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Predation by larvae of *Sepedon ruficeps* (Diptera: Sciomyzidae) and population dynamics of the adult flies and their freshwater prey

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Predation by larvae of *Sepedon ruficeps* (Diptera: Sciomyzidae) and population dynamics of the adult flies and their freshwater prey. - The biology, phenology, and population dynamics of the adults of *Sepedon ruficeps*, the most widely distributed species of Sciomyzidae in Africa, were studied in Benin in permanent and temporary freshwater habitats. The feeding behavior of the larvae, expressed as the number of snails consumed, varies as a function of the species of prey utilized (*Bulinus forskalii* or *Biomphalaria pfeifferi*), as a function of the sizes of the predator/prey, and as a function of the stages of development of the larvae. In relation to the snail-prey, the second- and third instar- larvae show a food choice varying according to the specific ethology of the prey attacked. In all cases, the third- instar larvae always consume the largest number of snails and indifferently attack all of the species of snails utilized in laboratory rearings. The larvae consume, equally well, *B. forskalii* that are healthy or parasitized by the larvae of trematodes. Curiously, in laboratory rearings, in the absence of snails, the larvae of *S. ruficeps* are equally capable of attacking and developing at the expense of *Aulophorus furcatus*, a small, freshwater, oligochaete annelid (Naididae).

Key-words: Diptera - Sciomyzidae - *Sepedon ruficeps* - predation - phenology - biology - freshwater snails - Oligochaeta.

INTRODUCTION

Since the publication by Berg (1953), Sciomyzid flies have been well known for the obligate malacophagous feeding of their larva. Throughout the world, 517 species have been described, of which 64 are from the Afrotropical Region. In this Region, 49

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species are in *Sepedon* Latreille and related genera, for which the keys to the genera, sub-genera, and species given by Verbeke (1950, 1961, 1963) are still useful. Knutson (1980) provided a catalog of the Afrotropical Sciomyzidae, and Miller (1995) presented a revised key to the genera. In regard to 2 monotypic Afrotropical genera known from only 1 or 2 females, Knutson & Vala (1999) described the male of *Tetanoptera leucodactyla* Verbeke and Vala *et al.* (2000b) described the male of *Verbekaria punctipennis* Knutson. The relationships of these genera were discussed in those publications.

With regard to the Sciomyzidae of the Republic of Benin, we have previously recorded the collection and distribution of 8 species, with the description of *Sepedon (Mesosepedon) knutsoni* (Vala *et al.*, 1994). We also have described the stages of development of *Sepedon (Parasepedon) trichrooscelis* Speiser, a parasitoid/predator of semi-terrestrial snails of the family Succineidae (Vala *et al.*, 1995). Furthermore, we have provided evidence of the obligate feeding by larvae of *Sepedonella nana* Verbeke on small, freshwater oligochaetes (Vala *et al.*, 2000a). The same observations were obtained with larvae of *Sepedon (Mesosepedon) knutsoni* (Vala *et al.*, 2002). At present, these two species are the only true sciomyzids known to have strictly non-malacophagous feeding behavior. In the laboratory, the larvae of *Salticella fasciata* Meigen (w. Palearctic Region) have been shown to have a tendency to feed on certain other kinds of invertebrates (Knutson *et al.*, 1970), as well as on their natural host, terrestrial snails (Knutson *et al.*, 1970, Vala, 1989, Coupland & Baker, 1995). In the course of our recent work, (Gbedjissi) has found that occasionally the larvae of *Sepedon (Parasepedon) ruficeps* Becker are also capable of feeding on the same freshwater oligochaetes as *S. nana* in laboratory rearings.

The biology of Afrotropical Sciomyzidae is very poorly known, with information on only 8 species of *Sepedon*, *Sepedonella nana*, and *Hydromya dorsalis* (Fabricius). In addition to the studies in Benin noted above, there are limited biological data on *S. ruficeps* from Ethiopia (Knutson *et al.*, 1967) and complete life cycles of *S.* (*P.*) *trichrooscelis* from Ghana (Knutson, 1999) and of *S.* (*P.*) *neavei* Steyskal, *S.* (*P.*) *testacea* Loew (Barraclough, 1983) and *S.* (*P.*) *scapularis* [Maharaj *et al.*, 1992; Appleton *et al.*, 1993 (including *S. neavei*)] from South Africa. The complete life cycle of *S.* (*P.*) *hispanica hispanica* Loew was presented by Knutson *et al.* (1967) from rearings in its limited distribution in Europe (se. Spain), and some data were presented for *S. h. ruhengeriensis* Verbeke from Nigeria by Knutson (1999). *Sepedon knutsoni* Vala *et al.*, and *S. umbrosa* Verbeke have recently been reared through the complete life cycle (Gbedjissi *et al.*, in prep.). The complete life cycle of the Palearctic *Hydromya dorsalis*, which extends into Ethiopia, was reported by Knutson & Berg (1963).

The present study is focussed on various aspects of the biology of *S. ruficeps*, the most widely distributed species of Sciomyzidae in the Afrotropical Region. It is known from Namibia and Botswana to Egypt, and from East Africa (Cape Verde Island, Senegal) through West Africa to the Arabian Peninsula (s. Yemen, Aden). Its altitudinal distribution is very broad, from a few meters above sea level (Cotonou, Benin; present data) to 4,000 m (Virunga, Democratic Republic of the Congo, Verbeke 1963).

In the perspective of attempts to control populations of the snail intermediate hosts of the larvae of trematodes in Benin we have, a) followed the seasonal changes of populations of *S. ruficeps* adults in 2 types of freshwater habitats, b) studied the food choice of the larvae vis-a-vis the autochthonous snails of different species and sizes, and, c) studied the feeding behavior of larvae on healthy snails and on those parasitized by larvae of trematodes. The results are discussed in relation to the meteorological conditions and the variations in populations of the snail prey during the study period.

Our data on *S. ruficeps* corroborate several key aspects of the extensive field and experimental laboratory data on typical, aquatic, predaceous sciomyzid larvae from the Nearctic, Palearctic, and Oriental Regions, and the limited data on other Afrotropical Sciomyzidae. Whereas there is a relative wealth of data on behavior and phenology from outside the Afrotropics, our information on the seasonal abundance of the adult flies and their larval prey, especially in comparing permanantly wet and seasonally dry habitats in relation to meteorological conditions, helps to fill a major gap in the knowledge of phenological aspects of tropical Sciomyzidae.

COLLECTING SITES

We investigated 6 freshwater localities in southern Benin during January to December 1996 which we have grouped into 2 types according to the permanent (P) or temporary (T) presence of water (Fig. 1). Three of these stations fit the definition of the permanent freshwater type: P1) Calavi, 15 km north of Cotonou, where captures were made along Nokoué Lake not far from a boat embarkation place. The vegetation, identical to that of the Cotonou locality (P2), is closely limited to cultures of *Thalia geniculata* L. (= *T. welwitchii* Ridl.) (Araceae) (which leaves are used to envelop the local corn food "akassa"); P2) Cotonou, which is a permanent, artificial pond near the Atlantic Ocean, regularly fed by polluted waste-water from the city. The coastal flora is degraded and includes *Ipomoea aquatica* Forsk. (Convolvulaceae), *Paspalum vaginatum* Sw. (Poaceae), *Typha australis* Shum. & Thonn. (Typhaceae), etc.; P3) Porto-Novo, a small, shallow, partly brackish water pond situated at the edge of the brackish lagoon. The site is strongly disturbed, with major production of vegetables requiring permanent, manual irrigation. The vegetation, always luxuriant, is typical of marshy areas having permanent water. Three stations of the temporary freshwater type have been followed: T1) Agnavo, 12 km NNW of Lokossa, an artificial impoundment made by the public works service of Mono Dept. During the rainy season, beside filamentous algae, we found *Ceratophyllum sp.*, *Leersia hexandra* Sw. (Lauraceae), *Ludwigia abyssinica* A. Rich. (Loganiaceae), *Nymphea* sp., etc.; T2) a well-delimited marsh in Cocotomey city, 15 km west of Cotonou. The main vegetation found here is *Ceratophyllum sp.* (Ceratophyllaceae), *Cyperus articulatus* L. (Cyperaceae), *Leersia hexandra* Sw. (Poaceae), *Lemna paucicostata* Hegel (Lemnaceae), *Ludwigia* sp. (= *Jussiaea* sp.) (Onagraceae), *Nymphea sp.* (Nymphaceae), *Pentodon pentandrus* (Shum. & Thonn.) Vatke (Rubiaceae), *Pistia stratiotes* L. (Araceae), *Typha australis*, etc.; T3) Djeffa, 14 km east of Cotonou and 600 m from the Cotonou-Porto-Novo road; the habitat is a temporary pond whose water depth may reach 2 m during flood periods. The flora here consists essentially of *Diplasium sammatii* (Kühn) (Athyriaceae), *Fuirena umbellata* Rottb. (Cyperaceae), *Ipomoea aquatica*, *Ludwigia abyssinica* A.

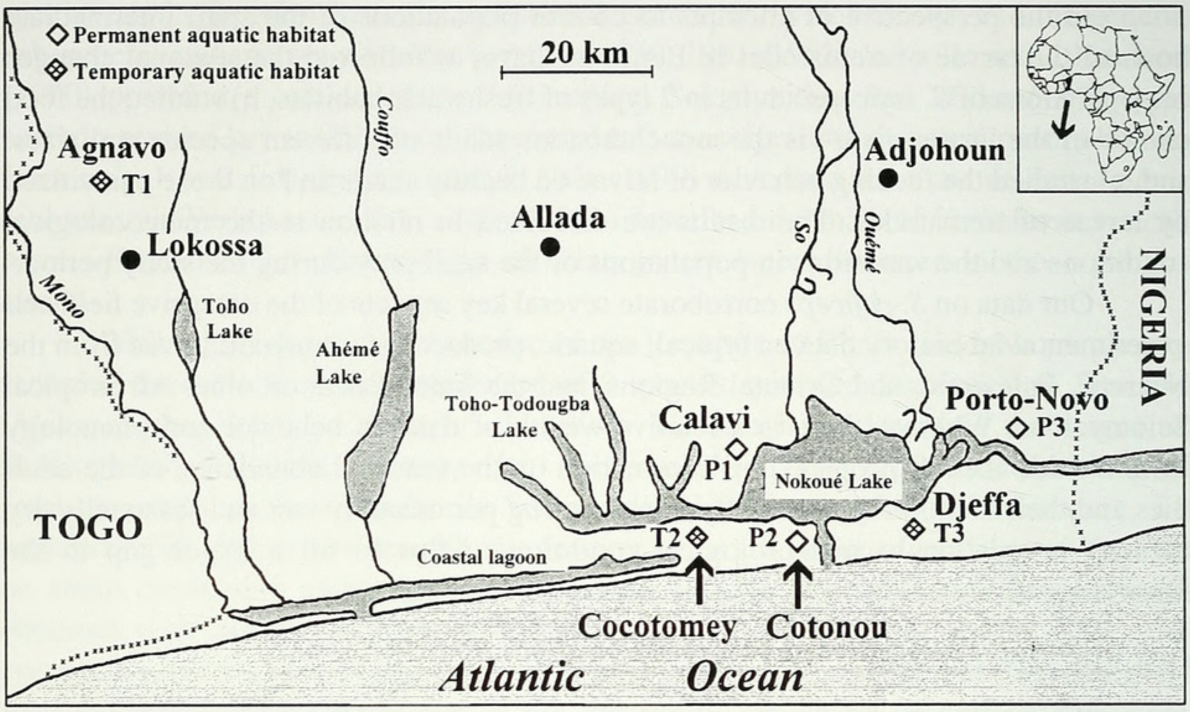

FIG. 1
Geographical distribution of the six studied stations in southern Benin.

Rich (Onagraceae), *Panicum laxum* Sw. (Poaceae), *Paspalum vaginatum*, *Thalia geniculata*, etc.

MATERIAL AND METHODS

Adults were collected from vegetation for 30 minutes every 15 days with a sweep net. In the laboratory adults were reared in plastic boxes (diameter 9 cm, heighth 11 cm) with a fine mesh aeration window. Inside each box were put wet cotton, a small container for water, and a small cup with honey and manioc flour as food. Experimental conditions were those of the laboratory with natural photoperiod (approximatively LD: 12:12), temperature from 25 to 32 C, and relative humidity of 70-85 %.

The rearing containers were examined daily. Eggs laid on the sides of the containers were recovered with the aid of a fine wet brush and placed for incubation on wet filter paper in Petri dishes. On hatching, the young larvae were placed in new Petri dishes with selected snail species. Each day, all of the dead or consumed snails were replaced by others of the same size.

The snails needed for the experiments were collected with a metallic net of 20 cm diameter, having a mesh of 1 mm. The 8-10 collections were made randomly during 30 minutes in a 20 x 2 m area or around the habitats when they were flooded, to accomodate the heterogeneity and variation in density of the snails. In the laboratory, the snails were reared and fed with plant material in order to have available the range of sizes of prey needed. For the predation experiments, the snails were divided into 3 size classes (diameter for planorbids, length for bulinids) : Pc (smallest sizes, < 3 mm), Mc (average sizes, 3-7 mm), and Gc (largest sizes, > 7 mm). Parasitized snails were identified by isolating each individual in a crystal container, 5 cm high, partly filled with fresh water. The daily observation of containers permitted determination of the eventual emergence of swimming cercariae from the snail host. The emission of cercariae was accelerated by illuminating the containers with a 100 W lamp for 30-60 minutes.

Three aspects of predation by the larvae of *S. ruficeps* were followed: a) the predatory behavior in the presence of only 1 species of snail prey, *Bulinus forskalii* (Ehrenberg) or *Biomphalaria pfeifferi* (Krauss), by placing together 1 larva (first, second, or third instar) and 3 snails of the same size class; b) the food preference vis-a-vis 1 or the other of 2 snail prey by placing together 1 larva of *S. ruficeps*, 3 *B. forskalii*, and 3 *B. pfeifferi* of the same size class; c) the behavior of the larvae as a function of the healthy or parasitized state of *B. forskalii* collected in Cocotomey.

Each experiment, with a minimum of 10 repetitions, was made in small Petri dishes with a water level of 3-5 mm, the water taken from the habitats of the snails. Two observations were made each day, at 9 AM and 3 PM. The statistical analysis of the results was made with the Wilcoxon test with a margin of error of 5 %.

RESULTS

Four species of Sciomyzidae were collected (Table 1). *Sepedon ruficeps* (larvae predatory primarily on freshwater snails) and *Sepedonella nana* (larvae predatory on small, freshwater oligochaetes) were collected at all of the stations. *Sepedon trichrooscelis* (larvae parasitoid/predatory on semi-terrestrial, hygrophilous *Succinea* sp.) was absent in the temporary habitats at Djeffa and Cocotomey, but very abundant in the perennial freshwater habitats except at Agnavo. *Sepedon knutsoni*, always collected in small numbers and originally described from Agnavo, is here reported from Cocotomey. Our recent laboratory studies and field observations of *S. knutsoni* show that the feeding behavior and the biology of larvae are similar to the behavior of *Sepedonella nana* larvae.

Concerning the freshwater pulmonate Gastropoda collected, some of which are intermediate hosts of trematodes having veterinary or medical consequences, the predominant are (Table 1): *Bulinus forskalii* (implicated in the transmission of *Schistosoma intercalatum* Fischer, *B. globosus* (Morelet), and *B. truncatus* (Audouin) (intermediate hosts of *S. haematobium* (Bilharz), *Biomphalaria pfeifferi* (intermediate host of *S. mansoni* Sambon), *Lymnaea natalensis* Krauss (intermediate host of cattle liverfluke, *Fasciola gigantica* (Cobbold) in Benin (Schillhorn Van Veen 1980; Assogba & Youssao 2001)) and the Physidae *Aplexa waterloti* (Germain). Among Planorbidae a small species (diameter more than 3 mm) is relatively abundant in some stations. The semi-terrestrial hygrophilous *Succinea* sp., living on emergent freshwater vegetation, frequents specific habitats. Prosobranch (operculate snails) were represented only by *Lanistes* spp. According to the station considered, all of these snails are not sympatric. All snails were identified with Brown & Kristensen's to key freshwater snails of West Africa (1993).

TABLE 1. Sciomyzidae and snails found in each freshwater station (data from 1996). +++, very abundant; ++, abundant; +, few; ±, present only from May to September in low numbers.

Taxon	Permanent water			Temporary water		
	Calavi P1	Cotonou P2	Porto Novo P3	Agnavo T1	Cocotomey T2	Djeffa T3
Sciomyzidae						
Sepedon knutsoni				±	±	
Sepedon ruficeps	++	++	++	++	++	++
Sepedon trichrooscelis	+++	+++	++	+		
Sepedonella nana	+	-	+	+++	++	-
Snails						
Biomphalaria pfeifferi		+++				
Bulinus forskalii	++	+	+	++	+++	
Bulinus globosus			+			++
Bulinus truncatus			+			++
Lanistes spp.		+		+	+	
Lanistes varicus	+		+			+
Lymnaea natalensis		+++		+		++
Aplexa waterloti	++	+		++		++
Planorbis sp.	++	++		++	++	
Succinea sp.	-	+	–	–		

A. Meteorological Information

In s. Benin, data collected at the meteorological station at the airport of Cotonou during 1996 (Fig. 2) showed 2 rainfall periods, characteristic of this zone of Africa. The major rainfall period extends usually from April to the beginning of August (> 50 mm) with the maximum precipitation occuring during 3 months (May, 259.6 mm; June, 512.3 mm; and July, 143.8 mm) and the minor rainfall period from September through November with a maximum of 112.8 mm occuring in October. The dry period extends from the end of November to the beginning of March with a near-total absence of rain during December and January. The annual temperature varies very little and presents 2 phases opposite to that of the rainfall. During the course of the heavy rains, the temperature decreases from 29.9 C (March) to 26.1 C (August) but increases from 26.2 C (September) to 29.9 C (March).

B. Development of populations of *Sepedon ruficeps* and of snails

B. 1. POPULATIONS OF *SEPEDON RUFICEPS* IN A TEMPORARY FRESHWATER HABITAT: COCOTOMEY STATION (T2).

At this station, selected as typical of a temporary freshwater habitat, the collections of *S. ruficeps* totaled 131 adults (67 males, 64 females). The changes in captures over time (Fig. 3) shows that the number of adults were zero through January to July. The population then increased to a very strong peak in October. We determined that the maximum captures were about 4 months after the heaviest rainfall, at the time when the habitat began to dry out. Here, *Bulinus forskalii* is the principal prey of the larvae of *S. ruficeps*. The presence of this snail was limited during the course of the year

(Table 2). From low numbers in June, its population increased progressively, somewhat in accord with the increase in water level, to reach a maximum in November as drying began. This maximum is explained by the decrease in water level which results in the concentration of snails that reproduce in the wet places thus remaining. From mid December, the quantity of snails diminished very rapidly and they were not collected by our method at the end of December. The habitat then was completely dry. Obviously, aestivating snails were hidden in the substrate cover and/or in cracks in the soil. Also, a certain number of snails were lost by predation (especially by birds). The mortality of the snails was also accentuated by the increased temperature of the water as it evaporated. During the completely dry period we collected several *B. forskalii* inside domestic wells and others partially buried in cracks in the soil. In this type of temporary freshwater habitat, due to the absence of water and the dispersal or disappearance of the snail population indispensable for the development of its larvae, *S. ruficeps* entirely disappeared from the habitat (Fig. 3).

TABLE 2. Numbers of *Bulinus forskalii* collected monthly during 1996 (per m^2) at the Cocotomey station (T2). (*, snails present in domestic well-water).

	Months											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
N snails/m^2	*0	*0	0	0	0	2	40	82	82	210	298	87
Status of habitat	Dry					Inundated				Low water level		

B. 2. POPULATIONS OF *SEPEDON RUFICEPS* IN A PERMANENT FRESHWATER HABITAT: COTONOU STATION (P2).

At Cotonou, of a total of 239 *S. ruficeps*, we found 121 males and 118 females. In contrast to the preceding habitat, adults were present throughout the year (Fig. 4). The curve of monthly captures is bell-shaped, with a peak number during the months of August (34 adults), September (38), and October (35). During the course of this chorology, the sex ratio remained essentially 1:1. As in the preceding case, the maximum numbers of adults is observed about 3 months after the strongest rains. There is thus a strong similarity between the development of the populations in the 2 types of stations. At Cotonou, the continual presence of *S. ruficeps* is explained by the permanent nature of the water.

As to the population level of snails, there is a large difference in the chorology in comparison to the preceding example. We particularly followed the development of the populations of the 2 most abundant species, *Biomphalaria pfeifferi* and *Lymnaea natalensis* (Fig. 5). For *B. pfeifferi*, we observed a unimodal bell-shaped curve with an important peak culminating at about 75-100 individuals per m^2 at the time of the minor period of rain during September through October. The curve of *L. natalensis* is different and bimodal. The first peak was in April (45 snails) with the appearance of the rains. The second was much more important (72 snails) and was found in August-September.

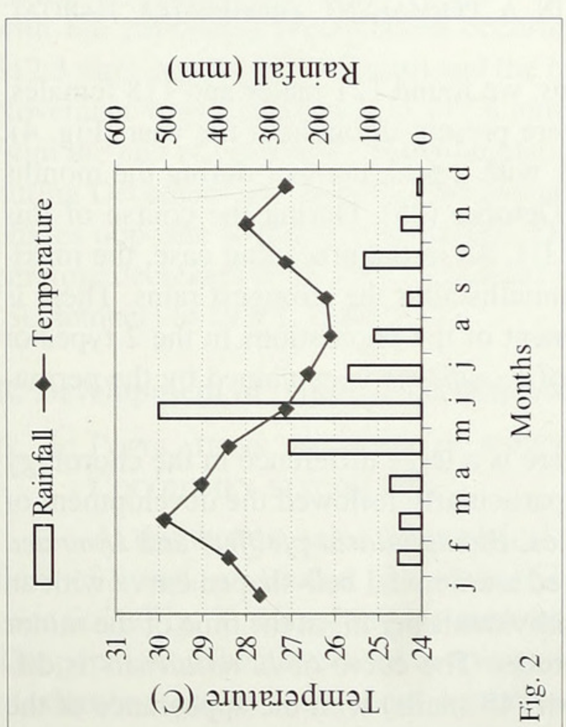

Fig. 2

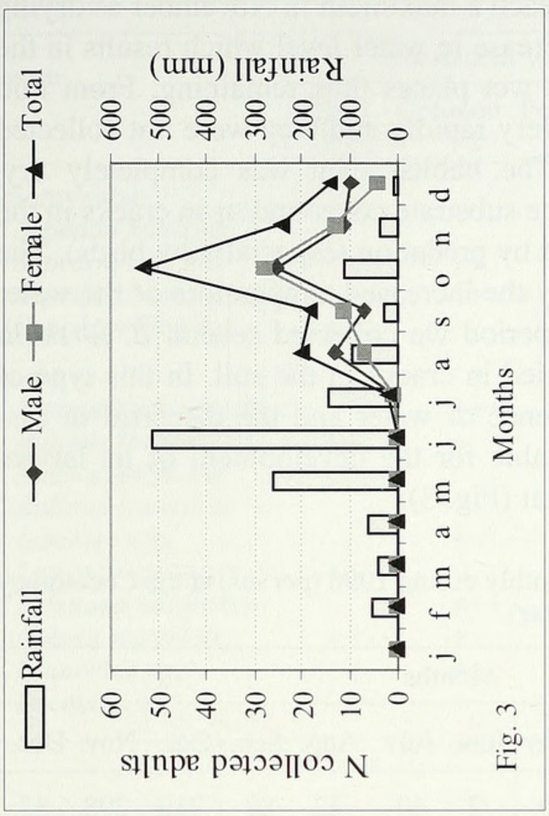

Fig. 3

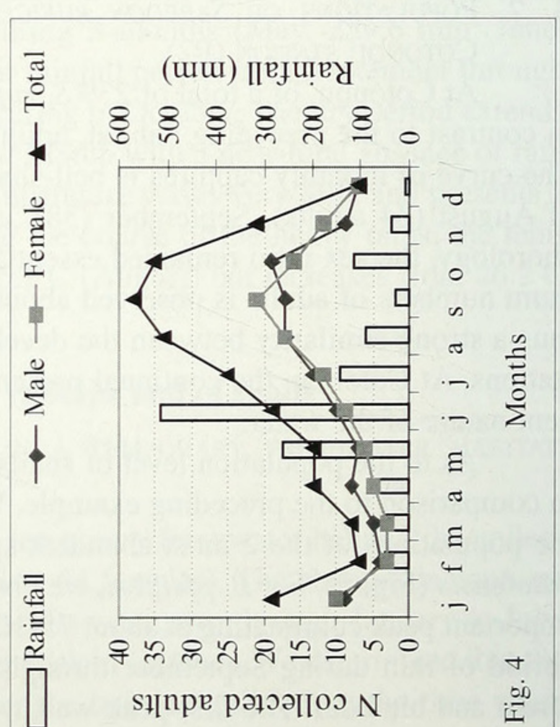

Fig. 4

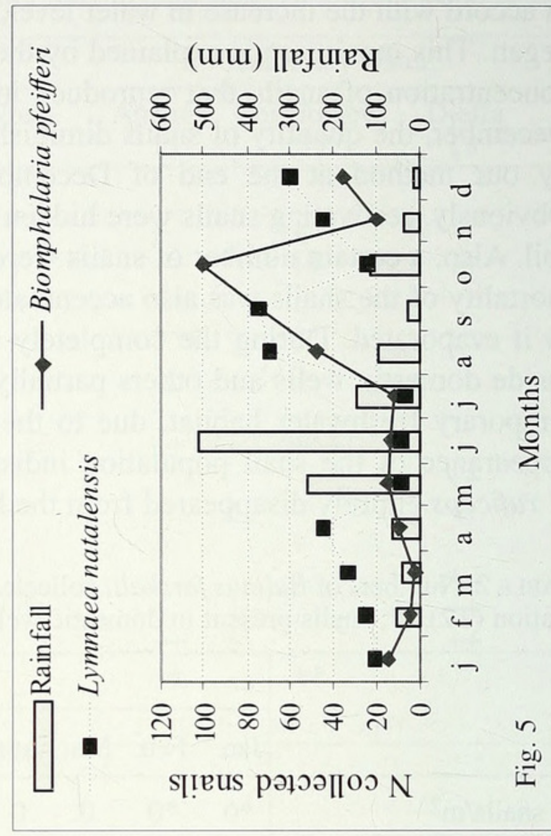

Fig. 5

At the Cotonou station, the maximum of captures of the 2 species of snails thus decreased. This situation, probably due to their respective periods of reproduction, is favorable for predation by larvae of *S. ruficeps*. In effect, the larvae have at their disposal, successively and for a long period, a variety of sizes of prey. In this habitat of permanent water the population peaks of the snails is when the level of water is low, resulting in an aggregation of individuals that are thus more easily collected. In contrast, at the time of the strong rains of May to July, the snails are dispersed, their drift is important, and the collection of snails is weaker.

C. Biology and feeding behavior in terms of the number and species of snails killed and eaten during the larval instars

In the laboratory, *S. ruficeps* adults lived about 3 months, with a larval development of 16-19 days. *S. ruficeps* appears to be a multivoltine species with several successive and overlapping generations in the course of the year.

The larvae of *S. ruficeps* avoid attacking the foot of the snail. Instead, the point of attack is preferentially the soft tissues of the head. The shells of snails of small sizes are rapidly and completely emptied; those of large sizes are killed quickly and completely emptied after several hours or are killed after 1 or 2 days. The larvae do not have necrophagous or detritivorous behavior and they never consume snails that have died naturally. The larvae of *S. ruficeps* fed on all of the freshwater snails under consideration, except the operculate *Lanistes* spp. We have limited the study of predation to *Bulinus forskalii* and *Biomphalaria pfeifferi*, which serve as intermediate hosts of human bilharziasis in Benin.

The average number of *B. forskalii* (Fig. 6) killed by larvae of *S. ruficeps* varied from 8.75 ± 1.9 (first stadium) to 42.18 ± 4.05 (third stadium). First-instar larvae readily attacked the size-classes Pc ($\bar{x}$ = 5.31 ± 1.33) and Mc ($\bar{x}$ = 2.78 ± 0.78), but attacked with difficulty the size-class Gc ($\bar{x}$ = 0.18). The several Gc snails killed and eaten by the first-instar larvae were all parasitized by bilharzian furcocercaria. That is to say, for most of the old snails the larval development of schistosomes had enough time to complete their entire cycle (from miracidia to furcocercaria) from bilharzian infested human populations (mainly by *Schistosoma haematobium*) living near water bodies.

The second- and third- instar larvae indifferently fed upon all sizes of *B. forskalii*. In comparison, omitting the size-class Pc, third instar larvae consumed 5 times more than the first instar and 3 times more prey than the second instar.

With *B. pfeifferi* as prey (Fig. 7), first instar larvae killed and ate all of the snails of class Pc ($\bar{x}$ = 4.96 ± 0.19), with difficulty those of class Mc ($\bar{x}$ = 0.12), and never

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Figs 2-5

2. Rainfall (histograms) and temperature (solid line) data during 1996 in Cotonou from meterological station of Cotonou. 3. Change in the *Sepedon ruficeps* population in the temporary habitat of Cocotomey. Rainfall is indicated during the same time (1996). 4. Change in the *Sepedon ruficeps* population in the permanent habitat of Cocotomey. Rainfall is indicated during the same time (1996). 5. Evolution of snail populations of *Lymnaea natalensis* and *Biomphalaria pfeifferi* during the year (1996) in function of rainfall in Cotonou.

those of class Gc. Second- instar larvae killed and ate individuals of classes Pc ($\bar{x}$ = 6.7 ± 1.57) and Mc ($\bar{x}$ = 3.1 ± 0.78) and none of Gc. Third-instar larvae attacked with success snails of all size-classes. For snails of class Pc, the third-instar larvae consumed 5 times that of the first instar and 4 times that of the second instar.

Independent of the prey species utilized, the small sizes were always much more extensively killed and eaten. During the development of the larvae, the number of snails killed increased distinctly. Certain larvae, having fed sufficiently, continued to attack and to kill snails without eating them. This strictly killing behavior or "wasteful feeding" has been reported for certain species of *Sepedon*, particularly by Neff & Berg (1966), and for other genera of aquatic, predacious Sciomyzidae by other authors. The size of the prey, especially for the first instar larvae, appeared also to be an important factor in predation, especially in the case of *B. pfeifferi*. Mature larvae of *S. ruficeps* were very efficient in killing snails, and this probably had a direct effect on the level of the snail population by destruction of the parents. On occasion, the efficacy of predation was limited by the secretion of mucous by the snails, which trapped and asphyxiated the larvae, notably small first- instar larvae.

In the presence of both *Bulinus forskalii* and *Biomphalaria pfeifferi* (Fig. 8), first-instar larvae did not show any food preference and killed and fed upon about 50 % of each species (Wilcoxon test). In contrast, in the other 2 instars, there was a strong tendency for preferential attack on *B. forskalii*, with 76.1 % (second- instar larvae) and 67.3 % (third- instar larvae) against, respectively, 23.9 % and 32.7 % of *B. pfeifferi*.

D. Parasitism and predation of *Bulinus forskalii*

Bulinus globosus and *B. truncatus* are known to be intermediate hosts of *Schistosoma haematobium*, and *B. forskalii* in the transmission of *S. intercalatum*. The dry habitat at Cocotomey permits a good understanding of the development of the prevalence of parasitization (Table 3). The rate of parasitism regularly increased in July to reach a peak in November. The rate then declined at the beginning of December. The increase seen was partly due to the frequenting of the habitat by numberous vertebrates (probably those infested with trematodes). The snails can be infested precociously because the individuals less than 3 mm have released cercaria. Three types of cercariae have been found among the snails collected at Cocotomey: cercarium type (no tail) in *B. forskalii*, xyphidiocercaria type (simple tail) in *L. natalensis* and *B. forskalii*, and furcocercaria type (bifid tail characterizing *Schistosoma* sp.) in *B. globosus*. Sometimes multiple parasitism (with definitive hosts being cattle, birds, etc.) by trematodes existed in the same snail.

The results (Fig. 9) show, no matter which stage is considered, that the larvae of *S. ruficeps* indifferently consumed parasitized or healthy *B. forskalii*. Here there also appeared higher consumption of parasitized snails of size-class Pc by first instar larvae (Wilcoxon test). When the larva attacks a parasitized snail, the cercariae are liberated into the water (because the immature stadia of the parasite, sporocysts or rediae, are destroyed). In choice experiments, Fontana (1972) showed that the aquatic predator *Dichetophora biroi* (Kertész) in Australia did not show any preference for *Lymnaea tomentosa* (Pfeiffer) infected or not with the cattle fluke, *Fasciola hepatica* L., and

TABLE 3. Annual rate of snail parasitism by schistosomiasis cercaria in Cocotomey station (T2) during 1996.

	Months											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
N tested	0	0	0	0	30	30	30	30	30	30	0	0
N parasitized	0	0	0	0	1	3	7	12	16	8	0	0
% parasitism	0	0	0	0	3.3	10.0	23.3	40.0	53.3	26.6	0	0
Status of habitat	Dry					Inundated				Low water level		

Lindsay (1982) showed the same for *Ilione albiseta* (Scopoli) in Ireland when offered infected or healthy *L. truncatula* Müller.

DISCUSSION

A. Phenology

In permanent freshwater habitats, *S. ruficeps* adults were present throughout the year. In habitats that dried out annually they disappeared with the evaporation of the water and the increasing rarity of the snail prey. It is possible that the species could pass the dry period in a dormant stage (most likely in the puparium or as an adult) but such aestivation has not been proved for any tropical species of Sciomyzidae. Considering the proximity of temporary and permanent freshwater habitats in many areas, it is unlikely that a species could be adapted to have small, dispersed portions of its population sensitive enough to extremely local conditions of dryness to effect a scenario of continuous breeding in wet areas and dormancy in dry areas. Rather, it is much more likely that there is extensive migration from drying areas to wet areas. Capture-mark-release-recapture studies and search for aestivating puparia (perhaps by experimental flooding) in temporary freshwater habitats in the tropics are needed areas of research.

The seasonal variation in populations of adults in relation to rainfall that we have noted conforms, in general, with observations in the Parc National de la Garamba (ne. Democratic Republic of the Congo, ex-Zaire) by Verbeke (1963). The meterological conditions, especially rainfall, at Garamba (about 5° N. lat.) and s. Benin (about 6° N. lat.) which are about 2,800 km distant, are rather comparable (Walter & Breckle, 1986). Verbeke (1963) provided a summary of collection dates of 787 specimens of 11 species of *Sepedon* and related genera captured between Dec. 1950 and Sept. 1952 in 16 types of habitats (a much broader range of habitats than those studied in the present paper). He compared the collection dates with average monthly rainfall, and concluded that these species fly throughout the year. Maximum abundance is in the dry season (Nov. to Feb.), and the curve of abundance of Sciomyzidae is inverse to that of precipitation. However, half of the specimens referred to by Verbeke (1963) were *Sepedon trichrooscelis* (subsequently shown by Vala *et al.* (1995) and Knutson (1999) to be atypical for *Sepedon* in being a parasitoid/predator of semi-terrestrial hygrophilous Succineidae) and the closely related, biologically unknown *S. lippensi* Verbeke. Furthermore, only 14 of the 399 specimens of *S. trichrooscelis* and *S. lippensi* were collected

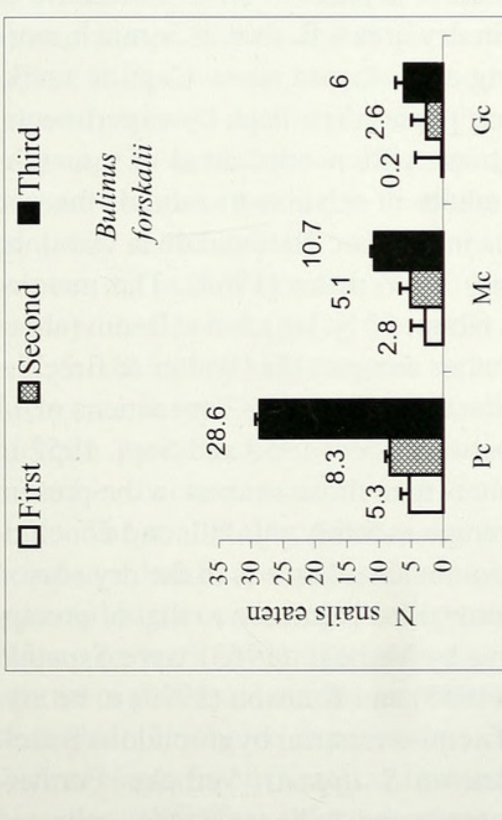

Fig. 6

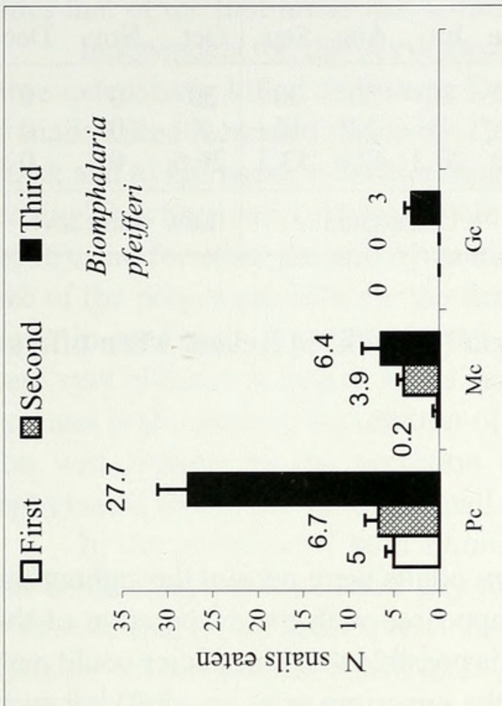

Fig. 7

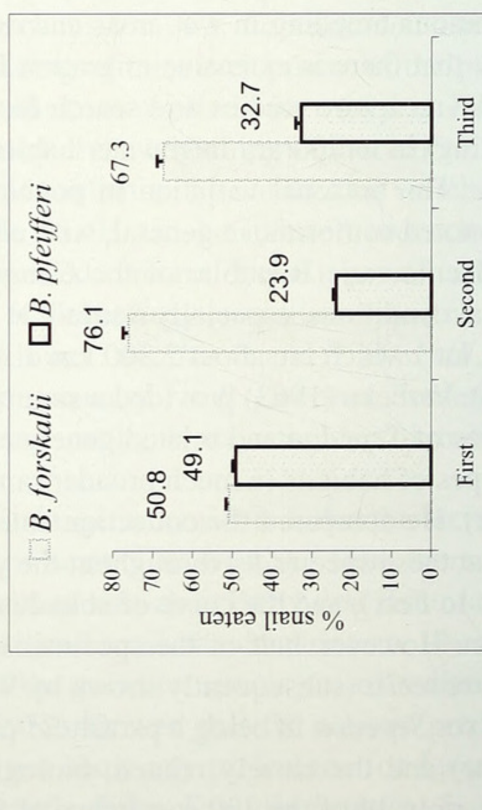

Fig. 8

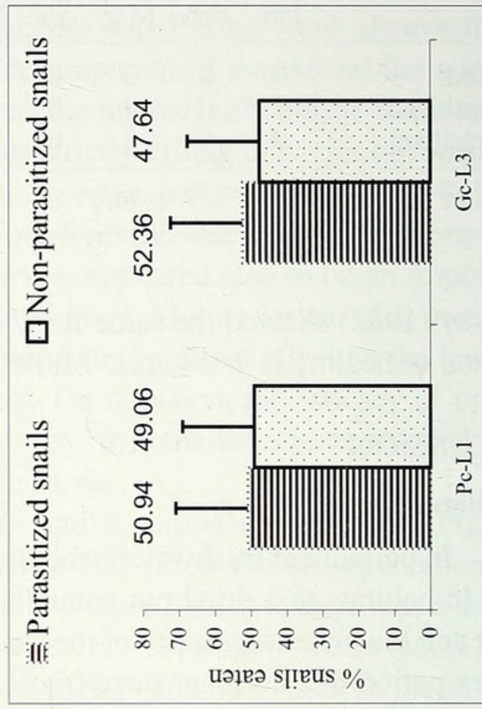

Fig. 9

during the 5 months of April through Aug., indicating that at least these species do not breed continously. However, Vala *et al.* (1995) concluded that *S. trichrooscelis* is multivoltine, based on lab rearings in which the entire life cycle required only 30 days and on limited field collections of immatures.

There are also data from the Neotropical Region that indicate that populations of adult Sciomyzidae are inversely correlated with rainfall. Knutson & Carvalho (1989) found that 172 specimens of 2 species of *Thecomyia* (probably aquatic predators) collected at 1 site near Belém, Brazil on 49 dates during 1977 and 1978 were taken just before and after the rainy season. Mello & Bredt (1978) made monthly collections of 5 species of *Sepedonea* Steyskal and 1 species of *Sepedomerus* Steyskal (aquatic predators) during 1975 and 1976 near Brasilia, Brazil and found that populations peaks occurred as the period of heaviest rainfall declined, with adults of some species found during every month of 1 of the years. Further research in tropical zones on voltinism (numbers of generations produced per year) and how species survive inclement conditions is needed, particularly in view of the use of aquatic predators for control of disease-carrying snails.

B. Predation

Predation by both aquatic and terrestrial sciomyzid larvae has been very extensively studied in primarily qualitative life history researches, rather extensively studied in lab experiments, and studied to a limited extent in field experiments. The majority of studies are on Northern Hemisphere species, in many genera, with the freshwater predators *Sepedon f. fuscipennis* Loew (Nearctic) and *Tetanocera ferruginea* Fallén (Holarctic) being especially well known. In tropical regions, there have been far fewer natural history and experimental studies. Three Oriental species of *Sepedōn* have been studied experimentally to some extent: *S. plumbella* Weidemann (Bhuangprakone & Areekul, 1973), *S. senex* Weidemann (Beaver, 1989), and *S. spangleri* Beaver (Sucharit *et al.*, 1976). Our data on *S. ruficeps* complement the 3 papers on freshwater, predaceous *Sepedon* spp. in the Afrotropical Region (Barraclough 1983; Maharaj *et al.*, 1992; Appleton *et al.*, 1993).

The larvae of *S. ruficeps* have a broad valence of predation on freshwater pulmonate snails. In nature, it seems that the larvae adapt their prey-choice to the simultaneous or successive presence of the snail prey, especially Bulinidae and Planorbidae, whose periods of reproduction and population peaks decrease during the year. This polyphagy explains, in part, the broad geographical distribution of many species

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FIGS 6-9

6. Number of *Biomphalaria forskalii* eaten by each larval stadium in presence of this species only. Pc, Mc, Gc, respectively small, medium and large sizes of snails. 7. Number of *Bulinus pfeifferi* eaten by each larval stadium in presence of this species only. Pc, Mc, Gc, respectively small, medium and great sizes of snails. 8. Relative (%) number of *Biomphalaria forskalii* and *Bulinus pfeifferi* eaten by each larval stadium when both snail species are present together. 9. Percentage of snails eaten by *Sepedon ruficeps* larvae according the presence or absence of trematode larvae and size of the snails. Pc, Gc, small and large sizes of snails eaten; L1, L3, larval stage.

of Sciomyzidae in the Afrotropical Region. Furthermore the freshwater oligochaete *Aulophorus furcatus* (Müller) constitutes without doubt an alternate prey for some Sciomyzidae in the absence of snail prey, as we have determined in the laboratory (unpublished data).

Its broad malacophagy also indicates that *S. ruficeps* represents a good possibility for control of the snail intermediate hosts of bilharziasis because the larvae feed upon healthy or infested snails, without choice, and on all sizes of snails. It is possible to envisage introductions of larvae into freshwater habitats, principally when the snails aggregate at the time preceding the drying of the habitat. As determined by Barraclough (1983) for the immature stages of *Sepedon (Parasepedon) testacea* and *S. neavei*, consumption by the larvae of *S. ruficeps* increases as a function of the age of the larvae and the type of snail prey.

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