

The Population Dynamics of
Wyeomyia smithii (Coq.)
(The Pitcher Plant Mosquito)
in Manitoba
and Northwestern Ontario

A Thesis
Submitted to the Faculty
of
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Martha Judit Farkas

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MARTHA JUDIT FARKAS

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ABSTRACT

The phenology of development in Wyeomyia smithii (Coq.) within the water-filled leaves of Sarracenia purpurea L. (the purple pitcher plant) was studied in bogs near The Pas and Patricia Beach, in Manitoba, and near Kenora, in Northwestern Ontario. Collections of eggs, larvae and pupae were made from 1982 to 1984 at Patricia Beach; eggs, larvae and pupae were collected at The Pas and Kenora only during 1983.

The phenology of W. smithii at the three locations was very similar. Overwintered larvae developed into adults by early July. Females laid eggs in newly opened leaves, as well as in the previous year's leaves. The largest portion of the resultant larvae entered a third instar diapause by mid-August, and remained in this instar until the following spring. A small percentage of the larvae reached the fourth instar at each site, and may have given rise to a second generation by the end of August.

Pitcher plant leaf size was found to be correlated with larval density.

Pupation rates as well as adult size and fecundity were not found to vary significantly among sites. There was a trend towards smaller and less fecund individuals as the season progressed.

Overwintering survival was low at Patricia Beach but relatively high at The Pas during the winter of 1983-1984.

A larval diet supplement added to pitcher plant leaves was found to hasten the rate of development of the contained larvae, as well as produce larger and more fecund adults.

FOREWORD

The format followed for this thesis is that of manuscript style. None of the manuscripts have been published, but they will be submitted for publication at a later date.

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INTRODUCTION

Sarracenia purpurea L., the purple pitcher plant, can be found growing primarily in glacial peat bogs, and may reach densities of nearly 7,500/ha. in the northeastern United States (Fish 1983).

It is an unusual plant in that it is carnivorous, primarily insectivorous. Insects are attracted to the pitcher-shaped leaves in order to feed on the secreted nectar. After having been directed by downward-pointing hairs onto a slippery inner surface, the insects slip and drown in the pitcher fluid. They are digested by plant-secreted proteolytic enzymes as well as by bacterial action (Fish and Hall 1978). The plants can survive without the nutrients derived from the decomposition of their insect victims, however their growth is enhanced in the presence of this nutrient supplement (Paterson and Cameron 1982). Amino acids, peptides and other nutrients from the insects are absorbed and utilized directly by the pitcher plant leaf (Fish and Hall 1978). Nitrogen derived from insect victims helps the plants to survive in nitrogen-deficient environments (Brower and Brower 1970).

Within the pitcher are a variety of symbiotic organisms that subsist on the pitcher plant's prey. Bacteria, rotifers, nematodes, copepods, mites and dipterous larvae inhabit the leaf fluid (Fish and Hall 1978). The pitcher's victims function as a food source for such organisms either

by being fed upon directly or else by acting as a substrate for microbial growth (Paterson 1971). My thesis research was directed at learning more about a dipterous inhabitant of the pitcher plant, Wyeomyia smithii (Coq.) (Diptera: Culicidae).

Studies on the population dynamics of W. smithii were carried out in what appear to be discrete bogs at three different sites: north of The Pas, Manitoba; east of Patricia Beach, Manitoba; and southeast of Kenora, in northwestern Ontario (Fig. 1). Although it is not known how long these three populations of Wyeomyia have been separated, the study was undertaken to determine whether isolation had acted on the populations to the extent that some of the life history parameters examined would show differences.

The effect of larval diet supplement on W. smithii development, i.e. on the rate of pupation and on adult size and fecundity, was investigated. It is known that 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 (Bradshaw 1983). In this study, an attempt was made to determine how the natural food supply within pitcher plants compared to a supplemented diet in terms of augmenting development.

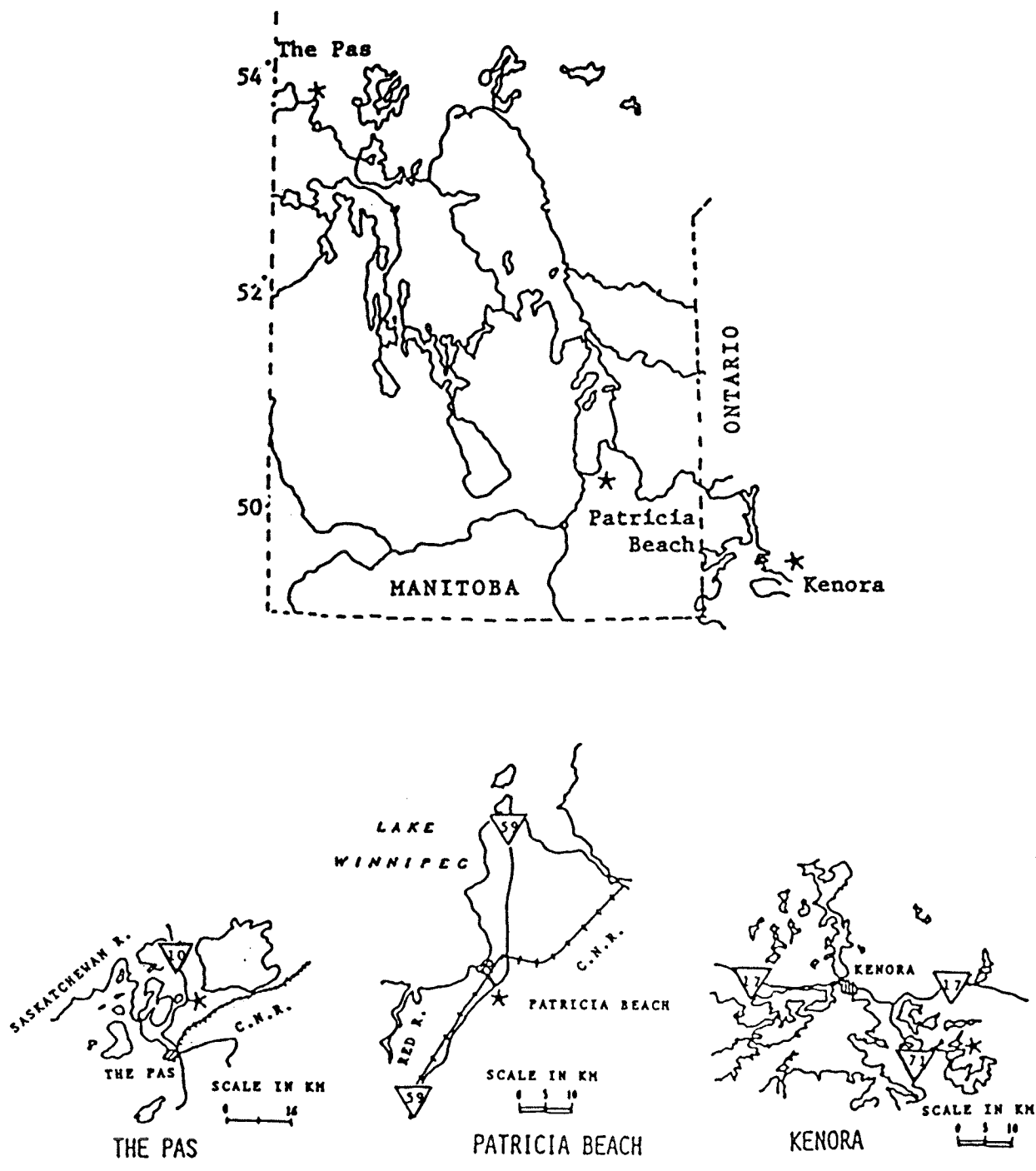


Fig. 1 Location of sampling sites (modified from Wiens, 1972).

LITERATURE REVIEW

The genus Wyeomyia belongs to a closely-knit tribe of mosquitoes called the Sabethini, which are primarily tropical in distribution. Its species are restricted almost entirely to container-type breeding places such as water in the axils of bromeliad leaves or in pitcher plants. The American Sabethini have evolved almost entirely within the tropical region. W. smithii arose from a tropical species that became sub-tropical and temperate as it spread into eastern North America (Ross 1964).

W. smithii was first designated as a new species in the genus Aedes by Coquillett (1901). It was named after Professor J.B. Smith, who provided the material for the taxonomic study. By 1904, it was placed in the genus Wyeomyia (Smith 1904).

Dodge (1947) described a new species of Wyeomyia which he named W. haynei. The larval characteristics of W. haynei, which were thought to distinguish it from W. smithii were: the presence of a small pair of dorsal anal gills; more numerous comb scales; and mesothoracic hair 13 equal to or smaller than prothoracic hair 13. In the adult, the presence of a patch of silvery scales on the scutellum in W. haynei were thought to distinguish it from W. smithii, which has dark scales. However, from its northern range in Canada to its southern range near the Gulf of Mexico, the obvious gradation of morphological as well as physiological

characters (e.g. anal papillae length, photoperiodic response, blood feeding habits, egg laying patterns) and reproductive success between geographically separated populations of the pitcher plant mosquito, indicate that there is only one species, viz, W. smithii (Bradshaw and Lounibos 1977). In this literature review, W. haynei will be referred to as southern W. smithii.

Distribution

W. smithii spends its egg, larval and pupal stages in the fluid held by the leaves of Sarracenia purpurea L., the purple pitcher plant (Istock et al. 1975; Goins and Folkerts 1976; Kingsolver 1979; Barton and Smith 1984). Its range is therefore limited by the distribution of S. purpurea. The distribution of this plant (Fig. 1) extends into northern Alberta and British Columbia (Cody and Talbot 1973), however W. smithii has not yet been recorded from these provinces. W. smithii has been reported from the following areas: Alabama (Goins and Folkerts 1976; Lounibos et al. 1982); Florida (Bradshaw 1980; O'Meara et al. 1981); Georgia (Darsie and Williams 1976); South Carolina (Weathersbee and Arnold 1948); North Carolina (Wray and Brimley 1943; Paris and Jenner 1959; Bradshaw 1980); Indiana (Siverly 1963); Ohio (Lang 1978); New York (Dodge 1947; Istock et al. 1975; Guirgis and Sanzone 1978; Bradshaw 1980); Minnesota (Price 1958); Michigan (Kingsolver 1979); New Jersey (Coquillett 1901; Dodge 1947; Coyne and Hagman 1970; Bradshaw and

Phillips 1980); Connecticut (Wallis and Frempong-Boadu 1967); Massachusetts (Lounibos and Bradshaw 1975; O'Meara et al. 1981); Wisconsin (Dodge 1947); Maryland (Paris and Jenner 1959; Bickley and Mallack 1978); Newfoundland (Haufe 1952; Mogi and Mokry 1980); Nova Scotia (Lewis and Bennett 1979); New Brunswick (Paterson 1971; Lewis and Bennett 1979); Quebec (Swales 1972; Maire and Aubin 1976); Ontario (Dodge 1947; Judd 1959; Smith and Brust 1971); Manitoba (Evans and Brust 1972) and Saskatchewan (Burgess and Rempel 1971). To summarize, W. smithii ranges south to north from the Gulf of Mexico, along the east coast United States into Canada, and east to west from Newfoundland to Saskatchewan. This corresponds to a distribution which extends from 30° N latitude in the southeastern United States to approximately 55° N in Manitoba (Bradshaw and Louinbos 1977).

At more southerly latitudes, various Sarracenia species other than S. purpurea overlap in their ranges and in their general habitat. In these areas, W. smithii is found in S. flava. However, these plants tend not to have standing water in the summer and the leaves senesce and die in the winter. Consequently, they do not provide a secure habitat for overwintering larvae. W. smithii is also found in hybrids between S. purpurea and the following: S. flava, S. leucophylla, S. rubra, and S. alata. The leaves of these plants contain standing water during the summer and a number of the leaves remain alive during the winter. It is possible that W. smithii overwinters in these leaves (Bradshaw 1983).

W. smithii must vacate overwintered leaves before the next growing season ends in order to survive. Since the total number of pitcher plants at a particular site remains relatively constant from year to year, and host-plant populations are restricted to discrete glacial peat bogs in the northern part of W. smithii's range, this mosquito must be adapted to colonize new leaves of the same plants year after year. Such an existence is in sharp contrast to that of mosquitoes which colonize ground pools of unpredictable occurrence and duration (Fish 1983).

Life History

Egg: The eggs of W. smithii are laid on the water surface or on the moist inner surface of pitchers (Evans 1971; Istock et al. 1975; Goins 1977)

A water soluble chemical from the plant tissues acts as an attractant to female W. smithii seeking ovipositional sites. A complete characterization of the substance is not yet available (Istock et al. 1975, 1983). In early spring and late summer, the adults preferentially select younger pitchers for ovipositional sites (Evans 1971; Istock et al. 1975, 1983; Kingsolver 1979; Mogi and Mokry 1980).

Since older leaves are less attractive to ovipositing mosquitoes, it is likely that the production or concentration of the chemical within the leaf tissue declines with increasing age of the leaf (Istock et al. 1983). This ovipositional bias is advantageous, since

brittleness and the probability of breaking and draining increase with the age of a pitcher (Istock *et al.* 1975). Old pitchers are distinguishable from new ones by evidence of winter frost damage on their surfaces (Mogi and Mokry 1980; personal observation).

W. smithii ovipositing in response to a specific chemical cue emanating directly from the habitat is a departure from ovipositional strategies known for species that occupy other aquatic habitats (Fish 1983). Aedes atropalpus (Coq.) (Kaipage and Brust 1973) and Culex tarsalis Coq. (Hudson and McLintock 1967) oviposit in pools where the attractant is provided by the medium in which larvae and pupae develop. A. aegypti (L.) and C. pipiens quinquefaciatus Say oviposit in response to bacterial excretory products which are indicators of larval food resources (Hazard *et al.* 1967). Ovipositional cues produced by existing or past resources would clearly be unsuitable for W. smithii for two reasons. Their habitat usually exists for only a single generation, and oviposition occurs before food resources become available (Fish 1983).

A positive correlation was found between the number of eggs laid and pitcher plant leaf size (Evans 1971; Paterson 1971). Eggs may be laid singly, or in small groups but it is evident that only a portion of a female's eggs are laid at a time (Evans 1971; Mogi and Mokry 1980; Bradshaw 1983). The ecological significance of such ovipositional behaviour for mosquitoes which breed in small container habitats may be

that it lessens the risk of placing eggs in leaves that may not collect rain water, as well as decreases intraspecific competition (Mogi and Mokry 1980).

It has been suggested by Bradshaw (1983) that individual W. smithii are able to distinguish leaves in which they have oviposited. In order to do so, they would need to rely on a marker, which signals that a leaf has recently been visited, or it would require that females remember the leaves into which they have oviposited. If either mechanism exists, it is likely that it is of short term duration, since under laboratory conditions, females may oviposit into the same leaf on more than one occasion.

Larva: The eggs of W. smithii hatch and first instar larvae begin to appear in pitcher plant leaves in late June and early July in the northern part of their range (Judd 1959; Evans 1971). First and second instars occur throughout July and early August, but third instars are predominant from the beginning of August (Evans 1971). In northern latitudes, W. smithii larvae enter diapause in the third instar and overwinter in the leaves of S. purpurea, frozen in a core of ice (Smith and Brust 1971), while southern W. smithii diapause in the fourth instar (Bradshaw and Lounibus 1977). This topic will be dealt with in more detail under the headings of diapause and overwintering mechanism.

The first, second and third larval instars of northern W. smithii each last three to four days (at 25° C) under

long-day conditions in the laboratory. The length of the fourth instar is about twice as long, and is thought to be needed to accumulate sufficient protein and lipid to ensure adequate reserves to produce yolk for the ovarian follicles of the adult female. Diapause by the third instar probably relates to trophic considerations, since this phenomenon postpones the fourth instar stage until the spring (Bradshaw and Lounibos 1972). Overwintered third instar larvae resume development in the spring as soon as temperatures exceed 15° C (Evans 1971). Mean temperatures are sufficiently high by the end of May to allow for uninterrupted development (Evans 1971, personal observation). Towards the end of June and during July, the majority of larvae moult to the pupal stage and begin to emerge as adults. These adults oviposit primarily into newly opened pitcher plant leaves, and the eggs give rise to a new generation of larvae. By late summer the majority of these individuals are in the third instar (resulting in a primarily univoltine population), however, a small percentage of the population can go beyond this stage and become imagoes. These individuals may contribute to a second generation if conditions are favorable (Evans 1971). In the case of more southern populations (e.g. Alabama), several generations occur during a season (Goins and Folkerts 1976).

W. smithii larvae feed by filtering particles arising from the decomposition of insects and other arthropods which fall into the pitchers. They probably also ingest protozoa,

bacteria, and suspended particulate material (Addicott 1974; Istock et al. 1975; Goins and Folkerts 1976; Fish and Hall 1978; Bradshaw 1983). There is a time lag in the field of several days between maximum insect capture by the newly opened leaves, and maximum egg hatch of W. smithii larvae. This delay would allow for bacterial and enzymatic factors to act on the captured prey of the pitcher, providing particulate matter for the young larvae (Fish and Hall 1978). Both the quantity and quality of larval diet has a significant effect on larval development, adult fecundity and adult longevity. In laboratory studies, it was found that those larvae reared on TetraMin[®] (a commercially available fish food) or on a TetraMin[®]-dog food combination, developed faster and ultimately yielded adults that lived longer and produced more eggs. It is probable that the high protein content of these diets produced such developmental patterns (Lillie and Nakasone 1982).

Smith (1904) noted that only rarely did a W. smithii larva come up to the water surface to breathe through its siphon. Evans (1971) concluded that the early instars, which primarily exhibit this behavior, must be respiring cutaneously. The large tracheated anal papillae are also used for respiration. Third instar larvae are capable of surviving under a film of oil for eight days without any significant mortality. The oxygen concentration of the medium probably dictates which method of respiration will be used. During June and July, fourth instar larvae spend the

majority of their time at the surface where direct contact is made with the air. At this time of year, the dissolved oxygen content of the water is lower due to higher temperatures. Early instars also spend more time at the surface when temperatures are high.

One piece of evidence which suggests that W. smithii has spread out in a northerly direction is the gradation of anal papillae phenotypes. The two other North American species of Wyeomyia; W. mitchelli and W. vanduzeei, and the southern, Gulf Coast of Mexico population of W. smithii, all have four long anal papillae of nearly equal length, and this is considered to be the primitive condition. As one proceeds farther north, the change in papillae length in W. smithii at first manifests itself as two long ventral and two short dorsal papillae, and further north, simply as two bulbous ventral papillae. When a northern population (two papillae phenotype) is crossed with the Gulf Coast population (four papillae phenotype) the F_1 hybrid will exhibit a papillary phenotype which is intermediate, and therefore reflects the relative equivalent latitudes of the parents. With regard to its physiology, since W. smithii larvae do not have to surface to respire, they can use their anal papillae as a respiratory surface. The reduction in the number and size of anal papillae may therefore reflect the increasing amount of dissolved oxygen available in the leaves of S. purpurea at more northerly (or southerly montane) areas (Bradshaw and Lounibos 1977).

Pupa: The pupal stage lasts approximately 6 days at 27° C (Evans 1971). In the field, the pupal period is more variable, since this time interval is inversely proportional to temperature (Clements 1963). In northern areas, pupae occur from late May and continue to appear throughout the summer, and may be found as late as early September (Judd 1959; Evans 1971). In the more southern parts of its range (e.g. Alabama), pupae occur in all but the coldest months (i.e. November, December) (Goins 1977).

Adult: In Ontario and Manitoba, adults are prevalent during July and August, although they can be found in the field from approximately the end of June to about mid-September (Evans 1971). More southern regions (e.g. Alabama) have adults present throughout the warmer portions of the year (i.e. March-October) (Goins 1977). Adults are most active during the daylight hours, with activity peaking in the afternoon (Evans 1971; Goins 1977). W. smithii adults are poor fliers, therefore a large portion of their time is spent resting within the hood of the pitcher plant, or hovering nearby (Wallis and Frempong-Boadu 1967; Evans 1971; Goins 1977). Copulation has only been observed in resting individuals. Under field conditions, mating has been observed to occur within the mouth of the pitcher plant (Evans 1971).

All W. smithii are autogenous for the first ovarian

cycle, whereas southern W. smithii may take blood for the second and subsequent ovarian cycles (Bradshaw 1980).

W. smithii will ingest honey (Smith and Brust 1971; Bradshaw and Lounibos 1972); fluid of hydrated raisins (Price 1958; Istock et al. 1975); fluid of hydrated apple slices (Evans and Brust 1972) or a sucrose solution (personal observation). Adults may feed on plant juices in nature, however laboratory studies have shown that they do not require such food to produce eggs (Istock et al. 1975). However, the longevity of carbohydrate-fed adults was greater than that of adults maintained without a carbohydrate source (Price 1958; Smith and Brust 1971; Lang 1978; Lillie and Nakasone 1982).

Ovarian Development and Bloodfeeding Pattern

W. smithii females are receptive to insemination as early as 0.5 hours after eclosion. Over 50% of all females tested were inseminated within the first four hours after emergence. In the field, male W. smithii hover around pitcher plants, probably to enhance their chances of encountering newly emerged and sexually receptive females (O'Meara and Lounibos 1981).

Autogeny for the first ovarian cycle occurs among all populations of W. smithii (Smith and Brust 1971; Bradshaw 1980; O'Meara and Lounibos 1981; O'Meara et al. 1981), but females from northern populations also have some degree of ovarian precocity (Smith and Brust 1971; O'Meara and

Lounibos 1981). Early reproductive maturation by advanced ovarian development at the time of adult eclosion is caused by an early release of juvenile hormone during the pupal stage. This mediates an early release of a gonotrophic factor from the head (O'Meara and Lounibos 1981).

The stylets of northern W. smithii appear to be functional (Hudson 1970), despite the fact that they are not used for hematophagy (Smith and Brust 1971; Bradshaw 1980; O'Meara and Lounibos 1981; O'Meara et al. 1981; Lounibos et al. 1982). These bloodfeeding habits support the theory that the range of W. smithii in North America has been extended from the south to the north. Southern W. smithii normally defer bloodfeeding until after the initial egg clutch has been deposited. Northern W. smithii have carried this trend to the extreme by not blood-feeding at all (Bradshaw 1980). Obligatory autogeny throughout the life of a female has been found to occur in populations north of and including New Jersey, i.e. greater than 40° N latitude (O'Meara and Lounibos 1981).

Southern W. smithii has been observed feeding on a wide variety of vertebrates including humans and turtles. Although autogeny for the first (or only) ovarian cycle is usually associated with the absence of suitable hosts, it is unlikely that this is the case in southern W. smithii.

The adaptive significance of bloodfeeding within this species probably relates to the different life history tactics of northern and southern W. smithii. The warmer

temperatures which exist in the more southerly part of the range of W. smithii lead to greater crowding which could result in smaller adults and lower fecundity. Northern W. smithii larvae live in habitats in which they develop relatively free from density-dependent constraints during the summer (see section on factors influencing larval development). Increasing fitness by blood-feeding in these large, relatively well nourished adults would be offset by the potential dangers of predation, desiccation etc., encountered while searching for and digesting a blood meal. Among southern W. smithii, crowding and/or warmer temperatures may result in nutritionally impoverished adults. In this case, hematophagy would increase the contribution to total reproductive effort made by the second and subsequent ovarian cycles. This is provided that adult W. smithii are able to extend the time over which they can exploit potential oviposition sites (Bradshaw 1980). Therefore, as W. smithii was expanding its range northward, stronger seasonal influences temporarily relieved the larvae of stress due to crowding. This led to the evolution of a strain of W. smithii which was wholly dependent on larval reserves for egg production (Lounibos et al. 1982).

Egg laying patterns of W. smithii also vary depending on the geographical origin of the mosquito. Individual females of southern (e.g. Florida) populations were found to initiate and complete all oviposition of their first

autogenous egg clutch within 3 days, with the majority of females laying their entire egg clutch within a 24 to 48 hour period. However, individual females from northern regions (e.g. Massachusetts) oviposited periodically during 10-11 days of observation. Each female deposited 3-5 egg clutches, separated by intervals of 1-3 days. The initial egg clutch (assumed to be represented by the first 1-3 days of oviposition) was the largest and averaged 64 eggs per female, and was not significantly different from the mean number of eggs (65) matured by females of the Florida strain in their first egg clutch. The cyclic ovipositional pattern observed in northern females is probably due to repeated ovarian developmental cycles. This conclusion was based on the following evidence: 1) females which had completed the deposition of their egg clutch during the previous 24 hours had ovaries which were only in the early stages of development; 2) ovipositing Massachusetts females were more fecund than Florida females, whereas those individuals which were not permitted to oviposit had the same level of fecundity as those from Florida. Florida females denied blood matured the same number of eggs whether allowed to oviposit or not. Egg retention apparently inhibited additional autogenous egg production in Massachusetts females; 3) Massachusetts females produced significantly more eggs (82) than they had ovarioles (67). Therefore some ovarioles in these females must have matured at least 2 eggs; 4) The maximum number of dilations in the pedicel of

individual ovarioles never exceeded and was usually equivalent to the number of egg clutches deposited. This was observed in both the northern strains of W. smithii (no blood-meal required) as well as in southern strains (blood-meal required) (O'Meara et al. 1981).

To summarize, geographical variation occurs in both blood feeding behavior and ovarian development. Northern W. smithii eclose with ovaries at an advanced stage of development and produce repeated egg clutches without blood-feeding (Smith and Brust 1971; O'Meara et al. 1981). Southern W. smithii emerge with undeveloped ovaries and produce only one egg clutch autogenously, with subsequent ovarian development dependent on bloodfeeding. Under natural conditions, resources may be less abundant and southern W. smithii may then consume blood for the second and subsequent ovarian cycle as well (Bradshaw 1980; O'Meara and Lounibos 1981; Lounibos et al. 1982)

Factors Influencing Larval Development

It has been suggested that a population of pitcher plant mosquitoes in a New York bog experienced an alternation of density-dependent and density-independent selection within the same season. The periods of density-dependence occurred in the spring and late fall, while density-independence occurred during the summer months when food was abundant. (Istock et al. 1976a). Life history phenotypes may range from fast-developing,

diapause-resisting, multivoltine forms, to slow-developing diapause-prone, univoltine types (Istock et al. 1976b). Since two major peaks of pupation existed within the population, the second pupal pulse could represent the univoltine types. This may reduce competition between the univoltine forms and the faster developing, multivoltine forms. A release from competition would confer a high reproductive potential to these slow-developing individuals despite the possible disadvantage of the univoltine modality. The seasonal separation of univoltine and multivoltine types may be due to the differential responses of individual larvae to diapause-terminating photoperiods (Istock et al. 1976a).

During the fourth instar, larvae accumulate a nutrient and energy reserve. Under conditions of food stress, a significant flexibility in the duration of this instar occurs, and is not observed in any other part of the life cycle. This flexibility increases the chances that an individual will store sufficient larval reserves in order to achieve adequate egg production as adults. Different larvae under food stress compensate to different degrees. Although pupal weight differences can be correlated with the duration of this last instar, they tend to have comparable fecundity. The consequence of prolonging the fourth larval instar is that the age of first reproduction is delayed (Moer and Istock 1980).

W. smithii live within the fluid of pitcher plant

leaves which may be subject to evaporation, and some degree of drought resistance is probably required. Bick and Penn (1947) have shown that W. smithii larvae are able to survive continuous drought for 192 hours. Periodic flooding for 30 minutes at 24 hour intervals was of no obvious benefit to W. smithii survival under dry conditions. This is contrary to what one would expect since periodic flooding would be thought to simulate slight rainfall fluctuations which would presumably help larval survival. Perhaps longer durations of flooding are necessary to confer survival value to the larvae.

In a Michigan bog, it was found that those pitchers existing in the shade had a cooler and less water-stressed microclimate than did those plants growing in the sun. Within these latter pitchers, fluid temperatures were elevated, causing W. smithii larvae to develop at a faster rate. A proportion of these mosquitoes were bivoltine, while shade-mosquitoes were exclusively univoltine. Despite such differences in generation times, sun and shade mosquitoes apparently had a similar mean fitness. Differential voltinism was balanced by increased mortality in those pitchers growing in the sun, since the probability of desiccation is higher (Kingsolver 1979).

Diapause

The more northern pitcher plant mosquitoes undergo a seasonal developmental arrest or diapause in the third

instar. This diapause is evoked and maintained by a short-day photoperiod and is averted or terminated by long days (Smith and Brust 1971; Bradshaw and Lounibos 1972, 1977; Evans and Brust 1972; Bradshaw 1976). Smith and Brust (1971) found that larval head capsule widths were good indicators of instar stage. This criterion was used to determine if diapause occurred while in the third instar.

The onset and termination of dormancy in W. smithii is a function of photoperiod and largely independent of temperature, since short days induce diapause at high as well as at low temperatures. Also, percent development (non-diapause) in third instar larvae increases with photoperiod regardless of temperature (Evans and Brust 1972; Bradshaw and Phillips 1980).

Under conditions of 12 hours light and 12 hours dark (12L:12D), diapause is induced in third instar W. smithii larvae when the eggs and subsequent first and second instar are kept at constant temperatures. However, some third instar larvae (2-3%) will moult to fourth instar, but only after 80-90 days (Evans and Brust 1972).

W. smithii relies upon photoperiodic cues for controlling not only a developmental arrest in the third instar, but the duration of the second instar as well. Long days promote rapid development in the second instar and prevent the onset of diapause while short days prolong development in potentially diapausing larvae. This was determined by exposing adults, as well as subsequent

progeny, to either short day conditions (12L:12D) or long day conditions (17L:7D). The duration of the egg stage and the first instar larvae was unaffected by daylength. However, if larvae were reared under the 12L:12D situation, the duration of the second instar stage was twice as long as that found with larvae reared under long day conditions. It is proposed that this prolongation of the pre-diapausing second instar is to allow for the necessary physiological adjustments before overwintering for several months in the frozen ice core of the pitcher. The extended second instar may also be a means of confirming seasonal cues provided by the changing environmental photoperiod. Cloud cover could cause an otherwise long day to appear shorter, and during daylengths which are close to the critical photoperiod, misdirection of development could occur. However, the longer duration of the second instar permits a truer assessment of the environment, that is, it ascertains whether daily illumination is increasing or decreasing (Bradshaw and Lounibos 1972).

Termination of diapause has been shown to depend on long daylengths. In laboratory studies on larvae from Massachusetts, 2 or more long days were required to terminate diapause in all individuals. Diapause was terminated in over 50% of the sample after 3 long days, and 100% after 4 or more long days (Bradshaw and Lounibos 1972). Growth of larvae is evident only a few days after transfer to long photoperiods (Smith and Brust 1971; Bradshaw and

Lounibos 1972).

Diapausing larvae which have been exposed to several long day cycles cannot be induced to reenter diapause if they are subsequently exposed to a short day regime. It is evident that although the photoperiodically maintained diapause is stable under short-day conditions, it is of a weak nature since it rapidly breaks down under long day regimes (Smith and Brust 1971).

Larvae which have overwintered for several months come out of diapause at the same long-day photoperiod which was required to terminate diapause in larvae which had only just begun to overwinter. Since photoperiod can maintain as well as break diapause, it probably helps to synchronize the seasonal cycles of W. smithii. However, in the more northern extension of its range (e.g. Kenora, Ontario) the critical photoperiod required to break diapause is not attained until late April (Smith and Brust 1971). Due to the low temperatures at this time of year, it is probable that temperature rather than photoperiod limits the rate of development in the spring (Smith and Brust 1971; Evans and Brust 1972).

The intensity of dormancy can also be correlated with latitude. Northern third instar larvae enter a strong diapause, i.e. three long days are required to terminate diapause in 50% of a sample population. As one proceeds southward the number of long days required to terminate diapause decreases to one long day and beyond this point,

larvae no longer diapause as third instars, but enter a strong fourth instar diapause. The strength of the diapause in the fourth instar continues to decline as one proceeds farther south (Bradshaw and Lounibos 1977).

Overwintering Mechanism

It is unlikely that overwintering third instar larvae freeze even when encased in ice for 6-7 months. The phenomenon of freezing point depression in larvae probably keeps them from freezing in nature (Evans and Brust 1972). Sufficient snow cover can provide enough insulation to keep the temperature within the spagnum (where pitcher plants grow) fairly constant and only slightly below freezing even during the coldest of winter months (Paterson 1971; Smith and Brust 1971; Evans and Brust 1972).

Larvae cannot survive sustained subzero temperatures for more than a few months. Likewise, they are unable to resist freezing at temperatures much below -5°C . In those areas where ground temperatures remain near 0°C all winter, it is likely that many larvae never freeze (Evans and Brust 1972).

The examination of dead larvae retrieved from winter pitcher samples in New Brunswick revealed that most of these individuals had food in the intestinal tract. All living larvae had empty guts. W. smithii stop feeding and void their gut contents before the pitcher content freezes. If retained, the gut contents serve as a major site for ice

crystal formation in the overwintering larvae, and therefore contribute to their death (Paterson 1971).

Cohabitants of Pitcher Plant Leaves

Along with W. smithii, representatives from two other dipteran families are found to be obligatorily associated with the pitcher plant. Metriocnemus knabi Coq. (Chironomidae) is dependent on the fluid filled pitcher leaves of S. purpurea for ovipositional and developmental sites (Wiens 1972). In addition, Blaesoxipha fletcheri (Aldrich) and Sarcophaga sarraceniae Riley (Sarcophagidae) also undergo larval development within the fluid of pitcher plant leaves (personal observation).

Competition among these coexisting organisms is minimized by resource partitioning (Fish and Hall 1978; Bradshaw 1983). A floating insect may be directly attacked by the sarcophagid. If the prey drowns and settles to the bottom, it is fed upon by M. knabi. Both organisms act as macro-decomposers in the system. This spatial distribution in the leaf minimizes interaction (Buffington 1970; Bradshaw 1983). Spatial segregation is also facilitated by differences in the respiratory mechanisms. Sarcophagids are almost entirely restricted to the surface of the pitcher plant fluid since they must breathe through their posterior spiracles (Fish and Hall 1978). W. smithii larvae may also surface periodically to breathe through their posterior spiracles, but they are also capable of respiring

cutaneously (Evans 1971). M. Knabi larvae remain submerged since they extract their oxygen directly from the water (Fish and Hall 1978).

As a result of the macro-decomposers, increased surface area of the victim becomes available to the bacteria, which are considered to be the micro-decomposers of the system. Bacteria are ingested by protozoans which are then fed upon by W. smithii larvae (Bradshaw 1983). Rotifers are also ingested by larvae (Addicott 1974). W. smithii may therefore feed on prey directly by consuming particulate material generated by macro-decomposer action or indirectly by feeding on micro-flora and fauna (Bradshaw 1983).

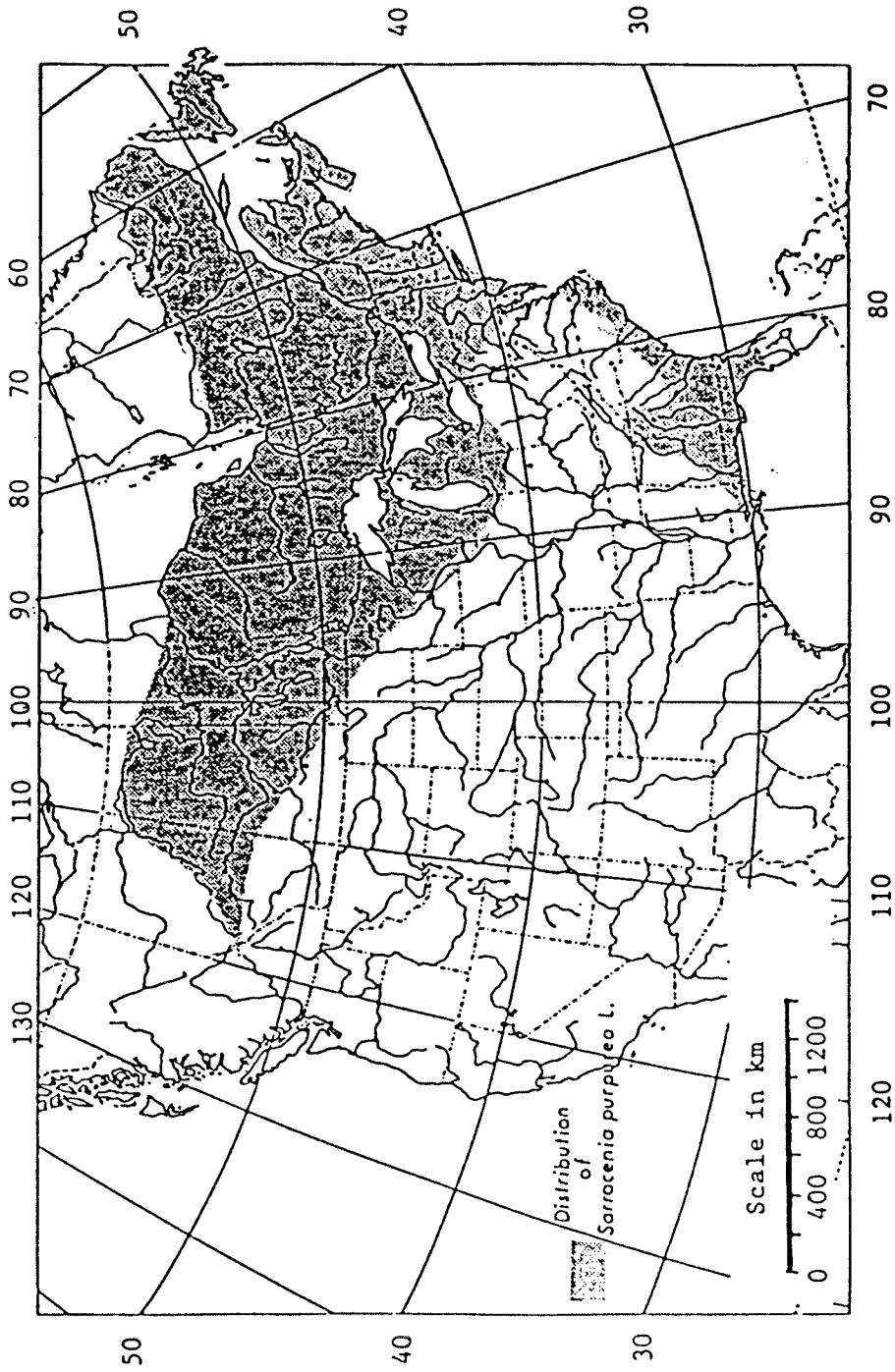


Fig. 1 Distribution of *Sarracenia purpurea* in North America (Evans, 1971)

Aspects of the Population Dynamics
of Wyeomyia smithii (Coq.)
(the Pitcher Plant Mosquito)
in Manitoba and Northwestern Ontario

INTRODUCTION

Wyeomyia smithii (Coq.) spends the egg, larval and pupal stages of its development in the fluid held by the leaves of Sarracenia purpurea L., the purple pitcher plant (Istock et al. 1975; Goins and Folkerts 1976; Kingsolver 1979). W. smithii has a distribution which extends from 30° N latitude in the southern United States, to near 55° N latitude in Manitoba (Bradshaw and Lounibos 1977).

Certain characteristics have been found to vary over the geographic range of this species. Four anal papillae exist in southern forms while only two occur in northern populations (Bradshaw and Lounibos 1977). Bloodfeeding patterns, ovarian development, and egg laying patterns also differ between southern and northern strains (Smith and Brust 1971; O'Meara and Lounibos 1981; O'Meara et al. 1981). In addition, southern populations diapause in the fourth instar, while northern forms overwinter as third instar larvae (Bradshaw and Lounibos 1977).

The purpose of my study was to learn more about the population dynamics of W. smithii in Manitoba and northwestern Ontario. All studies were carried out at three different sites: north of The Pas, Manitoba (approximately 54° N latitude); east of Patricia Beach, Manitoba (approximately 50° N latitude), and southeast of Kenora (approximately 50° N latitude), in northwestern Ontario.

The populations of W. smithii at the three sites occur

in what appear to be discrete bogs. One objective of the study was to determine whether isolation has affected the populations to the extent that some of the life history parameters examined would show differences among sites.

MATERIALS AND METHODS

In 1983, all three sites were monitored weekly or biweekly. In 1982 and 1984, only the Patricia Beach site was visited regularly to obtain data for the life history pattern study.

Life History Pattern

The general life history pattern of W. smithii was examined with respect to the two categories of pitcher plant leaves which exist in the bog. The distinction between the two types is made on the basis of age. One-year old pitcher plant leaves are those which formed the previous summer and have persisted into the next year. These leaf types are critical to the survival of W. smithii since it is in these leaves that the species overwinters as larvae. The other category consists of the new leaves i.e. the current year's growth.

The method by which the life history pattern of this insect was monitored consisted of randomly collecting 30 or more leaves of each age type at regular intervals. Old leaves were collected from April/May to August/September while new leaves were collected from July until August/September.

At all three sites, one or two leaves were removed from a rosette making sure that a full range of leaf sizes was obtained. This was done for both old and new leaves. The

leaves were examined in the laboratory for the various developmental stages of W. smithii. The volume of each pitcher leaf collected was determined by measuring how much water it could hold.

Comparison of Pupation Rates, Adult Size and Fecundity among Sites

Fifty, one-year old leaves at Patricia Beach, forty-six leaves at Kenora, and sixty-two leaves at The Pas were tagged and closely monitored throughout the sampling season. Only those leaves with ten or more larvae were tagged, using surveyor's tape. The total number of larvae occurring within each of the tagged leaves was recorded. Leaf tagging took place within a 1-2 km² area at all three sites.

Kenora and The Pas were monitored biweekly while Patricia Beach was visited every week, due to its close proximity to the University of Manitoba. Each time a site was visited, the contents of the tagged leaves were removed with a turkey baster and examined. Any pupae present were removed, and the rest of the pitcher plant fluid returned to the leaf. The number of pupae collected at each sampling was recorded and these pupae were brought back to the laboratory. Upon emergence, females were retained for approximately three days to allow for the autogenous development of their eggs. Wing length was measured for both sexes and used as a size parameter.

Overwintering Survival

Overwintering survival was investigated by collecting eighty or more pitcher plant leaves at The Pas and Patricia Beach sites in January as well as in April. In the laboratory, the contents of the leaves were examined for larval mortality. Meteorological data was provided by Environment Canada. Data from the Pine Falls weather station (approximately 33 km N.E. of Patricia Beach), and the Pinawa weather station (approximately 59 km S.E. of Patricia Beach), were used as substitutes for Patricia Beach data, since the latter does not have a meteorological station.

RESULTS AND DISCUSSION

Life History Pattern

The life history pattern of W. smithii at all three sites was determined by plotting the mean number of individuals per leaf of each developmental stage, for every sample of one-year old pitcher plant leaves (Fig. 1) and new leaves (Fig.2). Means were rounded off to the nearest 0.05. Since the number of leaves within a sample which contained no larvae would affect the overall mean for that sample, qualitative as well as quantitative trends will be discussed (the percentage of leaves within each sample which contained larvae is given in Table I).

Figure 1 depicts the mean number of W. smithii in one-year old leaves at all three sites. Only the third instar, fourth instar, and pupal stages are depicted in these graphs. The phenology of the mosquito within the leaves was similar at all three sites. Third instar larval numbers were high in the spring since this is the stage which has just overwintered. Larvae remained in the third instar until May despite the fact that photoperiods capable of terminating diapause had already occurred by mid to late April at latitudes such as those of The Pas (Brust, R.A. unpublished data), Kenora and Patricia Beach (Smith and Brust 1971). According to Smith and Brust (1971), cool spring temperatures are responsible for the delay in development during the spring. As soon as temperatures

became high enough so that larvae could resume development, the number of third instars decreased as they moulted into fourth instar larvae. According to Evans (1971), this occurs when temperatures exceed 15°C.

The Kenora site had a greater number of third instar larvae per leaf than the other two sites. This is probably related to leaf size and will be discussed more fully in the section on the relationship between leaf size and the number of thirds.

Fourth instar larvae were prominent in June at all three sites. They developed into pupae which were prevalent in late June and early July. The presence of pupae marks the period of adult emergence. Pupae were found in small numbers at Kenora and The Pas, but were not recovered from Patricia Beach. Although the fluid of sampled leaves was examined for pupal skins, they were difficult to detect due to organic debris within the pitcher plant leaf.

Female W. smithii preferentially oviposit into younger pitchers (Evans 1971; Istock et al. 1975; Mogi and Mokry 1980), however some females will oviposit into the old leaves, resulting in another generation of W. smithii in these leaves. From Fig. 1, it can be seen that third instar of the new generation began to appear in late July and early August at all three sites (the preceding first and second instar are not represented on these graphs). Third instar larvae enter diapause and remain in this stage in order to overwinter. At the latitudes of Kenora and Patricia Beach,

the critical photoperiod for W. smithii is approximately 15 hours (Evans and Brust 1972). At The Pas, a 16-16 1/2 hour photoperiod is required in order to achieve 50% diapause induction (Brust, R.A. personal communication). At all three sites, critical photoperiods are reached by mid to late August.

It is not yet known how important one-year old leaves are to the overwintering success of these mosquitoes. Presumably once the leaves are more than a year old, they are relatively risky environments due to the progressively deteriorating condition of the leaves.

Figure 2 depicts the mean number of the various stages of W. smithii which occurred in the new leaves, that is, the current year's growth. New leaves start to form in late May and early June. They begin to open during the early part of July and continue to do so until early August (Evans 1971; personal observation). Shortly after the leaves open, adult females which have recently emerged from the overwintered leaves will preferentially oviposit into these new leaves. They are attracted by a water soluble chemical emitted by the leaves (Mogi and Mokry 1980; Istock et al. 1983).

First, second, third, and fourth instars are depicted in Fig. 2. Eggs began to occur within the new leaves by early July (personal observation). First and second instars were evident from early July until the end of the sampling period (late August at The Pas, and early September at Patricia Beach and Kenora). Irregularities in the

phenological pattern of first and second instar larvae over the sampling season could be due to the fact that they are difficult to find within leaf samples because of their small size, and consequently may be underestimated. In addition, they are subject to higher larval mortality than are the later instars (Brust, R.A. personal communication), and detection of dead first and second instar larvae is unlikely.

The larvae began to moult to third instars by early August. The majority of these larvae will be in diapause and will develop no further than the third instar in order to overwinter. Once again, Kenora had greater numbers of third instar larvae than the other two sites.

At The Pas and Patricia Beach sites, fourth instar larvae were found in a number of pitchers. They were also found at Kenora, but in numbers too small to be represented on the graph. The presence of fourth instar larvae implies that these individuals developed quickly enough to miss the seasonal cue of shortening day lengths, while in the first and second instar (Evans and Brust 1972). It is possible that adults emerging from these fourth instars were able to contribute to a second generation of W. smithii.

The phenology of W. smithii at the Patricia Beach site over a three year period in one-year old leaves is depicted in Fig. 3. Although the duration of the sampling season varied from year to year, the general trends are the same as discussed for Figure 1. The mean number of third instar

larvae was relatively high in the spring of 1983 and 1984 since this is the overwintering stage. The numbers of thirds decreased as they developed into fourth instar larvae. The third instar of the new generation appeared in late July-early August in all three years.

The phenology of W. smithii in new leaves (Fig. 4) is similar to that described in Fig. 2. There were no apparent differences among years with respect to the general phenology. Since the sampling period in 1984 was of short duration, comparisons of these data with those of previous years are limited. In 1982 and 1983, first and second instar larvae were found in the leaves from July until the end of the sampling season. The long period over which first and second instar larvae occurred can be attributed to the prolonged emergence of females from the overwintered leaves, or possibly to the presence of a second generation within the leaves during the later part of the season. Third instar larvae began to appear in late July and in August. In both 1983 and 1984, fourth instar larvae occurred as well. Evidently, the early stages of these individuals developed rapidly and consequently missed the seasonal cue of shortening day lengths which induces diapause.

The Relationship between Leaf Size and the Number of Third Instar Larvae

The relationship between leaf size and the number of third instar larvae was examined during the spring. At this

time of year the population is relatively constant, since no emergence or ovipositional activity is occurring. Presumably late fall would also be a suitable time to examine this relationship. A correlation coefficient of approximately 0.3 was found between leaf size and the number of third instar larvae at each site (Table II). This correlation is significant at the 0.01 level, indicating that the number of larvae per leaf is related to leaf size. As leaf size increases, the number of individuals per leaf also increases.

In order to determine whether differences exist between sites with respect to leaf size and the number of third instar larvae, an analysis of variance was performed. It was found that significant differences (0.01 level) existed among the sites with respect to mean leaf size, as well as the mean number of third instars per leaf. To determine between which sites these differences arose, a Duncan's Multiple Range test was performed. Mean leaf size was found to differ significantly (0.05 level) among all sites (Table III). The Pas had the smallest leaves, Kenora the largest, while Patricia Beach had leaves of an intermediate size. The mean larval density within leaves at Kenora was found to vary significantly (0.05 level) from the other two sites (Table III). Not only did the Kenora site have the largest leaves, but these leaves also contained more larvae than did leaves from the other two sites. It has been reported that a positive correlation exists between the number of eggs laid

per leaf and the pitcher plant leaf size (Evans 1971; Paterson 1971). This may partially account for the relationship between mean leaf size and the mean number of third instar larvae per leaf. Larger leaves may also be able to attract more insect prey, resulting in more food per leaf. Those leaves would then be capable of supporting greater numbers of larvae.

Comparison of Pupation Rates among Sites

Figure 5 shows the percent pupation of W. smithii biweekly from June to August at all three sites in 1983. Only one major peak of pupation occurred at each site, with the majority of pupation occurring in July. Since Kenora and The Pas were monitored only every second week, any pupae which emerged between sampling intervals could not be accounted for. Due to the distances involved, The Pas and Kenora sites could not be sampled in comparable weeks, but only during alternating weeks. The earlier pupation peak at The Pas, compared to the Patricia Beach and Kenora sites, may be due to the timing of the visits.

Comparison of Adult Size and Fecundity among Sites

Adult male size, adult female size and fecundity were compared among sites (Table IV). As previously mentioned, only those pitcher plant leaves with ten or more larvae were tagged. The mean number of larvae per leaf recorded at the three sites is consequently higher in this study than in the

previous section dealing with the relationship between leaf size and the number of larvae per leaf (Table III). Once again, Kenora had greater numbers of larvae per leaf than did the other two sites. Despite varying larval densities, analysis of variance revealed no significant differences among sites with respect to adult male size, adult female size, or fecundity, at the 0.01 level of significance. Female size was always found to be significantly larger than male size.

Changes in Adult Size and Fecundity during the Sampling Season

The mean values for adult male size, and adult female size, and fecundity for the various sampling dates are given for The Pas (Appendix 1), Patricia Beach (Appendix 2) and Kenora (Appendix 3). Only those sampling date/size categories or sampling date/fecundity categories containing means which were comprised of three or more observations were included in the analyses (overall means in Table IV were also calculated using this data set). Since there were no significant differences among sites with respect to the various parameters, the measurements for each characteristic were plotted on the same graph without making a distinction as to which site they were derived from. Regression analysis revealed that the slopes of the lines for male and female wing length (Fig. 6) and fecundity (Fig.7) were significantly different from a slope of 0 at the 0.01 level,

indicating that a downward trend in size and fecundity exists over the sampling period.

A possible explanation for this decline can be found in the decreasing ability of the pitcher plant leaf to attract insect prey as the season progresses. Leaves are most effective at catching prey a short while after they first open. Fewer prey are caught as the leaf ages (Fish and Hall 1978; Bradshaw 1983). Any attraction that overwintered leaves would have towards potential prey would be expected to rapidly decline with time. Early in the season, adults emerging from the one-year old leaves are larger and more fecund since the leaves may be attracting more nectar-feeding insects to the leaves. Another possibility is that enough food material from the previous summer still remains in the leaves to adequately support the developing larvae. As the season progresses, fewer insects are caught as prey, and food left over from the previous year becomes depleted.

Overwintering Survival

Larvae are most susceptible to overwintering mortality during the October-December period since at this time of year they are relatively unconditioned to cold temperatures. Cold tolerance is gradually developed in response to the increasingly longer exposures to cold temperatures which W. smithii larvae experience as they overwinter (Evans and Brust 1972).

Two factors which greatly affect overwintering survival are the amount of snow cover, and the depth of water in the bog. Sufficient snow cover can provide enough insulation to keep the temperatures within the sphagnum (where the pitcher plants grow), fairly constant and only slightly below freezing during the coldest of winter months (Paterson 1971; Smith and Brust 1971; Evans and Brust 1972). The water depth in a bog can also provide thermal insulation, thereby influencing survival rates. For example, in 1970, standing water in a bog at Pinawa, Manitoba with a snow cover of 30-40 cm remained unfrozen until January (Brust, R.A. personal communication). The temperature differential between the ambient air temperatures and the bog results from the heat of crystallization during freezing, and the insulation provided by the snow cover (Brust, R.A.; Pruitt, W.O. Jr. personal communication).

The survival rate at Patricia Beach was lower than at The Pas in both January and April of 1984 (Table V). Larvae cannot resist freezing at temperatures much below -5°C (Evans and Brust 1972) and by November, air temperatures of -4°C were reached at both sites (Table VI). The depth of snow cover on the ground (Table VI) did not differ greatly between the two sites at the time the January samples were taken. Since snow depth was recorded only once a month, a more reliable insulation parameter may be cumulative snowfall (Table VI). The heavier snowfall at The Pas, especially during the critical months of October-December,

may be responsible for providing a more consistent source of insulation on a day to day basis for the larvae. In addition, the Patricia Beach site was fairly dry during the fall of 1983 while The Pas site had several cm of standing water. Dry conditions may have contributed to the lower survival rates observed at the Patricia Beach site.

Survival rates in the spring appear higher than during the winter at both sites (Table V). During spring thaws, dead larvae may deteriorate and therefore spring collections will appear to have smaller numbers of dead larvae. This causes survival rates during the spring to appear to be higher.

The low survival rate of W. smithii at Patricia Beach is reflected in Fig. 8, which depicts the mean number of larvae per leaf in 1983 and 1984. It is evident that the mean number of larvae in 1984 was consistently lower than in 1983. This is probably due to the low overwintering survival which occurred during that year. This does not necessarily mean that the W. smithii population at Patricia Beach is declining. Fewer individuals per leaf could result in less competition for food. The larger and more fecund mosquitoes would tend to counteract some of the detrimental effects of high winter mortality.

Table I. Percentage of One-Year Old and New Pitcher Plant Leaves Containing Larvae During the Sampling Season, 1982-1984.

Patricia Beach 1982			Patricia Beach 1983			Patricia Beach 1984			Kenora 1983			The Pas 1983		
Date	% Old Leaves With Larvae	% New Leaves With Larvae	Date	% Old Leaves With Larvae	% New Leaves With Larvae	Date	% Old Leaves With Larvae	% New Leaves With Larvae	Date	% Old Leaves With Larvae	% New Leaves With Larvae	Date	% Old Leaves With Larvae	% New Leaves With Larvae
June 30	32		April 29	56		May 14	42		April 28	73		May 5	53	
July 7	19		May 14	61		May 23	17		May 11	40		June 8	65	
July 21	25	70	May 17	42		May 31	25		May 19	59		June 23	59	
July 28	38	78	May 26	49		June 7	18		June 1	83		July 6	52	27
Aug. 11	28	70	June 6	67		June 14	42		June 15	68		July 20		56
Aug. 25	39		June 14	41		June 21	14		June 28	58		Aug. 9	39	68
Aug. 26		55	June 24	34		June 28	14		July 14	20	67	Aug. 26	47	62
Sept. 2	44	63	July 2	19	81	July 5	33		July 29	63	89			
Sept. 16	50	55	July 26	18	54	July 9	7	43	Aug. 15	34	22			
Sept. 30	39	67	Aug. 5	29		July 12	19	42	Sept. 4	81	81			
			Aug. 19		51	July 16	6	38						
			Aug. 23	36	50	July 19	13	53						
			Sept. 10	65	55	July 23	6	76						
						July 26	19	73						
						July 30		69						
						Aug. 2	38							
						Aug. 14	18							

Table II. Correlation Between the Number of Third Instar Larvae per Leaf and Leaf Size (Volume in ml) During the Spring, 1983

Site	Total No. of Leaves	Spearman Correlation Coefficient
The Pas	96	0.28 **
Patricia Beach	206	0.26 **
Kenora	150	0.25 **

**-significant at the 0.01 level of probability

Table III. Relationship Between the Mean Number of Third Instar Larvae per Leaf and the Mean Leaf Size (Volume in ml) During the Spring, 1983

Site	Total No. Of Leaves	Mean Volume(ml) \pm S.E.*	Mean Number of Third Instar per Leaf \pm S.E.*
The Pas	96	12.8 \pm 0.6 ^a	2.1 \pm 0.3 ^a
Patricia Beach	206	24.1 \pm 0.8 ^b	2.9 \pm 0.3 ^a
Kenora	150	36.7 \pm 1.4 ^c	4.3 \pm 0.5 ^b

*-Means followed by the same letter are not significantly different at the 0.05 level

Table IV. Comparison of Adult Size (wing length in mm) and Fecundity (number of eggs per female) Among Sites, 1983

Site	No. Leaves	Mean No. Larvae/Leaf ± S.E.	Mean Male Wing Length (mm) ± S.E.*	Mean Female Wing Length (mm) ± S.E.*	Mean Fecundity (No. Eggs per Female) ± S.E.*
The Pas	62	12.5 ±0.8	2.36 ±0.02 ^a n=76	2.59 ±0.03 ^b n=53	42.9 ±3.0 ^c n=43
Patricia Beach	50	14.8 ±0.7	2.26 ±0.02 ^a n=81	2.50 ±0.03 ^b n=59	37.7 ±2.8 ^c n=45
Kenora	46	22.4 ±1.6	2.31 ±0.02 ^a n=68	2.55 ±0.04 ^b n=50	35.6 ±4.4 ^c n=29

* means followed by the same letter are not significantly different at the 0.01 level

n=sample size

Table V. Overwintering Survival of Third Instar Larvae at Patricia Beach and The Pas, 1983-1984.

	Patricia Beach		The Pas	
	Total No. of Larvae Retrieved	% Survival	Total No. of Larvae Retrieved	% Survival
January	678	8.9	841	67.6
April	290	28.1	1350	89.6

Table VI. Meteorological Data for Pinawa, Pine Falls,
and The Pas, 1983-1984

Site	Meteorological Parameter	Oct. 1983	Nov. 1983	Dec. 1983	Jan. 1984	Feb. 1984	Mar. 1984	Apr. 1984
<u>Pine Falls</u>	Mean Temp. °C	5.3	-1.9	-20.9	-18.0	-7.6	-8.4	7.0
	Mean Min. Temp. °C	1.0	-4.3	-24.7	-23.6	-11.8	-14.1	0.3
	Cumulative Snowfall (cm)	0	19.0	13.5	22.0	11.5	11.0	0.0
<u>Pinawa</u>	Snow Cover (cm)	0	20	n/a	34	35	n/a	n/a
<u>The Pas</u>	Mean Temp. °C	4.7	-2.3	-22.4	-19.0	-7.9	-9.2	5.3
	Mean Min. Temp. °C	-0.3	-4.3	-26.9	-24.8	-13.2	-14.6	-0.5
	Cumulative Snowfall (cm)	3.0	37.5	12.3	32.9	13.0	13.0	13.0
	Snow Cover (cm)	0	14	18	28	15	2	6

n/a: not available

FIG. 1 MEAN NUMBER OF W. smithii IN ONE-YEAR OLD LEAVES, 1983

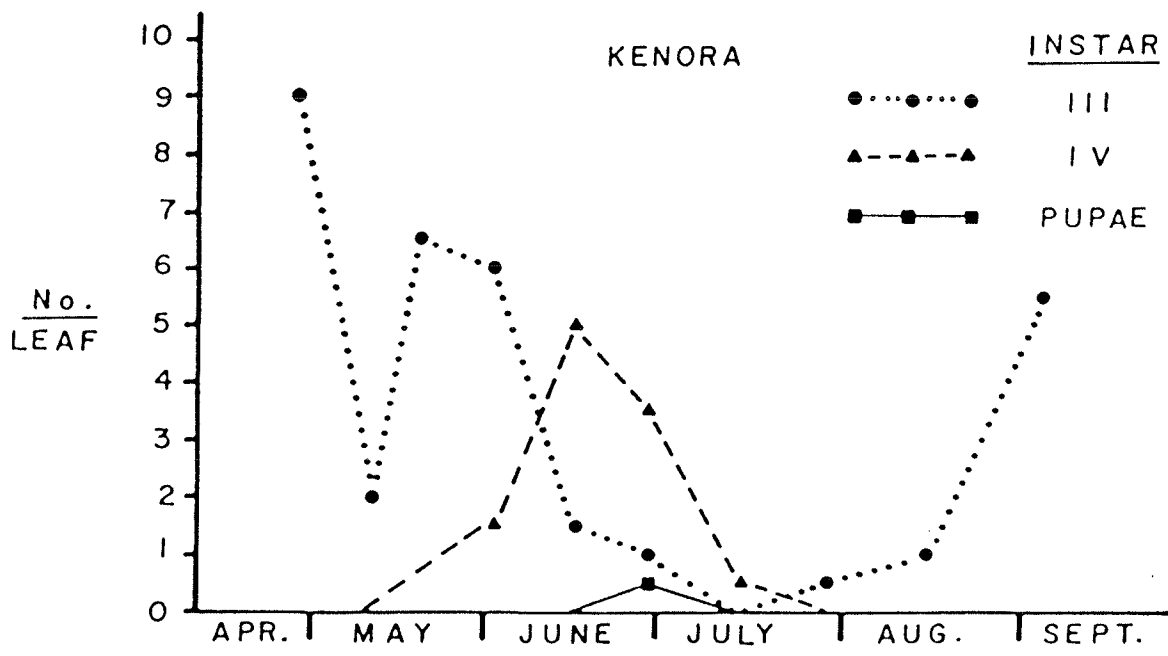
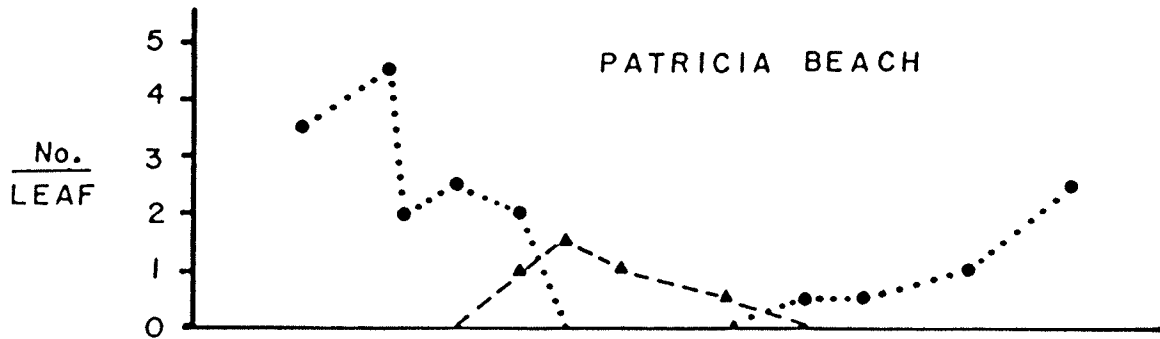
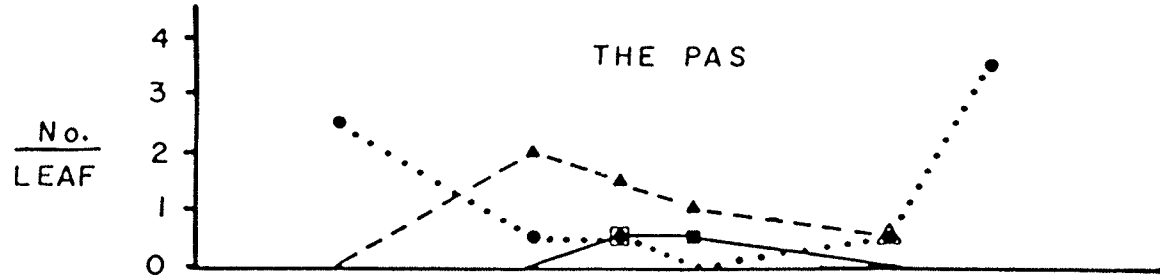


FIG. 2 MEAN NUMBER OF W. smithii IN NEW LEAVES, 1983

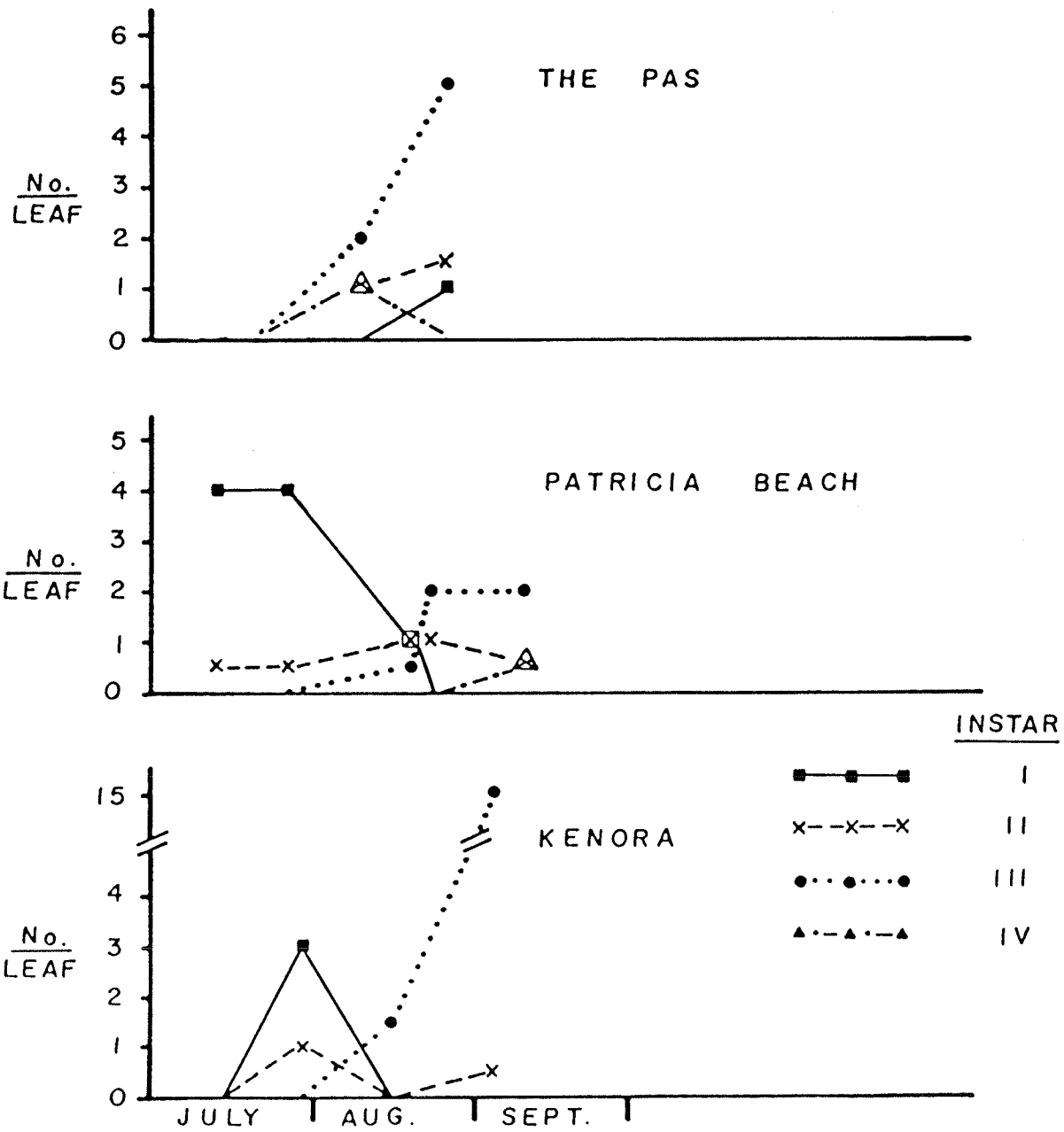


FIG. 3 MEAN NUMBER OF W.smithii IN ONE-YEAR OLD LEAVES AT PATRICIA BEACH, 1982-1984

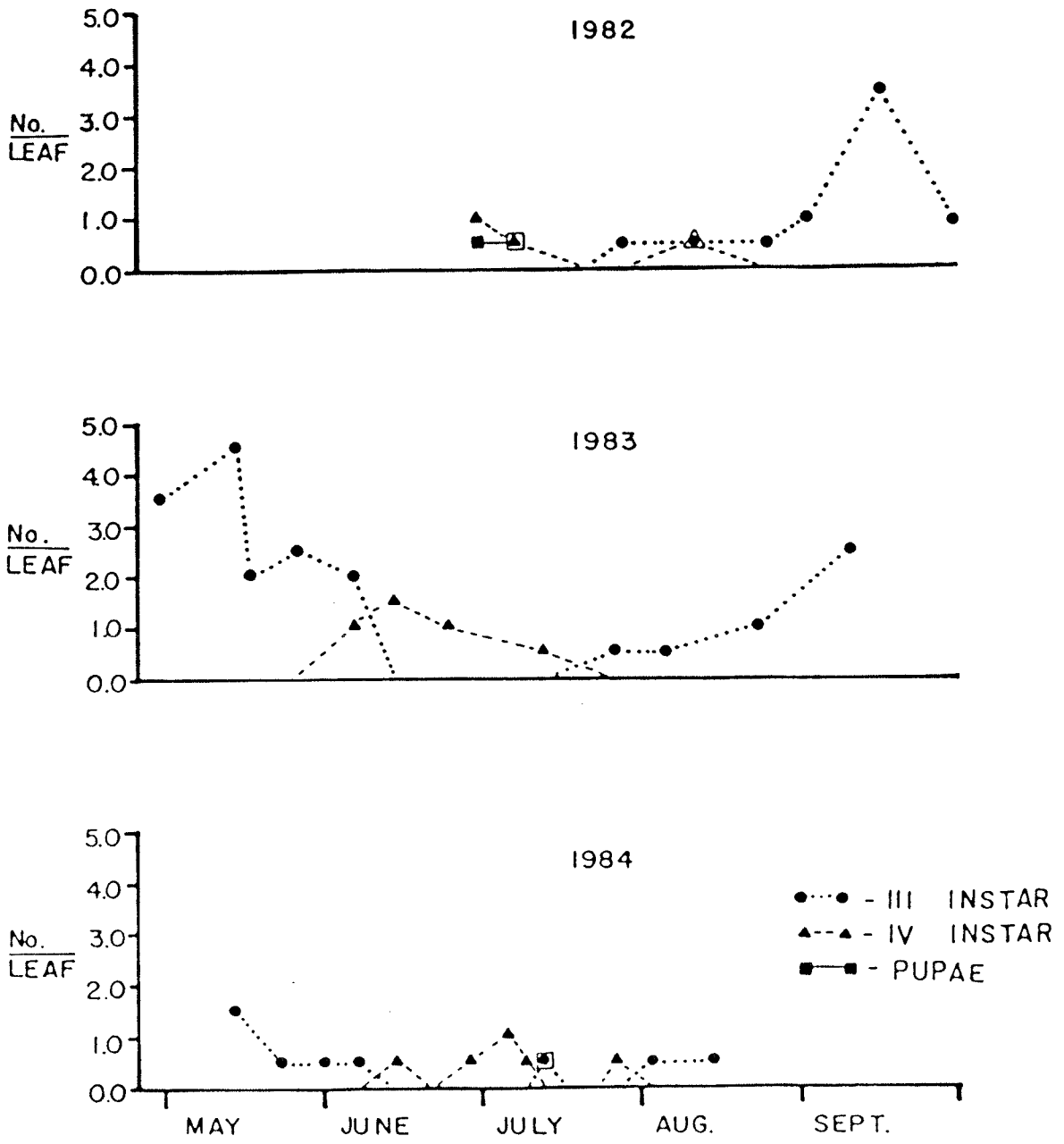


FIG. 4 MEAN NUMBER OF W. smithii
IN NEW LEAVES AT PATRICIA
BEACH, 1982 - 1984

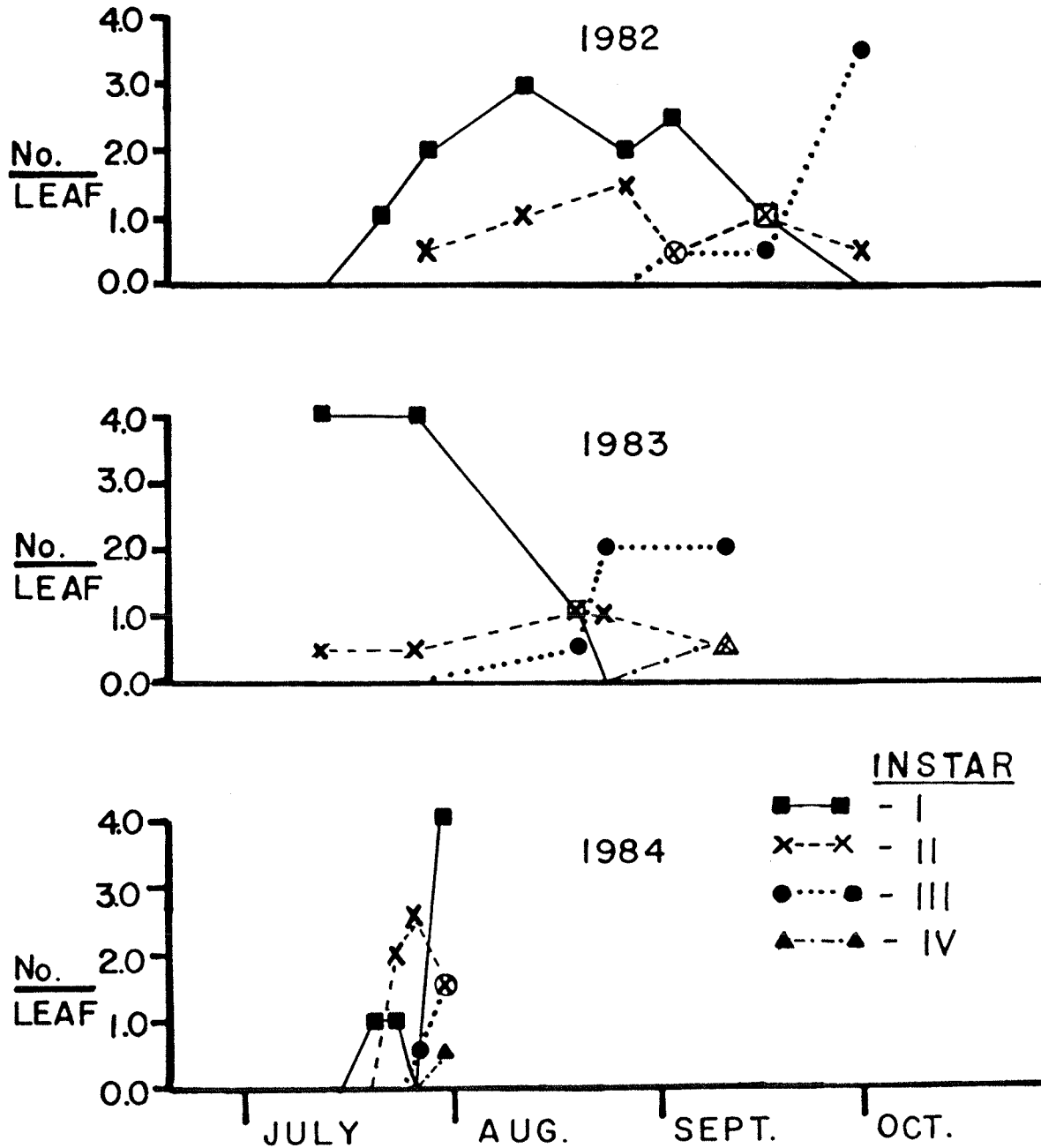


FIG. 5 PERCENT PUPATION OF W. smithii
BIWEEKLY FROM JUNE-AUGUST, 1983

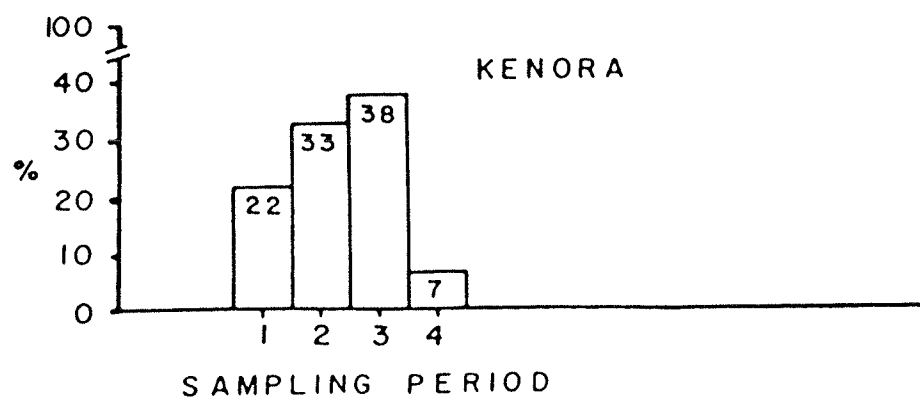
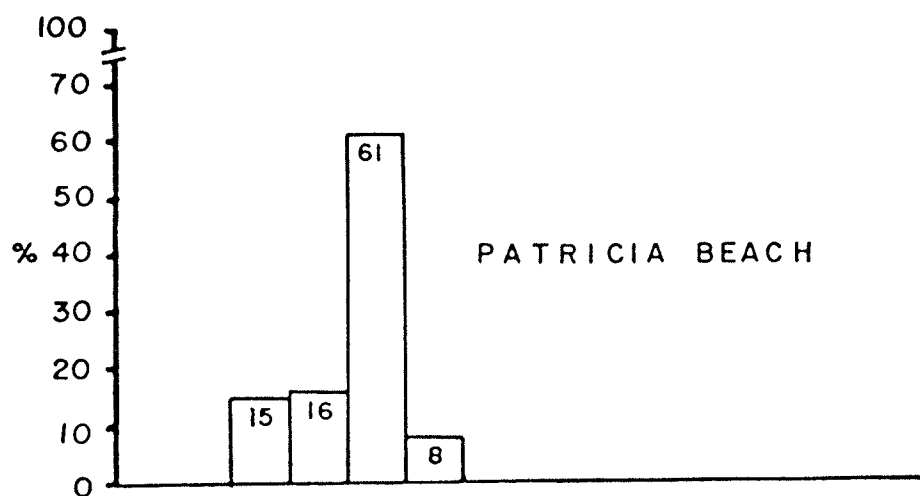
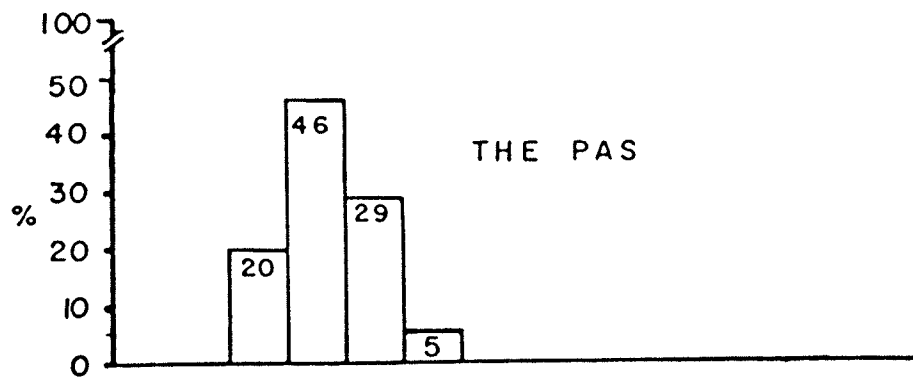


FIG. 6 CHANGES IN ADULT SIZE (MEAN WING LENGTH \pm S.E.) DURING THE SAMPLING SEASON, 1983.

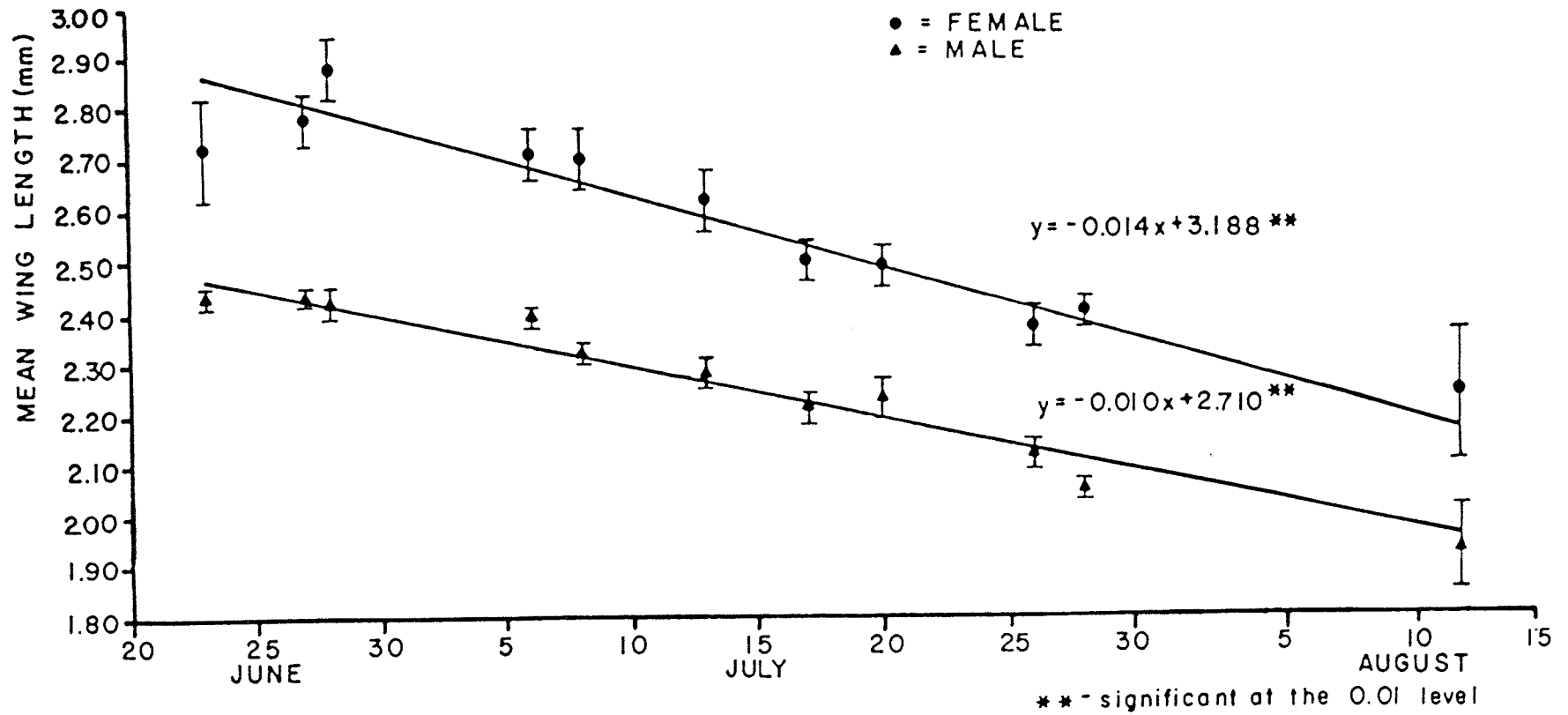


FIG.7 CHANGES IN FECUNDITY (MEAN NUMBER OF EGGS PER FEMALE ± S.E.) DURING THE SAMPLING SEASON, 1983

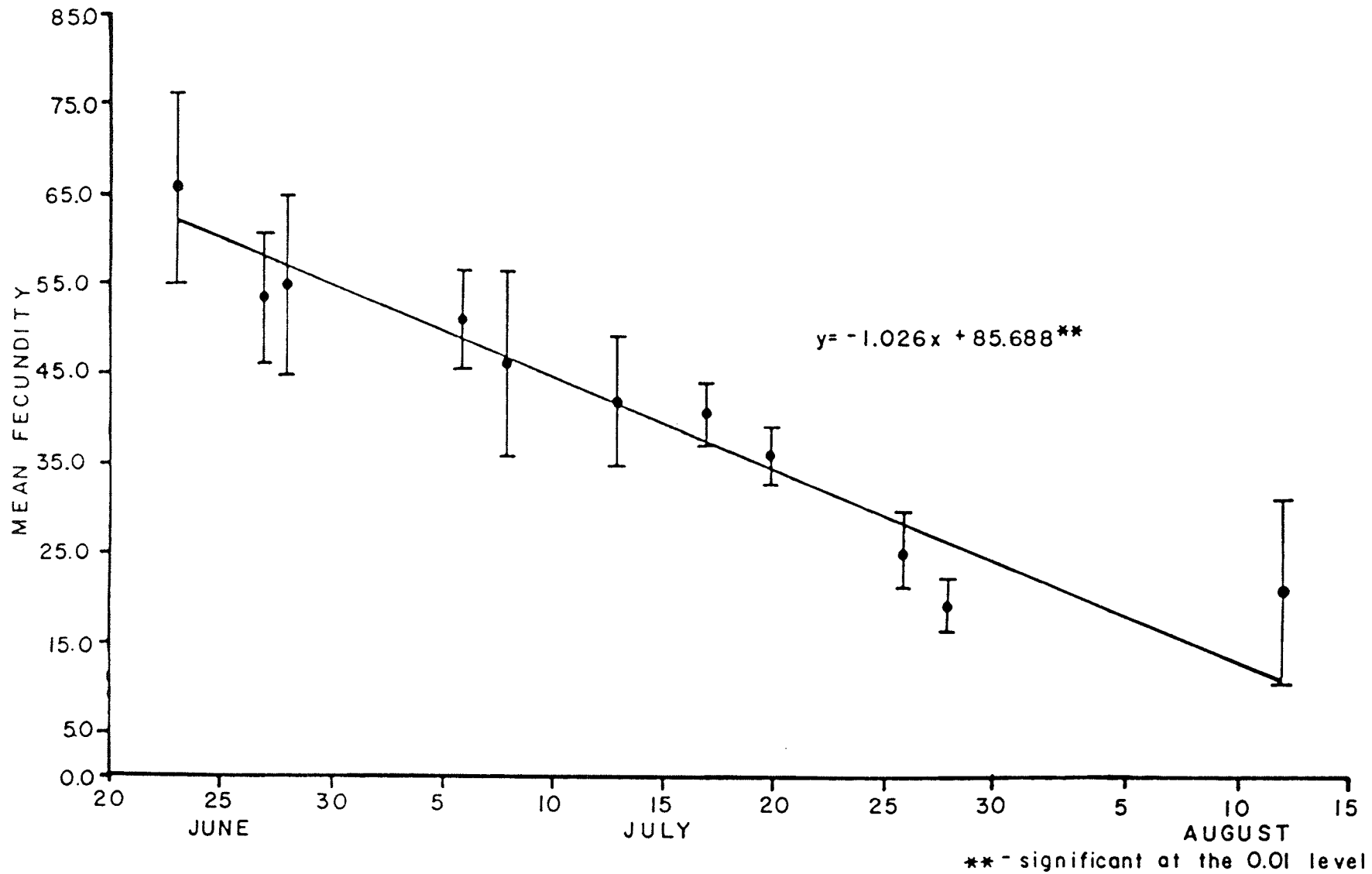
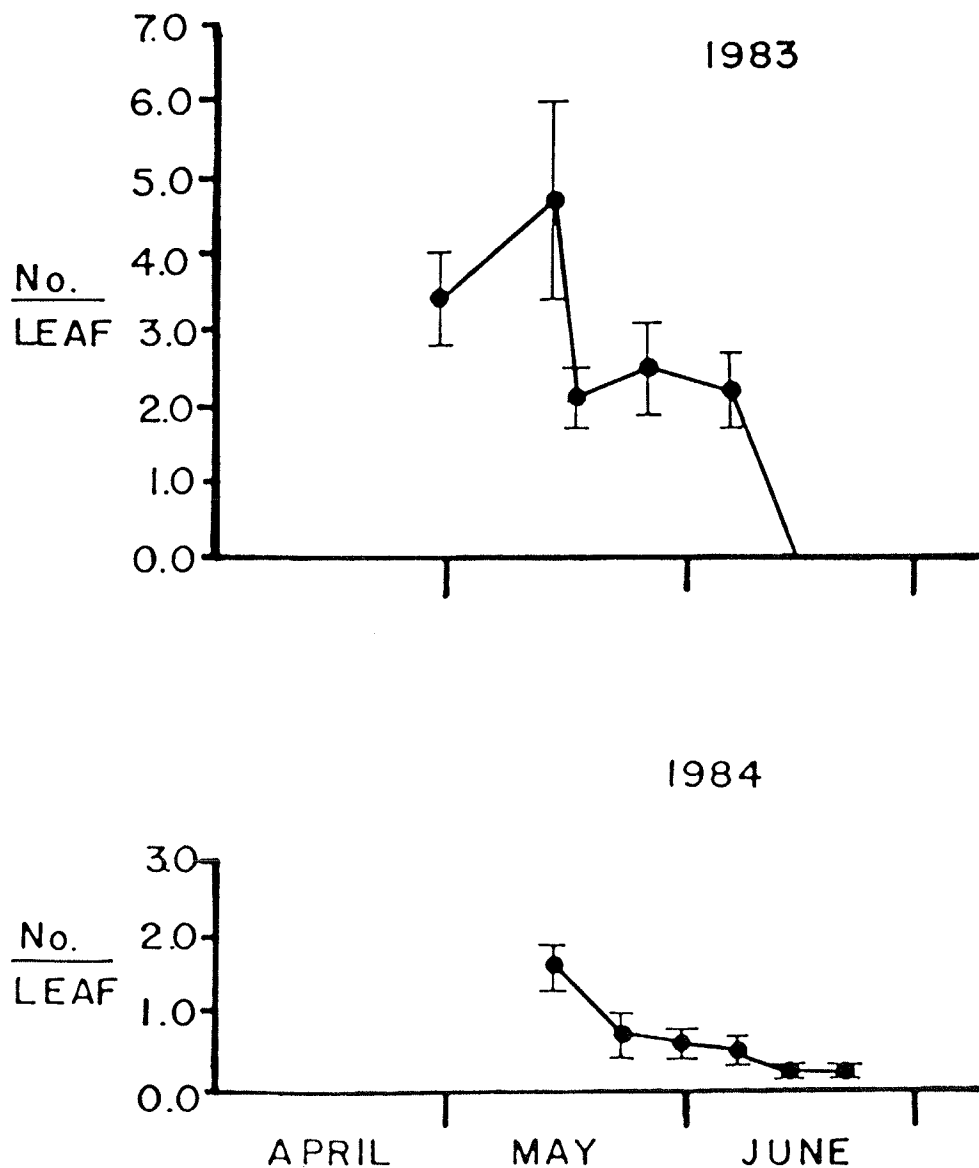


FIG. 8 MEAN NUMBER OF THIRD INSTAR LARVAE \pm S.E. IN ONE-YEAR OLD LEAVES AT PATRICIA BEACH, 1983-1984



The Effect of a Larval Diet Supplement on
Development in Wyeomyia smithii (Coq.)
Under Field Conditions

INTRODUCTION

Wyeomyia smithii (Coq.) (the pitcher plant mosquito) is one of a number of symbiotic organisms that subsist on the pitcher plant's prey (Fish and Hall 1978). Insects which drown in the pitcher plant fluid are fed upon by the macro-decomposers of the system viz. Metriocnemus knabi Coq. (Chironomidae), Blaesoxipha fletcheri (Aldrich) and Sarcophaga sarraceniae Riley (Sarcophagidae).

Macro-decomposer action on prey insects, as well as the decomposition of the cadavers, results in particles which are small enough to be filtered out of the water column by W. smithii larvae and ingested (Istock et al. 1975; Fish and Hall 1978). W. smithii larvae may also feed by ingesting the bacteria and protozoans found within the pitcher plant fluid (Addicott 1974; Istock et al. 1975; Fish and Hall 1978; Bradshaw 1983).

Both the quantity and quality of larval diet has a significant effect on larval development and adult fecundity (Lillie and Nakasone 1982). In this study, the effect of a larval diet supplement on W. smithii development, that is, on the rate of pupation, and on adult size and fecundity in the field, was examined in order to determine whether the natural food supply within the pitcher plant is as favourable for development as a supplemented diet. Since W. smithii is autogenous, it must synthesize and store the lipoproteins needed for egg production during the period of

larval development, as has been demonstrated for A.
atropalpus (Coq.) (Van Handel 1976).

MATERIALS AND METHODS

Comparison of Pupation Rates, Adult Size and Fecundity
Between Treatments

Pitcher plant leaves in bogs near The Pas and Patricia Beach, Manitoba, and Kenora, in northwestern Ontario, were monitored during the spring of 1983. The fluid contents of the leaves were removed and collectively placed into plastic buckets until approximately 1500 third instar larvae were collected. Some of the emptied leaves were tagged, using surveyor's tape. Fifteen third instar larvae and some fluid from the drained pitcher plant leaves were added to each of the tagged leaves. The number of larvae per leaf was standardized in order to reduce possible variability among individuals due to differing larval densities. The development of W. smithii in 92 one-year old pitcher plant leaves at Patricia Beach, 96 leaves at Kenora, and 100 leaves at The Pas, was monitored.

In 1984, only the Patricia Beach site was monitored, and leaves were selected that contained more than 5 larvae. The integrity of each pitcher plant leaf was not disturbed. In all, 79 leaves were tagged in the spring, and monitored throughout the summer.

The treatment consisted of periodically adding a diet supplement to half of the tagged pitcher plant leaves, the other half were used as controls. The main purpose of the diet supplement was to augment the natural food supply of

the larvae, not replace it. TetraMin[®] (a commercially available fish food) was selected as the diet since in laboratory studies, it was found that larvae reared on a TetraMin[®] or a TetraMin[®]-dog food combination developed faster and yielded adults that lived longer and produced more eggs than did those reared on other artificial diets (Lillie and Nakasone 1982). At the Patricia Beach site, 0.04 grams of ground-up TetraMin[®] (passed through an 80-mesh sieve), were added to the tagged leaves weekly, while at The Pas and Kenora, 0.08 grams were added biweekly. On subsequent visits, more food was added only if the pitcher plant fluid was relatively clear. If it exhibited a reddish tinge, indicating a TetraMin[®] surplus, no diet supplement was added. The fluid contents of the tagged leaves were replenished with distilled water to prevent dessication due to evaporation.

Each time a site was visited, the contents of the tagged leaves were removed with a turkey baster and examined for pupae. The number of pupae collected on each sampling date was recorded. These pupae were brought to the laboratory and reared in order to study the effect of a diet supplement on adult size and fecundity. Upon emergence, females were retained for a three day period to allow for autogenous egg development.

RESULTS AND DISCUSSION

Comparison of Pupation Rates Between Treatments

Figures 1,2,3 and 4 represent pupation rates at the various sites in both diet supplemented and unsupplemented pitcher plant leaves. The rate of pupation is represented as the percentage of the total number of pupae collected on each sampling date.

At The Pas site (Fig. 1), the peak of pupation occurred in early July in both the diet supplemented and unsupplemented individuals. However, differences are evident in the distribution of the incidence of pupation over time. The percentage of individuals which pupated early in the season is lower in the unsupplemented pitchers than in the supplemented plants. The incidence of pupation consequently follows a rather even distribution in this group, with the peak occurring about midpoint in the curve. In the diet supplemented pitchers, the peak of the curve is skewed to the left, since larvae pupated at a more synchronous rate, the majority becoming pupae by the beginning of July.

At the Patricia Beach site (Fig. 2), the peaks indicating percent pupation are lower in the population with a natural food supply than in that with a supplemented diet. In addition, the major peaks of pupation occurred at an earlier date (late June in the supplemented group as opposed to mid-July in the unsupplemented group).

The same pattern was evident at the Kenora site (Fig. 3). The peak pupation period was spread over two sampling periods in the unsupplemented pitchers, whereas in the other group, nearly 90% of the pupae were collected during the first visit.

In 1984, under conditions of naturally occurring larval densities within pitcher plant leaves (Patricia Beach site, Fig. 4), the rate of pupation was again enhanced in diet supplemented leaves. Pupation was earlier and more synchronous.

Comparison of Adult Size and Fecundity between Treatments

The effect of a larval diet supplement in 1983 on adult size and fecundity is shown in Table I. At all three sites, those individuals which came from leaves supplemented with TetraMin[®] were significantly larger and more fecund (0.01 level of significance) than those which did not receive a diet supplement. Females were consistently larger than males. Within the diet treatment and the control, size and fecundity did not vary significantly among sites.

Again in 1984 (Table II), the size of males and females was significantly larger and females were more fecund (0.01 level of significance) in those mosquitoes which received a diet supplement. Within treatments, no significant differences in size and fecundity were found among sites.

Changes in Adult Size and Fecundity during the Sampling Season

Changes in adult male size, adult female size and fecundity during the 1983 sampling season are given in Appendix 4, 5, and 6 respectively and include both diet supplemented and unsupplemented individuals. Appendix 7 shows the changes in size and fecundity which occurred at the Patricia Beach site in 1984. Only those sampling date/size categories or sampling date/fecundity categories, containing means which were derived from three or more observations were included in the analyses (means in Tables I and II were also calculated using these data sets).

For both the diet supplemented and unsupplemented mosquitoes, the values for male and female size (Fig. 5, Fig. 6), as well as fecundity (Fig. 7, Fig. 8), were plotted over time. Since it has already been shown for the 1983 data that no significant differences existed among sites when comparing size or fecundity (Table I), the values obtained for the various parameters measured were plotted according to sampling date only (Fig. 5, Fig. 7), and no distinction was made with regard to site. The best possible line through each set of points was obtained for each parameter-treatment combination by performing a regression analysis.

In 1983, male and female size were found to decrease over time in both the diet supplemented and unsupplemented mosquitoes, as demonstrated by the line slopes which

represent these sets of data (Fig. 5). The slopes differed significantly from 0 at the 0.01 level in all cases, indicating a decreasing trend. However, the decline in size is more pronounced in the unsupplemented individuals, since the slopes for the associated lines are greater. In 1984 (Fig. 6), the line slopes for the control individuals are also greater than that of their diet supplemented counterparts. However, within the control treatment, only male size was found to have a slope which differed significantly from 0 at the 0.01 level. Diet supplemented individuals did not show a significant change in size over the sampling period.

In 1983 (Fig. 7), fecundity among the diet supplemented mosquitoes was found to decline significantly (0.05 level) over the sampling season, whereas in 1984 (Fig. 8) fecundity did not change significantly over time. In the control treatment, a significant decline (0.01 level) occurred in 1983 (Fig. 7) but not in 1984 (Fig. 8). It should be noted however, that the slope of the line for the unsupplemented group in 1984 is greater than that found in the diet supplemented group, indicating an increased trend towards less fecund mosquitoes as the season progressed.

A primary factor which could explain the strong declines seen in size and fecundity among unsupplemented individuals is lack of adequate nutrition. Pitcher plant leaves progressively lose their ability to attract

nectar-feeding insects as they age. Most of the insects trapped by the plant would have been captured the previous summer, after the new leaves had filled with fluid (Fish and Hall 1978; Bradshaw 1983). When a food shortage exists, adult mosquitoes emerging earlier in the season, from one-year old leaves, should be larger and more fecund.

A significant decline in size (0.01 level) and fecundity (0.05 level) was also found among diet supplemented individuals (Fig. 5, Fig. 7), although it was not as pronounced as that found in the unsupplemented group. Since food was only added at weekly and biweekly intervals, larvae from the diet supplemented treatment could have experienced a food shortage for several days or even a week between feedings, especially at The Pas or Kenora.

An improved food supply leading to the earlier emergence of larger and more fecund mosquitoes may result in bivoltinism. The life history study (manuscript I, Fig. 2, Fig.4) showed that a few fourth instar larvae were present in the new leaves in August and early September (1983) as well as in late July (1984). Evidently, these larvae were able to develop quickly enough (while in the earlier instars) to avoid the seasonal cue of shortening daylengths which induces diapause. If the offspring of these individuals were able to reach the third instar larval stage before temperatures dropped much below a mean of 15°C, then a proportion of the population would be bivoltine.

At Kenora (Fig. 3) and Patricia Beach (Fig 2. and Fig. 4), 50% pupation occurred several days earlier in the spring among diet supplemented individuals. Earlier emergence may increase the proportion of individuals which could contribute to a bivoltine population at these sites.

Table I. Effect of a Larval Diet Supplement on Adult Size (Wing Length in mm) and Fecundity (Number of Eggs per Female) at the 3 sites, 1983.

Site	Treatment	Adult Male Size		Adult Female Size		Fecundity	
		Mean Wing Length in mm \pm S.E.	Sample Size	Mean Wing Length in mm \pm S.E.	Sample Size	Mean Number of Eggs per Female \pm S.E.	Sample Size
The Pas	Control	2.36 \pm 0.02 ^a	77	2.52 \pm 0.04 ^c	54	35.5 \pm 3.7 ^e	36
	Diet Supplement	2.48 \pm 0.01 ^b	87	2.87 \pm 0.02 ^d	58	66.9 \pm 3.3 ^f	46
Patricia Beach	Control	2.35 \pm 0.02 ^a	79	2.59 \pm 0.03 ^c	62	38.1 \pm 3.1 ^e	50
	Diet Supplement	2.55 \pm 0.01 ^b	118	2.98 \pm 0.01 ^d	102	80.9 \pm 1.6 ^f	94
Kenora	Control	2.38 \pm 0.02 ^a	81	2.64 \pm 0.02 ^c	59	43.6 \pm 2.6 ^e	44
	Diet Supplement	2.56 \pm 0.01 ^b	124	2.97 \pm 0.01 ^d	121	73.2 \pm 1.9 ^f	86

-Means followed by the same letter are not significantly different from each other at the 0.01 level of probability.

Table II. Effect of a Larval Diet Supplement on Adult Size (Wing Length in mm) and Fecundity (Number of Eggs per Female) at Patricia Beach, 1984.

Treatment	Adult Male Size		Adult Female Size		Fecundity	
	Mean Wing Length in mm \pm S.E.	Sample Size	Mean Wing Length in mm \pm S.E.	Sample Size	Mean Number of Eggs per Female \pm S.E.	Sample Size
Control	2.33 \pm 0.04 ^a	22	2.65 \pm 0.04 ^c	25	51.8 \pm 4.4 ^e	21
Diet Supplement	2.50 \pm 0.01 ^b	46	2.86 \pm 0.02 ^d	42	70.5 \pm 2.2 ^f	37

-Means followed by the same letter are not significantly different from each other at the 0.01 level of probability.

FIG. 1 PERCENT PUPATION OF
W. smithii AT THE PAS, 1983

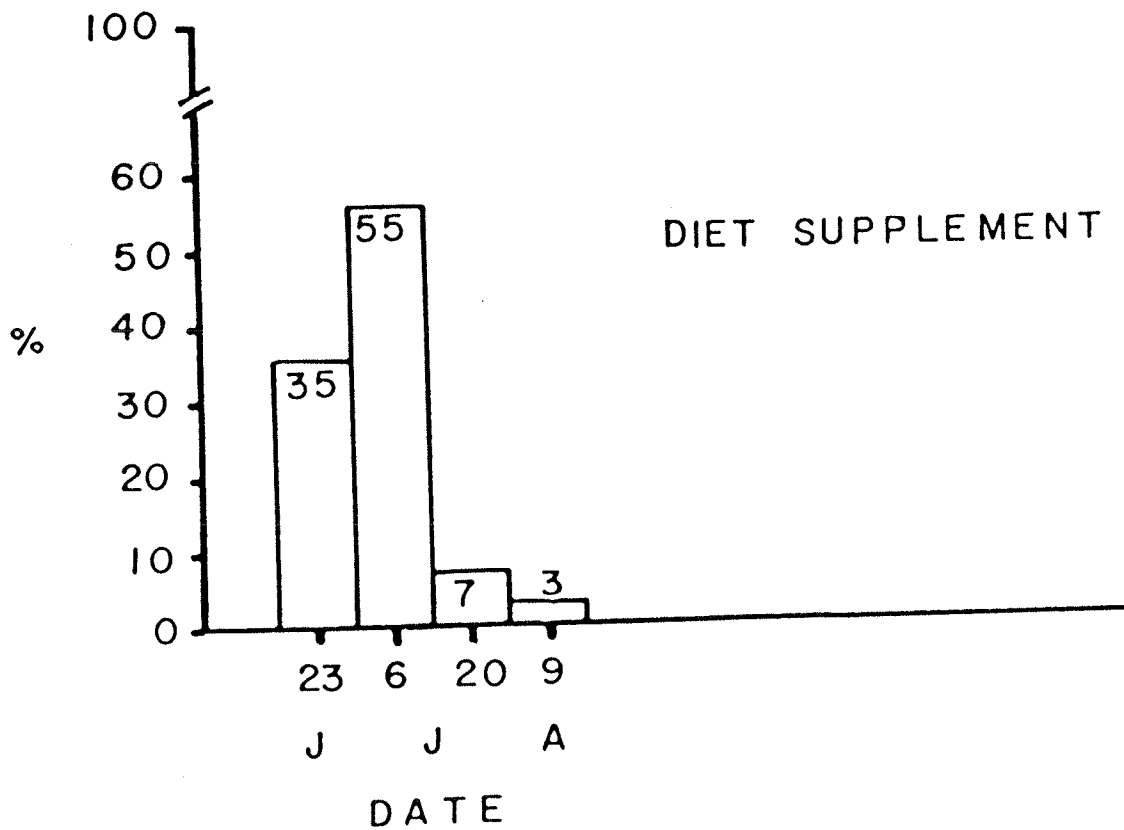
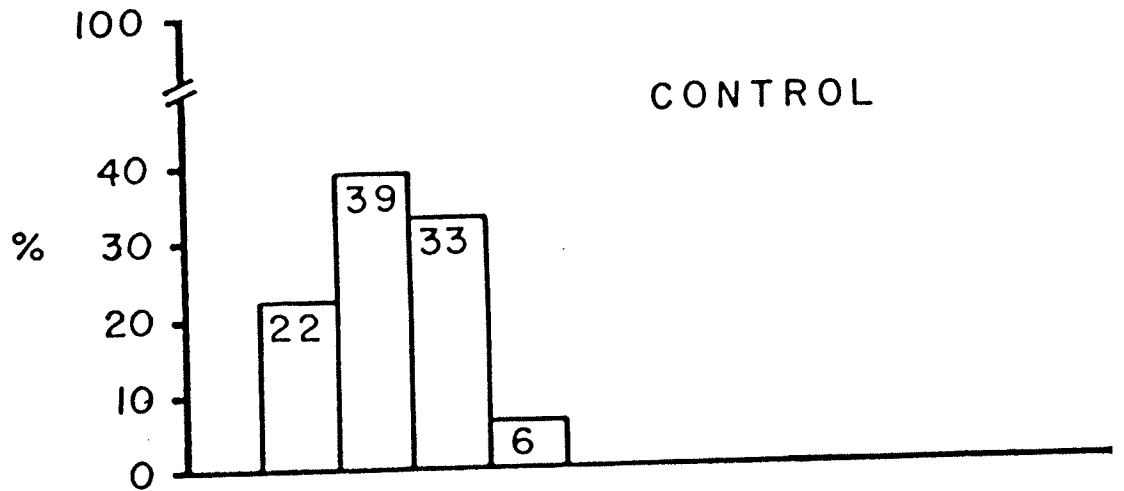


FIG.2 PERCENT PUPATION OF
W. smithii AT PATRICIA
BEACH, 1983.

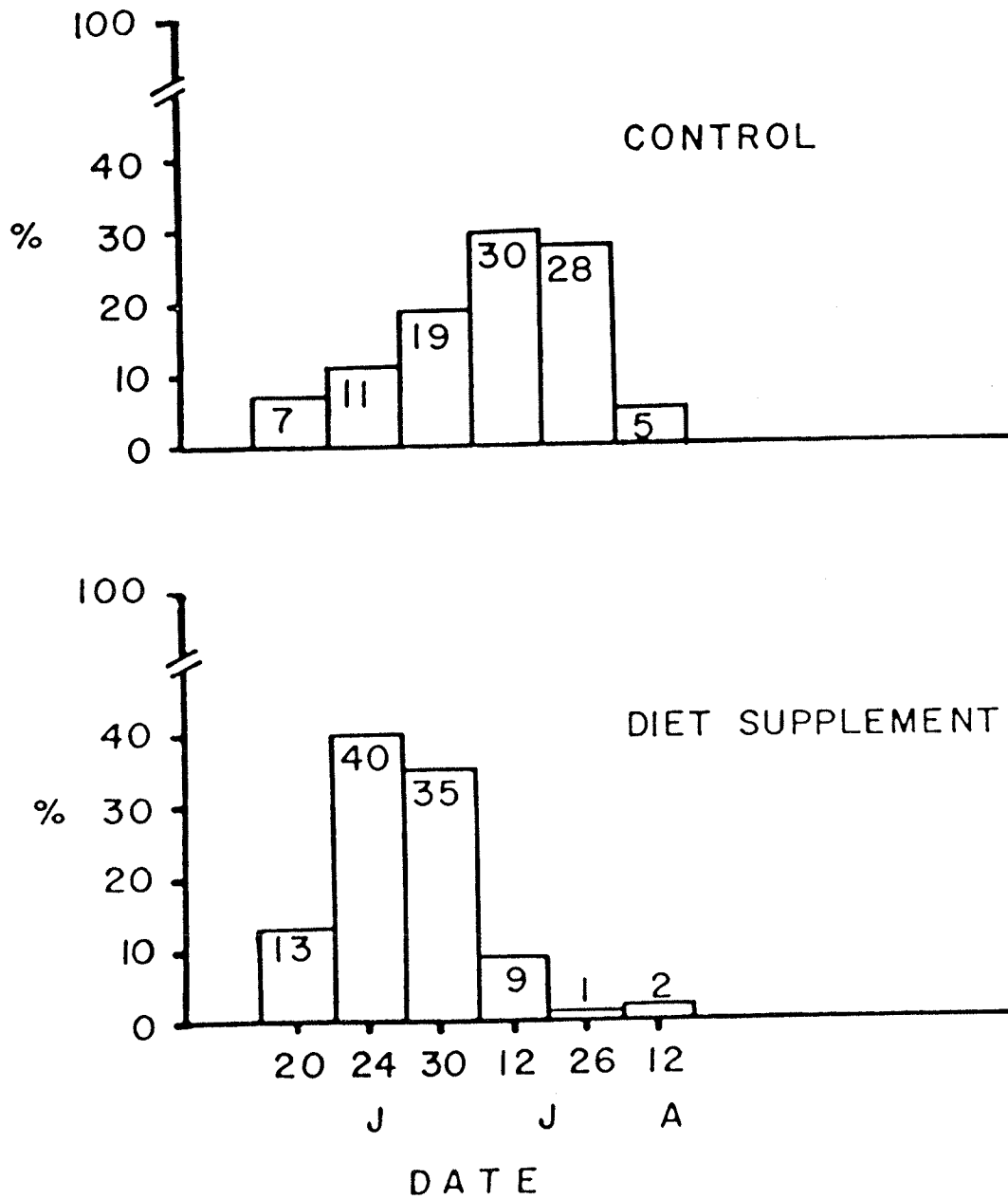


FIG.3 PERCENT PUPATION OF W.smithii
AT KENORA, 1983

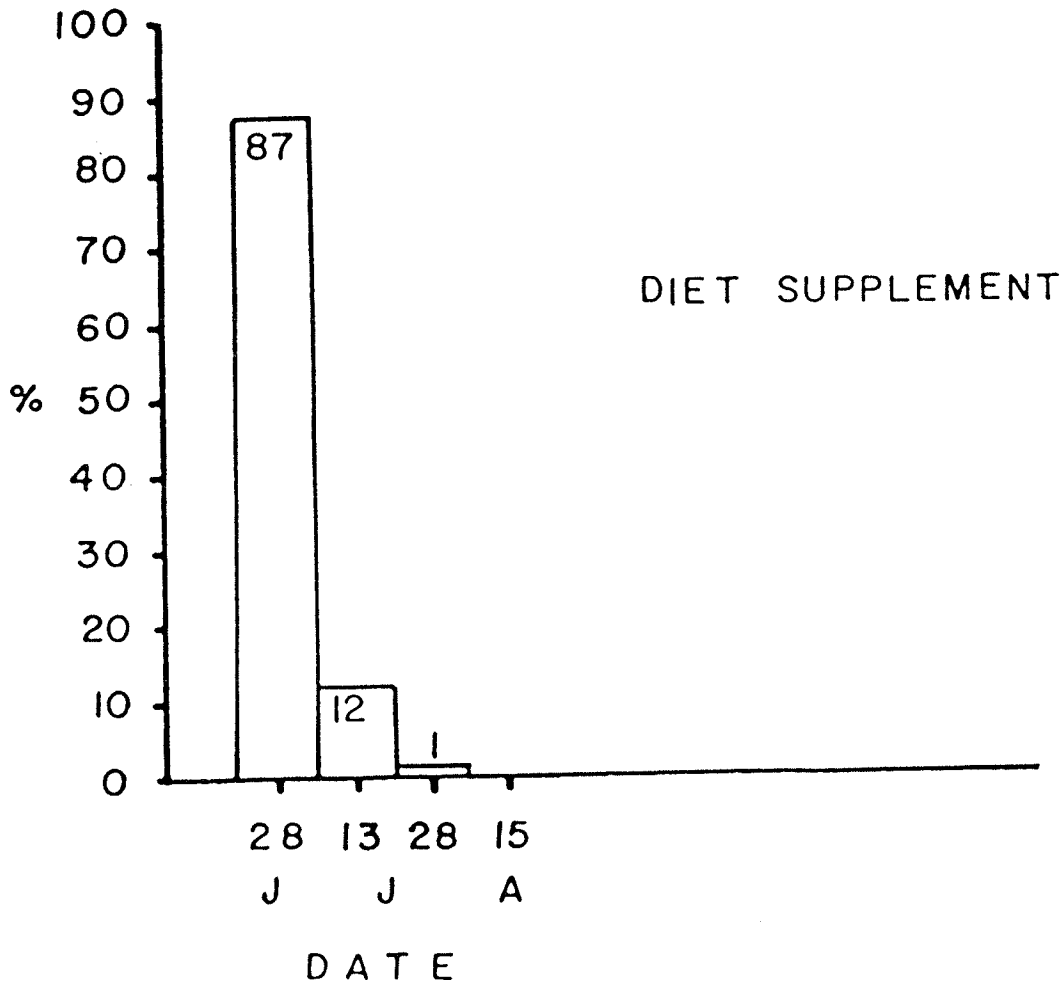
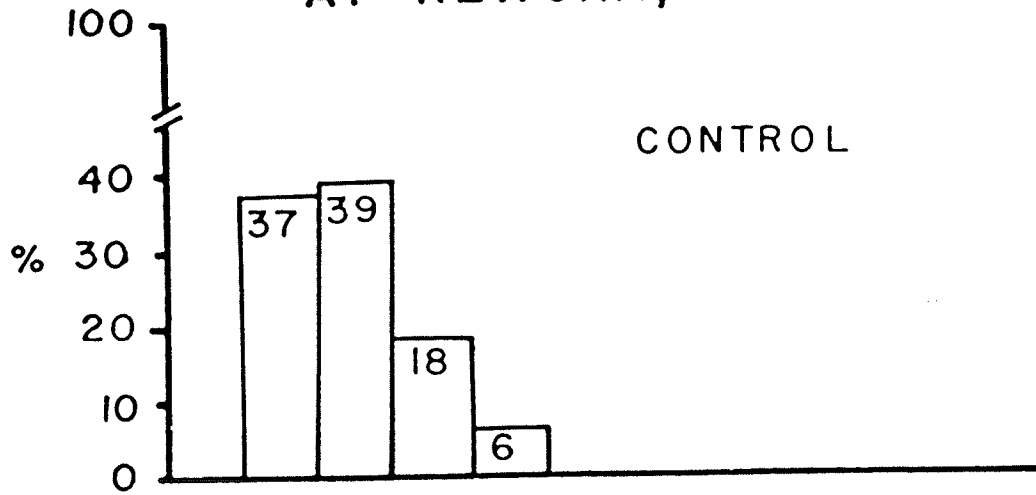


FIG. 4 PERCENT PUPATION OF
W. smithii AT PATRICIA
BEACH, 1984.

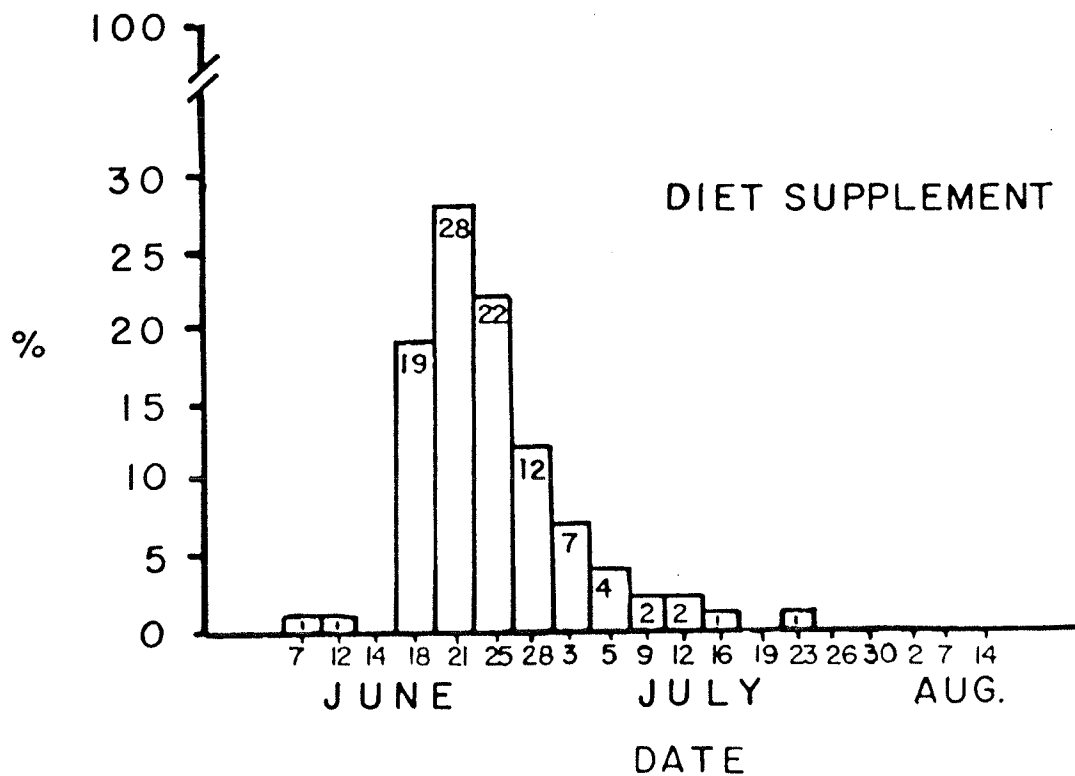
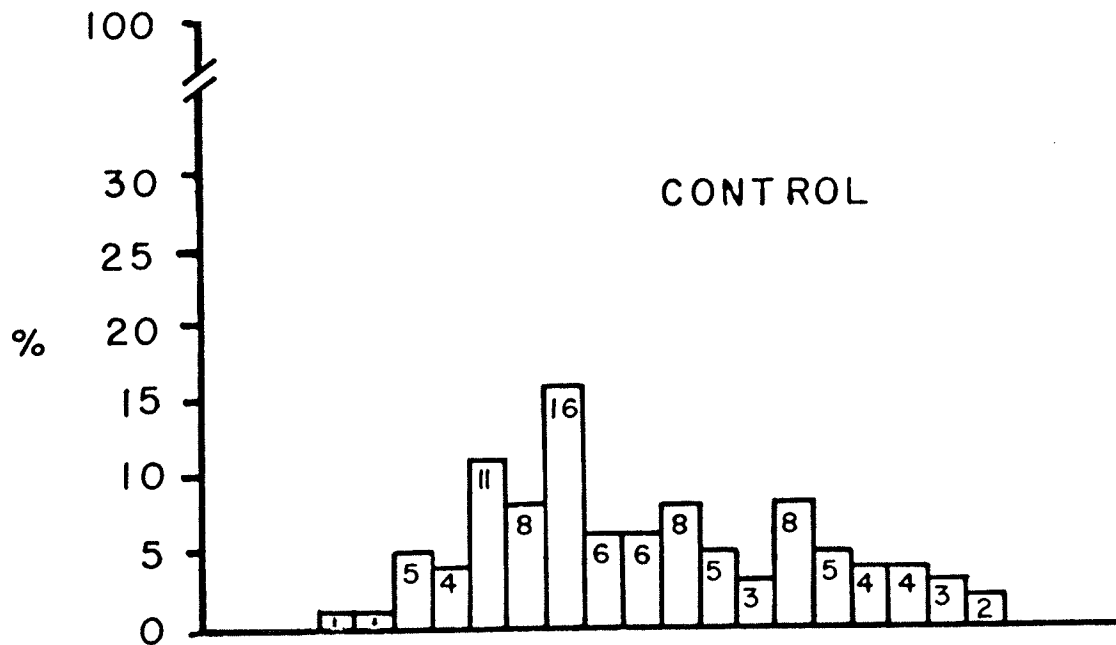
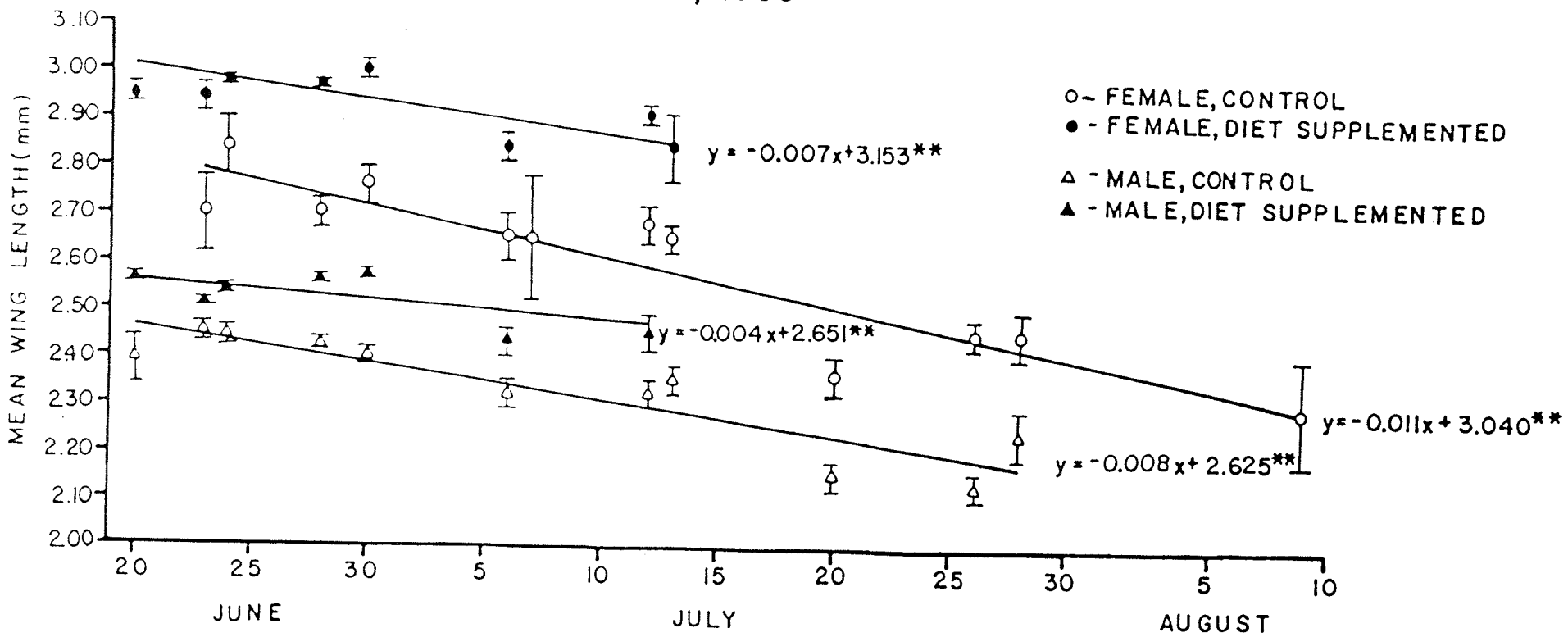


FIG.5 CHANGES IN ADULT SIZE (MEAN WING LENGTH ± S.E.)
 DURING THE SAMPLING SEASON WITHIN DIET SUPPLEMENTED
 AND CONTROL TREATMENTS, 1983



** - significant at the 0.01 level

FIG. 6 CHANGES IN ADULT SIZE (MEAN WING LENGTH \pm S.E.)
 DURING THE SAMPLING SEASON WITHIN DIET
 SUPPLEMENTED AND CONTROL TREATMENTS
 AT PATRICIA BEACH, 1984

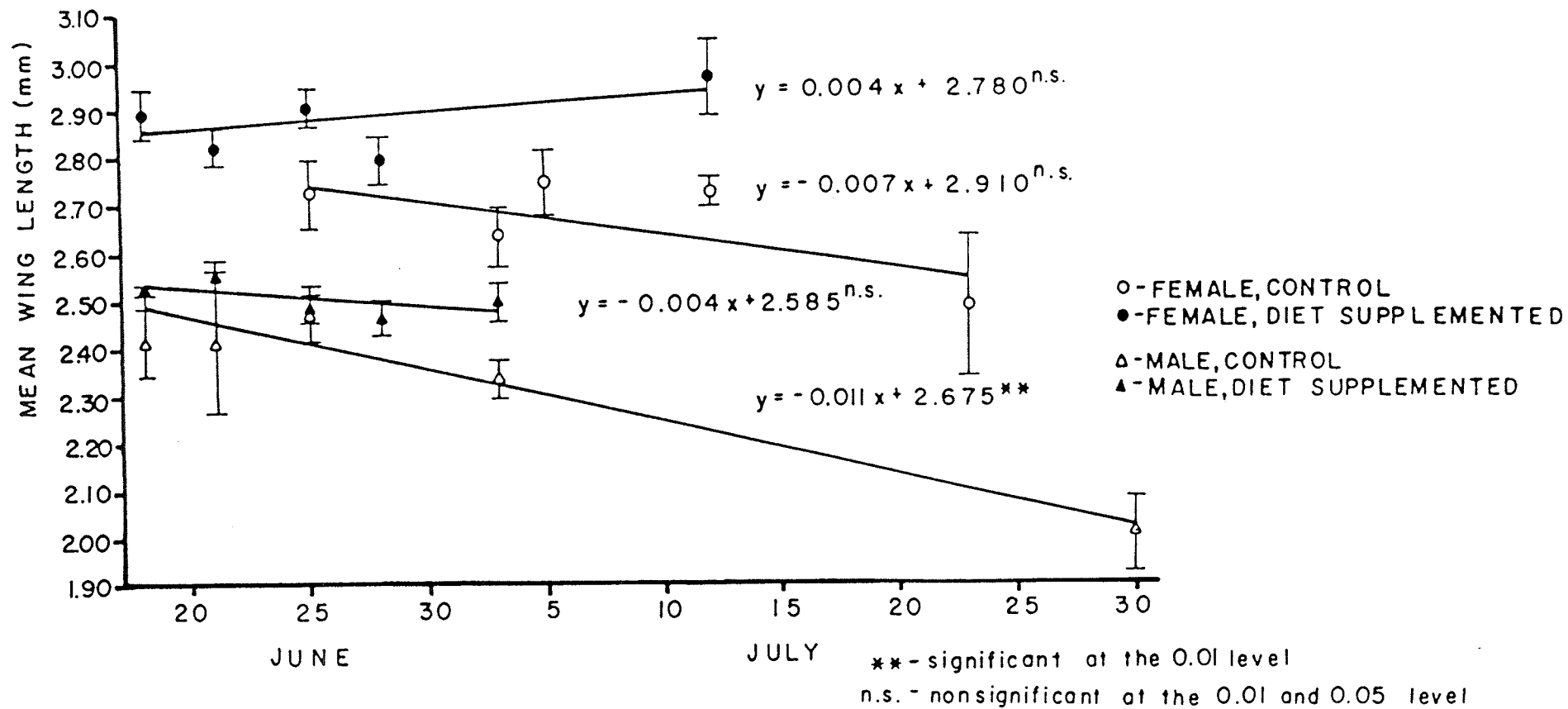


FIG.7 CHANGES IN FECUNDITY (MEAN NUMBER OF EGGS PER FEMALE \pm S.E.) DURING THE SAMPLING SEASON WITHIN DIET SUPPLEMENTED AND CONTROL TREATMENTS, 1983

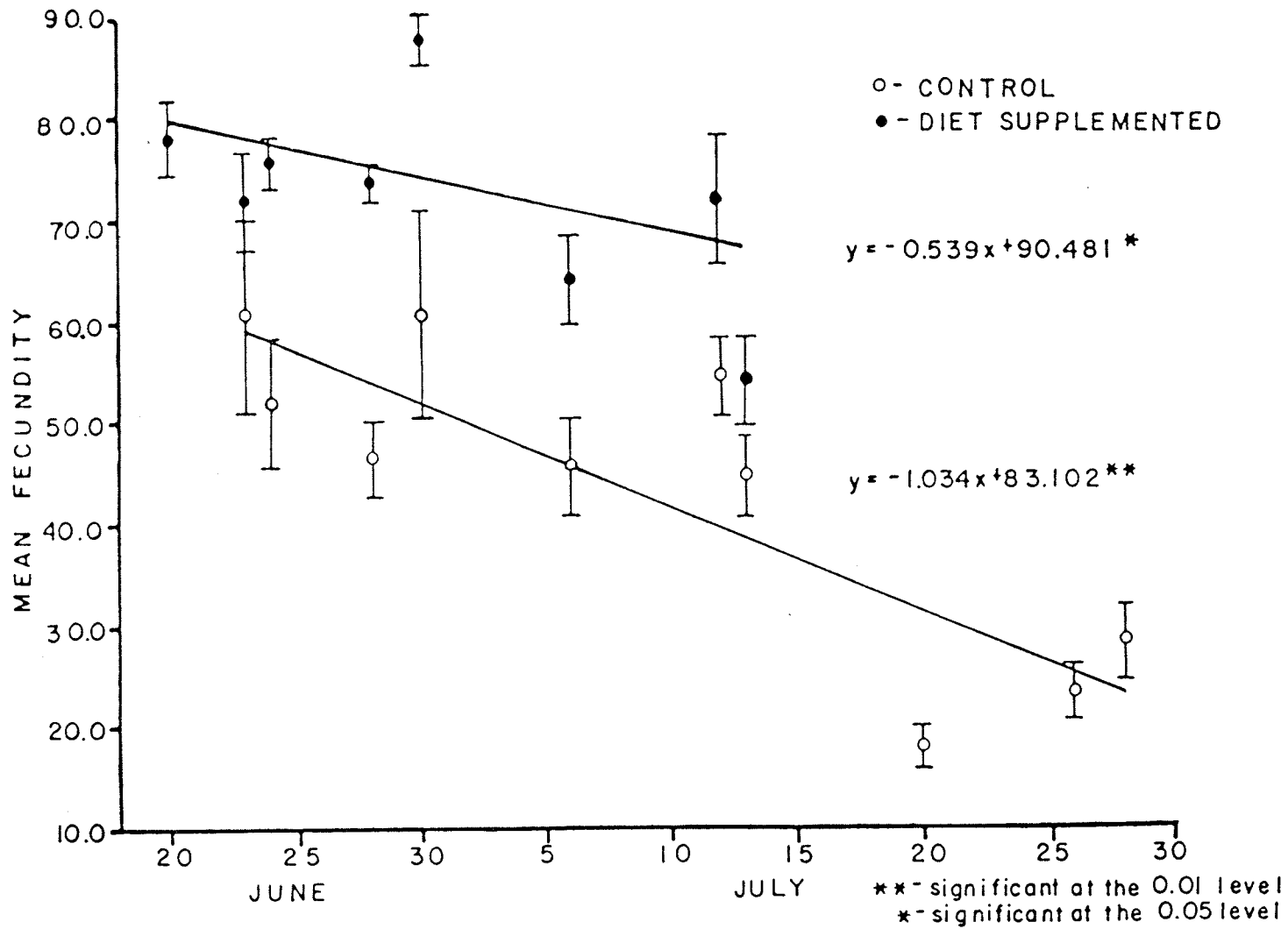
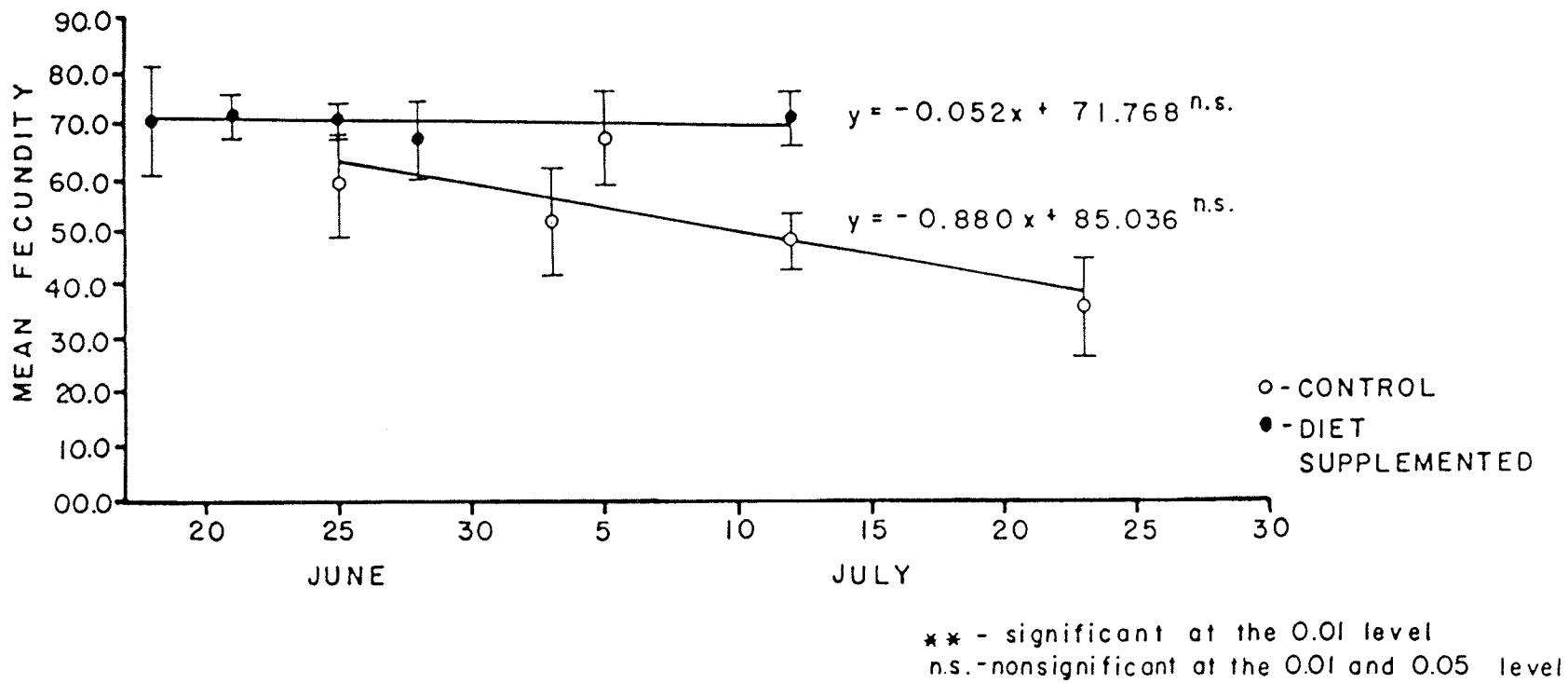


FIG. 8 CHANGES IN FECUNDITY (MEAN NUMBER OF EGGS PER FEMALE \pm S.E.) DURING THE SAMPLING SEASON WITHIN DIET SUPPLEMENTED AND CONTROL TREATMENTS AT PATRICIA BEACH, 1984



GENERAL DISCUSSION

The study of the life history pattern of W. smithii was undertaken in 1983 at three different sites (The Pas and Patricia Beach, Manitoba, and Kenora, in northwestern Ontario), and for three consecutive years (1982-1984) at Patricia Beach, Manitoba. No differences were found to occur among sites or years with respect to the general phenology of W. smithii in both one-year old and new leaves. In addition to similar phenologies, pupation times were also found to be similar at each site.

The presence of fourth instar larvae within new leaves makes it likely that these individuals produce a second generation. The incidence of bivoltinism, however, probably varies from year to year, depending upon spring and fall temperatures. In the United States, bivoltinism has been reported as far north as Michigan, although it only occurs in part of the population at this latitude (Kingsolver 1979). In the southern part of its range, several generations of W. smithii occur during a season (Goins and Folkerts 1976).

Although no overt differences were found among sites with respect to the life history parameters mentioned, it is likely that variation does occur between these populations. The critical photoperiod has been found to vary, being approximately an hour longer for larvae from The Pas than

for individuals from the other two sites (Brust, R.A. unpublished data).

The number of larvae per leaf in the spring was found to be correlated with leaf size. This relationship was found to exist within each site, as well as among sites, where the site with the largest mean leaf size (Kenora) also had the highest mean number of larvae per leaf. Similarly, the number of M. knabi (Chironomidae) larvae per leaf during the fall has been found to be correlated with leaf size (Paterson and Cameron 1982). Such relationships may simply be due to the fact that as the size of the habitat increases, W. smithii and M. knabi adults are more likely to lay their eggs there. Larger pitcher plant leaves may also be able to sustain greater numbers of larvae since they may attract more insect prey as food. Once they filled with water, the larger leaves would be more likely to provide the constant aquatic environment needed for development and overwintering.

Adult male size, adult female size and fecundity did not vary significantly among sites. Fecundity is the only characteristic of the three which has previously been measured for Manitoba W. smithii under field conditions. Evans (1971) found that the fecundity of females caught at Pinawa, Manitoba averaged 35 ± 2.5 eggs per female. This is comparable to an overall mean fecundity of 39.1 ± 1.9 (Manuscript I, Table IV) and of 39.2 ± 1.8 (Manuscript II,

Table I, control individuals) found in the present study in 1983. In 1984 (Manuscript II, Table II, control individuals), mean fecundity was higher (51.8 ± 4.4) than that obtained in 1983. In 1984, there were fewer larvae per leaf than in 1983. The larger food supply per larva may have given rise to more fecund females. It is also possible that the 1984 fecundity value may be an overestimate since it was calculated from 21 observations. The means for fecundity obtained in 1983 were each derived from over 100 observations.

Overwintering survival was low at Patricia Beach and high at The Pas during the winter of 1983-1984. This is contrary to the findings of Evans (1971) where larval survival was higher (50%) at Pinawa and Telford, Manitoba (locations comparable to the Patricia Beach site), than at The Pas, where survival was estimated at 25-35%. In order to understand why such variations in survival occurred, a detailed study of meteorological conditions would have been necessary.

The length of the fall critical period could have influenced larval survival (Pruitt, W.O. Jr. personal communication). This critical period is defined as the time interval between the fall overturn (when the temperature of the air falls below that of the surface substrate) and the hiemal threshold (when snow cover reaches a depth of 15-20 cm). During this period, temperatures in the upper substrate

can fluctuate quite markedly (Pruitt 1957), and if this occurs over an extended period of time, larval mortality can occur due to exposure to cold temperatures. The length of the fall critical period varies from year to year, but is usually shorter at The Pas due to its more northerly location (Pruitt, W.O. Jr. personal communication), and a shorter fall critical period may have contributed to the higher survival of larvae at The Pas in 1983.

Paterson (1971) found that a large number of terrestrial arthropods fell into pitcher plant leaves in New Brunswick, providing an abundant food supply for W. smithii larvae. This may be the case for larvae inhabiting young leaves, but the present study indicates that inadequate nutrition exists for the developing larvae within the pitcher plant fluid of overwintered leaves since diet supplementation enhanced the rate of larval development as well as increased adult size and fecundity. This supports the statement of Lounibos et al. (1982), that food stress undoubtedly occurs among larvae, especially after the leaves have passed peak attractivity, since the prey insects which drown in the fluid of S. purpurea are of a transient nature.

Larvae which were given a diet supplement pupated more synchronously and at an earlier date. Conversely, pupation among those individuals which did not receive a diet supplement occurred at a later date and was distributed over a longer period of time. Pupation is delayed among those

individuals which exist on an inadequate diet since the duration of the fourth instar larval stage is extended under such conditions (Moeur and Istock 1980; Lounibos et al. 1982).

Overall mean fecundity among diet supplemented individuals was similar in both 1983 (75.1 ± 1.2) and 1984 (70.5 ± 2.2). The number of eggs per female among diet supplemented individuals in 1983 was almost double that found in the control group, whereas in 1984, fecundity was increased by approximately one third. Diet supplemented individuals were also larger, and under natural conditions, this may enable them to live longer, thereby increasing the time period over which oviposition could take place.

In laboratory studies on northern strains of W. smithii, females reared from TetraMin[®]-fed larvae averaged 90.1 ± 6.0 eggs per female (Lillie and Nakasone 1982), and 86.5 ± 1.9 eggs per female (O'Meara et al. 1981). The higher fecundities recorded from these laboratory reared populations, where food was not a limiting factor for development, supports the suggestion (Manuscript II) that in the present study, larvae experienced food shortages between feedings, and consequently females did not develop a full complement of eggs.

SUMMARY

1. The phenology of W. smithii was similar between sites at The Pas and Patricia Beach, Manitoba, and Kenora, in northwestern Ontario in 1983.
2. The phenology of W. smithii was similar during all three years (1982-1984) at Patricia Beach.
3. The presence of fourth instar larvae in new leaves at all three sites indicates that a small percentage of the population may be bivoltine.
4. The number of third instar larvae per leaf was found to be positively correlated with leaf size (volume in ml).
5. Leaf size varied significantly between the sites. Kenora had the largest leaves, The Pas had the smallest leaves, and Patricia Beach had leaves of an intermediate size.
6. Larval density within leaves in the field was higher at Kenora than at the other two sites, probably due to the larger average leaf size at this site.
7. Pupation rates did not vary significantly between sites.
8. Adult male size, adult female size and fecundity did not vary significantly between sites.
9. Overwintering survival was much higher at The Pas than at Patricia Beach during the winter of 1983-1984.
10. Larvae which received a diet supplement were found to pupate earlier and more synchronously than did the control individuals.

11. TetraMin[®]-fed larvae developed into adults which were significantly larger and more fecund than the control individuals.
12. Mosquitoes which did not receive a diet supplement decreased in size and fecundity during the course of the sampling season, due to the decreasing amount of nutrition available to them.
13. Mosquitoes which received a diet supplement also declined in size and fecundity as the season progressed, although it was not as pronounced as in the unsupplemented group. Evidently, some degree of food shortage was experienced between feedings.

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Appendix 1. Changes in Adult Size (wing length in mm) and Fecundity (number of eggs per female) during the Sampling Season at The Pas, 1983

Sampling Period	Mean Male Wing Length (mm) \pm S.E. n	Mean Female Wing Length (mm) \pm S.E. n	Mean Fecundity (No. of Eggs per Female) \pm S.E. n
June 23	2.43 \pm 0.02 n=28	2.72 \pm 0.10 n=5	65.7 \pm 10.7 n=3
July 6	2.39 \pm 0.02 n=25	2.71 \pm 0.05 n=20	51.0 \pm 5.5 n=14
July 20	2.23 \pm 0.04 n=23	2.49 \pm 0.04 n=28	35.9 \pm 3.2 n=26

n=sample size

Appendix 2 Changes in Adult Size (wing length in mm) and Fecundity (number of eggs per female) during the Sampling Season at Patricia Beach, 1983

Sampling Period	Mean Male Wing Length (mm) \pm S.E. n	Mean Female Wing Length (mm) \pm S.E. n	Mean Fecundity (No. of Eggs per Female) \pm S.E. n
June 27	2.43 \pm 0.02 n=21	2.78 \pm 0.05 n=8	53.3 \pm 7.2 n=7
July 8	2.32 \pm 0.02 n=17	2.70 \pm 0.06 n=7	46.0 \pm 10.3 n=5
July 17	2.21 \pm 0.03 n=22	2.50 \pm 0.04 n=21	40.6 \pm 3.5 n=18
July 26	2.12 \pm 0.03 n=18	2.37 \pm 0.04 n=20	25.0 \pm 3.6 n=12
Aug. 12	1.93 \pm 0.08 n=3	2.23 \pm 0.13 n=3	20.7 \pm 10.3 n=3

n=sample size

Appendix 3. Changes in Adult Size (wing length in mm) and Fecundity (number of eggs per female) during the Sampling Season at Kenora, 1983

Sampling Period	Mean Male Wing Length (mm) \pm S.E. n	Mean Female Wing Length (mm) \pm S.E. n	Mean Fecundity (No. of Eggs per Female) \pm S.E. n
June 28	2.42 \pm 0.03 n=34	2.88 \pm 0.06 n=10	54.7 \pm 9.9 n=7
July 13	2.28 \pm 0.03 n=20	2.62 \pm 0.06 n=12	41.9 \pm 7.2 n=10
July 28	2.05 \pm 0.02 n=14	2.40 \pm 0.03 n=28	19.3 \pm 2.8 n=12

n=sample size

Appendix 4. Changes in Adult Male Size (Wing Length in mm)
 During the Sampling Season Within Diet Supplemented
 and Control Treatments, 1983.

Site	Sampling Date	Control		Diet Supplement	
		Mean Wing Length in mm \pm S.E.	Sample Size	Mean Wing Length in mm \pm S.E.	Sample Size
The Pas	June 23	2.45 \pm 0.02	43	2.51 \pm 0.01	55
	July 6	2.32 \pm 0.03	19	2.43 \pm 0.03	32
	July 20	2.15 \pm 0.03	15		
Patricia Beach	June 20	2.39 \pm 0.05	10	2.56 \pm 0.01	33
	June 24	2.44 \pm 0.02	20	2.54 \pm 0.01	41
	June 30	2.40 \pm 0.02	15	2.57 \pm 0.01	38
	July 12	2.32 \pm 0.03	22	2.45 \pm 0.04	6
	July 26	2.13 \pm 0.03	12		
Kenora	June 28	2.42 \pm 0.02	51	2.56 \pm 0.01	124
	July 13	2.35 \pm 0.03	21		
	July 28	2.24 \pm 0.05	9		

Appendix 5. Changes in Adult Female Size (Wing Length in mm)
 During the Sampling Season Within Diet Supplemented
 and Control Treatments, 1983.

Site	Sampling Date	Control		Diet Supplement	
		Mean Wing Length in mm \pm S.E.	Sample Size	Mean Wing Length in mm \pm S.E.	Sample Size
The Pas	June 23	2.70 \pm 0.08	5	2.94 \pm 0.03	17
	July 6	2.65 \pm 0.05	25	2.84 \pm 0.03	41
	July 20	2.36 \pm 0.04	20		
	Aug. 9	2.29 \pm 0.11	4		
Patricia Beach	June 20			2.95 \pm 0.02	15
	June 24	2.84 \pm 0.06	3	2.98 \pm 0.01	39
	June 30	2.76 \pm 0.04	10	3.00 \pm 0.02	42
	July 7	2.65 \pm 0.13	3		
	July 12	2.68 \pm 0.04	18	2.91 \pm 0.02	6
	July 26	2.45 \pm 0.03	31		
Kenora	June 28	2.70 \pm 0.03	25	2.97 \pm 0.01	117
	July 13	2.65 \pm 0.03	24	2.84 \pm 0.07	4
	July 28	2.45 \pm 0.05	10		

Appendix 6. Changes in Fecundity (Number of Eggs per Female)
 During the Sampling Season Within Diet Supplemented
 and Control Treatments, 1983.

Site	Sampling Date	Control		Diet Supplement	
		Mean Fecundity (Number of Eggs/Female ± S.E.)	Sample Size	Mean Fecundity (Number of Eggs/Female ± S.E.)	Sample Size
The Pas	June 23	60.6 ± 9.6	5	72.0 ± 4.9	16
	July 6	45.7 ± 4.9	15	64.2 ± 4.4	30
	July 20	18.0 ± 2.2	16		
Patricia Beach	June 20			78.2 ± 3.7	13
	June 24	52.0 ± 6.4	3	75.8 ± 2.5	37
	June 30	60.8 ± 10.3	4	87.8 ± 2.4	39
	July 12	54.6 ± 3.9	16	72.0 ± 6.4	5
	July 26	23.4 ± 2.8	27		
Kenora	June 28	46.5 ± 3.8	19	73.9 ± 1.9	83
	July 13	44.8 ± 4.0	20	54.3 ± 4.5	3
	July 28	28.4 ± 3.8	5		

Appendix 7. Changes in Adult Size (Wing Length in mm) and Fecundity (Number of Eggs per Female) During the Sampling Season Among Diet Supplemented and Control Treatments at Patricia Beach, 1984.

Treatment	Sampling Date	Adult Male Size		Adult Female Size		Fecundity	
		Mean Wing Length in mm \pm S.E.	Sample Size	Mean Wing Length in mm \pm S.E.	Sample Size	Mean Number of Eggs per Female \pm S.E.	Sample Size
Control	June 18	2.41 \pm 0.07	3				
	June 21	2.41 \pm 0.15	3				
	June 25	2.47 \pm 0.06	4	2.72 \pm 0.07	3	58.3 \pm 9.8	3
	July 3	2.33 \pm 0.04	9	2.63 \pm 0.06	9	51.7 \pm 10.0	6
	July 5			2.74 \pm 0.07	5	67.0 \pm 8.8	4
	July 12			2.72 \pm 0.03	4	48.0 \pm 5.2	4
	July 23			2.48 \pm 0.15	4	35.8 \pm 9.2	4
	July 30	2.00 \pm 0.08	3				
Diet Supplement	June 18	2.52 \pm 0.01	17	2.89 \pm 0.05	8	70.5 \pm 10.3	4
	June 21	2.55 \pm 0.03	9	2.82 \pm 0.04	14	71.4 \pm 4.1	14
	June 25	2.48 \pm 0.03	9	2.90 \pm 0.04	13	70.4 \pm 3.0	12
	June 28	2.46 \pm 0.04	5	2.79 \pm 0.05	4	67.0 \pm 7.2	4
	July 3	2.49 \pm 0.04	6				
	July 12			2.96 \pm 0.08	3	71.0 \pm 5.0	3