STUDY OF EFFECT OF SEPEDON SENEX W. (SCIOMYZIDAE) LARVAE ON SNAIL VECTORS OF MEDICALLY IMPORTANT TREMATODES

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ABSTRACT

Laboratory experiments were carried out to determine the potential value of Sepedon senex W. in the control fresh—water snail populations. Prey selection by Sepedon senex W. larvae, their consumption capacity, survival, and their ability to kill snail prey were determined. The effects of prey and predator densities on the rate of predation were investigated, and the searching, killing and consumption efficiencies of Sepedon senex W. larvae were determined. Observations of the vertical distribution of certain fresh—water snails in aquaria and preliminary studies on mass rearing of Sepedon senex W. were carried out.

Killing selection and efficiency of the larvae depended on the relative sizes of snails and larvae. The daily consumption of the larvae depended on their stage of development and increased with prey density but decreased with increasing larval density. When searching for prey, the rate of movement of larvae increased with decreasing distance between predator and prey (P < 0.05). Searching efficiency increased with prey density and increasing age of the larvae. The later instar larvae detected snails from longer distances and sooner than the younger ones. Younger larvae spent much more time handling snail prey than older larvae. Handling time increased slightly with prey density.

Most of the non-operculate snails studied were distributed at a depth of 0-1 cm, which is within reach of Sepedon senex W. larvae.

Protein food for adults increased larval consumption, conversion efficiency, growth rate, and shortened the developmental period at every stage. Larvae fed with live snails had higher conversion efficiency, and higher growth rates than those fed with freshly crushed snails. The conversion efficiency of the larvae increased with age. There was a tendency for the female population to increase when adult S. senex were fed with protein—rich food.

INTRODUCTION

According to Alcata¹ the most important parasitic disease of cattle in the Hawaiian Islands is caused by liver flukes (Fasciola gigantica). Liver fluke infection in the Hawaiian Islands dates back to at least 1892, when it was first reported on Kauai, Oahu, Maui, and Molokai. About 57% of animals slaughtered at that time were infected with flukes and economic losses were large. The intermediate hosts of Fasciola gigantica in Hawaii are Lymnaea ollula Gould and Pseudosuccinea columella Say which are commonly found in streams, and on taro and water—cress plants.

There are three important phases in the life cycle of flukes: (1) development in the intermediate host; (2) encystment on vegetation; and (3) development in cattle.

Attempts are being made to control the parasite through biological control of the snail hosts. Lampyrid species, *Proturis hebes* Porter, *Colophotia praeusta* Esch, *Luciola cruciata* and *L. laterclis* Motsch, have been released directly into the field to control *Lymnaea ollula* and *Achatina fulica* Bowdich, but none of the insects were recovered.^{2,13}

C.O. Barg³ was the first to notice the malacophagous habit of sciomyzid larvae. A decade later not less than 143 species of Sciomyzidae became known but the natural history of about two – thirds of the known species remains to be investigated. All have been found to be malacophagous during their larval stages in the water. Most species are able to kill non-operculate snails but Hoplodictya setosa (Coquillett) can attack and feed on operculate snails.² The possible value of Sciomyzidae in the biological control of medically important snails was recognized early in the study of the immature stages of this family at Cornell University.³ Experiments were soon conducted to determine the ability of marsh fly larvae to attack Lymmaea ollula, the Hawaiian snail host of the giant liver fluke of cattle.^{2,13} Experiments on snail hosts of liver flukes included experimental introductions of Sciomyzidae in Hawaii, Guam and Australia. A sciomyzid species from Central America is now established on all four of the major islands of Hawaii and on Guam. It is known to kill Lymnaea ollula Gould in nature as well as in the laboratory and is believed to be effective in reducing snail populations.² Berg⁴ concluded that (1) since public pressure against widespread use of broad spectrum toxicants is increasing rapidly, alternative methods of snail control to extensive application of molluscicides should be developed as quickly as possible; (2) there is no valid reason to discount the possibility of biological or integrated control of snails before these methods have been adequately tested; and (3) snial-killing Sciomyzidae (Diptera) constitutes one of the groups of natural enemies of snails that may have value in biological control. However much more research on the basic biology and ecology of these flies is needed. Only about one - third of the Sciomyzidae have been studied. Laboratory and field testing of biological control must be carried out to confirm that sciomyzid species are the most promising agents for the control of certain snail species. Most of the 143 species Berg studied at that time live in relatively cool climates and probably could not colonize warm regions where trematode diseases cause great problems. He suggested that research must be extended into the tropics.⁴

During 1967-70, I studied the biology and ecology of British Sciomyzidae while in the United Kingdom. On returning to Thailand I began studying Thai species of Sciomyzidae.⁵

Thailand suffers from many trematode diseases, including intestinal, liver and lung flukes which infect man, cattle and other domestic animals. Most of the intermediate hosts of flukes are lymnaeid and planorbid snails, for example, *Indoplanorbis exustus* Deshayes and *Lymnaea* (Radix) auricularia rubiginosa Michelin.

As Berg concluded, sciomyzid larvae differ remarkably among themselves in habitat, adaptations, mode of attack, and choice of host and prey, so that specificity of feeding of predacious sciomyzid larvae is a necessary and important aspect to study. The ability of the larvae to attack and destroy snails is a basic attribute to be determined if these larvae are to be effective as biological control agents.⁴

In the present study, in order to determine if Sepedon senex W., a Thai species of Sciomyzidae, could be effective in controlling fresh—water snails, seven main aspects were investigated:

- (1) prey selection by Sepedon senex W. larvae;
- (2) snail consumption capacity and survival of Sepedon senex W. larvae;
- (3) ability to kill snail prey;
- (4) effects of prey and predator densities on the rate of predation;
- (5) searching, killing and consumption efficiency of Sepedon senex W. larvae;
- (6) vertical distribution of fresh-water snails in aquaria; and
- (7) preliminary studies on mass rearing of Sepedon senex W.

Sepedon senex W. was used in the experiments because it is one of the larger sciomyzids found in Thailand. Three fresh—water snail species (intermediate hosts of important flukes in Thailand) were used as prey: the non—operculate Indoplanorbis exustus Deshayes, Lymnaea (Radix) auricularia rubiginosa Michelin, and Gyraulus convexiusculus Hutton. The experiments are described below.

MATERIALS AND METHODS

1. Prey selection by Sepedon senex W. larvae

In order to investigate how the larvae select and attack their prey, snails of different sizes and different species were exposed to single larvae of various instars for 24 hours. Each trial consisted of a single larva and snails of different species or sizes confined in a dish 5 cm in diameter and 1.5 cm in height in water 1 cm deep. Ten replicates of three experiments were set up. In the first experiment, a single first instar larva 1.39-1.65 mm in length was exposed to three *G. convexiusculus* of different diameters; 1.39-1.65 mm, 2.36-3.00 mm and 3.80-3.82 mm. In the second trial, a single second—instar larva 2.60-2.78 mm in length was confined in a dish with four snails; two *G. convexiusculus* 2.70-3.00 mm and 3.60-3.90 mm in diameter, one *I. exustus* 4.86-5.00 mm diameter and

one *L. auricularia rubiginosa* 4.17-5.00 mm. In the third experiment, a single third instar larva 4.17-4.86 mm in length was exposed to two *I. exustus* 4.86-5.21 mm and 5.70-8.00 mm diameter, and two *L. auricularia rubiginosa* 4.17-4.28 mm and 6.05-7.00 mm diameter.

2. Consumption capacity and survival of Sepedon senex W. 'arvae

G. convexiusculus of various diameters and first instar larvae which had killed their prey successfully were employed in these experiments. In order to determine their capacity to consume snails, S. senex larvae were fed daily with G. convexiusculus 1.5-4.0 mm in diameter. One hundred snails and 10 larvae were confined in a 45 cm diameter bowl containing water 10 cm deep. The number of snails given daily was more than sufficient. The numbers of dead snails and larvae were recorded and these were replaced daily to keep prey and predator density constant. The larvae replaced were of the same length as the dead ones. Ten replicates were carried out.

3. The ability of Sepedon senex W. larvae to kill snail prey

It is well established that variation in prey and predator density affects the rate of predation. 8,9 In order to determine the appropriate densities of the snail prey and appropriate stage of larvae for maximum prey consumption, all three instar larvae of S. senex larvae and G. convexiusculus of 2-3 mm diameter were used in the experiments. Predator and prey were confined together in 5 cm diameter dishes with 1 cm depth of water. The exposure duration was 24 hours. The average number of snails killed was recorded. A larva was exposed to snails at five different densities, 4, 6, 8, 10, and 12. Ten replicates were carried out.

4. Effects of prey and predator density on the rate of predation

All three larval instars of *S. senex* and *G. convexiusculus* of 4–5 mm diameter were used in the experiments. Six different densities of each instar, 1, 5, 10, 15, 20, and 25 per dish, were exposed to 12 different snail densities: 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, and 60. Five replicates of each experiment using first instar larvae and three replicates of each experiment using second and third instar larvae were carried out. The larvae and snails were confined together in 9 cm diameter dishes with 1 cm depth of water for 24 hours. The average number of snails killed was recorded.

5. Searching, killing and consumption efficiency of Sepedon senex W. larvae

In order to determine the behaviour of all three larval instars of *S. senex* and their ability to search, kill and consume snail prey at different prey densities, three replicates of experiments on each instar using 6 different prey densities were carried out. Six prey densities of 1, 4, 6, 8, 10 and 12 snails were used. A single larva and snail prey were placed at opposite sides of petri dishes 9.2 mm in diameter with water 5 mm deep. The movement of the larvae was traced and marked every minute until the larva attacked the snail prey. The time spent in moving was recorded for four intervals of distance from snail prey: 92–70,

69-47, 46-24 and 23-1 mm. The time spent in searching and consuming snail prey was recorded until satiation.

6. Vertical distributions of certain fresh water snails

Sepedon spp. larvae possess a hydrophobic spiracle disc at the posterior end for breathing air. This disc floats on the surface of the water. A big air bubble in the gut also helps to enable larvae to hold snails much bigger than themselves afloat while consuming them. Because the larvae breath air, they can submerge completely only for a short time. Therefore they cannot attack snails in deep water. To investigate the possibility of using sciomyzid larvae as agents to control non-operculate snail populations, their vertical distribution was investigated. The vertical distribution of three species of non-operculate snails, Indoplanorbis exustus Deshayes, Lymnaea auricularia rubiginosa Michelin, and Gyraulus convexiusculus Hutton, was studied in the laboratory. Three species of snails (250 individuals of each) were kept together in aquaria (45×30×30 cm.) with 22 cm of water. An aerator was applied to each of the three aquaria. Ten days were allowed for acclimation of the snails. The numbers of snails at various depths were recorded. Ten replicates were carried out.

7. Preliminary studies on mass rearing of Sciomyzidae

Techniques for mass rearing of control agents also need to be developed before a control programme be put into practice. Increasing sciomyzid production could be accomplished by increasing egg production, reproductive period or growth rate. Chock (1961) noticed that egg production of sciomyzids increased when snail tissue was added to the food of adults. In the laboratory, using the techniques of Knutson, Is sciomyzid larvae were reared to produce eggs throughout the year. I found that sciomyzid larvae cannot kill operculate snails but feed on them when these snails are freshly crushed. When the snail supply was limited, the larvae were reared successfully from hatching to pupation on crushed operculate snails. The mortality of newly hatched larvae appeared to be less when fed on crushed snails, even when living, pulmonate snails of suitable size were present.

In order to investigate the effects of adult and larval food on growth and development of *S. senex*, two types of experiments were carried out. In the first experiments adults were reared on four different recipes of food: (A) honey: dry milk – 3:5, (B) honey: dry milk: yeast – 3:5:2, (C) honey: dry milk: crushed snail – 3:5:1, (D) honey: dry milk: yeast: crushed snail – 3:5:2:1. A pair of *S. senex* were reared in 4 oz. jars and were investigated every second day. Seven to nine replicates were carried out. The second experiments were done to rear larvae from the first experiments. Larvae from adults fed with each food recipe were used in experiments to investigate the effects of larval food on growth and development of *S. senex*. In one set of experiments, larvae were fed with live snails; in another, they were fed with freshly crushed snails. Individual larvae were reared in plastic dishes 4 cm in diameter filled with 2.5 mm of water, and 40 live *G. convexiusculus* or a similar number of freshly crushed snails were given daily, which was more than sufficient. The length of

larvae and the number of snails eaten daily were recorded. The results of the experiments were expressed in terms of dry weight. Larval and snail dry weights were obtained from the length or diameter and dry weight relationship curves. The moulting, pre—oviposition and incubation periods were recorded. Ten replicates were performed. For the larvae of the flies fed with D—recipe food, similar experiments were done using 5 cm diameter plastic dishes filled with 1 cm depth of water.

RESULTS

1. Prey selection by Sepedon senex W. larvae

Table 1 shows that *S. senex* larvae killed snails selectively depending on the relative sizes of the larvae and snail prey, and on snail species. All instars of larvae killed snails with diameters as wide as approximately twice the length of the larvae. The larvae selected smaller snails more often than larger ones. The later instar larvae killed snails more efficiently. In all trials, *L. auricularia rubiginosa* were not attacked.

2. Consumption capacity and survival of Sepedon senex W. larvae

S. senex larvae consumed 112-135 snails at an average rate of 124.6 ± 7.64 (mean \pm S.D.) G. convexiusculus of 1.5-4.0 mm diameter during their larval life. Consumption capacities of the first, second, and third instar larvae were approximately 6.00 ± 9.17 , 48.00 ± 18.33 , and 96.00 ± 6.15 snails, respectively. The average percentage survival of larvae was approximately 50.00 ± 6.15 (mean \pm S.D.) and increased approximately in proportion with the developmental stage (Table 2). Third instar larvae had the highest percentage survival rate with the smallest deviation from the mean.

3. Ability of Sepedon senex W. larvae to kill snail prey

The effect of prey density on the rate of predation of the three larval instars of S. senex is shown in Figure 1. For all larval stages, the number of snails eaten per larva per day increased with snail density. Maximum daily consumptions of the individual larvae of the first, second and third instars were 3, 6, and 10 snails of 2-3 mm diameter, respectively. The later instars had greater ability to kill snails at all prey densities studied (Fig. 1).

4. Effects of prey and predator densities on the rate of predation

The average rate of predation increased with prey density (Fig. 2) but decreased with predator density for all instars (Figs. 2 & 3). The ability of the larvae to kill snails at all prey and predator densities increased with age (Figs. 2 & 3). The highest possible daily consumption of 4-5 mm G. convexiusculus by first, second, and third instar larvae, when alone, were approximately 1,3 and 4 snails per larva respectively.

5. Searching, killing and consumption efficiency of Sepedon senex W. larvae

At similar distances from snail prey, third instar larvae moved faster than younger larvae (Fig. 4). The first and the second instar larvae moved faster as they approached snail prey but the rate of movement of the third instar larvae from 1 to 92 mm away from snail prey was more or less constant at approximately 15 mm per minute.

Figure 5 shows that searching time decreased with increasing prey density but handling time (killing and consuming time) increased with prey density. Developmental stage showed more obvious effects on rate of predation than did prey density. The third instar larvae of *S. senex* had the highest efficiency of searching and handling prey at all levels of prey density.

6. Vertical distribution of fresh-water snails

Figure 6 shows the average percentage of distribution at different depths for three species of snails. All three species of snails studied preferred to be near the water surface, 0-1 cm depth. More than 66 to approximately 94 percent (mean \pm S.D. = 85.10 ± 19) of *I. exustus* were located at 0-1 cm depth, 72.5-100 percent (mean \pm S.D. = 87.70 ± 8.00) of *L. auricularia rubiginosa* and 75.80-95.80 percent (87.30+7.40) of *G. convexiusculus* preferred to be at similar depths.

7. Preliminary studies on mass rearing of Sciomyzidae

The incubation period of eggs, growth rate, developmental periods of the larvae, and the preoviposition period of progenies from flies fed with high protein food were shorter than those of larvae from parents fed with low protein food (P < 0.05; Table 3, Fig.7)

Larvae from flies fed with live snails had shorter developmental periods and higher growth rates than those fed with freshly crushed snails. Developmental periods of larvae reared in 4 cm diameter plastic dish with 2.5 mm depth of water and those reared in 5 cm dish with 1 cm depth of water were not significantly different (P > 0.05).

Table 3 shows that the larvae from flies fed with higher protein food had higher growth rates and higher conversion efficiency than those fed with low protein food. The larvae consumed more tissue of live snails than of crushed snails. Conversion efficiency and growth rates of larvae fed with live snails were higher than of those fed with crushed snails.

All of the first instar larvae seemed to consume approximately equal amounts of food per day but this was not so for the later stage larvae. Second and third instar larvae from parents fed with higher protein food consumed more food per day. The conversion efficiency of the larvae increased with age.

DISCUSSION

Smaller larvae possess smaller and weaker mouth – hooks than older larvae. When an encounter with snail prey takes place, the larva usually crawls around the shell, probes about and may touch the snail's body. When the larva's mouth – hook pierces the snail tissue, a local contraction occurs. This contraction is usually followed rapidly by a violent retraction of the snail into its shell. The larva is often pulled into the aperture by the snail. Being attacked, the snail secretes mucus which may close the spiracular openings of the fly larva and kill it. Smaller larvae suffer more than the larger ones from this contraction and secretion resulting in unsuccessful attack. *L. auricularia rubiginosa* secretes larger

quantities of more a viscous material which makes it difficult for sciomyzid larvae to kill them (Table 1). In other studies,⁵ when the larvae were fed with only *L. auricularia rubiginosa*, they were able to kill and consume the snails. In this study, different species and/or different sizes of snails were available in each trial. The larvae selected and attacked the most vulnerable snails. Larvae of all instars attacked and killed pulmonate snails of suitable size (Table 1). First instar larvae only 1 mm long were able to kill snails (*I. exustus*) 3 mm in diameter. Larger snails were often killed when they were attacked by several larvae simultaneously.⁵ Large third instar larvae attacked large snails, and also had a higher overall ratio of successful attacks than the younger, smaller larvae (Table 1), resulting in their higher survival (Table 2). Percentage survival of first instar larvae was in the same range as the percentage of snails killed by first instar larvae, which explains the high mortality of this larval instar, (Tables 1 & 2). Newly hatched larvae that failed to kill a snail in the first few days after hatching eventually died.

Average survival of *S. senex* larvae in the laboratory was approximately 50%, probably much higher than would occur in nature. In trials in which predatory fauna were confined with *S. senex* larvae overnight, the larvae were consumed. Predatory fauna used were those found in the same habitals as the larvae, i.e., dragonfly nymphs (*Epophthalmia frontalis* Selys), (2) fish *Poecilia reticulatus*, *Tricopsis vittatus*, *Rasbora* sp., and young *Channa striatus*. The number of mosquito larvae 2–4 mm in length required to satiate these predators was 7–50 per predator per day depending on predator species.^{6,7} The length of the first and second instar larvae of *S. senex* used in these studies was in the same range as that of the mosquito larvae. This suggested that mortality of sciomyzid larvae is probably more than 50% in nature.

In the laboratory with no enemies of the sciomyzid larvae present, mortality decreased proportionately with larval stage (Table 2). The third instar larva had the highest percentage survival.

Solomon stated that rate of predation depended on prey and predator densities and that the total number of prey killed is equal to the number of prey killed per predator multiplied by the number of predators. ¹⁰ Figures 2 and 3 show increasing rates of predation by single larvae of all instars with increasing prey density, since less time is spent on searching. When satiation was reached the rate of predation levelled off. The first, second and third instar larvae reached satiation when predatory rates were 3, 6 and 10 snails (2–3 mm diameter *G. convexiusculus*) per larva per day, respectively, which were the highest possible killing efficiencies at prey densities of not less than 10 snails. Solomon called this changing of predation rate due to prey density a "functional response".

The highest possible killing efficiency depended on the relative sizes of prey and predator. When 4-5 mm diameter G. convexiusculus were given daily to single larvae of S. senex, the satiation levels of the first, second and third instars were 1, 2 and 4 snails, respectively (Fig. 2). At this size, the highest possible rate of consumption of the larvae was reached when a single larva was confined with forty or more snails.

In Figure 1, the functional response curves of the first and second instars were of Type I and that of the third instar was of Type III suggested by Holling, but in Figure 4 the functional response curves of all larval stages were between Type I and Type II. The ability of *S. senex* larvae to kill snails increased with age (Fig. 1 & 2) but decreased with predator density (Fig. 2 & 3). The higher the predator densities, the lower the number of snails consumed until the functional response curves reached equilibria which were lower than the maximum possible consumption due to interference and competition between larvae. Therefore, not only prey and/or predator densities but also the realtive sizes of predators and prey affect the rates of predation. Later instar larvae are bigger and able to kill and consume more efficiently (Tables 1 & 4). Larvae confined with snails at high density consumed more snails, grew faster, and hence increased their ability to kill snails. Murdoch refered to this behaviour as "developmental response". 11

Since the prey density at which the highest possible consumption rate would occur depended on species and size of prey, the best proportion of *S. senex* larvae to *G. convexiusculus* to achieve control of snail numbers would seem to be 1:40, providing there was no mortality of predators.

The later instar larvae attacked and consumed more snails because of their bigger mouth—hooks and body size. Also they have higher efficiencies of searching and detecting prey. At similar distances from snail prey, third instar larvae moved faster toward their prey than younger larvae. The first and the second instar larvae moved faster as they approached closer to snail prey, indicating that the nearer they were to their prey, the more accurately they could detect its position. Larvae moved randomly at the begining but more directly toward the snail as they locate their prey. The increase in the rate of movement started from the release point, 92 mm away from prey, indicating that larvae can detect their prey at a distance of 92 cm or more. Third instar larvae moved directly from the release point with constant rate of movement toward their prey. Thus, not only the stage of development but also the distance between predator and prey influences searching time.

The searching and handling time of larvae of all developmental stages varied with prey density (Fig. 5). Increased snail prey density shortened searching time but slightly prolonged handling time because of interference. First instar larvae spent more time in searching and handling their prey than second and third instar larvae. This resulted in the higher predation rate of the later instar larvae, especially at high prey densities.

S. senex cannot attack snails in deep water, and can attack only non-operculate snails. The snail species used in this experiment are medically important, non-operculate pulmonates which require air for respiration, and so prefer to be near the surface. Most remained at 0-1 cm depth in aquaria. In nature some are occasionally found floating at the water surface, especially L. auricularia rubiginosa and I. exustus. Most of these snails are found in nature crawling on aquatic plants or on the side of man-made ponds at the water surface or a few cm above the surface.

This suggests that if the population density of sciomyzid larvae is high enough to kill all snails within reach, the snail population might be effectively reduced.

In order to find the best food for sciomyzid flies and larvae to attain high production in mass rearing, experiments to determine the effects of adult and larval food quality on growth and development were carried out. The larvae from flies reared with high protein food seemed to be stronger, ate more food per day, and hence had a higher growth rate and a shorter developmental period. Flies emerging from these larvae also had a shorter preoviposition period. Wigglesworth stated that protein food is necessary for egg and yolk production which is important for growth of larvae. ¹⁷

Sciomyzid larvae are predacious in nature and will not eat crushed snails which have started to decay. This possibly lowered the daily consumption of the larvae fed with crushed snails. In addition, the nutritional quality of the dead snails may not equal that of live snails. The conversion efficiencies of every instar (from flies fed with A-D food recipes) fed with live snails were higher than those of larvae fed with crushed snails. This conversion efficiency increased with age. This led to the lower growth rate and longer developmental period of larvae from parents fed with low protein food and fed on crushed snails (Table 3, Fig. 7).

These results suggest that in releasing sciomyzid larvae directly into the field to control fresh water snails, the relative sizes of snails and larvae, and the densities of both predator and prey, need to be taken into consideration.

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บทคัดย่อ

เพื่อทราบว่าจะใช้ Sepedon senex W. ควบคุมประชากรของหอยน้ำจืดได้หรือไม่ จึงได้ทดลองถึงการเลือก ทำลายเหยื่อ ปริมาณการกิน การอยู่รอด ความสามารถในการฆ่าเหยื่อของตัวอ่อนของแมลง Sepedon senex W. และ ทดลองถึงผลของความหนาแน่นประชากรเหยื่อและผู้ล่าต่ออัตราการล่า ประสิทธิภาพในการค้นหา การฆ่าและกิน เหยื่อของ Sepedon senex W. ศึกษาถึงการกระจายของหอยน้ำจืดในแนวคิ่ง และทดลองเบื้องต้นเกี่ยวกับการผลิต Sepedon senex W. จำนวนมาก

การเลือกทำลายเหยื่อและประสิทธิภาพในการฆ่าเหยื่อของตัวอ่อนขึ้นอยู่กับขนาดของหอยและตัวอ่อน ปริมาณการกินอาหารต่อวันขึ้นอยู่กับระยะการเจริญของตัวอ่อน และเพิ่มขึ้นเมื่อประชากรเหยื่อเพิ่ม ลดลงเมื่อ ประชากรตัวอ่อนเพิ่มขึ้น ในการค้นหาเหยื่อตัวอ่อนจะเคลื่อนที่เร็วขึ้นเมื่อยิ่งเข้าใกล้เหยื่อ (p < 0.05) ประสิทธิภาพ ในการค้นหาเพิ่มขึ้นเมื่อความหนาแน่นประชากรเหยื่อเพิ่มขึ้นและเมื่อตัวอ่อนมีอายุมากขึ้น ตัวอ่อนที่มีอายุมาก สามารถตรวจพบเหยื่อที่ระยะห่างกว่า และก้นหาเหยื่อได้เร็วกว่าตัวอ่อนที่มีอายุน้อย ตัวอ่อนอายุน้อยใช้เวลาในการฆ่าและกินเหยื่อมากขึ้นอีกเล็กน้อยเมื่อประชากรเหยื่อเพิ่มขึ้น

หอยที่ศึกษาไม่มีฝาปิด ส่วนใหญ่ของหอยเหล่านี้ ชอบอยู่ที่ผิวน้ำที่ความลึกประมาณ 0-1 เซนติเมตร ซึ่ง อยู่ในระดับที่ตัวอ่อนของ Sependon senex W. เข้าถึงได้

การเลี้ยงตัวเต็มวัยของ Sepedon senex W. ด้วยอาหารมีโปรตีนทำให้อัตราการกินและอัตราการเจริญของ ตัวอ่อนเพิ่มขึ้น ระยะการเจริญทุกระยะสั้นลง ตัวอ่อนที่กินหอยมีชีวิตมีประสิทธิภาพในอาการเปลี่ยนอาหารมาเป็น เนื้อเยื่อ และอัตราการเจริญสูงกว่าตัวอ่อนที่กินหอยตาย ประสิทธิภาพในการเปลี่ยนอาหารมาเป็นเนื้อเยื่อมากขึ้นเมื่อ อายุมากขึ้น ประชากรของแมลงเพศเมียมีแนวโน้มเพิ่มขึ้นเมื่อเลี้ยงตัวเต็มวัยด้วยอาหารที่มีโปรตีนสูง

TABLE 1 Selective killing of some medically important snails by *Sepedon senex* W. larvae expressed as percentage killed

Larval instar	Larval length	Snail diameter (mm)	% Killed	
1	1.39 – 1.53	(G) 1.39-1.65	9.87	
		(G) 2.36-3.00	5.72	
		(G) $3.80-3.82$	0	
2	2.60 - 2.78	(G) $2.70 - 3.00$	92.73	
		(G) $3.60-3.90$	89.47	
		(I) 4.80 - 5.00	40.59	
		(R) $4.17 - 5.00$	0	
3	4.17 - 4.86	(1) 4.86 - 5.21	42.05	
		(1) 5.70 - 8.00	38.04	
		(R) $4.17 - 4.28$	0	
		(R) $6.05 - 7.00$	0	

G - Gyraulus convexiusculus Hutton

TABLE 2 Developmental period and survival of *Sepedon senex* W. when fed with live *Gyraulus convexiusculus* Hutton

	Moulting period (day)	% Survival
1 st In	2.30 + 1.70	6.00 + 9.17
2 nd In	2.78 + 0.78	48.00 + 18.33
3rd In	3.62 + 1.25	96.00 + 6.15

^{1 -} Indoplanorbis exustus Deshayes

R - Lymnaea (Radix) auricularia rubiginosa Michelin

TABLE 3 Developmental period of *Sepedon senex* W. from parents fed with four different food recipes (A-D) when fed with live and freshly crushed *Gyraulus convexiusculus* Hutton

Food of parent flies	Food of larvae	1 st Instar larval period (day) M±S.D	2 nd Instar larval period (day) M±S.D	3 rd Instar larval period (day) M±S.D	Pupal period (day) M±S.D	Preoviposi- tion period (day) M±S.D	Incubation period (day) M±S.D	Sex ratio
A	l.sn.	3.30 ± 0.48	2.80 ± 0.42	3.80 ± 0.42	8.80 ± 1.31	8.60 ± 0.89	3.00 ± 0.68	
	c.sn.	7.25 ± 0.71	7.38 ± 0.92	6.75 ± 0.71	11.88 ±1.89	12.33 ± 2.52	3.05 ± 0.64	5:3
В	l.sn.	3.11 ± 0.33	2.44 ± 0.53	3.78 ± 0.44	7.66 ± 0.87	8.60 ± 0.84	2.68 ± 0.48	
	c.sn.	6.71 ± 0.76	7.28 ± 0.98	6.71 ± 0.75	10.29 ± 0.95	11.33±1.53	2.80 ± 0.41	3:4
С	l.sn.	3.00 ± 0.00	2.10 ± 0.20	3.60 ± 0.52	6.40 ± 0.70	8.60 ± 0.55	2.63 ± 0.49	
	c.sn.	6.33 ± 0.87	7.11 ± 0.33	6.33 ± 0.87	9.89±1.54	9.75 ± 1.50	2.78 ± 0.52	4:5
D	l.sn.	2.00 ± 0.00	2.00 ± 0.00	3.50 ± 0.53	5.40 ± 0.70	8.80 ± 0.10	2.56 ± 0.51	
	c.sn.	5.86 ± 0.69	7.00 ± 0.00	6.28 ± 0.95	9.28 ± 1.49	9.65 ± 0.58	2.72 ± 0.46	4:3
D*	l.sn.	2.30 ± 1.70	2.78 ± 0.78	3.62 ± 1.25	5.24 ± 0.51	8.87 ± 0.01	2.50 ± 0.61	
	c.sn.	5.24 ± 0.13	6.25 ± 0.73	6.78 ± 0.86	7.32 ± 1.01	9.02 ± 0.51	3.07 ± 0.41	NR
D**	c.sn.	4.89 ±1.46	3.84±1.35	3.40 ± 0.49	5.00 ± 1.00	10.75 ± 5.34	3.09 ± 0.79	NR

A - honey + dry milk

B - honey + dry milk + yeast

C - honey + dry milk + crushed snail

D - honey + dry milk + yeast + crushed snail

^{* -} reared in 5 cm diameter dish with 1 cm depth of water

^{** -} Beaver, 1977

^{1.}sn. - live snail

c.sn. - crushed snail

NR - not recorded

TABLE 4 Food consumption and growth rate (mg dry weight/larva/day) of Sepedon senex W. larvae from parents fed with four different food recipes (A-D) when fed with live and freshly crushed Gyraulus convexiusculus Hutton.

Food of parent flies	Snail food of larvae	1 st Instar larvae		2 nd Instar larvae		3 rd Instar larvae	
		Consumption	growth	Consumption	growth	Consumption	growth
Α	live	2.25	0.012	3.04	0.35	3.21	0.47
	crushed	1.34	0.0055	1.72	0.131	2.11	0.182
В	live	2.25	0.013	3.15	0.40	3.32	0.57
	crushed	1.36	0.006	1.83	0.132	2.21	0.236
С	live	2.25	0.016	3.18	0.46	3.32	0.57
	crushed	1.36	0.0064	1.87	0.134	2.25	0.296
D	live	2.34	0.020	3.19	0.48	3.35	0.59
	crushed	1.37	0.0069	1.91	0.136	2.44	0.309

A - honey + dry milk

TABLE 5 Conversion efficiency (growth rate: food consumption rate) of Sepedon senex W. larvae from parent flies fed with four different food recipes (A-D) when fed with live and crushed Gyraulus convexiusculus Hutton

Food of parent flies	Snail food of larvae	Conversion efficiency (%)				
		1 st Instar larvae	2 nd Instar larvae	3 rd Instar larvae		
A	live	0.5	12.0	15.0		
	crushed	0.4	8.0	9.0		
В	live	0.6	13.0	16.0		
	crushed	0.4	7.0	11.0		
С	live	0.7	14.0	17.0		
	crushed	0.5	7.0	13.0		
D	live	0.8	15.0	18.0		
	crushed	0.5	7.0	13.0		

A - honey + dry milk

B - honey + dry milk + yeast

C - honey + dry milk + crushed snail

D - honey + dry milk + yeast + crushed snail

B - honey + dry milk + yeast

C - honey + dry milk + crushed snail

D - honey + dry milk + yeast + crushed snail



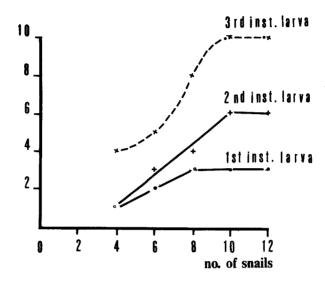


Fig. 1 Functional response curves of the three larval instars of Sepedon senex W. fed with Gyraulus convexiusculus Hutton 2-3 mm in diameter.

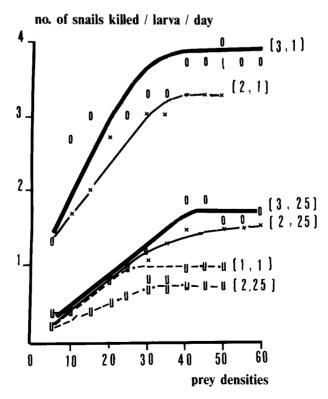


Fig. 2 Functional response of Sepedon senex W. fed with Gyraulus convexiusculus Hutton 4-5 mm in diameter at different prey and predator densities. Figures in parentheses are (larval instar, predator density)

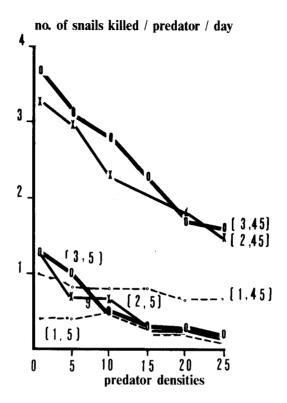


Fig. 3 Rate of predation and ability to kill snails (Gyraulus convexiusculus Hutton) of Sepedon senex W. larvae at different prey and predator densities.

Figures in parentheses are [larval instar, prey density].

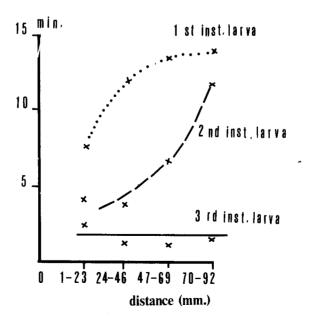


Fig. 4 Time (minutes) spent in moving 22 mm at four different distance intervals between *Sepedon senex* W. larvae and *Gyraulus convexiusculus* Hutton prey.

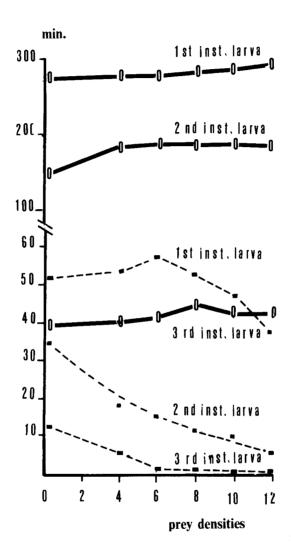


Fig. 5 The searching and handling time of Sepedon senex W. larvae at different prey densities.

searching handling

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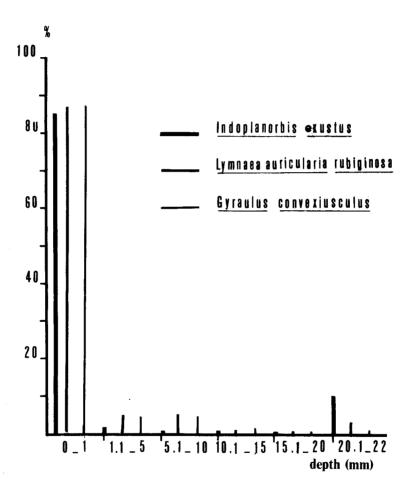


Fig. 6 Vertical distribution of *Indoplanorbis exustus*, *Lymnaea auricularia rubiginosa*, and *Gyraulus convexiusculus* in aquaria.

