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Laboratory Study of Cannibalism in *Sphodromantis viridis* Forskal (Mantodea: Mantidae): Effects of Prey Availability, Habitat Structure, and Predator Density

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ABSTRACT

A laboratory study to evaluate the role of available preys, habitat structure and mantid density on the cannibalism among developmental and adult individuals of *Sphodromantis viridis* Forskal was investigated. Prey availability strongly reduced cannibalism within individuals of the same age and others of different ages. Complex habitat structure provides shelter for mantid individuals although it could not prevent cannibalism. High density of mantid nymphs or adults increased cannibalism. Rates of cannibalism increased as the mantid ages increased. First, second and third instar nymphs did not have any cannibal's activity. On the other hand, adult females had the greatest cannibals' activity. Mantid individuals could not cannibals upon higher-age individuals; inversely the later instar nymphs and the adults could not eat (cannibals) the earlier nymphs probably as a result of difficulties of catching behavior. Mantid cannibalism occurred in the presence or absence of preys, through a simple or complex habitat structure and low or high predator's density. This adaptive behavior might improve the chances of survival and provide a defended degree of the mantid against interspecific predation.

Key Words: Cannibalism, *Sphodromantis viridis*, prey availability, habitat structure, and predator density

INTRODUCTION

Cannibalism or intraspecific predation is common in the wide taxonomic groups (Elgar and Crespi, 1992). Observations of cannibalism in an organism lead to a variety of attitudes. Crowding and stress promoting cannibalism was considered merely a laboratory artifact (Tartabini, 1991 and Britz and Pienaar, 1992).

Cannibalism has been documented in at least 10 insect orders (Elgar and Crespi 1992) and probably remains undescribed in many others. Predatory insects seem particularly prone to cannibals and so the behavior can be problematic in the mass production of beneficial species for biological control purposes. For example, Duelli (1981) reported that cannibalism occurred to varying degree in all eleven species of Chrysopidae that he examined. Michaud (2003) found that commercially packed larvae of *Chrysoperla plorabunda* cannibalised at rates that reduced their numbers by 20 % per day after hatching. Cannibalism is prevalent when food resources are limited and reduces competition for these resources (Hopper *et al.*, 1996, Samu *et al.*, 1999 and Dixon, 2000). Accordingly, starvation can enhance cannibalism (Agarwala and Dixon 1992). Consequently, cannibalistic interactions depend on the availability of food resources and therefore the nutritional condition of predators.

Habitat structure is an important factor for both distribution and foraging behavior of the predators (Werner and Anholt, 1993 and Elkin and Baker 2000). Density-dependent cannibalism has also been reported for many predators (Dixon, 2000 and Michaud 2003).

One group of generalist arthropod predators that has been the subject of numerous experimental studies is the praying mantids (Mantodea – Mantidae). Mantids are common in many terrestrial systems (Hurd and Eisenberg, 1990; Hurd, 1999). Because of their potential for broad impacts, mantids have been manipulated to study the details of predator-prey interactions and the impact of generalist predators on community structure and dynamics in early succession habitat (Hurd and Eisenberg, 1990 and Moran *et al.*, 1996). The foraging behavior and sexual cannibalism of *Sphodromantis viridis* Forskal during mating was investigated in details (Younes, 2003). However, little is known on cannibalistic interactions between and within both nymphs and adults.

The main objective of this study is to determine the vulnerability of the various developmental instars as well as adults of *S. viridis* to cannibalism and in particular the effect of available preys, habitat structure and mantid density on this vulnerability. Another objective of this study is determination whether the various instars / stages of the mantid will readily attack and eat each other.

MATERIALS AND METHODS

Stock culture

S. viridis egg cases (ootheca) were obtained from fields in Fayoum Province, Egypt and stored at 5° C in plastic container kept moist with wet paper towels. When needed, egg cases were incubated at 22° C until the mantids emerged. *S. viridis* nymphs pass through 12 instars to reach adult stage (Zohdy and Younes 2003). The cannibals used through this study were the twelve nymphal instar (24h old) and also newly emerged adults (2-4 days old). As a result of the mantid changes their preys through their development, the fruit fly, *Drosophila melanogaster* adults were used as preys for 1st, 2nd, and 3rd nymphal instars. The house fly, *Musca domestica* adults were used as preys for the 4th, 5th and 6th nymphal instars. Beyond 6th instar, *Schistocerca gregaria* nymphs and adults were used as preys.

Cannibalism among *S. viridis* nymphs

Experiments of the mantid nymphs were set up in transparent plastic containers (30 x 30 x 20 cm). Influence of prey availability, habitat structure and predator density on the cannibalistic behavior of the mantid nymphs was investigated in a three factorial design resulting in 6 treatments. Factors were prey availability (with or without), predator density (low or high) and habitat structure, simple (with 50 cm stalks long scattered in the cup) or complex (with 100 cm stalks long scattered in the cup). Ten replicates each with 10 mantid individuals were set up in each treatment. Five mantids were used for low predator density while ten mantids were used for high density. Preys were added in excess to exclude competition.

Cannibalism among adults

Cages of 60 x 60 x 40 cm were used for determining cannibalism among adults. 100 and 200 cm long stalks scattered in the cages were used for low and high habitat structure, respectively. Adults of 2-4 days old were starved for 24 h before using them in the experiments.

Cannibalism among different S. viridis age class

Effects of prey availability, habitat structure and predator density on tendency of *S. viridis* different ages to eat one another was determined. Five mantid individuals of the same age (for example 1st nymphal instar) were used with another five individuals of 2nd, 3rd,.... 12th, females or males and so on. Each experiment was repeated ten times using new mantid individuals and new preys. Preys were used in accesses except in case of determining the cannibalism activity of the predator without preys. All experiments, including rearing of preys and predators were carried out in a rearing room at a constant temperature of 24±2°C and a photoperiod of L16: D8.

Statistical analysis

Values of the mean differences were statistically analyzed using unpaired t-test analysis using Graph Pad software, (2002).

RESULTS AND DISCUSSION

Cannibalism among similar age individuals

Effects of prey availability, habitat structure and predator density were presented in table (1). Data showed that, the first three nymphal instars could not exhibit cannibalistic behavior whereas all other nymphs and adults exhibited cannibalism behavior. The rate of cannibalism (mean or percentage) varied among nymphs and adults according to the experimental factors. Results of the effect of prey availability (with or without) on the cannibalism (Table 1) showed non significant differences ($P > 0.05$) through 4th, 5th, 6th, 10th, 11th and 12th instar. Significant differences ($P < 0.05$) were obtained through 7th instar ($t = 2.15$, $df = 18$, $P < 0.05$), 8th instar ($t = 2.29$, $df = 18$, $P < 0.05$) and 9th instar ($t = 2.09$, $df = 18$, $P < 0.05$).

Habitat structure (simple or complex) was more affected on the cannibalism of the mantid nymphs and adults (Table 1). Significant differences ($P < 0.05$) were obtained by 5th, 6th, 7th, 8th, 9th, 10th, 11th and 12th instars while non significant difference ($t = 1.99$, $df = 18$, $P > 0.05$) was obtained with the 4th instar. In case of adult stage, significant difference was obtained only with females ($t = 3.22$, $df = 18$, $P < 0.01$). The same effect of habitat structure on the mantid cannibalism was obtained by the predator density (Table 1). This means that, significant differences in the mean number of individuals eaten (cannibalism) were obtained by 5th, 6th, 7th, 8th, 9th, 10th, 11th, and 12th instar while non significant difference was obtained by the 4th instar ($t = 1.57$, $df = 18$, $P > 0.05$). Considering

Table (1): Effect of prey availability, habitat structure and predator density on the mean number of *S. viridis* eaten (cannibalized) in 24 h by similar-age individuals

Predator instar / stage	Prey availability		Habitat structure		Predator density	
	With Mean ± SE	Without Mean ± SE	Simple Mean ± SE	Complex Mean ± SE	Low Mean ± SE	High Mean ± SE
N1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
N2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
N3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
N4	0.7 ± 0.26	1.1 ± 0.27	0.7 ± 0.21	0.2 ± 0.13**	0.1 ± 0.01	0.4 ± 0.16
N5	1.5 ± 0.88	2.1 ± 0.2	0.9 ± 0.17	0.2 ± 0.13**	0.3 ± 0.15	1.1 ± 0.31*
N6	1.9 ±0.23	2.4 ± 0.16	1.2 ± 0.2	0.4 ± 0.16**	0.6 ± 0.22	1.6 ± 0.3*
N7	2.3 ± 0.2	2.9 ± 0.18*	1.5 ± 0.16	0.7 ± 0.21**	0.9 ± 0.23	1.8 ± 0.24*
N8	2.8 ± 0.21	3.3 ± 0.15*	1.9 ± 0.17	1.1 ± 0.23*	1.1 ± 0.17	1.9 ± 0.23*
N9	2.9 ± 0.23	3.5 ± 0.16*	2.3 ± 0.21	1.5 ± 0.26*	1.5 ± 0.16	2.2 ± 0.20*
N10	3.3 ± 0.21	3.5 ± 0.16	2.6 ± 0.22	1.7 ± 0.21**	1.7 ± 0.21	2.6 ± 0.22**
N11	3.6 ± 0.16	3.7 ± 0.21	2.4 ± 0.16	1.6 ± 0.16**	2.1 ± 0.23	3.1 ± 0.22**
N12	3.8 ± 0.15	3.9 ± 0.21	2.8 ± 0.24	1.9 ± 0.17**	2.4 ± 0.26	3.2 ± 0.20*
Female	4.2 ± 0.23	4.6 ± 0.18	3.4 ± 0.22	2.3 ± 0.26**	2.8 ± 0.24	3.5 ± 0.16*
Male	0.1 ± 0.01	0.1 ± 0.01	0 ± 0	0 ± 0	0.1 ± 0.01	0.2 ± 0.13

(N) is the predator nymphal instar; * significant difference (P> 0.05); ** significant difference (P> 0.01).

the adults, significant difference was obtained by the adult female (t = 2.33, df = 18, P < 0.05).

Figures (1, 2 and 3) demonstrated the effect of prey availability, habitat structure and predator density on the percent cannibalism. Zero percent was obtained by the first three nymphal instars and also by the effect of habitat structure on the cannibalism of the mantid males. On the other hand, adult females had the high percentage of cannibalism within them, which were 42 and 46 % with and without prey available; 34 and 23 % with simple and complex habitat structure; 28 and 35 % with low and high predator density, respectively.

Cannibalism among different age-classes

Data obtained in tables (2, 3 and 4) indicate that, the incidence of cannibalism depends upon both the age-structure of the mantid and other factors as prey availability, habitat structure or predator density. By measuring the incidence of cannibalism among individuals of different ages of 1st, 2nd and 3rd instars showed a zero tendency to eat any individuals. On the other hand, they were eaten by many individuals had greater-ages. Thus, the early stages were potentially at great risk of death from cannibalism. Percentage of cannibalism determined showed great values when predators were without preys, in a simple habitat structure or in a highly density.

Data also showed that, mantid individuals could not eat others of higher ages, *i. e.* cannibalism found with the same ages or with younger individuals. Although 12th nymphal instar and adult females had the great values of cannibalism with others, they could not cannibal on the smaller nymphs as a result of difficulty of catching them. The maximum percent cannibalism was obtained by mantid females. They had great values to cannibal their own and so others individuals. Males had smaller values to cannibal their own or others.

Some authors have suggested that, the incidence of cannibalism is simply a consequence of frequency of encounters between co specifics and their relative vulnerability (Agarwala and Dixon, 1992 and Stevens, 1992), *i.e.* cannibalistic attack rates are determined by the probability of encountering vulnerable individuals.

Results from this study, concluded that food limitation was not a complete explanation of cannibalism in *S. viridis*. Wagner *et al.* (1999) found that cannibalism by larvae of *Harmonia axyridis* could reduce developmental time under conditions of limited prey availability, although there were no measurable benefits when food was abundant.

Cannibalism among *S. viridis* was affected by habitat structure. Complex habitat structure reduced cannibalism among *S. viridis* individuals. Obviously, the complex structure created refuges for the mantid individuals. Thompson (1987), Convey (1988) and Scheu (2001) noticed that, complex habitat structure may reduce interference through the predators due to lower encounter rates. Among praying mantids, a preference for habitats of high structural complexity had been documented (Balderson, 1991 and Rentz, 1996). On the other hand, Dong and Polis (1992)

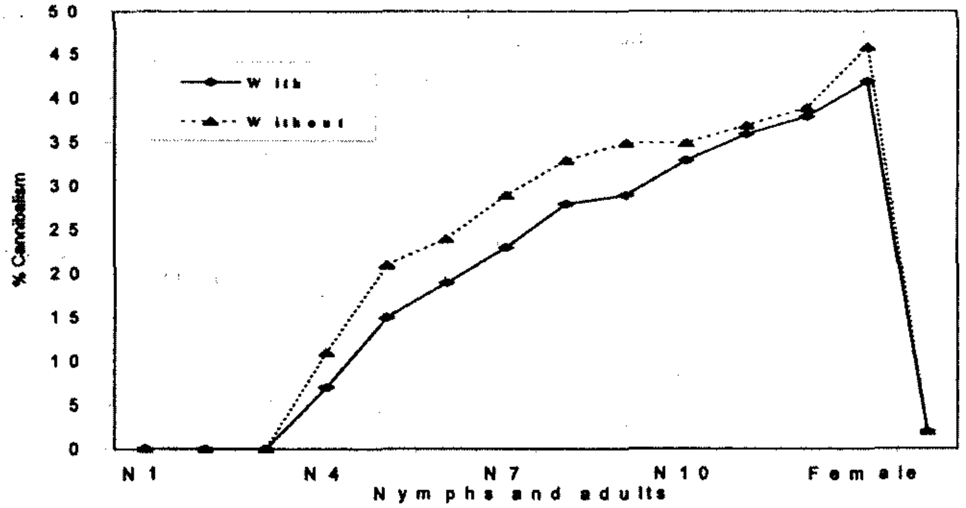

Figure (1): Percentage of *S. viridis* eaten within own individuals (% Cannibalism) in 24 h with or without preys.

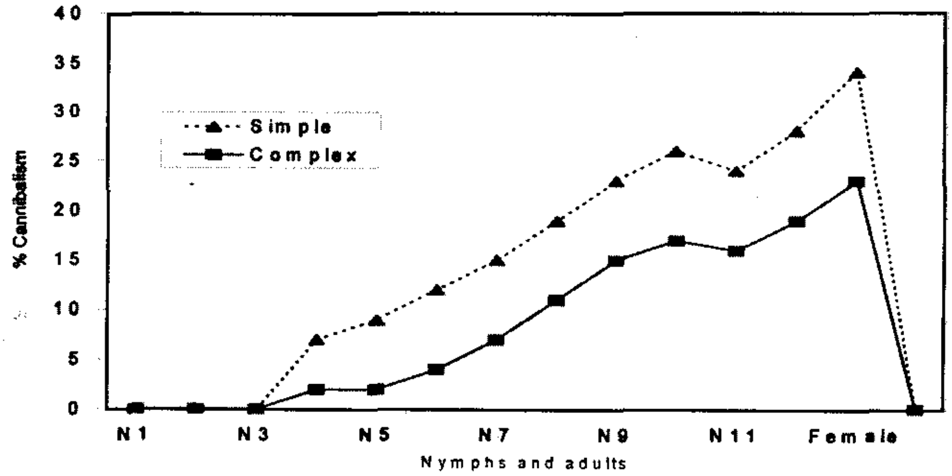

Figure (2): Percentage of *S. viridis* eaten within own individuals (% Cannibalism) in 24 h with simple or complex habitat structure.

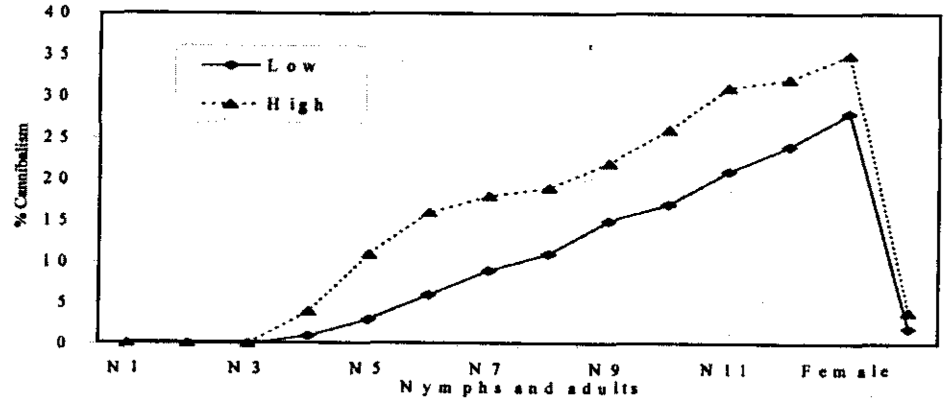

Figure (3): Percentage of S. viridis eaten within own individuals (% Cannibalism) in 24 h with low or high predator density.

Table (2): Effect of prey availability (with or without) on the percentage of *S. viridis* eaten (cannibalized) in 24h by individuals of their own and other ages

Predator Instar / stage	Condition	% cannibalism													
		N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12	Female	Male
N4	With	14	17	14	7	--	--	--	--	--	--	--	--	--	--
	Without	22	20	18	11	--	--	--	--	--	--	--	--	--	--
N5	With	4	10	12	15	15	--	--	--	--	--	--	--	--	--
	Without	8	15	17	23	21	--	--	--	--	--	--	--	--	--
N6	With	3	8	10	7	17	19	--	--	--	--	--	--	--	--
	Without	6	11	14	24	26	24	--	--	--	--	--	--	--	--
N7	With	--	8	6	12	19	21	23	--	--	--	--	--	--	--
	Without	--	15	14	20	28	33	29	--	--	--	--	--	--	--
N8	With	--	--	6	12	19	17	25	28	--	--	--	--	--	--
	Without	--	4	15	20	28	34	38	33	--	--	--	--	--	--
N9	With	--	--	4	4	16	22	28	24	29	--	--	--	--	--
	Without	--	--	8	16	29	39	45	49	35	--	--	--	--	--
N10	With	--	--	--	10	18	25	29	34	30	33	--	--	--	--
	Without	--	--	--	18	22	36	43	39	35	35	--	--	--	--
N11	With	--	--	--	4	12	24	22	28	28	30	36	--	--	--
	Without	--	--	--	16	20	35	47	42	39	36	37	--	--	--
N12	With	--	--	--	8	12	28	30	35	30	34	35	38	--	--
	Without	--	--	--	20	25	39	45	46	53	46	40	39	--	--
Female	With	--	--	--	--	18	15	24	39	40	40	48	52	42	54
	Without	--	--	--	12	22	20	30	46	45	49	58	58	46	68
Male	With	--	--	--	--	--	--	--	--	--	--	--	--	--	2
	Without	--	--	--	2	4	2	4	8	12	4	2	2	--	2

Table (3): Effect of habitat structure (simple, complex) on the percentage of *S. viridis* eaten (cannibalized) in 24h by individuals of their own and other ages

Predator Instar / stage	Habitat	% cannibalism													
		N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12	Female	Male
N4	Simple	12	17	15	7	--	--	--	--	--	--	--	--	--	--
	Complex	5	9	12	2	--	--	--	--	--	--	--	--	--	--
N5	Simple	13	11	17	18	9	--	--	--	--	--	--	--	--	--
	Complex	6	7	8	9	2	--	--	--	--	--	--	--	--	--
N6	Simple	14	16	18	11	14	12	--	--	--	--	--	--	--	--
	Complex	--	6	8	4	5	4	--	--	--	--	--	--	--	--
N7	Simple	--	24	28	24	19	18	15	--	--	--	--	--	--	--
	Complex	--	8	14	18	12	10	7	--	--	--	--	--	--	--
N8	Simple	--	12	30	34	29	26	24	19	--	--	--	--	--	--
	Complex	--	4	8	12	14	12	14	11	--	--	--	--	--	--
N9	Simple	--	--	15	22	33	36	28	25	23	--	--	--	--	--
	Complex	--	--	6	10	16	22	18	17	15	--	--	--	--	--
N10	Simple	--	--	2	18	27	34	36	40	33	26	--	--	--	--
	Complex	--	--	--	10	15	22	24	27	21	17	--	--	--	--
N11	Simple	--	--	--	12	22	29	38	44	40	36	24	--	--	--
	Complex	--	--	--	8	11	14	21	23	20	18	16	--	--	--
N12	Simple	--	--	--	6	17	26	29	37	46	40	35	28	--	--
	Complex	--	--	--	2	5	8	10	15	11	19	20	19	--	--
Female	Simple	--	--	--	4	12	20	28	34	44	48	46	42	34	46
	Complex	--	--	--	--	8	10	14	16	20	22	26	22	23	30
Male	Simple	--	--	--	2	4	2	4	2	2	4	4	--	--	2
	Complex	--	--	--	--	--	--	2	2	2	4	2	--	--	--

Table (4): Effect of predator density (low and high) on the percentage of *S. viridis* eaten (cannibalized) in 24h by individuals of their own and other ages

Predator Instar/stage	Predator density	% cannibalism													
		N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12	Female	Male
N4	Low	6	8	4	2	--	--	--	--	--	--	--	--	--	--
	High	18	20	12	4	--	--	--	--	--	--	--	--	--	--
N5	Low	10	14	16	10	3	--	--	--	--	--	--	--	--	--
	High	15	22	24	16	11	--	--	--	--	--	--	--	--	--
N6	Low	8	10	12	14	10	6	--	--	--	--	--	--	--	--
	High	12	18	22	28	20	16	--	--	--	--	--	--	--	--
N7	Low	--	4	5	10	15	14	9	--	--	--	--	--	--	--
	High	6	10	26	35	40	26	18	--	--	--	--	--	--	--
N8	Low	--	--	2	8	12	16	14	11	--	--	--	--	--	--
	High	2	4	16	28	38	40	28	19	--	--	--	--	--	--
N9	Low	--	--	--	6	10	18	22	18	15	--	--	--	--	--
	High	--	--	4	14	22	30	40	36	22	--	--	--	--	--
N10	Low	--	--	--	2	14	20	26	27	20	17	--	--	--	--
	High	--	--	--	12	26	34	42	44	36	26	--	--	--	--
N11	Low	--	--	--	2	10	18	30	34	32	26	21	--	--	--
	High	--	--	--	8	22	30	38	46	48	40	31	--	--	--
N12	Low	--	--	--	4	8	12	14	18	20	22	24	24	--	--
	High	--	--	--	10	16	28	40	48	52	48	40	32	--	--
Female	Low	--	--	--	8	20	22	20	16	17	16	18	20	28	32
	High	--	--	--	16	30	36	40	46	56	48	45	40	35	38
Male	Low	--	--	--	--	--	--	--	--	--	--	--	--	--	2
	High	--	--	--	2	4	4	2	2	4	4	2	2	--	4

considered population density as a key factor for the population dynamics of cannibalism. This study also indicated that mantid individual cannibalism was a predator density-dependent behavior in both nymphs and adults.

It is also well known from theoretical studies that cannibalism can have an important effect on population structure and dynamics. This effect can be positive: for example, Kohlemeier and Ebenhoh (1995) showed that cannibalism by the predator can in some cases lead to a higher long term predator stock size. Bobisud (1976) reported that sufficiently restricted cannibalism in the prey can lead to increase equilibrium population sizes. Furthermore, cannibalism can enable a population to survive when food is scarce-the so- called lifeboat effect (Van den Bosch *et al.* 1988). On the other hand, Van den Bosch and Gabriel (1997), using an age-structured model, stated that "increasing the cannibalistic pressure decreased the adult and large juvenile population density irrespective of parameter values".

Overall, on the positive side, the length of a mantid stadium being sensitive to cannibalism improve the chances of surviving to find prey, eliminates potential competitors and ensures future availability of food when preys are scarce. In conclusion, cannibalism appears to be a strategic behavior worthy of study in other species of predacious insects, both in light of its theoretical implications for population dynamics and for its potential ramifications on the effectiveness of these predators as biological control agents.

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