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1996

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TOP-DOWN CASCADE FROM A BITROPHIC PREDATOR IN AN OLD-FIELD COMMUNITY[1]

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Abstract. We tested the hypothesis that a bitrophic (third and fourth level) arthropod predator can exert a cascading, top-down influence on other arthropods and plants in an early successional old field. First-stadium mantids, *Tenodera sinensis,* were added to replicated open-field plots in numbers corresponding to naturally occurring egg hatch density and allowed to remain for ≈2 mo. Sticky-trap dispersal barriers around both control and mantid-addition plots allowed us to monitor emigration of arthropods continuously during the experiment. Biomass of herbivores, carnivores, and plants, and abundances of arthropod taxa within plots were determined at the beginning, middle, and end of the experiment.

The impact of mantids on the community was a top-down trophic cascade, beginning at the fourth trophic level and evident at each of the lower three levels. Mantids induced marked behavioral responses in other predators, but interference among predators did not prevent the trophic cascade. The most common predators, cursorial spiders, emigrated from mantid addition plots in significantly greater numbers than from controls. This behavioral response may have resulted from avoidance of predation or competition.

Mantids decreased biomass of herbivorous arthropods through predation, and this decrease in turn increased biomass of plants. Therefore, these generalist predators were able to decrease herbivory enough to affect plant growth. This and other recent studies indicate that top-down effects can be important in structuring terrestrial communities. Ours is the first example of a top-down cascade by a generalist arthropod predator in a nonagricultural ecosystem and illustrates the importance of detecting behavioral responses in studies of trophic interactions.

Key words: arthropod assemblages; behavioral responses; herbivore load; intraguild interactions; mantids; old fields; predator load; predators, bitrophic and generalist; Tenodera sinensis; *top-down forces; trophic cascades.*

INTRODUCTION

The importance of top-down vs. bottom-up forces in trophic level interactions has been the topic of recent debate in ecology. No real agreement has been reached on the importance of top-down and bottom-up forces in terrestrial systems (Hunter and Price 1992, Power 1992, Strong 1992). A strict dichotomy between these two processes may be counterproductive, as it is likely that both top-down and bottom-up forces interact to structure all communities (Menge 1992). However, the question remains: in which communities and under what conditions are top-down or bottom-up forces important?

The effects of generalist predators on prey assemblages is complicated by the fact that they occupy two trophic levels (third and fourth) at the same time. Such bitrophic predators (sensu Hurd and Eisenberg 1990*a*)

have a tendency to produce intraguild interactions such as predation (Polis et al. 1989, Hurd and Eisenberg 1990*a*), exploitation competition (Spiller 1984, Hurd and Eisenberg 1990*b*), interference competition (Spiller 1984, Wise 1993), and predator avoidance behavior (Stamps 1983, Moran and Hurd 1994). These interactions can result in both direct and indirect effects on arthropod assemblages (Risch and Carroll 1982, Hurd and Eisenberg 1984*b*, 1990*a*, Fagan and Hurd 1991, 1994, Riechert and Bishop 1990). How interactions within the generalist predator guild influence plant assemblages is poorly understood, and may not be straightforward. For example, spiders eat pollinating insects, which may negatively affect plants, but also eat seed predators, which may benefit plants (Louda 1982).

In spite of the argument by Price et al. (1980) that enemies of herbivores are mutualists of plants, there have been relatively few studies investigating the effects of predators on plants in terrestrial systems. Studies detecting top-down effects in terrestrial commu-

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nities have focused on arthropod specialists such as hymenopteran parasitoids (Gomez and Zamora 1994). Studies with parasitoids typically involve only one or a few host insects and therefore have little chance of detecting effects on very diverse systems such as terrestrial insect communities. Other top-down studies have shown effects of vertebrate predators on plant growth and reproduction (Altegrim 1989, Spiller and Schoener 1990, 1994, Marquis and Whelan 1994, McLaren and Peterson 1994, Dial and Roughgarden 1995). Generalist arthropod predators are less well studied, although it is clear that they can exert important influences on arthropod assemblages, including herbivorous arthropods that can be important to plant succession (Brown 1985). We have found no experimental evidence in the literature that generalist arthropod predators affect primary producers in complex natural communities; however, Riechert and Bishop (1990) found that introduced spider predation decreased leaf damage in a garden test system.

Possible mechanisms by which trophic cascades function have not been well investigated in terrestrial systems, although the role of behavior has been noted in several aquatic studies (Werner et al. 1983, Douglas et al. 1994, Hill and Lodge 1994). Behavior is an important component of predator–prey interactions (Lima and Dill 1990, Anholt and Werner 1995) and thus should not be ignored in design of cascade experiments.

The most abundant generalist predators in old-field communities in our study area are mantids and spiders. The most common mantid in the mid-Atlantic region of the United States is the Chinese mantid (*Tenodera sinensis*), which often reaches high densities upon emergence in the spring (Hurd and Eisenberg 1984*a*, Eisenberg and Hurd 1990). This is a semelparous univoltine insect that hatches in the spring, matures late in summer, oviposits in autumn, and is killed by frost at the end of the growing season. As mantids mature they become the largest arthropod predators in old fields, capable of preying on virtually any arthropod and even small vertebrates. Numerous species of cursorial spiders make up a diverse assemblage (Hurd and Fagan 1992) that co-occurs with mantids. A number of experiments have demonstrated that realistic densities of mantids in old-field communities can have profound effects on other predators as well as on herbivorous arthropods (Hurd and Eisenberg 1984*b*, 1990*a*, Fagan and Hurd 1991, 1994, Moran and Hurd 1994). Therefore, they are bitrophic (Hurd and Eisenberg 1990*a*).

We designed the present study to examine the effects of a mantid population on the lower three trophic levels in an early successional old-field community. Specifically, we tested whether these bitrophic generalist predators can exert a cascading (sensu Carpenter et al. 1985), top-down effect on: (1) biomass of carnivores, herbivores, and plants; (2) numerical abundance of both lower arthropod trophic levels; and (3) behavior of cursorial spiders, which are usually the numerically dominant members of the generalist arthropod predator guild in such systems.

MATERIALS AND METHODS
Study site

The study site was a large field located in northern New Castle County, Delaware. It had been periodically cut for hay in recent years (last time in fall 1993) so that at the beginning of the study aboveground plant biomass was low. The major plant species present initially were *Trifolium pratense, Poa* sp., *Viola papilionacea, Phleum* sp., *Lynchis alba,* and *Allium* sp. There was not an established population of mantids at the beginning of the study, but a diverse assemblage of insects and other arthropods was present (M. D. Moran, *personal observation* from previous year). Approximately 30 m from the south side of experimental plots was a line of trees, and the other three sides of the plots were on the edges of large open fields.

Experimental design

During April of 1994 12 6 × 6 m plots were established in pairs, resulting in six groups composed of two plots each. Each treatment and control plot within a pair was separated by 3 m while each pair of plots was separated from other pairs by 20 m. Treatment plots (receiving mantids) and control plots (no mantids) were systematically interspersed (i.e., alternating) within the pairs of plots (Hurlbert 1984). Each plot was bounded by an 0.5 m wide black plastic barrier that was stapled to furring strips placed around the outside edge of the plot. The day before introduction of mantids, a 6-cm band of Tangletrap (Tanglefoot Company, Grand Rapids, Michigan) was painted in a broad stripe down the middle of the barrier to trap emigrating mantids and spiders. Tangletrap was periodically reapplied during the course of the experiment to maintain stickiness. Mantids and spiders caught on the inside edge of the Tangletrap stripe were considered emigrants; any individuals found on the outside edge were considered to be immigrants and thus were ignored. Although many other arthropods were captured in these traps, the numbers have been shown to be too low to produce statistically significant barrier effects on arthropod assemblages within the plots (Fagan and Hurd 1994, Moran and Hurd 1994). Therefore, we regard this as an open-field experiment.

Mantid oothecae were collected from New Castle County, Delaware, during early spring 1994. These were weighed to determine expected numbers of emerging nymphs from each ootheca according to a regression provided by Eisenberg and Hurd (1977). Oothecae were introduced into treatment plots from 8 May to 14 May. Nine oothecae, corresponding to an initial density of $\approx 64.6 \pm 5.47$ hatchlings/m² (mean $\pm$ 1 SE), were added to each plot in a uniform spatial pattern at a density of one ootheca/4 m². Ootheca dispersion generally is highly aggregated within fields, and two oo-

thecae occur in the same 1 m² in the field roughly 30% of the time (Eisenberg and Hurd 1990), so that the range of emergence in any given 1 m² that contains one to two oothecae would be from 26 nymphs for a single small ootheca, to 764 for two large oothecae (Eisenberg and Hurd 1977). Therefore our experimental density was within normal range, and well below maximum. Thus, this manipulation does not artificially establish enhanced predator densities ("predator augmentation," sensu Price 1987), but rather establishes a normal density of predators at a suitable site that has not yet been colonized.

Oothecae were not added to the plots until emergence had begun from individual oothecae, so that mantid introduction occurred over several consecutive days. This was done to verify that all oothecae were viable. Oothecae were added to plots as evenly as possible, so that all received their full complement at the same time. The experiment was allowed to run from 8 May until 11 July, encompassing the period of maximum productivity for producers (Al-Mufti et al. 1977) and arthropod consumers (Hurd and Wolf 1974) in north temperate old-field ecosystems.

Sampling methods

Arthropod samples were taken by D-Vac for all plots. A coordinate was randomly selected on the south side of each plot and a D-Vac sample taken on a transect across the plot, encompassing an area of 1.05 m². The samples were sorted according to trophic level (herbivore or carnivore) and order, then counted and weighed (dry mass after 24 h at 60°C). Plant biomass was determined by removing all living aboveground plant material from three randomly selected 0.25-m² quadrats within each plot. Plants were then dried in an oven at 60°C, and weighed. Although these sampling techniques are destructive, the total area removed by sampling was only 6.25% for the plants and 8.75% for arthropods, which we regard as negligible.

On 5 May all plots were sampled for arthropods and plants to determine initial (pre-manipulation) conditions for all three trophic levels. We took two additional samples following mantid introduction, on 8 June and 10 July. Beginning on 11 May when more than half of the mantids had been introduced inside the plots, spiders and mantids were removed from the Tangletrap barriers every day at sunrise and sunset to distinguish diurnal emigration from nocturnal emigration. The stadium of each mantid stuck in the trap was recorded and body length of spiders was measured.

Predator load, defined as biomass of carnivores (including mantids) divided by total arthropod biomass (Fagan and Hurd 1994), was calculated for the arthropod samples. Herbivore load was calculated as biomass of herbivorous arthropods/100 g plant biomass (Root 1973).

Statistical analyses

The emigration of mantids and spiders was analyzed by a G test (Sokal and Rohlf 1981), where the expected ratio of diurnal and nocturnal movement was taken from the average lengths of diurnal and nocturnal periods (1.63:1) during the experiment. An F_{max} test indicated that variances of treatments were unequal for herbivore abundance, herbivore biomass, herbivore load, carnivore abundance, and carnivore biomass, so these data were log-transformed. Carnivore load was calculated as a proportion and therefore was arcsine-transformed. Number of spiders emigrating early and late in the experiment, carnivore abundance and biomass, herbivore abundance and biomass, carnivore load, and herbivore load were analyzed by multivariate repeated-measures MANOVA employing profile analysis (von Ende 1993). For the plant biomass data, a mean was first calculated from the three samples taken from each plot (Hurlbert, 1984), and these were then subjected to profile analysis. In profile analysis, a significant Time effect indicates that the response variable in question increases or decreases over time while the Treatment × Time interaction indicates whether the time trends differ between treatments. For comparison of spider emigration during the day and night, total numbers of spiders emigrating during the course of the experiment were analyzed by three-way ANOVA with treatment (mantid addition or control), blocks, and time (day or night) as the three factors. Abundance of each arthropod order during the final sample time was analyzed by two-way ANOVA. Multiple comparisons in our study were subjected to sequential Bonferroni (Rice 1989) to adjust the alpha value for multiple statistical tests.

RESULTS

During the 1st mo of the study, mantids progressed through the first two stadia. During the 2nd mo they developed more rapidly, reaching the sixth stadium by the end of the study. *Tenodera sinensis* has seven nymphal stadia; therefore, this study encompassed most of the juvenile stage.

By the end of the experiment, dispersal of mantids (mean ± 1 SE) from treatment plots was 37.01 ± 2.79% of initial added density. No mantids were ever caught emigrating from control plots. Mantids were more likely to disperse during the day than at night (Table 1): ≈90% of mantid nymphs caught in dispersal barriers were collected at the end of each day (i.e., dispersed during daylight hours). Although there were significant differences among plots (heterogeneity), the bias toward daytime movement was consistent. Cursorial spiders, on the other hand, exhibited no clear preference for day or night movement in control or treatment plots and within-plot dispersal patterns did not differ significantly from expected (Table 2).

The addition of mantids had a significant effect on

TABLE 1. G test analysis of day and night movement for *T. sinensis* using an expected ratio of 1.63:1, which corresponds to the average ratio of day to night during the course of the experiment.

Plot no.	Day (no.)	Night (no.)	Ratio D:N	G	P†
1	738	50	14.76:1	431.3	<0.001
2	622	45	13.82:1	356.9	<0.001
3	841	85	9.89:1	403.4	<0.001
4	862	93	9.27:1	397.0	<0.001
5	800	87	9.20:1	342.2	<0.001
6	669	54	12.39:1	358.2	<0.001
Total				2289.0	<0.001
Heterogeneity				284.0	<0.001

† Indicates significance after sequential Bonferroni correction.

TABLE 2. G test analysis of day and night movement for cursorial spiders from control and treatment plots. We used an expected ratio of 1.63:1, which corresponds to the average ratio of day to night during the course of the experiment. There were no significant values after sequential Bonferroni correction.

Plot no.	Day (no.)	Night (no.)	Ratio D:N	G	P
Control plots					
1	25	18	1.38:1	0.39	>0.50
2	10	25	0.40:1	4.05	<0.05
3	28	21	1.33:1	0.34	>0.50
4	45	26	1.73:1	0.06	>0.75
5	21	22	0.95:1	3.45	>0.05
6	27	25	1.08:1	1.98	>0.10
Total				10.27	>0.05
Heterogeneity				4.87	>0.75
Treatment plots					
1	33	19	1.74:1	0.08	>0.50
2	33	24	1.38:1	0.30	>0.50
3	40	18	2.22:1	1.20	>0.10
4	41	41	1:1	5.02	<0.05
5	48	35	1.37:1	0.45	>0.50
6	46	34	1.35:1	0.83	>0.10
Total				7.88	>0.10
Heterogeneity				5.86	>0.10

diurnal and nocturnal emigration of spiders from experimental plots (Fig. 1A, three-way ANOVA). The interaction between Treatment and Time was nonsignificant, while the main effects of Treatment and Time were significant (Table 3). So spiders left the treatment plots in greater numbers than control plots, both day and night.

The number of spiders emigrating from the experimental plots declined during the course of the experiment (Fig. 1B, profile analysis, Wilks' lambda = 0.0196, $F_{1,5}$ = 249.69, $P < 0.001$). There was a significant treatment effect on the numbers of spiders emigrating from plots during the course of the experiment and this effect appeared to be greatest early in the experiment, as the significant Treatment × Time interaction indicates (Wilks' lambda = 0.3949, $F_{1,5}$ = 7.661, $P = 0.039$).

Because we took the initial arthropod samples before mantid additions, we cannot calculate a meaningful estimate of predator load from the first sample. However, since the mean number of mantids present at hatching was 64.6 mantids per square metre we can assume pred-

ator load was elevated initially in treatment plots. Analysis of the second and third D-Vac samples showed no significant overall Time effect on predator load (profile analysis, Wilks' lambda = 0.9642, $F_{1,5}$ = 0.186, $P = 0.685$). However, the Treatment × Time interaction was significant (Wilks' lambda = 0.3028, $F_{1,5}$ = 11.51, $P = 0.019$, Table 4). Since confidence intervals overlap the means during the final sample (7/10), predator load did not differ between treatment and control plots at that time.

There was a significant increase over time for both abundance of carnivores (profile analysis, Wilks' lambda = 0.123, $F_{2,4}$ = 14.22, $P = 0.015$, Fig. 2A) and
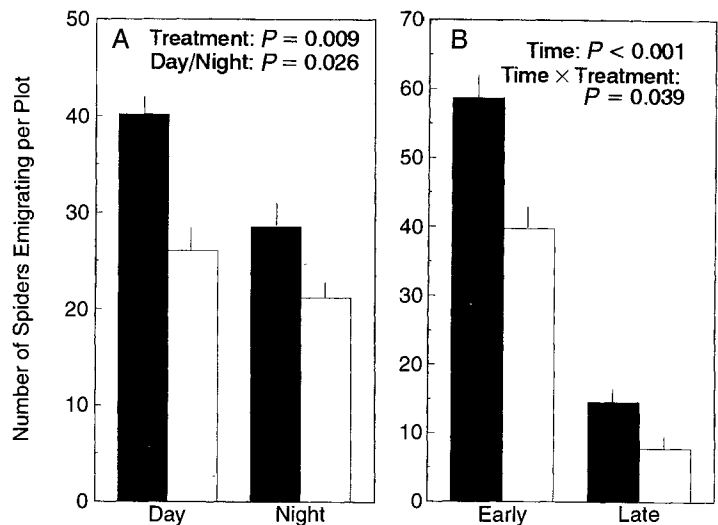

FIG. 1. (A) Comparison of emigration rates for total number of cursorial spiders caught during the day and the night. Significantly more spiders emigrated from treatment plots and during the day (three-way ANOVA). (B) Same comparison for those cursorial spiders caught early in the experiment (Days 1–30) and late in the experiment (Days 31–60). There was a significant Time and a significant Treatment × Time interaction (profile analysis). All data are mean + 1 SE. Solid bars = treatment plots, open bars = control plots.

TABLE 3. ANOVA table for analysis of spider emigration between plots during day and night. Treatment refers to effect of mantid addition. Time refers to the effect of day vs. night emigration.

Source of variation	SS	df	F	P
Treatment	693.375	1	16.376	0.009
Time	408.375	1	9.645	0.027
Block	850.708	5		
Treatment × Time	70.041	1	1.654	0.255
Error	211.708	23		

TABLE 4. Predator load (mean and 95% confidence intervals) from D-Vac samples during the course of the experiment. MANOVA: Time, $P = 0.685$; Treatment × Time, $P = 0.019$.

Date	Treatment $\bar{X}$	Treatment CI	Control $\bar{X}$	Control CI
8 June	0.10	0.04	0.03	0.02
10 July	0.07	0.04	0.08	0.06

biomass of carnivores (Wilks' lambda = 0.025, $F_{2,4} = 77.22$, $P < 0.001$, Fig. 2B). However, there was no mantid effect because Treatment × Time interactions for both carnivore abundance and carnivore biomass were nonsignificant.

There was significant increase over time for herbivore abundance (profile analysis, Wilks' lambda = 0.021, $F_{2,4} = 95.17$, $P < 0.001$, Fig. 3A) and herbivore biomass (Wilks' lambda = 0.001, $F_{2,4} = 3276.93$, $P < 0.001$, Fig. 3B) during the course of the experiment. There was no effect of mantid addition on herbivore abundance, but herbivore biomass was significantly depressed relative to control by mantid additions, as indicated by the significant Treatment × Time interaction (Wilks' lambda = 0.054, $F_{2,4} = 35.15$, $P = 0.002$, Fig. 3B).

Herbivore load increased over the course of the experiment (Fig. 4A), as indicated by the significant Time effect (profile analysis, Wilks' lambda = 0.006, $F_{2,4} = 350.12$, $P < 0.001$). There was also a significant Treatment × Time effect (Wilks' lambda = 0.206, $F_{2,4} = 7.73$, $P = 0.042$) showing that increased herbivore load over time was depressed by mantid addition (Fig. 4A).

Biomass of the lowest trophic level we examined, the plant assemblage, increased over time (profile analysis, Wilks' lambda = 0.071, $F_{2,4} = 25.98$, $P = 0.005$, Fig 4B). Plant biomass also exhibited a significant Treatment × Time effect (Wilks' lambda = 0.161, $F_{2,4} = 10.41$, $P = 0.026$), as the plant biomass diverged between treatment and control plots during the course of the experiment. At the end of the experiment, plant biomass was ≈30% higher in mantid addition plots.

Homopterans and dipterans were the dominant groups within the arthropod assemblage (Fig. 5). Abundance of most orders of arthropods were slightly lower in the control plots though none of the effects on individual orders was statistically significant (two-way ANOVA).

DISCUSSION

Intraguild behavioral effects

Other than in some aquatic studies (see *Introduction*), most studies of top-down effects have overlooked the potentially important role of behavior. It is clear from our results that dispersal is a potentially important
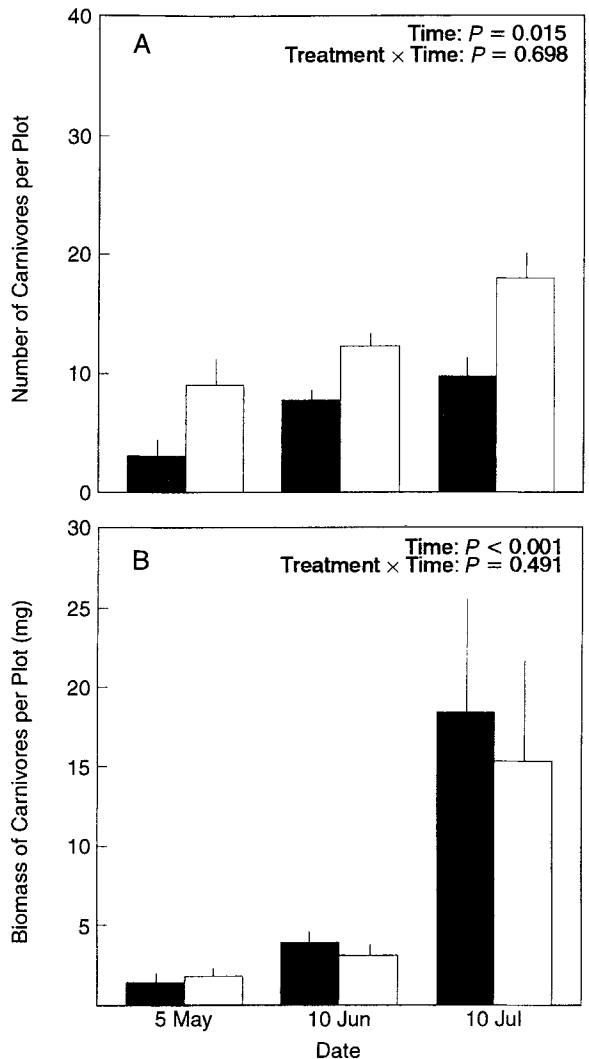

FIG. 2. (A) Comparison of the abundance of carnivorous arthropods other than mantids captured in D-Vac samples during the course of the experiment. There was a significant Time effect while the Treatment × Time interaction was nonsignificant (profile analysis). (B) Comparison of the biomass of carnivorous arthropods other than mantids captured. There was a significant Time effect while Treatment × Time interaction was nonsignificant (profile analysis). All data are mean + 1 SE. Solid bars = treatment plots, open bars = control plots.
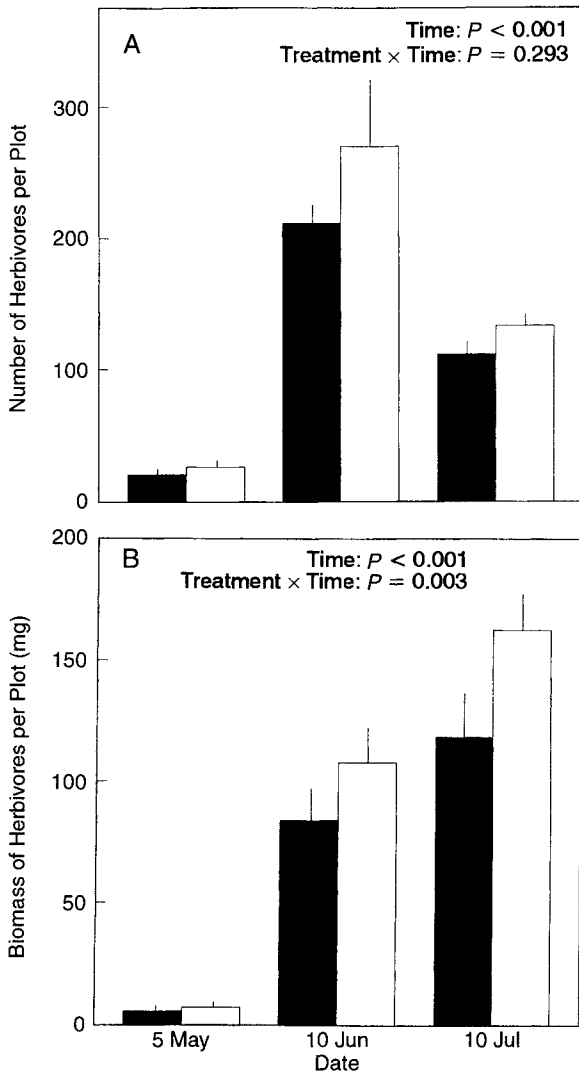
FIG. 3. (A) Comparison of the number of herbivorous arthropods captured in D-Vac samples during the course of the experiment. Both the Time effect and the Treatment × Time effect were nonsignificant (profile analysis). (B) Comparison of the biomass of herbivorous arthropods captured. There was a significant Time effect and a significant Time × Treatment interaction (profile analysis). All data are mean + 1 SE. Solid bars = treatment plots, open bars = control plots.
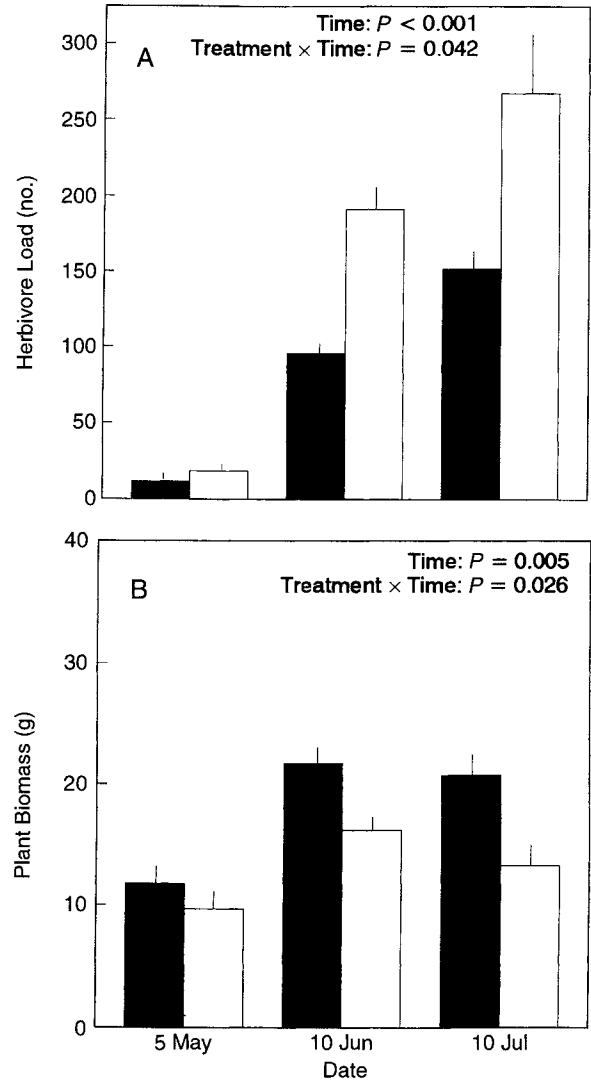

FIG. 4. (A) Comparison between treatment and control plots for herbivore load. There was a significant Time effect and a significant Treatment × Time interaction (profile analysis). (B) Comparison between treatment and control plots for the dry mass of aboveground plant biomass. There was a significant Time effect and a significant Treatment × Time interaction (profile analysis). All data are mean + 1 SE. Solid bars = treatment plots, open bars = control plots.

aspect of intraguild predator effects in this old-field arthropod assemblage.

Spiders showed no bias toward diurnal or nocturnal dispersal in treatment or control plots. However, mantids caused more emigration from treatment plots than from controls. This response could be either predator avoidance behavior, or numerical response to lowered prey abundance for spiders resulting from competition with mantid nymphs. Mantids exhibited a striking bias toward diurnal dispersal, which is consistent with their role as visual predators (Maldonado and Rodriguez 1972). This does not rule out predator avoidance (Moran and Hurd 1994) as a mechanism for inducing spider

movement, however, since mantid nymphs can feed in the dark if prey make physical contact (Hurd et al. 1989).

Although the treatment effect on spiders early in the season when mantid densities were high could well have been predator avoidance, the late season response was more likely a result of competition between mantids and spiders for prey. Even though the number of mantids in the plots was very low by the time of the last sample (i.e., probably too low to cause predator avoidance behavior), early prey depletion may have had a residual competitive effect on spiders. However,
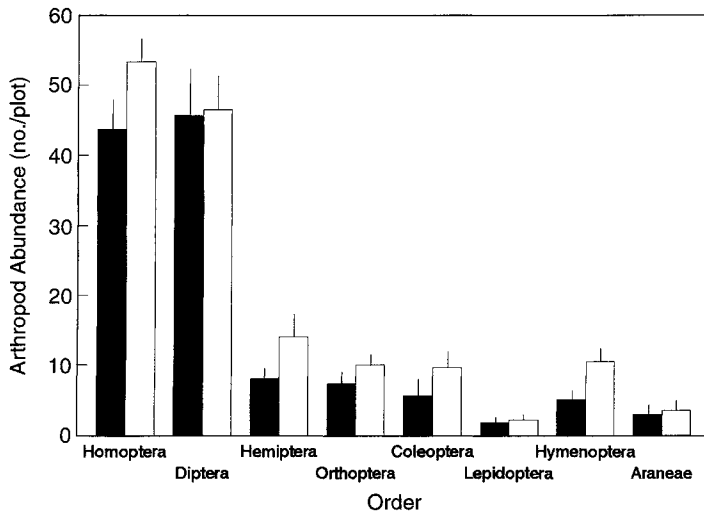
FIG. 5. Comparison between treatment and control plots for the numerical abundance of different arthropod orders (two-way ANOVA for each order). No order was significantly affected by mantid additions. All data are mean + 1 SE. Solid bars = treatment plots, open bars = control plots.

we cannot invoke competition with certainty based on our data. According to Wise (1993) only one other study (Schaefer 1975) examined intraguild interactions in cursorial spiders, and was unable to distinguish between competition and predation as a mechanism for negative intraguild effects.

The fact that mantids grew faster during the 2nd mo than during the 1st mo may be explained by a seasonal increase in both prey availability (Hurd and Rathet 1986) and temperature (Hurd et al. 1989). However, conditions within the plot apparently were not optimal, since more than a third of the initial mantid population emigrated from treatment plots. Density of mantid nymphs at egg hatch is locally very high, causing rapid dispersal over short distances within the habitat (Fagan and Hurd 1994). The proportion of initial mantid numbers that disperse increases with increasing density. In an earlier study (Hurd and Eisenberg 1984a) dispersal ranged from 3% at low initial density (3 mantids/m²) to 7% at high initial density (30 mantids/m²); our initial density was about twice that of the high-density treatment in that experiment.

Cascading trophic effects

The impact of adding generalist predators to this old-field community was a trophic cascade that extended to plants. Adding mantids did not result in a sustained elevation of predator load in treatment plots through the experimental period. This is in contrast with an earlier study (Hurd and Eisenberg 1984a) in which predator load remained higher in treatment plots throughout the season because increasing body size of mantids compensated for mortality and dispersal. However, a much greater proportion of initial mantid density emigrated in the present experiment than in that earlier study. In fact there were so few left in plots by the end of the study that our last D-Vac sample failed to capture any, although we did visually detect some survivors in treatment plots. The observed magnitude of mortality

is not surprising; in a 3-yr study of an unmanipulated population of *T. sinensis,* survivorship from egg hatch to adult was <10% (Hurd et al. 1995).

In spite of the behavioral effects of mantids on spiders, we detected no significant effect on abundance or biomass of intermediate predators, including spiders. We suggest a compensation between survivorship and dispersal: as more spiders emigrated from treatment than control plots, survivorship of spiders that remained in treatment plots may have been higher than in control plots. In contrast to our findings in this study, mantids had significant effects on spider densities in previous experiments (Hurd and Eisenberg 1990a, Fagan and Hurd 1991, Moran and Hurd 1994).

Our data suggest that the cascade effect bypassed intermediate predators and acted directly to reduce herbivore biomass. Abundances of all orders of herbivorous arthropods were lower in treatment plots although these reductions were not significant. This seems to indicate that mantid nymphs had weak effects that were diluted over the entire spectrum of potential prey. Therefore, generalist predators like these mantid nymphs exert different effects on the plant community than would a specialist predator attacking only one or a few prey items. Another effect of enhanced primary production on consumers may be increased fecundity, which would show up as higher abundance and secondary productivity the following season (Hurd and Wolf 1974). In any case, that mantids can exert strong direct and indirect effects on herbivorous arthropods has been documented by Hurd and Eisenberg (1984b, 1990a) for *T. sinensis,* and by Mook and Davies (1966) and Fagan and Hurd (1991, 1994) for another temperate mantid, *Mantis religiosa.*

The substantial increase in plant production as a result of mantid addition to treatment plots occurred during the time of peak biomass accumulation for both producers and consumers in this seasonal old-field community. Further study is warranted to determine if

other parameters such as seed production are similarly affected, and to determine which plant species respond. We only examined total plant biomass, but the dominant plant species were *Poa* sp., *Trifolium pratense,* and *Viola papilionacea,* and it seems likely that these species were responsible for much of the increased plant growth.

CONCLUSIONS

Our results constitute the first evidence of which we are aware that a generalist arthropod predator can produce a top-down cascade that extends to the primary producer level in a complex, nonagricultural terrestrial community. The intraguild interactions we observed did not prevent the cascade from proceeding down through herbivores to the producer trophic level. The food web dynamics found in this study thus resemble those that Spiller and Schoener (1990, 1994) observed for top vertebrate predators (*Anolis* lizards). In their case lizards had a positive effect on primary producers by reducing herbivory even though they also had strong interactions with intermediate predators (i.e., spiders). These studies and ours do not support models that predict top predators increase herbivory on plants by reducing intermediate predators (Fretwell 1977, Oksanen et al. 1981). Diehl (1993) concluded that when the top predator is substantially larger than intermediate predators, top-down effects can become stronger, and our study supports this conclusion.

The role of top-down effects is not well understood in highly diverse systems such as terrestrial arthropod assemblages (Hunter and Price 1992, Power 1992, Strong 1992). Our results indicate generalist arthropod predators can exert significant top-down effects to the producer trophic level. This does not preclude bottom-up forces from being important in our community, but our study was not designed to detect them.

Finally, few studies to date have specifically addressed the role of behavior in community-level trophic interactions. Our data suggest that behavioral effects may indeed be important and need to be considered in trophic studies. Very few studies have been able to distinguish between competition and predator avoidance as causes for behavioral effects (but see Hacker and Bertness 1995). Therefore, future experiments should be designed to examine behavioral responses of consumers, herbivores as well as carnivores, to determine potential mechanisms. Terrestrial arthropod assemblages in secondary successional communities are widespread and abundant, and therefore deserve particular attention in this regard. If arthropod predators exert control on herbivores, and herbivores are important to plant succession (Brown 1985), then the influence of generalist predators on terrestrial community dynamics may be pervasive.

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