentages, the eggs produced by our 2018 cohort (226) might be expected to produce 14 adults in the fall of 2019, five or six of which would be females, but might range from zero to as many as 38 with 15 females. However, L.E.H. was able to find no mantids at the site on 19 September 2019, and thorough inspection on 4 November 2019, following frost, turned up no oothecae.

As the growing season continues to get longer and warmer, female mantids will begin to produce their first oothecae earlier in the fall. However, females of this species are capable of producing at least four oothecae, with 8–10 d between subsequent oviposition (Eisenberg et al. 1981). Therefore, if prey are abundant enough and for long enough, continued egg production over the extended fall offers a chance of successful recruitment from later oothecae, potentially a preadapted measure to survive global warming. However, the evidence is that mantid reproduction is markedly food-limited at the end of the season (Hurd 1999), or at least nitrogen-limited (White 1993). Finally, the pressures on *T. a. sinensis* will also apply to other insects and spiders with similar univoltine, semelparous life cycles as they face a rapidly changing seasonal environment.

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