Cohabiting With the Enemy: Comparative Population Ecology of Two Mantid Species in a Successional Old Field

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Abstract

Two praying mantids, *Tenodera aridifolia sinensis* Saussure and *Tenodera angustipennis* Saussure, are commonly found in the same old-field habitats in the eastern United States and in much of temperate zone Asia. Naturally established populations of these two species were studied intensively over two consecutive years (2010 and 2011) in an old field in southeastern Virginia, to compare life history features relevant to how they coexist, or whether one or the other of them is likely to be more successful in the same habitat. Populations of both species declined about 50% from 2010 to 2011 (adults from 47 to 21 for *T. a. sinensis*; 37 to 20 for *T. angustipennis*), but *T. a. sinensis* oviposited 10 oothecae and *T. angustipennis* only one in 2011. *Tenodera a. sinensis* was more abundant in the study site in both years, hatched earlier, and matured and oviposited earlier than *T. angustipennis*. Fewer females of both species survived to maturity in 2011 than in 2010, possibly indicating a reduction in prey or habitat suitability in 2011. We suggest that *T. angustipennis* will always be at a disadvantage as a result of its smaller body size, because of interspecific predation (and potentially competition) from its congener, lower clutch size, and susceptibility to egg parasitism. Further, environmental variability across field habitats and years profoundly affects populations of both species in successional old fields.

Key words: competition, guild, population regulation, praying mantid, predator coexistence

How similar species coexist in a resource-limited environment is the question underlying the principle of competitive exclusion (Hardin 1960). The answer to this question is embodied in the concept known as guild (Root 1967), in which common resources are partitioned by morphological or behavioral differences among potential competitors, such that each species has a nonoverlapping temporal or spatial portion of the resource niche space.

Two praying mantid species, *Tenodera aridifolia sinensis* and *Tenodera* (or *Paratenodera*) *angustipennis*, are members of the arthropod generalist predator guild that commonly share the same habitats in Asia (Yan et al. 1981) and in eastern North America (Rathet and Hurd 1983). These two mantids are widely distributed in Asia, and are now common in much of the eastern United States. *Tenodera a. sinensis* first appeared near Philadelphia, PA, in 1896 (Laurent 1898), and *T. angustipennis*, which is 10–15% shorter in body length, has been present in the United States at least since 1926 (Jones 1933, Gurney 1950). These two species share a long residence time in temperate zone communities, hatching in the spring and maturing over the summer to oviposit in the fall and die at the first killing frost. However, there are several factors elucidated in earlier

studies that lead us to hypothesize that *T. angustipennis* is likely to be less abundant and less persistent than its congener in fields where both occur.

As with many predators in nature, both *Tenodera* species are food limited in nature (Matsura et al. 1975, Eisenberg et al. 1981, Matsura and Morooka 1983, Matsura and Nagai 1983). Although similar in body size and breadth of diet, they differ in the timing of egg hatch in the spring, with *T. a. sinensis* hatching about 2 wk earlier than *T. angustipennis* (Hurd 1988). *Tenodera angustipennis* perches and oviposits higher in vegetation of the successional old fields they share as habitats, perhaps reducing contact with its larger congener (Hurd and Eisenberg 1989, Eisenberg and Hurd 1993, Hurd 1999). These niche differences may help explain how these two mantids might coexist, but competition avoidance is not the only factor. Experimental studies (Hurd 1988, Snyder and Hurd 1995) have shown that intraguild predation between these species can be important, with the earlier-hatching and consequently larger *T. a. sinensis* able to eat its smaller congener.

Another factor is that these two species differ in the number of eggs produced and in the vulnerability of their egg masses to

parasitism. The (fewer) eggs of *T. angustipennis* in each ootheca have a relatively thin layer of froth surrounding the egg mass, which allows parasitoid wasps (*Podagrion mantis* Ashmead: Fox (1939)) to reach the egg layer with their ovipositors, whereas the much thicker froth surrounding eggs of *T. a. sinensis* prevents successful oviposition. Because the rate of parasitism of mantid eggs is positively density-dependent (Fagan and Polarin 2001), egg loss to parasites may be an important contributing factor for regulating populations of *T. angustipennis* (Rose and Hurd 2016).

Although aspects of the ecology of these two species have been studied separately, there are few comparative studies of their population biology and life histories in a shared habitat. Rose and Hurd (2016) reported on a 7-yr assessment of reproductive output for these two species in a successional field where both species had become naturally established. The results of that study indicate that *T. angustipennis* was initially more abundant than *T. a. sinensis*, possibly owing to earlier colonization of the site, but that the population of *T. angustipennis* declined thereafter while *T. a. sinensis* abundance increased steadily over the first 6 yr. Decline in the population of *T. angustipennis* was hypothesized to be at least partly the result of increasing egg parasitism by a wasp, which does not occur in oothecae of *T. a. sinensis*. In the seventh year, *T. angustipennis* was virtually absent from the study area and *T. a. sinensis* declined sharply, plausibly because the site had become dominated by trees, reducing the availability of suitable open-field habitat for both mantids. Here, we report on the complete life cycles of these mantids over two growing seasons in a different area of the same field to compare life history characteristics that may be important to understanding how (or whether) these two closely related members of the same guild partition their environment.

Materials and Methods

Study Site

Our 2-yr study was conducted in an old field known as the Dixon Tract, on the Eastern Shore of Virginia National Wildlife Refuge, in extreme southern Northampton County, VA (latitude 37.136; longitude -75.964). The 890- by 340-m (~30-ha) property was undergoing secondary succession after the former agricultural field became part of the refuge in September 2006 (www.fws.gov). In early June 2010, when the first searches for mantids were made, the field had a mixture of grasses, shrubs, and young trees. The site was bordered on the west by a ribbon of dense pine forest, beyond which lay the Chesapeake Bay, by U.S. highway 13 on the east, and by commercial and residential properties to the north and south. Little bluestem (*Schizachyrium* spp.) and panic (*Panicum* spp.) grasses, goldenrods (*Solidago* spp.), and dog fennel (*Eupatorium capillifolium*) were the dominant herbaceous plants, and groundsel bush, *Baccharis halimifolia*, up to 3 m in diameter, was the dominant shrub. Scattered eastern red cedar trees, *Juniperus virginianus*, were the common small tree, and the common vines were Japanese honeysuckle (*Lonicera japonica*) and creeping blackberry (*Rubus argutus*). (A more complete list of vegetation on the Dixon Tract is available at <http://www.fws.gov/northeast/easternshore/>). Southern Northampton County narrows to a point of land between the Atlantic Ocean and Chesapeake Bay, producing a maritime climate with long hot summers, late frosts (often in December), short mild winters, and cool springs.

Sampling Procedure

We established a marked area of 1562 m² near the western edge of the old field, with boundaries marked by 76-cm blue surveyors'

flags. In 2010, we visited each plot twice a week for a total of 36 visits, from 14 June to 31 October. In 2011, we searched 25 times at regular intervals from 11 April to 16 October. During each visit, we searched for mantids while slowly walking back and forth in the same manner, and for the same period of time (i.e., comparable sampling effort), ~4 h. Each imago was given a unique number on the prothorax using an indelible marker. In brief, we recorded the life history milestones for both species over the course of both growing seasons. We also searched for oothecae each visit, beginning with the appearance of adult mantids, and marked the location of each ootheca with colored plastic flagging to prevent repeated counts.

Definitive identification and sex of each species cannot be determined in the field until the third instar is reached, at which point the two species differ in the color of a spot between the prothoracic coxae: pale yellow in *T. a. sinensis* and bright orange in *T. angustipennis*. However, as *T. angustipennis* hatches 2 wk later than its congener, the substantial size difference in nymphs by the time both were present in the field could be used to tell them apart early in the season. Sex can also be determined from the third instar on, because the ventral side of the sixth abdominal segment of a female begins to overgrow the seventh and eighth segments by this developmental stage, eventually resulting in adult females with six visible abdominal segments and males with eight. Other morphological differences in adults, such as the much longer antennae in males and the thicker bodies of females, further differentiate the sexes in both species. Oothecae are easily identified, those of *T. angustipennis* being long and quite narrow, whereas those of *T. a. sinensis* have a much thicker layer of froth surrounding the eggs, which makes them about as wide as long (i.e., more spherical).

Results

The number of *T. a. sinensis* in the field plot was higher than the number of *T. angustipennis* individuals during both years of the study, but numbers of both species were lower during the growing season of 2011 than in 2010 (Fig. 1A). This decline was especially true for *T. angustipennis* (Fig. 1B). Although sampling did not begin until 2 June in 2010, it was apparent by the instars (reflected by body lengths) of nymphs collected at that time that hatching of *T. a. sinensis* had occurred earlier than that of *T. angustipennis*. In 2011, sampling began in April, and younger nymphs of *T. a. sinensis* were already present then, but not those of *T. angustipennis*. Oothecae of both species from which nymphs have emerged can be identified by the open scales over the egg chamber that line the dorsal surface, and we have always found this occurring first in *T. a. sinensis*. Nymphs of *T. angustipennis* were not found until mid-June, indicating a consistent asynchronous egg hatch phenology between these two species as often has been described in the literature (Hurd 1999 and references therein).

In addition to lower numbers of individuals in 2011 than in 2010, some important stages in the life cycle were delayed in 2011 compared with the previous year (Table 1). The appearance of the first adults of both species was later by about 2 wk (first imago, Table 1). On the other hand, the first sampling date when all individuals were adults was about 3 wk earlier in 2011 than 2010 for *T. a. sinensis*, but delayed only 5 d for its congener. The first ootheca for *T. angustipennis* was found ~2 wk (2010) to 10 d (2011) after that of *T. a. sinensis*. The first ootheca for *T. a. sinensis* was found a week later in 2011 than in 2010, but only 3 d later for *T. angustipennis*. The last ootheca for both species was found later in 2010 than 2011. For *T. a. sinensis*, the time between when all individuals were

Fig. 1. (A, B) Numbers of individual mantids of both species encountered each month (combined samples for the month) during the growing seasons of 2010 (dark bars) and 2011 (open bars).

Table 1. Timing of attainment of adulthood and reproduction in the two mantid species in 2010 and 2011, and difference in time (days) of events between years (2011 dates minus 2010 dates)

Species	Year	First adult	All adult	First ootheca	Last ootheca
TS	2010	15 July	27 Aug.	14 Sept.	28 Oct.
	2011	30 July	5 Aug.	22 Sept.	16 Oct.
	Difference =	+15 d	–22 d	+8 d	–12 d
TA	2010	21 Aug.	31 Aug.	29 Sept.	21 Oct.
	2011	5 Sept.	5 Sept.	2 Oct.	16 Oct.
	Difference =	+15 d	+5 d	+3 d	–5 d

"All adult" is the first date on which all mantids found were adults. TS—*T. a. sinensis*; TA—*T. angustipennis*.

adult and first ootheca was 2.5 wk in 2010, but 47 d (6.5 wk) in 2011, whereas this interval for *T. angustipennis* was 29 d in 2010 and 27 d in 2011.

Numbers of individual adult females (NF) were about twice as high in 2010 as 2011, and the numbers of oothecae (NO) deposited were also higher in 2010 for both species (Table 2). However, the per capita number of oothecae (O/F) actually increased between years for *T. a. sinensis*, but decreased substantially for *T. angustipennis*: 20 *T. angustipennis* females produced only a single ootheca among them (i.e., 5%) in 2011. The densities of oothecae (O/m²) for both species deposited closer to the edge of the field were much lower than those found in the center of the field by Rose and Hurd (2016). In both areas of the field, densities of *T. angustipennis* oothecae declined markedly between 2010 and 2011, but not those of *T. a. sinensis*.

Table 2. Numbers of individual adult female mantids (NF) detected during 2010 and 2011, numbers (NO) and densities (O/m²) of oothecae, and fecundity (O/F)

Year	Species	NF	NO	O/F	O/m ²	O/m ² (R&H) ^a
2010	TS	47	7	0.149	0.004	0.130
	TA	37	10	0.270	0.006	0.192
2011	TS	21	4	0.190	0.003	0.170
	TA	20	1	0.050	0.001	0.082

^aResults from 2010 and 2011 taken from concurrent study (Rose and Hurd 2016) are included for comparison. TS—*T. a. sinensis*; TA—*T. angustipennis*.

Discussion

As predicted, *T. a. sinensis* was more successful than *T. angustipennis*, both in terms of larger population size and greater reproductive success. It is also evident that 2010 was a better year for both species than 2011. An indication of this was the month-longer time in 2011 than in 2010 between the time when all *T. a. sinensis* were adults and the appearance of the first ootheca; however, the interval was roughly the same in both years for *T. angustipennis*. In addition to prey scarcity, which directly affects reproduction in mantids (Eisenberg et al. 1981), factors in the abiotic environment such as temperature and rainfall can change from year to year and impact reproductive output (Hurd et al. 1995, 2001). Of course, these factors also act on other arthropod species that constitute prey for mantids.

The population decline in *T. angustipennis* from 2010 to 2011 that we report here is generally in agreement with a decline in reproductive output nearer the center of this same field in the same years, as reported by Rose and Hurd (2016). Although mantid densities were not measured in that study, the large difference (two orders of magnitude) in ootheca density for both species between sites in this field (comparing O/m² and O/m² (R&H) in Table 2) suggests that population density of both species was much lower closer to the edge of the field than in the center, which could be a consequence of higher predation rates by insectivorous birds that use the trees at the edge to perch and watch for insect prey (Ries and Fagan 2003). Although incidence of parasitic wasps in oothecae of *T. angustipennis* may have accounted for the decline in this species in the center of the field, as suggested by Rose and Hurd (2016), we found no evidence of egg parasitism in our plots closer to the edge. That is, the small round holes left by wasps leaving oothecae were never seen, although it is possible that wasp emergence had not yet occurred. Therefore, we have no direct evidence for the reason that *T. angustipennis* declined between years more than its congener. However, there is still the possibility of intraguild predation, in which the larger *T. a. sinensis* could prey on its smaller congener, as has been observed in the field (Snyder and Hurd 1995). Although possible, the low density of mantids at this site suggests that encounters between the species must have been few.

The present study was conducted during only 2 yr of the concurrent 7-yr study reported by Rose and Hurd (2016). However, the decline in *T. angustipennis* that Rose and Hurd observed in the center of that field during those same 2 yr continued until that species virtually disappeared from the field 4 yr later. That final year of their study (2015) only a single *T. angustipennis* ootheca was located, compared with a peak of 120 oothecae in 2010. In the meantime, *T. a. sinensis* continued to thrive (judging by ootheca abundance) until a sharp decline in ootheca abundance between 2014 (171 oothecae) and 2015 (66 oothecae). At that point, the field had become

dominated by trees and was in the early stages of forest succession, which is not a typical habitat for either species.

A potentially surprising result of our study was the small number of oothecae recorded (Table 2) compared with the numbers of marked and numbered adult females in our study site. In 2010, 47 female *T. a. sinensis* produced 7 oothecae (15%) and 37 *T. angustipennis* females produced 10 oothecae (27%). The proportion of oothecae to females in 2011 was slightly higher for *T. a. sinensis* (19%), but much lower for *T. angustipennis* (5%), another indication that the *T. angustipennis* population was in decline. We have no comparable data from other studies for *T. angustipennis*, but during 3 yr of a study of a *T. a. sinensis* population in Maryland (Hurd et al. 1995), ootheca/female ratios were 13% (1990), and 7% (1991), dropping to 0.4% in 1992, a year when the number of adult females was at its highest, but anomalously cool summer temperatures slowed development so that most of them did not live long enough to oviposit before the killing frost at the end of the season. The following year (1993), no mantids were found in that field. It would appear that the majority of female mantids of either species in these studies that manage to survive to adulthood generally either fail to mate, lack sufficient energy and nutrients to produce an ootheca, or die from predation, starvation, or frost before they can oviposit.

One of the problems with studying the comparative ecology of these two mantid species is that their nymphs (and thus the two species) cannot be distinguished until the third instar, some weeks along the developmental pathway. Our study confirms that *T. a. sinensis* hatches earlier than *T. angustipennis* in eastern Virginia, in part because on 2 and 3 June 2010, we collected 209 20–25-mm nymphs from the western edge of the Dixon tract and raised them in the laboratory on fruit flies and domestic crickets for a few weeks. All nymphs that reached the third-instar stage had the yellow spot and thus were confirmed as *T. a. sinensis*. Furthermore, during a 4 April 2009 visit to the Dixon tract by the junior authors, we photographed a small salticid spider eating nymphs as they eclosed from a *T. a. sinensis* ootheca. On 10 March 2012, all three authors observed nymphs hatching from a *T. a. sinensis* ootheca on a tall *Baccharis halimifolia* bush in the same old field, so we have hard evidence that *T. a. sinensis* hatches early in eastern Virginia. Over 7 annual March–early April visits to the site, Rose and Hurd (2016) never saw nymphs hatching from any of 332 *T. angustipennis* oothecae we counted. We therefore assume that the nymphs we recorded in April and May 2011 (Fig. 1) were those of *T. a. sinensis*. By mid- to late June, the two species could be reliably distinguished and so the values recorded thereafter give a true picture of their relative numbers: in each month, *T. a. sinensis* was almost always more numerous than *T. angustipennis*.

Although the first imagoes were observed a month earlier for *T. a. sinensis* than for *T. angustipennis* in both years (Table 1), by the end of August in both years (5 September for *T. angustipennis* in 2011), all mantids of both species had become adults. Thus, despite hatching some weeks later than *T. a. sinensis*, *T. angustipennis* caught up in the race to achieve adulthood by the end of summer by having one fewer instar (Matsura et al. 1975).

It is still an open question what selective pressures are responsible for the divergence in egg hatch phenology between these sibling species that puts *T. angustipennis* at a disadvantage when cohabiting in a field with *T. a. sinensis*, i.e., that works against coexistence. The fact that *T. a. sinensis* hatches earlier than *T. angustipennis* could reduce prey size overlap, and thus interspecific competition, but it also promotes interspecific predation by the always-larger *T. a. sinensis* (Snyder and Hurd 1995). The fact that *T. angustipennis* oviposits

much higher on trees than *T. a. sinensis* (Hurd 1999) would seem to preadapt it to occupying successional fields at least a bit longer into early forest succession, but that did not seem to help it succeed in our study site. The parasite load on *T. angustipennis* reported by Rose and Hurd (2016) could certainly reduce or eliminate it from fields, with or without the presence of its sibling species, but we did not examine *T. angustipennis* oothecae collected at the site reported here for signs of parasitism. Interspecific predation (and possibly interspecific competition) from *T. a. sinensis* and parasitism by wasps both work against success of *T. angustipennis* in old-field habitats, but the frequency with which these two species are found together suggests that even if *T. a. sinensis* will eventually dominate as the top predator in the arthropod assemblage, *T. angustipennis* manages to persist for at least long enough to propagate and supply potential colonists to nearby fields that are as yet unoccupied by *T. a. sinensis* or the parasitoids. This suggests that *T. angustipennis*, which must be present in appreciable numbers before its parasite can establish a population, should have better dispersal abilities than its congener (i.e., gets there first). Thus, *T. angustipennis* might be considered a fugitive species (Hutchinson 1951) that must always be a step ahead of its congener (and its parasite) to avoid extirpation. This is a hypothesis that remains to be explored.

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