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# **PHYTOTELMATA:**

## **Terrestrial Plants as Hosts for Aquatic Insect Communities**

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# INTERACTION BETWEEN THE MOSQUITO *WYEOMYIA SMITHII*, THE MIDGE *METRIOCNEMUS KNABI*, AND THEIR CARNIVOROUS HOST *SARRACENIA PURPUREA*

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## SUMMARY

(1) The water-filled leaves of the purple pitcher plant, *Sarracenia purpurea*, serve as host to a variety of organisms including bacteria, protozoans, mites, midges, mosquitoes, and flies.

(2) Prey captured by host leaves constitute the resource base of this community and the inhabitants partition this resource in spatial distribution and trophic level.

(3) Intra- and interspecific encounter of overwintering mosquitoes, *Wyeomyia smithii*, and midges, *Metriocnemus knabi*, from Florida to Canada along with competition experiments in the field and laboratory indicate that both species are now more self- than other-regulated. Consequently, they should be able to coexist indefinitely.

(4) Although prey capture by the host leaf is a limiting resource for *W. smithii*, oviposition site selection behavior by the females assures that their offspring will develop in an environment characterized by increasing resources and the highest probability of future survivorship.

(5) Gas and nitrogen production and consumption by insects and leaves suggest that the interaction between the plant and its inhabitants is mutualistic.

(6) Although both the plant and its arthropod guests appear to benefit from the symbiosis and at least *W. smithii* exhibit several specialized adaptations to living in *S. purpurea*, no convincing evidence exists that *S. purpurea* has evolved specifically in response to its arthropod symbionts. Thus, as pointed out by Istock et al. (this volume), the system cannot be described as coevolved.

(7) Along with *Sarracenia purpurea*, *W. smithii* are found in *S. flava* and hybrids between *S. purpurea* and *S. flava*, *S. leucophylla*, *S. rubra*, and *S. alata*.

(8) As measured by the incidence of pupae in the field, *W. smithii* probably realize as high a level of fitness during the summer in *S. flava* or *S. flava* X *S. purpurea* hybrids as they do in *S. purpurea* itself; however,

since all of the *S. flava* and most of the hybrid leaves die back in the winter, survivorship in winter is greatest in *S. purpurea* whose leaves persist.

(9) Variation in emergence success from pitcher plants other than *S. purpurea* and their hybrids with *S. purpurea* may explain part of the heritable variation in oviposition site selection behavior described by Istock et al. (this volume).

## INTRODUCTION

The genus, *Wyeomyia*, consists of about 100 species of which all but 1 live in the new world tropics (Stone et al. 1959) and are container inhabitants (Lane 1953). In North America, two species, *Wyeomyia vanduzeei* Dyar & Knab and *W. mitchellii* (Theobald) occupy bromeliads on peninsular Florida and *W. smithii* (Coq.) lives only within the water-filled leaves of the purple pitcher plant, *Sarracenia purpurea* L. (Fig. 1). The first major study of *W. smithii* was made by Smith (1901), who mistook them for another species: "as *Culex pungens* it did not strike me as especially odd that the larva should be in the leaf pitchers" (Smith 1904). Smith subsequently placed some overwintering larvae in a jar in his laboratory on January 22, and noted that they did not metamorphose until March of the same year. Although Smith believed that *W. smithii* enters an adult diapause, it has been shown subsequently that they undergo larval dormancy, the onset, maintenance, and termination of which is mediated by photoperiod (Smith & Brust 1971; Evans & Brust 1972; Bradshaw & Lounibos 1972, 1977). Smith also believed that *W. smithii* showed no inclination to bite (Smith 1902, 1904), a conclusion confirmed on many subsequent occasions (Owen 1937; Matheson 1944; Price 1958) although Hudson (1970) noted that females appear adequately equipped for biting. It is now known that *W. smithii* is capable of blood feeding in the southern part of its range (Bradshaw 1980). *W. smithii* from all latitudes may undergo the first ovarian cycle without taking blood. During subsequent cycles, however, a blood meal is required among southern but not northern females (Bradshaw 1980; O'Meara et al. 1981). The early descriptions of *W. smithii* therefore were observations of northern, not southern females.

Based primarily on the structure of the anal papillae of the larvae, Dodge (1947) described a new species of pitcher-plant mosquito, *W. haynei*, from southern (North and South Carolina) latitudes. However, Bradshaw & Lounibos (1977) found pitcher-plant *Wyeomyia* from the Gulf Coast to be inter-fertile with those from New England and that the hybrid between an Alabama and Massachusetts population was physiologically and morphologically identical to *W. haynei* from North Carolina. They therefore concluded that *haynei* was a geographical race and that only one species of mosquito, *W. smithii*, inhabits *S. purpurea* in North America.

A variety of organisms regularly lives within the leaves of *S. purpurea* including bacteria, algae, protozoans, rotifers, small crustaceans, mites, and three common species of insects (Judd 1959; Hegner 1926; Hepburn et al. 1920; Addicott 1974; Knab 1905; Smith 1901; Wray & Brimley 1943). The insects consist of a sarcophagid fly, *Blaesoxipha fletcheri* (Aldrich), a chironomid midge, *Metriocnemus knabi* Coquillett, and *W. smithii*. *B. fletcheri* larvae are typical cyclorrhaphous maggots whose enlarged posterior spiracles help prevent their submergence. The larvae hang from the water surface and scavenge voraciously on dead, trapped victims floating on the surface (Forsyth & Rob-



FIG. 1. The purple pitcher plant, *Sarracenia purpurea*, growing in a northern bog. The three pitchers in the foreground represent, left to right, a fully opened hardened pitcher, a mature bud about to open, and a freshly opened leaf (within the last 48 hours). Note the rain-catching hood with downward pointing hair towards the smooth, slippery inner surface of the leaf. The *Sphagnum* moss and ericaceous shrubbery are characteristic of northern pitcher-plant habitats.

ertson 1975). *M. knabi* dwell within the detritus at the bottom of the leaf which maintains a high level of oxygen, despite the presence of respiring organisms (Paterson 1971; Cameron et al. 1977). *M. knabi* both scavenge for particulate material and bore into drowned victims which have descended to the base of the pitcher-plant leaf. A large insect withdrawn from the bottom of the leaf is usually a veritable Medusa of writhing *M. knabi* larvae. *W. smithii* is a filter feeder and, like mosquitoes in other containers (Kato & Toriumi 1951; Maguire et al. 1968; Frank & Curtis 1977) is an efficient grazer, not only of small particulate material but also of bacteria, protozoa, and small rotifers (Addicott 1974). The coexistence of *W. smithii* with these insects in a finite habitat has been the subject of some speculation (Buffington 1970; Paterson 1971), but little experimentation. Competition among various container inhabiting mosquitoes has resulted in reduced survivorship (Istock et al. 1976), in prolonged larval development (Lang 1978; Moeur & Istock 1980; Istock et al. 1975, 1976; Frank & Curtis 1977; Frank et al. 1977; Smith 1902), and in actual or surmised displacement of one species by another in time and/or space (Seifert 1980; Pittendrigh 1950a, 1950b, 1950c; Kurihara 1957, 1958, 1959a, 1959b, 1960). In the present paper, I shall consider some interactions between *W. smithii* and *M. knabi*, between these inquilines and their plant host, and between oviposition behavior in *W. smithii* and predatory behavior in *S. purpurea*.

#### GEOGRAPHY OF ENCOUNTER AND INTERACTIONS BETWEEN *M. KNABI* AND *W. SMITHII*

The range of *W. smithii* overlaps that of *M. knabi* from the Gulf of Mexico (30° N latitude) to central Canada (ca 55° N latitude) (Bradshaw & Lounibos 1977; Evans 1971; Burgess & Rempell 1971; Haufe 1952). However, stating the range over which two species overlap says little about the degree to which they actually encounter each other or compete. To estimate the degree of inter- and intraspecific encounter, overwintering populations of both species were sampled from 30-54° N latitude (Fig. 2). Since *W. smithii* and *M. knabi* both overwinter in a state of larval diapause (Bradshaw & Lounibos 1972, 1977; Smith & Brust 1971; Evans & Brust 1972; Paris & Jenner 1959), sampling the larval population of the overwintering generation therefore samples the entire population. Many leaves during this time of year are devoid of either *W. smithii* or *M. knabi* and the mean densities of the two species would give little indication of the degree to which they might affect either themselves or each other. Consequently, Lloyd's (1967) indices of intra- and interspecific encounter were used. Intraspecific encounter, or mean crowding, is given by

$$\bar{X}^* = \frac{\sum (X_i)(X_i - 1)}{\sum X_i}$$

where  $X_i$  is the number of individuals of species X in the *i*th leaf. Interspecific encounter of Y by X is then

$$Y/X^* = \frac{\sum X_i Y_i}{\sum X_i} .$$

Figure 3 shows the degree of intra- and interspecific crowding along a geographic gradient. Mean crowding of *W. smithii* (Fig. 3A) ranged from 3-80

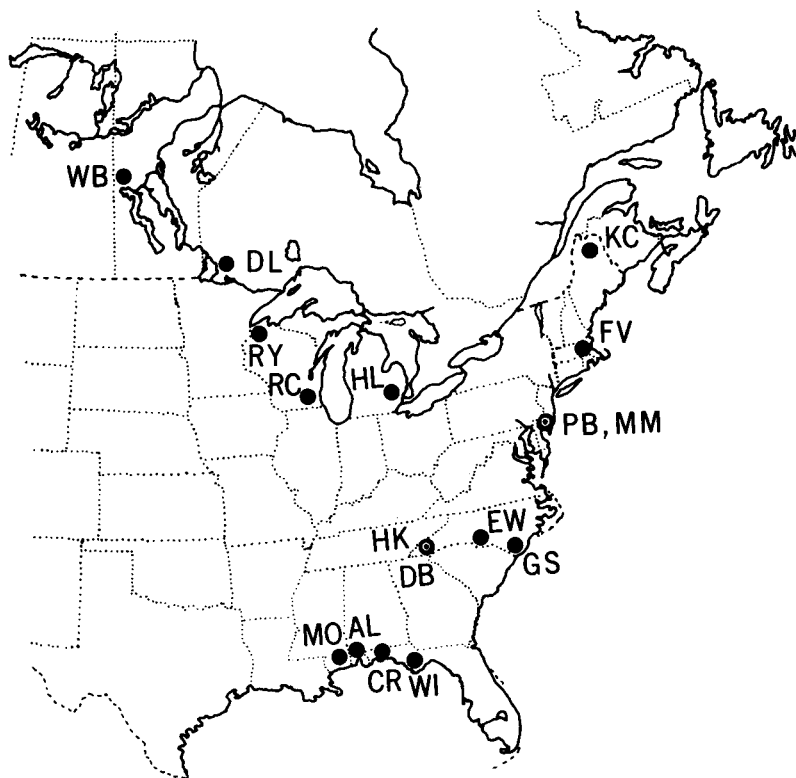


FIG. 2. The pitcher-plant and *Wyeomyia smithii* localities considered in this chapter: CR and WI are at 30°N, GS at 35°N, PB and MM at 40°N, FV, HL, and RC all at 42.5°N, DL at 49°N, and WB at 54°N. HK and DB are high elevation (900 m) localities in the southern Appalachians.

and was inversely correlated with latitude. Mean crowding of *W. smithii* at low latitudes but high altitudes resembled populations further north than would be predicted from their latitude alone. Interspecific encounter of *M. knabi* by *W. smithii* showed no significant geographical trends (Fig. 3B) and averaged, over their range, about 40 *M. knabi* encountered by the average *W. smithii*. Mean crowding of *M. knabi* averaged about 50 and also showed no consistent geographical trend (Fig. 3C). The encounter of *W. smithii* by *M. knabi* ranged from 3-50 and showed an inverse relationship with latitude and altitude (Fig. 3D). These data show that *W. smithii* encounter mainly other *W. smithii* in the southern and mainly *M. knabi* in the northern part of their range; the reverse pattern holds for *M. knabi*. The implication is that interspecific competition, if it exists, might be most intense for *W. smithii* in the north and for *M. knabi* in the south.

To estimate the presence and/or degree of intra- and interspecific competitive factors impinging upon *M. knabi* and *W. smithii*, different densities of midges and mosquitoes were exposed to a finite resource in the laboratory. To each of a series of *S. purpurea* leaves, 20 ml of water and three drops of bacterial-protozoan inoculum from pitcher-plant water collected in the field (New Jersey) were added. Then, 10, 20, 40, or 80 wild-caught, diapausing late

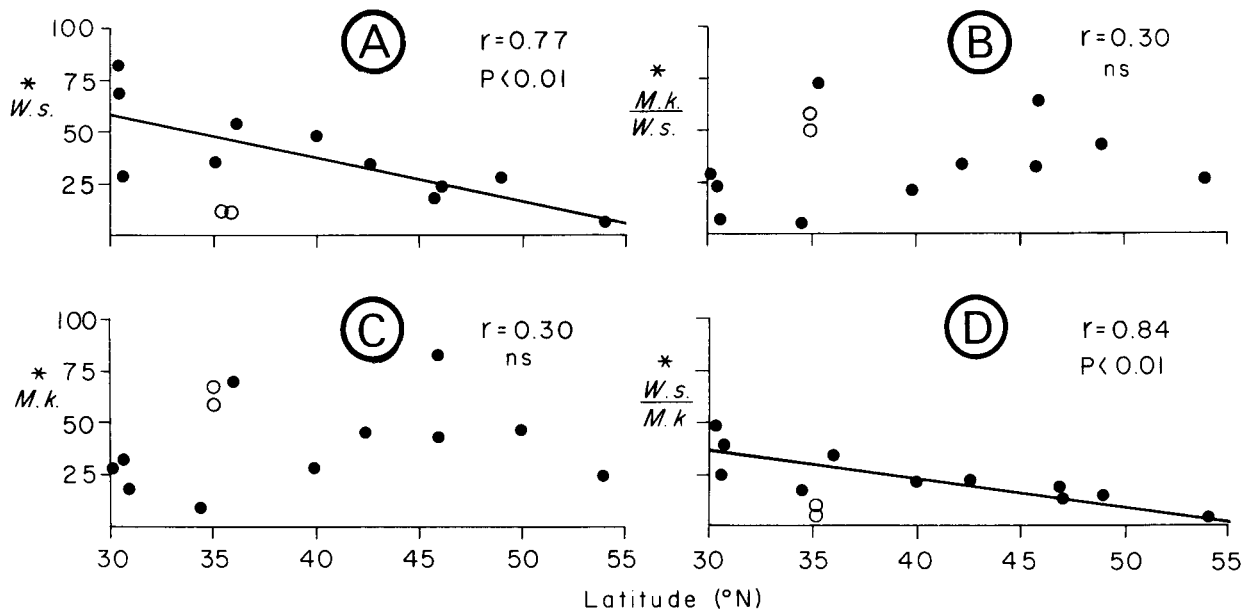


FIG. 3. Geographical variation in inter- and intraspecific crowding of overwintering larvae. \*W.s. and \*M.k., intraspecific crowding of *W. smithii* and *M. knabi* respectively; Open circles indicate high elevation localities in North Carolina (DB and HK in Fig. 2).

instars of *M. knabi* were combined with 10, 20, 40, or 80 wild-caught, diapausing third instars of *W. smithii*, both species originating from New Jersey. For controls, 10, 20, 40, or 80 larvae of each species were exposed only to themselves, without an interspecific competitor. The plants were placed on long-day photoperiod (L:D = 14:10) in humidity chambers at  $25 \pm 2^\circ\text{C}$  underneath a light bank to maintain the plants. Finally, the leaves were fed size-matched, mature mealworms (*Tenebrio* sp.) at a rate of one mealworm (0.10–0.13 g wet weight) every two days for six days. Three replicates were run at each density except 80 *W. smithii* with 80 *M. knabi* where insufficient animals were available. Each leaf was examined daily for the presence of pupae of *M. knabi* or *W. smithii*. After 40 days the leaves were sucked out, their contents censused, and the experiment terminated.

Figure 4 shows the pupation successes of *M. knabi*. The density of both *M. knabi* and *W. smithii* affected pupation success of *M. knabi*. While no straightforward, linear relationship emerges, it would appear that *M. knabi* realizes greatest pupation success at about 20 *M. knabi* per leaf with success declining at both higher and lower densities. The number of *W. smithii* had little effect on pupation of *M. knabi* up to a density of 20 *W. smithii* per leaf after which the presence of *W. smithii* in higher concentrations appeared to inhibit pupation of *M. knabi*. Two-way analysis of variance revealed significant effects of both *W. smithii* ( $F_{4,38} = 5.4$ ;  $P = 0.001$ ) and *M. knabi* ( $F_{3,38} = 8.5$ ;  $P < 0.001$ ). The interaction term had no significant effect on pupation success of *M. knabi* ( $F_{12,38} = 1.7$ ;  $P > 0.10$ ) so that the influences exerted by either other *M. knabi* or *W. smithii* were additive. Altogether,

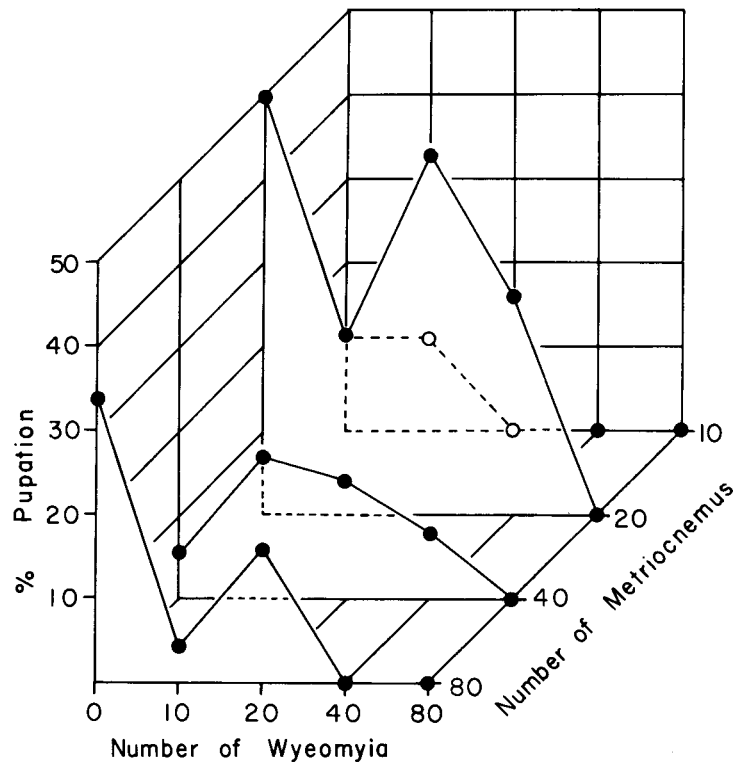


FIG. 4. Pupation success of *Metriocnemus knabi* at various densities of *M. knabi* and *W. smithii*.

the density of *M. knabi* explained about 24% and the density of *W. smithii* another 18% of the variation in pupation success of *M. knabi*. Among those *M. knabi* which did metamorphose, rate (Log(100/days)) of development was not affected by the density of either *W. smithii* or *M. knabi* ( $F_{13,24} = 1.63$ ;  $P = 0.16$ ). Interspecific competitive effects do not appear to be strongly impinging upon *M. knabi* and, in any event, are not greater than the effect of *M. knabi* on itself. The data in Figure 4 suggest that intraspecific crowding will inhibit development of *M. knabi* more at lower levels than will interspecific crowding and Figure 3 shows that the mean crowding of *M. knabi* on itself (ca 50 *M. knabi* per *M. knabi*) is greater than or equal to the mean crowding of *W. smithii* on *M. knabi* (ca 3-50 *W. smithii* per *M. knabi*). The results in the laboratory, when compared with the level of encounter in nature therefore indicate that, for *M. knabi*, intraspecific interactions predominate over interspecific competition.

Among *W. smithii*, pupation success was proportional to the density of *W. smithii* ( $F_{3,38} = 10.7$ ;  $P < 0.001$ ) (Fig. 5) but not significantly affected by the density of *M. knabi* ( $F_{4,38} = 1.0$ ;  $P > 0.40$ ). Altogether, intraspecific effects accounted for 36% of the variation in percent pupation whereas interspecific effects accounted for less than 5%. Among those *W. smithii* which do pupate, rate of development (Fig. 6) was negatively correlated with *Wyeomyia* density but positively correlated with *Metriocnemus* density. Two-way analysis of variance again showed no significant interaction term in either percent or



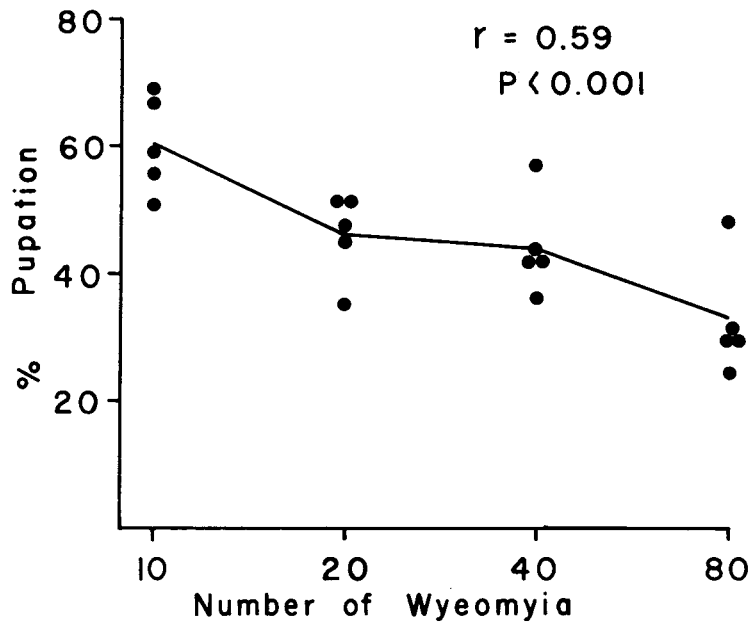


FIG. 5. Pupation success of *W. smithii* at various densities of *W. smithii*. The plot is two dimensional since the density of *M. knabi* had no significant effect on the pupation success of *W. smithii*.

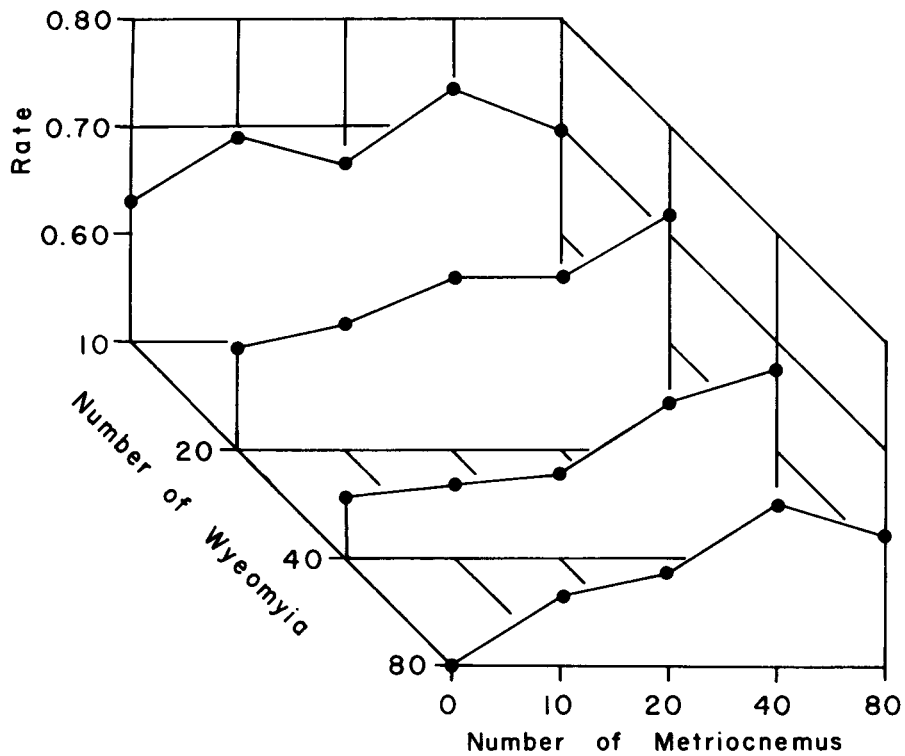


FIG. 6. Rate of development ( $\log(100/\text{days})$ ) of *W. smithii* at various densities of *W. smithii* and *M. knabi*. Note that the rate of *Wyeomyia* development is inhibited by other *Wyeomyia* but enhanced by *Metriocnemus*.

rate of development so that the inter- and intraspecific effects were additive. In nature (Fig. 3), intraspecific crowding of *W. smithii* is proportional to latitude whereas the mean crowding of *M. knabi* on *W. smithii* (ca 40 *M. knabi* per *W. smithii*) shows no consistent latitudinal trend. In the north, population levels of *W. smithii* are low, and, as indicated by the results in Fig. 3, there should be little inter- or intraspecific effects to impede development of *W. smithii*. In the south, *W. smithii* is more likely to be self-crowded, but these intraspecific crowding effects, if anything, are more likely to be abated, rather than augmented, by the presence of *M. knabi*.

Experiments designed to show competitive interactions in the laboratory have indicated for both *M. knabi* and *W. smithii* that, if competitive interactions exist at all, intraspecific competition exceeds interspecific competition. These results predict that each species would become self-limiting at a lower level of crowding than it would become limiting to the other. Hence, these two species should be able to co-exist indefinitely in the leaves of *S. purpurea*.

#### PLANT-INQUILINE INTERACTIONS

The unopened leaves of *Sarracenia* are sterile and the high amount of proteolytic activity found in the pitcher-plant "liquor" is probably due to the combined actions of plant-originated, bacterial, and autolytic enzymes, the latter two introduced by the drowned victims (Hepburn *et al.* 1920; Hepburn & St. John 1927). Even with endogenous bacterial and autolytic enzymes, the victims are encased in a rigid exoskeleton so that the breakdown products of insect protein may not be immediately available to the plant, either in the form of amino acids or ammonia, the primary products of bacterial action (Hepburn & St. John 1927). To estimate the possible role played by the arthropod inhabitants of *S. purpurea* in nutrient release, leaves of intact *S. purpurea* or glass jars (5 cm diameter by 4.7 cm height) were filled with 20 ml distilled water, 3 drops of fluid from pitcher-plants (New Jersey), and 1.5 meal worms (*Tenebrio* sp., 0.15-0.20 g wet weight). Groups of 3 leaves or jars each received 10 third instar, diapausing *W. smithii*, 10 third or fourth instar, diapausing *M. knabi*, 10 *W. smithii* plus 10 *M. knabi*, or nothing (control). Since pitcher-plant leaves are highly effective at taking up small nitrogenous compounds (Hepburn *et al.* 1920), the glass jars were necessary inert controls to assess the degree to which products were liberated into the water. Nitrogen content of the water was then determined by reaction with Nessler's reagent.

Figure 7 shows that the nitrogen level in leaves of *S. purpurea* rarely rose above 1 mg%, regardless of the occupants in the leaf. By marked contrast, nitrogen levels in glass jars rose as high as 10 mg% in the presence of *W. smithii* and/or *M. knabi*. The presence of *Wyeomyia* and *Metriocnemus* in any combination accelerated the appearance of nitrogen in the jar water when compared with their absence (Fig. 7A). Nitrogen levels in jars rose to a higher total level when *W. smithii* was the sole species of insect present (Fig. 7C) but the initial rate of nitrogen appearance was higher when *M. knabi* was the sole species in the jar (Fig. 7B). When both insects were present (Fig. 7D), a rapid initial appearance of nitrogen rose to a level of nitrogen characteristic of jars with *W. smithii* alone. The differences in the initial rate of nitrogen liberation between *M. knabi* (Fig. 7B) and *W. smithii* (Fig.

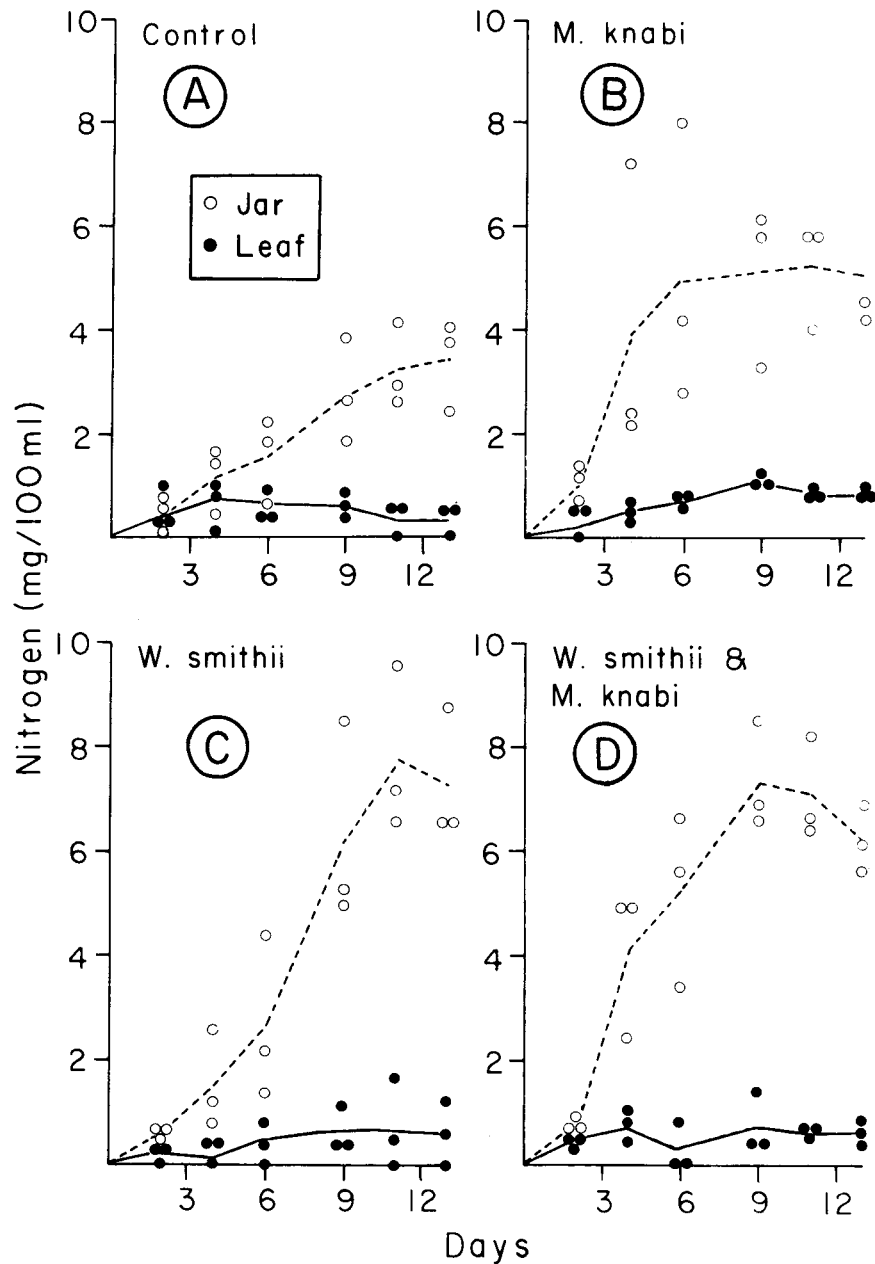


FIG. 7. Appearance of soluble nitrogen in the water of leaves and jars after the addition of prey (mealworms) and the inquilines shown in the upper left corner of each graph. The lines connect means and points plot the actual values for triplicate jars or leaves.

7C) may be due to the observation that *M. knabi*, unlike *W. smithii*, may eat its way directly into drowned victims, thus disrupting the integrity of their cuticle and increasing the surface area available for bacterial action. *W. smithii* larvae are mainly grazers upon bacteria, protozoans, and small particulate material in the "plankton" zone of the leaf or on the surface of the detritus on the bottom. Thus, although they may have to wait for the victims

to break down or for a victim-bacterial-protozoan food chain to develop, *W. smithii* may be preventing substantial amounts of nitrogen from being bound in bacteria, protozoans, or both. These results thus (1) confirm earlier conclusions (Hepburn *et al.* 1920) that leaves are highly effective at absorbing available nitrogenous compounds, and (2) that the presence of *W. smithii* and/or *M. knabi* accelerates the production of plant-available nitrogen in the water.

One might well imagine that all of this digestive activity would greatly increase the oxygen demand of the system. Indeed, jars that are covered rapidly become fetid and neither *M. knabi* nor *W. smithii* can long survive in the system. In addition, I have observed leaves in nature which have caught large insects, millipedes, or slugs, whose contents are red in color, foul in odor, and devoid of living *W. smithii* or *M. knabi*. However, the great majority of leaves with abundant inquilines and victims contain clear water with little or no odor. This observation suggests regulation by the plant of its internal environment. Cameron *et al.* (1977) found that, despite considerable oxygen demand by the system, leaves of *S. purpurea* in New Brunswick (Canada) maintained a high level of oxygen, even if the air-water interface was sealed with mineral oil. Inert test tubes did not exhibit this regulatory ability. However, the simple addition of oxygen is not sufficient since, with abundant inquilines, there would still be a considerable build-up of carbon dioxide.

To confirm the observations of Cameron *et al.* (1977), and to investigate the regulation of carbon dioxide, two experiments were run. In the first (Fig. 8A), helium-stripped water was added to leaves of *S. purpurea* which were then maintained on a 16:8 light:dark regimen or in constant darkness. In the second experiment (Fig. 8B), helium-stripped water was charged with

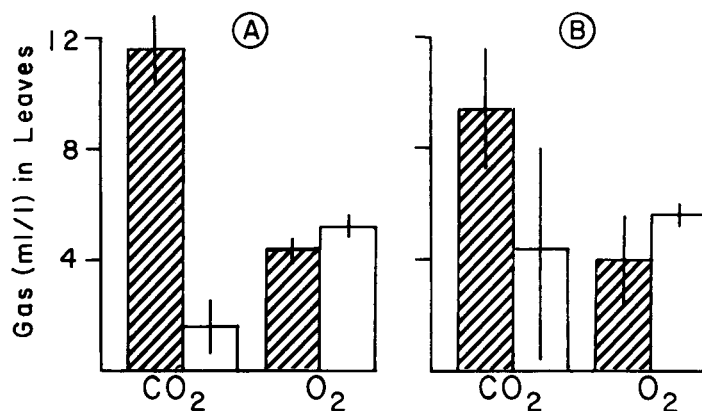


FIG. 8. Concentration of gas (ml/l) in the water of pitcher-plant leaves after (A) 48 and (B) 72 hours. In (A), the water was stripped of gases with helium, resulting in a trace of oxygen and no detectable carbon dioxide at the start of the experiment. In (B), the water was stripped of gases with helium and then charged with 18.8 ml/l of carbon dioxide and 2.5 ml/l of oxygen at the start of the experiment. In each case, replicates were maintained in constant darkness (shaded bars) or on long-days (16L:8D, open bars) and the samples taken during the eleventh hour after lights-on. Vertical bars show  $\pm 2$  standard errors.

18.82 ml/l of carbon dioxide and 2.5 ml/l of oxygen and added to leaves in the light (L:D = 16:8) or dark (constant darkness) as above. Immediately after the addition of the water, the leaves were sealed with melted grease (Vaseline). At the end of 48 (first experiment) or 72 (second experiment) hours, the carbon dioxide and oxygen levels were determined with a Fisher gas partitioner. Figure 8 shows that carbon dioxide increased in leaves with no carbon dioxide added and decreased in leaves charged with an initially high concentration of carbon dioxide. In both cases, carbon dioxide levels were lower in the light than in the dark. In both experiments oxygen levels rose to about 4-6 ml/l but there was no significant effect of light or dark. The results of these initial experiments are thus in agreement with Cameron et al. (1977), in that the leaves of *S. purpurea* provide an oxygen-enriched environment and appear to do so with little regard to lighting. In addition, the leaves are even more effective in removing carbon dioxide from the water, particularly in the presence of light. The implication here is that, regardless of the mechanism involved, at times later in the day when high temperatures will both increase inquiline metabolism and reduce oxygen solubility, the plant will also be removing carbon dioxide at its greatest rate.

The adaptive significance of the gas relationships in leaves of *S. purpurea* may be twofold. First, by infusing oxygen and removing carbon dioxide as well as nitrogenous end products, the plants are maintaining healthy inquiline populations which, in turn, increase the turnover of prey into plant-available nitrogen. Second, actively photosynthesizing plants have a ready sink into which they can move oxygen in the same direction as the natural gradient and, at the same time, possess a ready reservoir of carbon dioxide. The latter point may be far from trivial. Leaves of *S. purpurea* in nature may lie recumbent upon the bog mat or savannah or may be embedded in a mat of *Sphagnum* moss. At this level in a bog, convection is minimal (Kingsolver 1979) and temperatures are high, averaging 25-30°C during the day and sometimes reaching levels as high as 40°C (Evans 1971; Bradshaw 1980). At such temperatures in the full sun, photosynthesis will be high and is most likely to be limited by carbon dioxide, especially if the leaves are surrounded by moss, wiregrass, or other vegetation. *S. purpurea*, unlike the moss or wiregrass, however, has its own internal carbon dioxide generator whose output could be expected to increase with temperature (respiration of the bacterial, protozoan, and arthropod inquilines).

#### OVIPOSITION BEHAVIOR AND ITS CONSEQUENCES

Numerous observers (Smith 1902, 1904; Istock et al. 1975; Istock 1978; Paterson 1971; Mogi & Mokry 1980) have noted that *W. smithii* prefer to oviposit in leaves of the present rather than the previous year's crop. Fish & Hall (1978), working with northern (42.5°N) *W. smithii*, noted further a preference for the younger leaves of the current year's crop. It is therefore not surprising that the instar distribution of *W. smithii* along the Gulf Coast (Fig. 9) is strongly associated with different age classes of leaves. The very youngest leaves (rank 1) contained exclusively eggs and first instars. The next oldest leaves (rank 2) contained abundant larvae consisting mainly of second and third instars. Older leaves (ranks 3 and 4) contained fewer, more mature larvae and pupae. These data, along with the observations cited above, support the concept that *W. smithii* in general select only the youngest leaves for oviposition and that the resultant larvae then mature as the leaf ages.

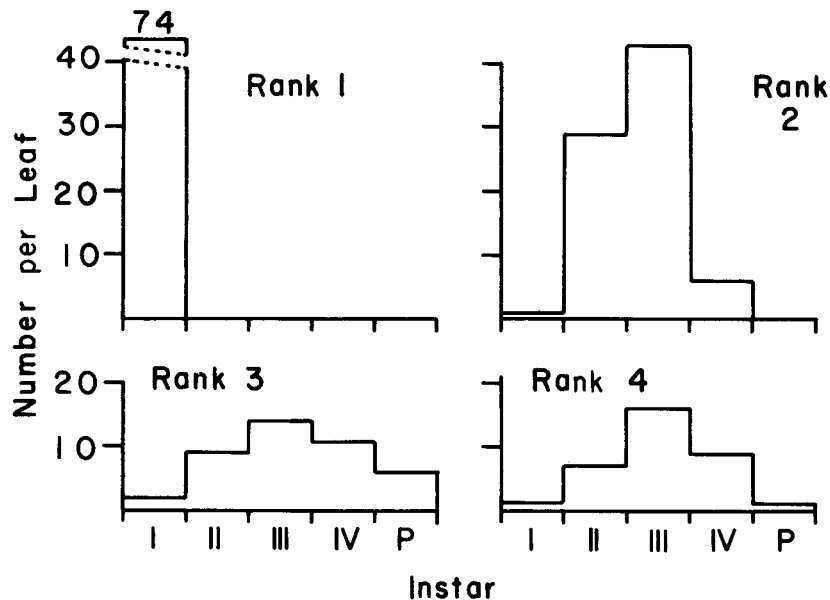


FIG. 9. Instar distribution of *W. smithii* in leaves of different ages, October 23, 1978, in north Florida (WI). Rank 1 leaves are the youngest. The bars represent the mean number of each instar in 2-5 leaves among 4 plants within a 100-square meter area.

This pattern of oviposition repeats in the laboratory (Fig. 10). If provided with *S. purpurea* grown on water tables in a constant environment (long days, L:D = 16:8 at 23°C), *W. smithii* originating from Florida to Maine (30-46°N) all select younger leaves (Fig. 10A-F). This pattern persists, regardless of the number of eggs in the leaves (Fig. 10G-I). In Figure 10G, *W. smithii* laid a total of 84 eggs of which 53 were in the youngest leaf. This figure is reasonable given the densities of eggs found by Mogi & Mokry (1980) or given the densities of first instars encountered along the Gulf Coast (Fig. 9). Even when more eggs are oviposited, the youngest leaf continues to receive the bulk of them. In Figure 10H and Figure 10I, females laid 179 and 1163 eggs in the youngest leaf. Ovipositing females thus selected newer leaves with densities of eggs an order of magnitude greater than observed in the field in preference to older leaves with far lower densities.

While working in north Florida, I observed an ovipositing female. At the time I was censusing leaves of *S. purpurea*, and three mature plants with many leaves each were within my immediate view. The adult female flew into the vicinity, flew to the first plant and into several leaves. She lingered only in the youngest leaf, exhibiting the typical up-and-down, bobbing flight pattern of ovipositing *W. smithii* as well as other sabethine mosquitoes. Three times I observed her abdomen dip in flight and later inspection revealed 3 fresh, untanned eggs among the others on the water surface in the leaf. She then left the leaf and that plant and proceeded to the next two plants and repeated the behavior. Finally, she returned to the original plant, selected the youngest leaf, exhibited the up-and-down, bobbing flight pattern but de-

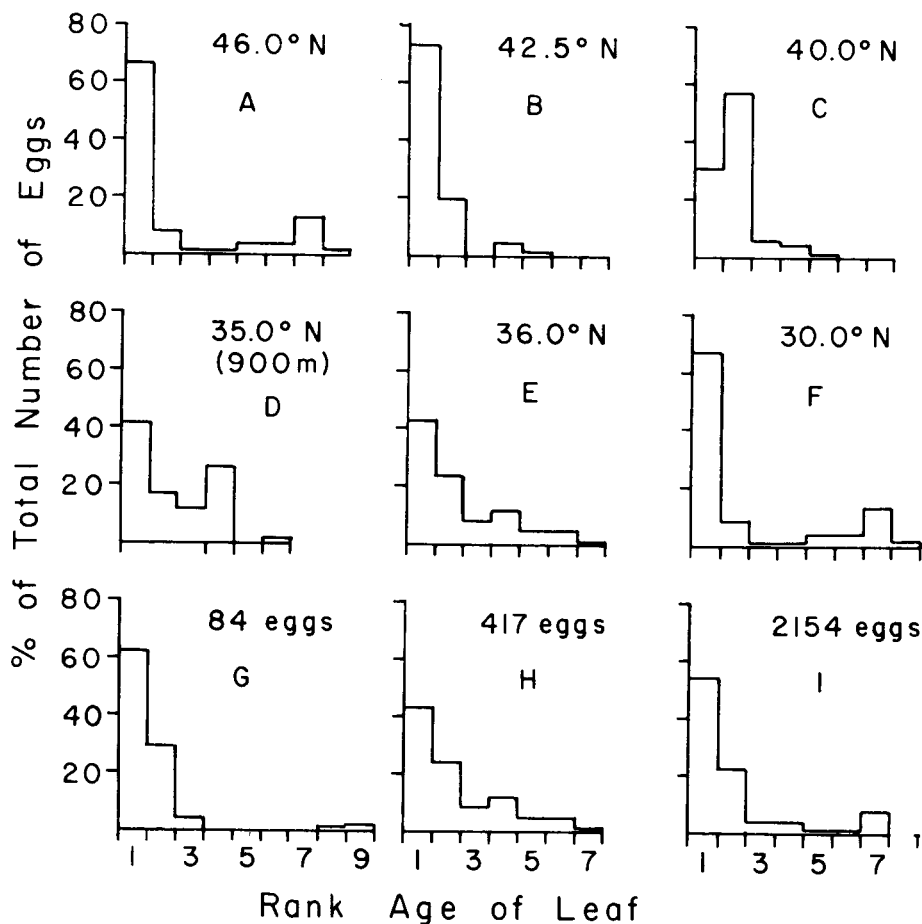


FIG. 10. Oviposition site selection behavior by *W. smithii* in the laboratory (23°C and long-day (16L:8D) photoperiod). A-F, variation in behavior due to geography of origin (localities shown in Fig. 2); in all experiments the adult population oviposited between a total of 400 and 500 eggs in three days. G-I, variation in behavior of adults from 36°N due to total number of eggs oviposited; the total number of eggs laid is shown at the top of G-I.

posited no eggs. These non-oviposition flights were repeated in the youngest leaves of the remaining two plants, again with no new eggs being deposited. The female then left the area. These observations in nature confirm the laboratory results (Fig. 10) and field distribution of eggs (Mogi & Mokry 1980) or larvae (Fig. 9) (Fish & Hall 1978).

The field observations suggest that individual *W. smithii* are able to distinguish leaves in which they have oviposited. The female I observed showed a high degree of discrimination, spending the most time at the same leaf on two successive visits to each of three plants within a few minutes time; yet, she deposited no eggs on the second visit. It would appear either that she had left some sort of marker to signal that she had recently visited that leaf or that she was capable of remembering recently visited leaves. The marker or remembrance is likely of short term duration since, under laboratory conditions (Fig. 10) females are clearly depositing more than a few

eggs into a single leaf. The up-and-down, bobbing flight pattern may thus constitute a period of final leaf assessment by the female before she commits a portion of her reproductive potential to that leaf.

The bulk of the published work on *W. smithii* has dealt with mosquitoes collected from pitcher plants at about 35°N latitude and northwards. Only a few papers mention *W. smithii* collected further south (Bradshaw & Lounibos 1977; Dodge 1947; Bradshaw 1980; O'Meara *et al.* 1981). Yet, it is at these latitudes that various *Sarracenia*, other than *S. purpurea*, overlap in their ranges (McDaniel 1971) and in their general habitat (personal observations), in particular, *S. flava* L., *S. rubra* Walt., *S. leucophylla* Raf., and *S. alata* (Wood). No investigator has ever reported on the occurrence of *W. smithii* in any of these other species or in their hybrids with *S. purpurea*.

The leaves of *S. purpurea* remain alive and hold water throughout the entire year, including the winter; leaves of *S. flava*, *S. leucophylla*, *S. alata*, and, to a lesser extent, *S. rubra* tend not to have standing water in the summer and the leaves senesce and die in the winter. Hence, these species tend not to provide a secure habitat for overwintering *W. smithii*. Where *S. purpurea* occurs with other species, hybrids are frequent (Fig. 11) (Bell



FIG. 11. *S. purpurea* (left), *S. flava* (right), and their  $F_1$  hybrid (center) showing the easily recognized, intermediate character of the latter.



1949, 1952). Among the hybrids between *S. purpurea* and these plants, the leaves contain standing water during the summer and a number of them remains alive during the winter. Invariably, *W. smithii* are found overwintering in these leaves (Fig. 12).

During the summer in north Florida, *W. smithii* are equally frequent in both *S. purpurea* and its hybrids with *S. flava* (Figs. 11, 13). Furthermore, during this time of year, of 50 leaves of *S. flava* examined, 21 had standing water and over half of the leaves with water also contained *W. smithii*, although at lower densities than in either *S. purpurea* or the *S. purpurea-flava* hybrids (Fig. 13). Of the 161 *W. smithii* recovered from *S. flava*, 5 of them, or 3.1% were pupae. By contrast, 2.8% of the 951 mosquitoes in *S. purpurea* and 1.8% of the 1111 in the hybrids were pupae. Apparently, *Wyeomyia* do not fare poorly in *S. flava* during the summer but clearly do not survive in senescent, dead leaves of *S. flava* during the winter. *S. flava* thus provides a good resource during the summer but a predictably poor one during the winter. The rock-pool mosquito, *Aedes mariaae* (Sergent and Sergent), switches its oviposition preference from open rock pools during the summer to enclosed rock holes during the fall under the influence of photoperiod (Coluzzi *et al.* 1977). Given the response of larval *W. smithii* to photoperiod (Smith & Brust 1971; Evans & Brust 1972; Bradshaw & Lounibos 1972, 1977), it would not be surprising to find oviposition site preference of adults similarly attuned to seasonal cues.

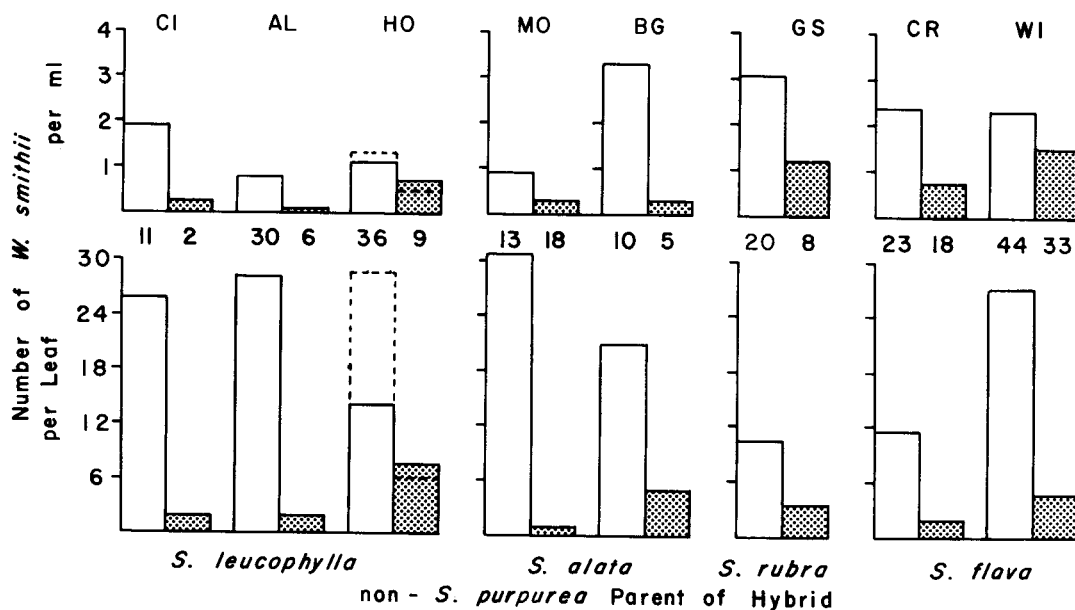


FIG. 12. Occurrence of *W. smithii* in *Sarracenia purpurea* (open bars) and its hybrids (shaded bars) with *S. leucophylla*, *S. alata*, *S. rubra*, and *S. flava*. Localities of collection are shown at the top of the figure and are illustrated in Figure 2, except CI, 30 km northwest of AL, HO, 16 km west of CR, BG, 24 km south of AL, MO, and BG, were sampled during the winter of 1972-73; HO (dashed outline), GS, CR, and WI were sampled during the winter of 1973-74. The bars plot means with the number of leaves sampled shown along the x-axis between the two sets of histograms.

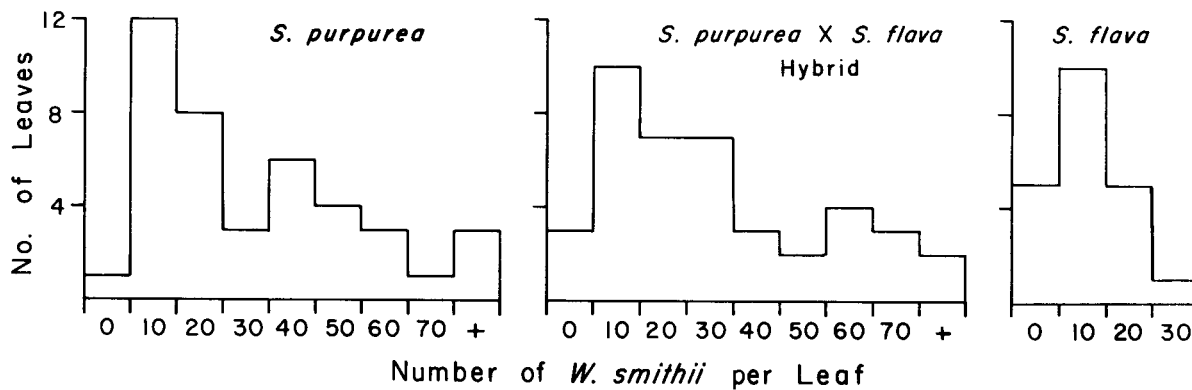


FIG. 13. Occurrence of *W. smithii* in *S. purpurea*, *S. flava*, and their  $F_1$  hybrid during July, 1978, in north Florida (WI). The first column of the histogram shows number of leaves with no *W. smithii*, the second column the number of leaves with 1-10 *W. smithii*, and so on.

The data in Figure 13 suggest that *W. smithii* do about as well in hybrids as they do in *S. purpurea*; however, the winters of 1972-73 and 1973-74, during which the data in Figure 11 were taken, were warmer than normal. During the winter of 1976-77, it was colder than normal and all of the *S. purpurea-flava* hybrids in North Carolina (GS) and most leaves of those in northern Florida (WI, CR) had senesced and died. Thus, *S. flava* and its hybrids provide a resource whose reliability varies both between seasons and between years.

The lower seasonal and annual predictability of the hybrids and, to a lesser extent, the seasonal opportunities in *S. flava*, may account for a portion of the heritable variation in oviposition site selection behavior described by Istock *et al.* (this volume). This relationship would be expected in Florida where both *S. flava* and its hybrids with *S. purpurea* occur frequently. In northern latitudes where *S. purpurea* is the only *Sarracenia* present, heritable variation in *Wyeomyia* oviposition behavior may in part be a reflection of a southern ancestry. If, indeed, evolution in *W. smithii* has proceeded from south to north as proposed by Bradshaw & Lounibos (1977), then northern *W. smithii* may still be expected to accept southern hybrids for oviposition.

To examine this possibility, *W. smithii* from either a northern locality (FV), approximately 1,000 km from the next nearest *S. flava*, or from northern Florida (WI) were exposed simultaneously to *S. purpurea* and hybrids between *S. purpurea* and *S. flava* in the laboratory. In each replicate, the plants were matched so that the youngest leaves of *S. purpurea* and of the hybrids had opened within 48 hours of each other.

When given the choice between *S. purpurea* and its hybrid with *S. flava*, *W. smithii* from Florida oviposited into *S. purpurea* taking only leaf age, but not volume (leaf size) into account (Table 1). At the same time, females ovipositing into the hybrids responded to both age and size. The hybrids used in this experiment were larger (mean volume = 52.8 ml) than the *S. purpurea* (mean volume = 16.04 ml) and contained the majority (88%) of the eggs.

TABLE 1. Step-wise regression of egg allocation (log percentage of eggs laid in all leaves) on leaf age (log days since opened) and size (log volume of water if leaf filled to capacity).

<i>W. smithii</i> ovipositing		Step	Variable	Reduction in sums of squares	t*	P	a	b	c
from	into								
north Florida	<i>S. purpurea</i>	1	age	0.378	3.58	<0.01	0.68	-0.32	
		2	size	0.039	1.16	>0.05			
	hybrid	1	age	0.339	3.86	<0.01			
		2	size	0.222	2.66	<0.05	0.71	-0.88	0.80
Massachusetts	<i>S. purpurea</i>	1	age	0.593	7.30	<0.01			
		2	size	0.225	4.90	<0.01	0.87	-0.72	0.65
	hybrid	1	age	0.357	3.81	<0.01			
		2	size	0.233	2.40	<0.05	0.33	-0.71	0.99

F-test for parallel regression planes:  $F_{2,34} = 4.70$ ;  $P < 0.05$

F-test for parallel axes: age,  $F_{1,34} = 7.05$ ;  $P < 0.01$

size,  $F_{1,34} = 3.28$ ;  $P > 0.05$

F-test for parallel regression planes:  $F_{2,29} = 0.48$ ;  $P > 0.05$

t-test for equality of intercept:  $t = 0.78$ ;  $P > 0.05$

\* t, t statistic; P, associated probability; a, b, c: coefficients in the regression equation,  $Y = a + b(\text{age}) + c(\text{size})$

When leaf age of hybrids was adjusted to take leaf volume into account, hybrids exhibited a younger "equivalent age" but a steeper decline in apparent attractability than *S. purpurea* (Fig. 14A). In nature during the summer (Fig. 15), very young instars of *W. smithii* predominate in younger leaves of *S. purpurea*, older instars in older leaves. In the hybrids, a large proportion of younger instars persists, even among moderately older (6 wks) leaves, probably reflecting the larger size of the hybrids. The age distribution of *W. smithii* in nature thus reflects their oviposition behavior in the laboratory.

When given a choice between *S. purpurea* and its hybrid with *S. flava*, *W. smithii* from Massachusetts did not discriminate according to parentage (Table 1); there was no significant difference between the two regression planes representing *S. purpurea* or hybrids in either slope or intercept (Table 1). Thus, when attractability is plotted as a function of equivalent age, the two plots overlap and a common line can be fitted to them (Fig. 14B). *Wyeomyia* from the north did, however, discriminate according to age and size of the leaf (Table 1).

These experiments and observations show that oviposition behavior in the laboratory is a complex function of leaf age, size, and plant parentage. *W. smithii* from the north where *S. purpurea* is the sole pitcher plant allocate

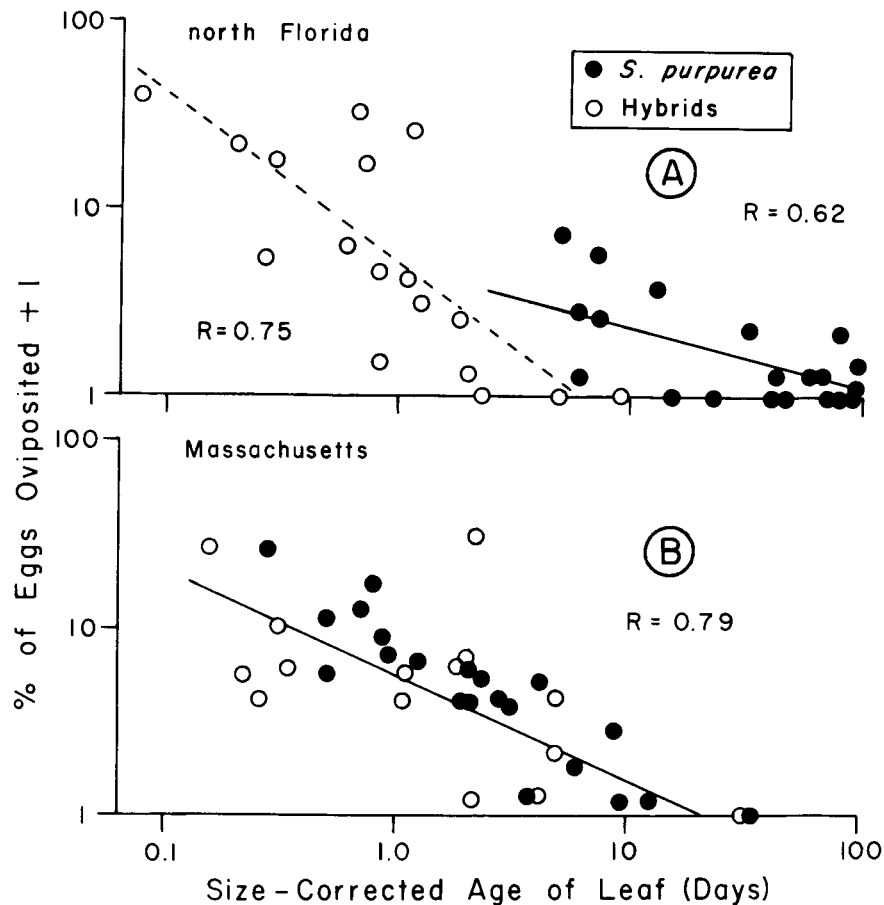


FIG. 14. Attractability to *W. smithii* (percentage of eggs oviposited) of *S. purpurea* and its  $F_1$  hybrid with *S. flava* in the laboratory. Adult *W. smithii* were exposed simultaneously to both *S. purpurea* and hybrids in two replicates each for mosquitoes from north Florida (WI) or Massachusetts (FV). Number of eggs oviposited were converted to percent of total oviposited during each replicate experiment so that replicates could be plotted on the same axes and pooled. Age of leaves were corrected for size from regression coefficients given in Table 1. Note in A that the difference in size between *S. purpurea* and the hybrids displaces the plots from one another; were they to be plotted on a scale of absolute age, the hybrids would contain a higher percentage of eggs, especially in the young and middle aged leaves.

their eggs according to the first two parameters alone. *W. smithii* from a southern locality with both *S. purpurea* and *S. flava* and hybrids, allocate their eggs according to all three parameters.

The distribution of *Sarracenia* species may explain some of the variability in oviposition behavior but it does not explain why younger leaves should be selected over older ones. Several observations and experiments indicate the selection for younger leaves relates to the abundance and timing of prey availability to the leaf. To examine both prey capture by *S. purpurea* and oviposition by *W. smithii* in a southern pine savannah, all the leaves of

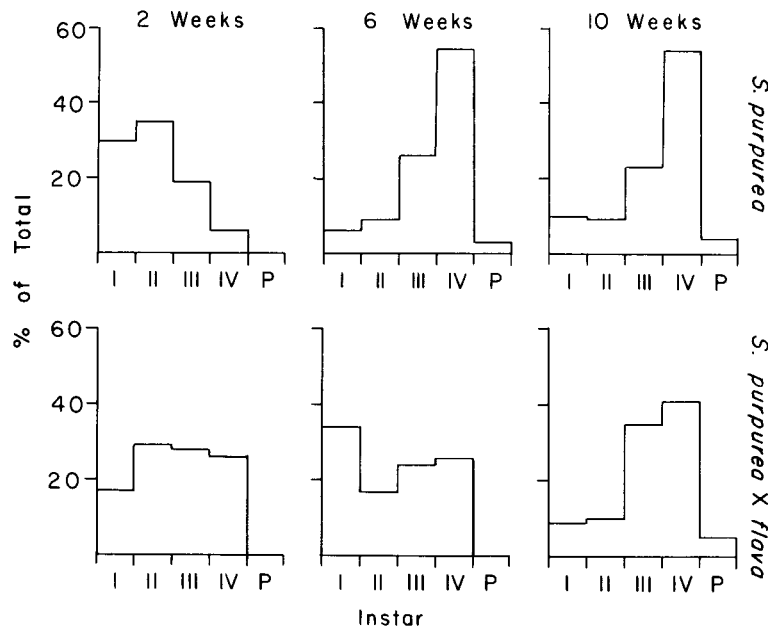


FIG. 15. Instar distribution of *W. smithii* in leaves of *S. purpurea* and its F<sub>1</sub> hybrid with *S. flava* in north Florida (WI). Age of leaves is shown at the top of the figure. Leaves had been marked when they opened with indelible pens and were censused July 28, 1978.

6 *S. purpurea* were sucked dry, rinsed three times with distilled water, and left, half-filled with distilled water, for 3 weeks. At the end of this time, all the intact leaves were destructively sampled and examined for inquilines and victims. To avoid counting victims which we might have missed in the original flushing of the leaves, we scored prey as only those insects and spiders which still retained heads or cephalothoraces intact on the thorax or abdomen. Figure 16 shows that in nature, the very youngest leaves contained the most *W. smithii* and that their abundance declines exponentially with rank age of the leaf. By contrast, it is not the youngest, but rather the penultimate leaves of *S. purpurea* which captured the most prey. These results show that along the Gulf Coast in the field, *W. smithii* are attracted to leaves before the time of maximum prey capture. The very important points here are that (1) as *W. smithii* develop, older stages will encounter increasing resources; (2) the resources available in a leaf are transient and not constantly being renewed; and (3) consequently, *W. smithii* oviposited into an older leaf will encounter competition from older instars for a reduced resource.

Leaves do not lead an entirely safe existence and there are caterpillars (*Exyra* spp., Lepidoptera: Noctuidae) which attack them specifically (Jones 1921; Higley 1885; Brower & Brower 1970). These caterpillars begin by chewing a low hole in the leaf which prevents further build-up of water and then spinning a web over the orifice, preventing entrance of more victims. In addition, older leaves may become brittle, fracture, and drain (Forsyth & Robertson 1975) and may frequently become fractured by frost during the winter (Istock *et al.* 1975; personal observations in North Carolina, New Jersey,

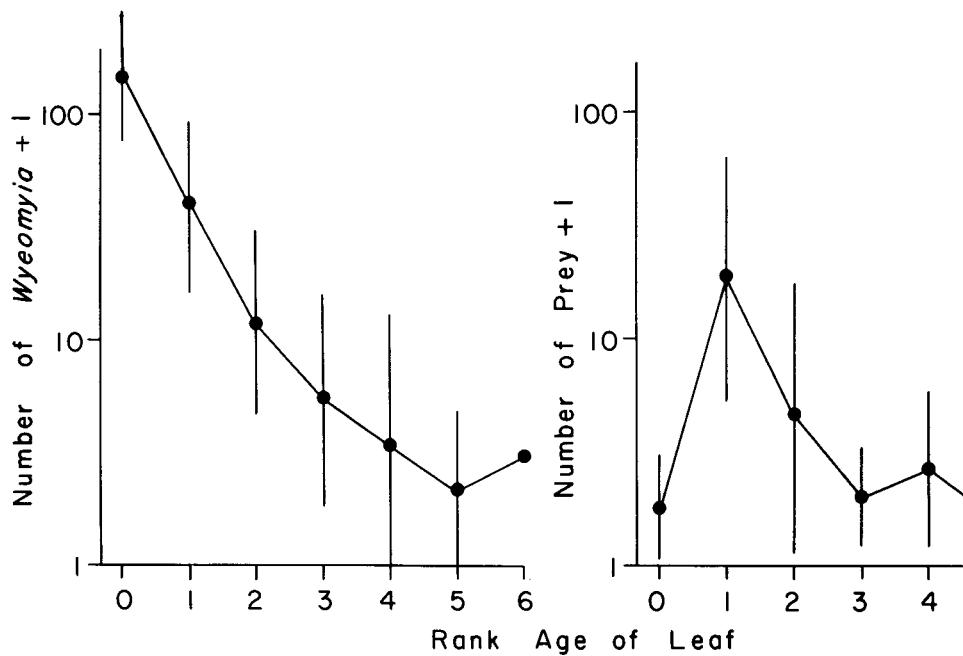


FIG. 16. Prey capture and *W. smithii* attraction in north Florida by pitcher-plant leaves of various ages. Each point represents the mean of 3-7 leaves except rank age = 6 where only 1 leaf was available; vertical bars show  $\pm 2$  standard errors.

and Michigan). Given finite probabilities of continuing to be an active predator, pitcher plants may have realized the greatest fitness by restricting carnivory to the earliest ages after the leaves have hardened. It is important to remember that the cessation of predatory behavior does not terminate its benefit to the plant since a leaf is still capable of photosynthesis. One can then visualize three stages in the life of a leaf. Initially, it is a nursery for its inquilines, primarily *W. smithii*; secondarily it is a carnivore; and, finally, it is a primary producer.

The above observations provide circumstantial evidence that *W. smithii* are limited by prey captured by their host and that, to maximize fitness, they must hatch into younger rather than older leaves. To examine the basis for prey capture as a limitation for *W. smithii*, a series of leaves in north Florida was censused weekly from the third to the tenth week after they had opened in early July. Weekly censuses noted the number of each instar, including pupae, and resulted in estimates of biomass, determined by weighing a known number of each instar and thereby obtaining the required instar-dry weight conversion factor. The pupae were removed and their weight added cumulatively into the biomass of *W. smithii* sustained by the leaf. During the tenth week of leaf age, the leaves were destructively sampled, the biomass of *W. smithii* was calculated on the basis of instars present and pupae produced, and the number of head capsules of victims captured was counted. Figure 17 shows that both the total biomass sustained and pupae emerging from the leaf were dependent upon the number of prey captured by the leaf. These results provide direct evidence that prey capture is limiting both

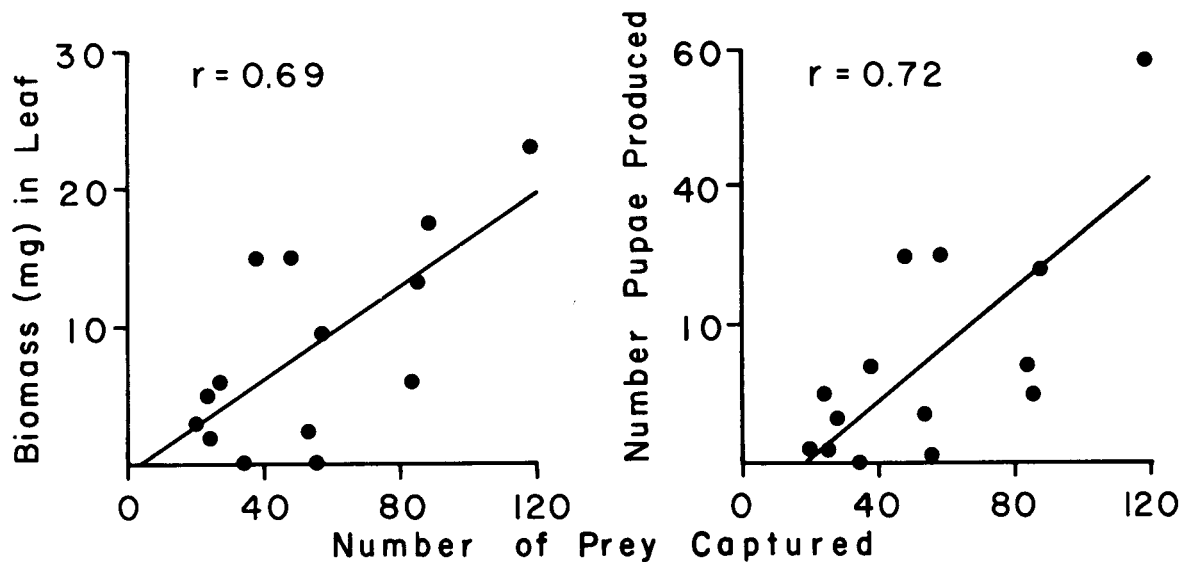


FIG. 17. Biomass of *W. smithii* sustained and pupae produced by leaves with varying prey capture. Pupae were censused and removed weekly; the biomass of larvae was determined after 10 weeks and includes the cumulative biomass of pupae produced in the interim.

growth and metamorphosis of *W. smithii* in nature, at least in the southern portion of their range.

To assess the impact of intra- and interspecific competition on *W. smithii* in the south (WI), either 100 first instars of *W. smithii*, 50 mixed, early instars of *M. knabi*, or a small amount of water (control) was added to a series of similar sized leaves which had opened within one week of each other. The leaves were censused once a week for 8 consecutive weeks and the number of prey captured by the leaf determined as above. The addition of either *W. smithii* or *M. knabi* was not found to have a significant effect on the biomass of *W. smithii* maintained by a leaf ( $F_{2,26} = 3.26$ ;  $P > 0.05$ ) (Fig. 18). However, the addition of extra *W. smithii*, but not *M. knabi* decreased the number of pupae per unit resource (prey) ( $F_{2,26} = 6.07$ ;  $P < 0.01$ ). These results support the earlier conclusion that *W. smithii* should, at the southern extent of their range, be more limited by other *W. smithii* than by *M. knabi*.

To examine whether leaf age had a significant impact on survivorship, 200, 100, 50, or 0 (control) first instars of *W. smithii* were added to leaves of various ages. The first instars were collected from other leaves on the same day that the experiment started. On October 10, *W. smithii* were added to leaves of rank 1 (youngest) through rank 5. The leaves were then left undisturbed until January 30 of the following year when they were again censused for survivorship. Percentage survivorship was then calculated as:

$$\frac{(100) (\text{mean \# larvae in experimental leaf} - \text{mean \# larvae in control leaf})}{\text{\# larvae originally added to experimental leaf}}$$

Probability of survivorship ranged from 25-47% among larvae in the rank 1 leaves (Fig. 19) but only 0-15% among the leaves of older rank where survivorship averaged 1/2 to 1/5 as high. Thus, females which would oviposit into

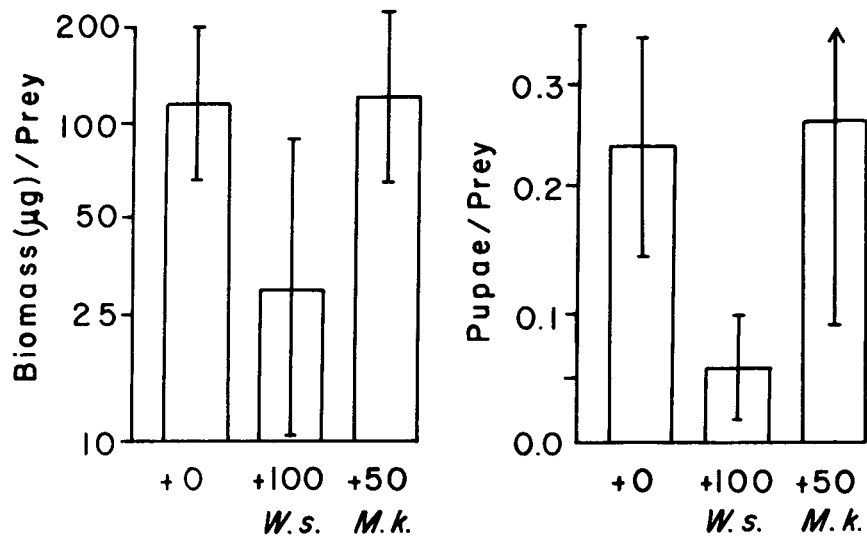


FIG. 18. Biomass of *W. smithii* sustained and pupae produced per unit prey in leaves with no supernumerary inquilines (0, control), with 100 first instars of *W. smithii* added (+ 100 *W.s.*), or with 50 mixed instars of *M. knabi* added (+ 50 *M.k.*).

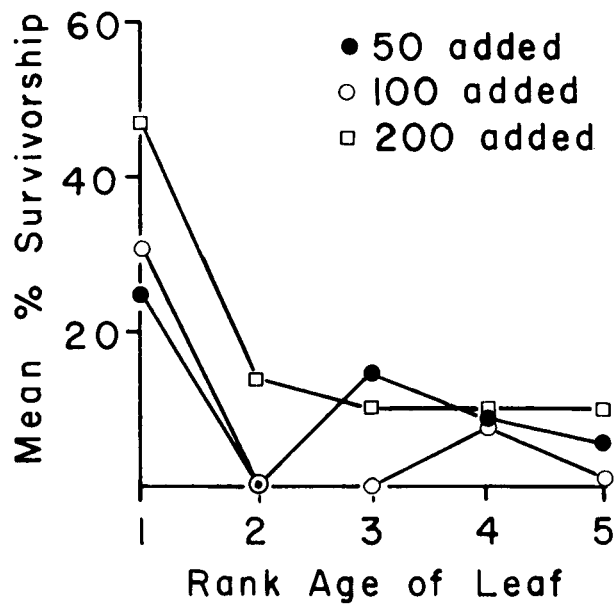


FIG. 19. Survivorship of first instar *Wyeomyia* introduced into leaves of various ages, rank 1 being the youngest.



older leaves could, on the average, expect reduced probabilities of survivorship among their offspring and could expect higher overwintering survivorship the younger the leaf into which they oviposited in the fall.

#### CONCLUSIONS

The leaves of the carnivorous purple pitcher plant, *Sarracenia purpurea*, act as host for a number of organisms including pitcher bacteria, protozoans, mites, midges, mosquitoes, and flies. These species apparently coexist throughout most of their ranges. In the present study, overwintering populations of *W. smithii* encountered considerable numbers of *M. knabi* (Fig. 3) but competition between these species would appear to be minimal, even when they are forced to overlap in time (Figs. 4-6). In fact, under very crowded conditions, *M. knabi* may even benefit *W. smithii* (Fig. 6). Both laboratory (Figs. 5-6) and field (Fig. 18) studies support the contention that *W. smithii* are more limited by other *W. smithii* than by *M. knabi* and that the two species should be able to coexist indefinitely.

Resource partitioning may involve stage of trophic utilization rather than time per se. The resource base of the community consists of prey consumed by *S. purpurea* and its use follows the nitrogen pathway illustrated in Figure 20. The dead victim may be attacked directly by *B. fletcheri* or, upon drowning and settling to the bottom, by *M. knabi*. These inquilines, one limnetic and one benthic, then act as macro-decomposers in the system. This spatial distribution in the leaf would suggest that they do not interact to a great extent; indeed, *B. fletcheri* is a classic case of a self-limited species (Forsyth & Robertson 1975). As a result of the macro-decomposers, increased surface area of the victim becomes available to bacteria, the micro-decomposers in the system. Bacteria are then grazed by protozoans which, in turn, become prey for *W. smithii*. Thus, *B. fletcheri* and *M. knabi* use the prey directly while *W. smithii* may use it directly by consuming particulate material generated by macro-decomposer action or indirectly by grazing upon the micro-flora and fauna. This course of events is supported by the observation that *M. knabi* liberate nitrogen from a victim faster than *W. smithii* (Fig. 7) but that the presence of *W. smithii* results in higher levels of dissolved nitrogen, presumably because they prevent nitrogen from being bound in living micro-flora and fauna.

The host leaves of *S. purpurea* rapidly take up dissolved nitrogen (Fig. 7) (Hepburn et al. 1920), infuse oxygen into the water (Fig. 8) (Cameron et al. 1977), and, particularly during the light, remove carbon dioxide (Fig. 8). The plant provides dinner (prey) for its inhabitants and then cleans up the leftovers (carbon dioxide and nitrogenous end products of their metabolism) while enriching the environment with oxygen. In return, the plant obtains a ready supply of nitrogen and carbon dioxide as well as a sink into which to flush oxygen. Thus, rather than presenting a case of intense competition for limited resources in a finite environment, the relationships revolving around *S. purpurea* and its arthropod inhabitants appear to be mutually beneficial.

In addition to *Sarracenia purpurea*, *W. smithii* may be found in *S. flava* and in natural hybrids between *S. purpurea* and *S. flava*, *S. rubra*, *S. leucophylla*, and *S. alata* (Figs 12-15). The hybrids represent a resource whose

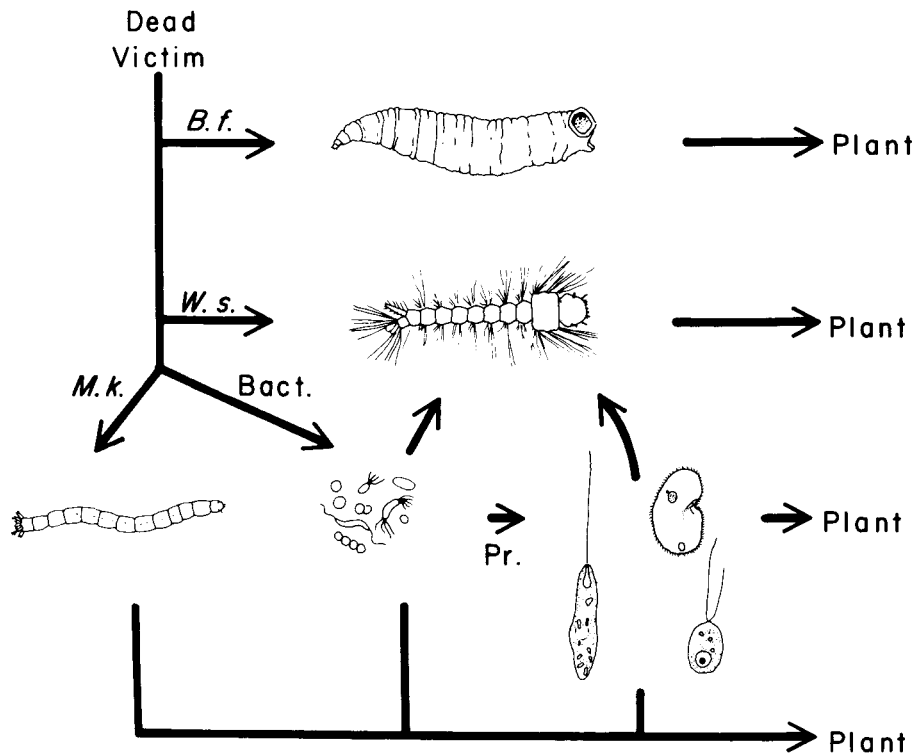


FIG. 20. Nitrogen flow in leaves of *S. purpurea* from a dead victim, through various inhabitants, to the plant. The victim may be attacked directly by *Blaesoxipha fletcheri* (B.f.), *Metriocnemus knabi* (M.k.), or bacteria (Bact.). Through the action of these decomposers, the victim may be broken down to small enough particles to be filtered by *Wyeomyia smithii* (W.s.). Bacteria, exploiting the increased surface area made available through the action of macrodecomposers (*B. fletcheri* and *M. knabi*) may be grazed by *W. smithii* or by protozoans (Pr.), the latter of which can then also be grazed by *W. smithii*. At each step of this food web, the inhabitants of the leaf provide plant available nitrogen in the form of the end products of their metabolism.

predictability varies both between seasons and years. Oviposition site selection behavior by *W. smithii* is a complex function of plant parentage, size, and age of host leaf as well as the range of host species to which the ovipositing population had been exposed (Table 1; Fig. 14). Of these parameters, age of leaf is consistently the most important character assessed by an ovipositing female.

Although not limited by their interactions with *M. knabi* (Figs. 5-6, 18), *W. smithii* are limited by the prey captured by their host. The number of prey captured by a leaf determines both the biomass of mosquitoes sustained in that leaf and the eventual pupation and emergence success of those mosquitoes (Fig. 17). Pitchers are not most effective at catching prey when they first open, but at a later time. Prey capture then peaks and declines so that older and the very youngest leaves catch few prey (Fig. 16). *W. smithii* appears to anticipate the build-up of leaf victims by selecting primarily the very youngest leaves for oviposition (Figs. 10, 16) and so maximizes the probability of future survivorship (Fig. 19).

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## REFERENCES

- Addicott, J. F. (1974). Predation and prey community structure: an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. *Ecology*, 55, 475-492.
- Bell, C. R. (1949). A cytotaxonomic study of the Sarraceniaceae of North America. *Journal of the Elisha Mitchell Scientific Society*, 65, 137-166.
- Bell, C. R. (1952). Natural hybrids in the genus *Sarracenia*. I. History distribution and taxonomy. *Journal of the Elisha Mitchell Scientific Society*, 68, 55-79.
- Bradshaw, W. E. (1980). Thermoperiodism and the thermal environment of the pitcher plant mosquito, *Wyeomyia smithii*. *Oecologia* (Berlin), 46, 13-17.
- Bradshaw, W. E. & Lounibos, L. P. (1972). Photoperiodic control of development in the pitcher-plant mosquito, *Wyeomyia smithii*. *Canadian Journal of Zoology*, 50, 713-719.
- Bradshaw, W. E. & Lounibos, L. P. (1977). Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. *Evolution*, 31, 546-567.
- Brower, J. H. & Brower, A. E. (1970). Notes on the history and distribution of moths associated with the pitcher-plant in Maine. *Proceedings of the Entomological Society of Ontario*, 101, 79-83.
- Buffington, J. D. (1970). Ecological considerations on the habitation of pitcher-plants by *Wyeomyia smithii* and *Metriocnemus knabi*. *Mosquito News*, 30, 89-90.
- Burgess, L. & Rempel, J. G. (1971). Collection of the pitcher-plant mosquito, *Wyeomyia smithii* (Diptera: Culicidae), from Saskatchewan. *Canadian Entomologist*, 103, 886-887.

- Cameron, C. J., Donald, G. O. & Paterson, C. G. (1977). Oxygen-fauna relations in the pitcher-plant *Sarracenia purpurea* L, with reference to the chironomid *Metriocnemus knabi* Coq. *Canadian Journal of Zoology*, 55, 2018-2023.
- Coluzzi, M., Di Deco, M. & Gironi, A. (1977). Influenza del fotoperiodo sulla scelta del luogo di ovideposizione in *Aedes mariaae* (Diptera, Culicidae). *Parassitologia*, 17, 121-130.
- Dodge, H. R. (1947). A new species of *Wyeomyia* from the pitcher-plant. *Proceedings of the Entomological Society of Washington*, 49, 117-122.
- Evans, K. (1971). The bionomics of *Wyeomyia smithii* (Coquillett), the pitcher-plant mosquito (Diptera: Culicidae: Sabethini). Unpublished M.Sc. Thesis, University of Manitoba.
- Evans, K. H. & Brust, R. A. (1972). Induction and termination of diapause in *Wyeomyia smithii* (Diptera: Culicidae), and larval survival studies at low and subzero temperatures. *Canadian Entomologist*, 104, 1937-1950.
- Fish, D. & Hall, D. W. (1978). Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher-plant, *Sarracenia purpurea*. *American Midland Naturalist*, 99, 172-183.
- Forsyth, A. B. & Robertson, R. J. (1975). K reproductive strategy and larval behavior of the pitcher-plant sarcophagid fly, *Blaesoxipha fletcheri*. *Canadian Journal of Zoology*, 53, 174-179.
- Frank, J. H. & Curtis, G. A. (1977). On the bionomics of bromeliad-inhabiting mosquitoes. IV. Egg mortality of *Wyeomyia vanduzeei* caused by rainfall. *Mosquito News*, 37, 239-245.
- Frank, J. H., Curtis, G. A. & Evans, H. T. (1977). On the bionomics of bromeliad-inhabiting mosquitoes. II. The relationship of bromeliad size and the number of immature *Wyeomyia vanduzeei* and *Wy. medioalbipes*. *Mosquito News*, 37, 180-192.
- Hegner, R. W. (1926). The protozoa of the pitcher-plant (*Sarracenia purpurea*). *Biological Bulletin*, 50, 271-276.
- Hepburn, J. S. & St. John, E. Q. (1927). A bacteriological study of the pitcher liquor of the Sarraceniaceae. *Transactions of the Wagner Free Institute of Science (Philadelphia)*, 11, 75-83.
- Hepburn, J. S., St. John, E. Q. & Jones, F. M. (1920). The absorption of nutrients and allied phenomena in the pitchers of the Sarraceniaceae. *Journal of the Franklin Institute*, 189, 147-184.
- Higley, W. K. (1885). The northern pitcher-plant or the side-saddle flower, *Sarracenia purpurea* L. *Bulletin of the Chicago Academy of Science*, 1, 41-55.
- Hudson, A. (1970). Notes on the piercing mouth parts of three species of mosquitoes (Diptera: Culicidae) viewed with the scanning electron microscope. *Canadian Entomologist*, 102, 501-509.
- Haufe, W. O. (1952). Observations on the biology of mosquitoes (Diptera: Culicidae) at Goose Bay, Labrador. *Canadian Entomologist*, 84, 254-263.
- Istock, C. A. (1978). Fitness variation in a natural population. *Evolution of Insect Migration and Diapause*. (Ed. by H. Dingle) pp. 171-190. Springer-Verlag, New York.
- Istock, C. A., Vavra, K. J. & Zimmer, H. (1976). Ecology and evolution of the pitcher-plant mosquito: 3. Resource tracking by a natural population. *Evolution*, 30, 548-557.
- Istock, C. A., Wasserman, S. S. & Zimmer, H. (1975). Ecology and evolution of the pitcher-plant mosquito: 1. Population dynamics and laboratory responses to food and population density. *Evolution*, 29, 296-312.

- Jones, F. M. (1921). Pitcher-plants and their moths. *Natural History*, 21, 296-316.
- Judd, W. W. (1959). Studies of the Byron Bog in southwestern Ontario. X. Inquilines and victims of the pitcher-plant, *Sarracenia purpurea* L. *Canadian Entomologist*, 91, 171-180.
- Kato, M. & Toriumi, M. (1951). Studies on the associative ecology of insects. IV. Synecological analysis of the larval association of mosquitoes in the bamboo thicket. *Science Reports of Tōhoku University, Fourth Series, Biology*, 19, 152-160.
- Kingsolver, J. G. (1979). Thermal and hydric aspects of environmental heterogeneity in the pitcher-plant mosquito. *Ecological Monographs*, 49, 357-376.
- Knab, F. (1905). A chironomid inhabitant of *Sarracenia purpurea*, *Metricnemus knabi* Coq. *Journal of the New York Entomological Society*, 13, 69-73.
- Kurihara, Y. (1957). Synecological analysis of the biotic community in microcosm. II. Studies on the relations of Diptera larvae to Protozoa in bamboo containers. *Science Reports of Tōhoku University, Fourth Series, Biology*, 23, 139-142.
- Kurihara, Y. (1958). Synecological analysis of the biotic community in microcosm. III. Studies on the relations of Diptera larvae to Protozoa in the containers made of bamboos of different ages. *Science Reports of Tōhoku University, Fourth Series, Biology*, 24, 15-21.
- Kurihara, Y. (1959a). Synecological analysis of the biotic community in microcosm. IV. Studies on the relations of Diptera larvae to pH in bamboo containers. *Science Reports of Tōhoku University, Fourth Series, Biology*, 25, 165-171.
- Kurihara, Y. (1959b). Synecological analysis of the biotic community in microcosm. VIII. Studies on the limiting factor in determining distribution of mosquito larvae in the polluted water of bamboo containers, with special reference to relation of larvae to bacteria. *Japanese Journal of Zoology*, 12, 391-400.
- Kurihara, Y. (1960). Biological analysis of the structure of microcosms, with special reference to the relations among biotic and abiotic factors. *Science Reports of Tōhoku University, Fourth Series, Biology*, 26, 269-296.
- Lane, J. (1953). *Neotropical Culicidae*. Univ. of Sao Paulo, Sao Paulo.
- Lang, J. T. (1978). Relationship of fecundity to the nutritional quality of larval and adult diets of *Wyeomyia smithii*. *Mosquito News*, 38, 396-403.
- Lloyd, M. (1967). "Mean Crowding." *Journal of Animal Ecology*, 36, 1-30.
- McDaniel, S. T. (1971). The genus *Sarracenia* (Sarraceniaceae). *Bulletin of Tall Timbers Research Station*, 9, 1-36.
- Maguire, B., Belk, D. & Wells, G. (1968). Control of community structure by mosquito larvae. *Ecology*, 49, 207-210.
- Matheson, R. (1944). *Handbook of the Mosquitoes of North America*. Comstock Publishing Company, Ithaca.
- Mœur, J. E. & Istock, C. A. (1980). Ecology and evolution of the pitcher plant mosquito. IV. Larval influence over adult reproductive performance and longevity. *Journal of Animal Ecology*, 49, 775-792.
- Mogi, M. & Mokry, J. (1980). Distribution of *Wyeomyia smithii* (Diptera, Culicidae) eggs in pitcher plants in Newfoundland, Canada. *Tropical Medicine*, 22, 1-12.

- O'Meara, G. F., Lounibos, L. P. & Brust, R. A. (1981). Repeated egg clutches without blood in the pitcher plant mosquito. *Annals of the Entomological Society of America*, 74, 68-72.
- Owen, W. B. (1937). The mosquitoes of Minnesota, with special reference to their biologies. *Technical Bulletin of the Minnesota Agricultural Experiment Station*, 126, 1-75.
- Paris, O. H. & Jenner, C. E. (1959). Photoperiodic control of diapause in the pitcher plant midge, *Metriocnemus knabi*. *Photoperiodism and Related Phenomena in Plants and Animals* (Ed. by R. B. Withrow), pp. 601-623, American Association for the Advancement of Science, Washington, D.C.
- Paterson, C. G. (1971). Overwintering ecology of the aquatic fauna associated with the pitcher plant, *Sarracenia purpurea* L. *Canadian Journal of Zoology*, 49, 1455-1459.
- Pittendrigh, C. S. (1950a). The quantitative evaluation of *Kerteszia* breeding grounds. *American Journal of Tropical Medicine*, 30, 457-468.
- Pittendrigh, C. S. (1950b). The ecoclimatic divergence of *Anopheles bellator* and *A. homunculus*. *Evolution*, 4, 43-63.
- Pittendrigh, C. S. (1950c). The ecotopic specialization of *Anopheles homunculus*; and its relation to competition with *A. bellator*. *Evolution*, 4, 64-78.
- Price, R. D. (1958). Notes on the biology and laboratory colonization of *Wyeomyia smithii* (Coquillett) (Diptera: Culicidae). *Canadian Entomologist*, 90, 473-478.
- Seifert, R. P. (1980). Mosquito fauna of *Heliconia aurea*. *Journal of Animal Ecology*, 49, 687-697.
- Smith, J. B. (1901). Some notes on the larval habits of *Culex pungens*. *Entomological News*, 12, 153-157.
- Smith, J. B. (1902). Life-history of *Aedes smithii* Coq. *Journal of the New York Entomological Society*, 10, 10-15.
- Smith, J. B. (1904). *Report of the New Jersey State Agricultural Experiment Station upon the mosquitoes occurring within the state, their habits, life histories, etc.* MacCrellish and Quigley, Trenton, New Jersey.
- Smith, S. M. & Brust, R. A. (1971). Photoperiodic control of maintenance and termination of larval diapause in *Wyeomyia smithii* (Coq.) (Diptera: Culicidae) with notes on oogenesis in the adult female. *Canadian Journal of Zoology*, 49, 1065-1073.
- Stone, A., Knight, K. L. & Starke, H. (1959). *A Synoptic Catalog of the Mosquitoes of the World (Diptera, Culicidae)*. Entomological Society of America, Washington, D. C.
- Wray, D. L. & Brimley, C. S. (1943). The insect inquilines and victims of pitcher-plants in North Carolina. *Annals of the Entomological Society of America*, 36, 128-137.