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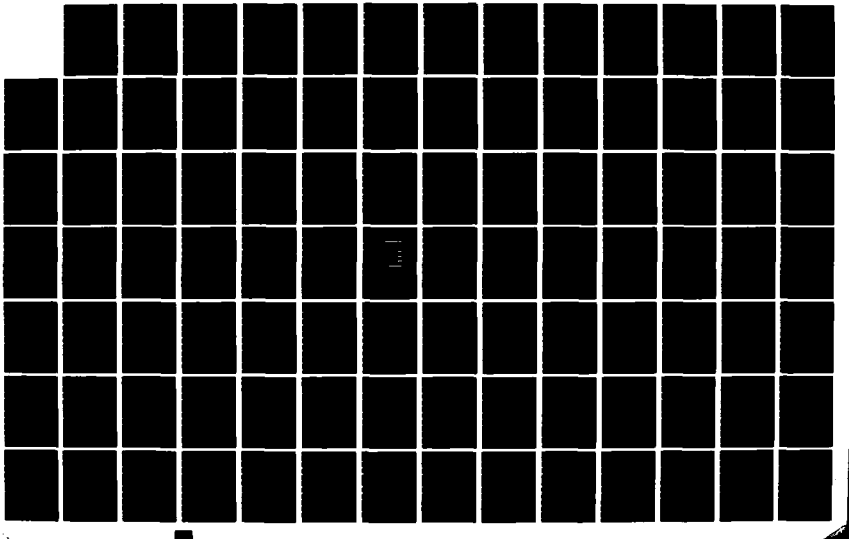

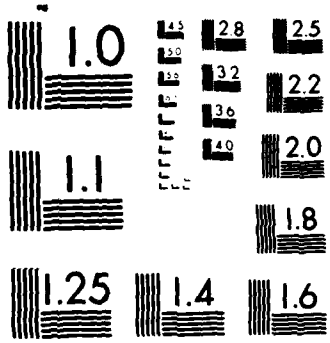

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ECOLOGY OF POSTLARVAL STAGES OF CHIGGER MITES

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The ecology of chiggers presents a complex and multidimensional set of ecological questions. The research conducted here represents a two-pronged approach to answering the most fundamental of these questions: What are the endogenous constraints which act to regulate chigger populations within a particular environment? How do chigger populations interact with their associated biotic community? To answer these questions, a combination of research was conducted combining both laboratory and field approaches.

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Eight microhabitats were sampled for postlarval Eutrombicula alfreddugesi (Oudemans) and E. splendens Ewing. Five microhabitats (soil, surface litter, tree holes, tree stumps and logs) yielded postlarvae. In the samples taken no postlarvae were found in Spanish moss, vertebrate nests or tree bark. Tree stumps yielded the most postlarvae, the greatest percent of samples with postlarvae, and the most postlarvae per 100 grams of habitat. Soil yielded the second highest number of postlarvae but contained the lowest percent of samples with postlarvae, and contained the fewest postlarvae per 100 grams of habitat.

Soil arthropod communities were analyzed and compared between sites with and without chigger larvae in three habitats: old field, woods, field-woods combined. Sites significantly higher in Mesostigmata, a primarily predaceous suborder, were devoid of chiggers. Analysis of soil communities at the generic level showed positive chigger sites significantly higher in species diversity. Competitive exclusion is hypothesized to be acting on chiggers at less diverse sites. An undetermined genus of acarid mite, known predators on quiescent postlarval stages, was significantly higher at negative chigger sites. The collembolan Folsomia, a known food source of postlarvae, and the mite Nanorchestes, a potential food source, were significantly higher at positive chigger sites.

Models of development rate and development time distribution were developed from laboratory investigations of each stage in the life cycle of Eutrombicula alfreddugesi Oudemans. The developmental rate models provide thermodynamic descriptions of the underlying biophysical mechanisms responsible for the developmental processes and are accurate descriptors of the development of each stadia ($R^2>0.90$). The distributions of development time, for each stadium, at each temperature have similar shapes and can therefore be described by a single normalized distribution which is independent of temperature. A Weibull function accurately models the normalized distribution of emergence as a function of physiological time for every stage of the life cycle

(R^2>0.95). The development of the deutonymph is unusual because the development rate does not respond systematicly to temperature change. Deutonymph cohorts may be subdivided into rapid and slow development morphs. The proportion of deutonymphs able to develop rapidly within the population increases as the temperature rises. The increase in the rapid morph is accurately described by a biophysical model (R^2-0.98) which suggests that the ratio of rapid developing deutonymphs is regulated by a secondary level of enzyme processes.

Fecundity of new E. alfreddugesi females was modeled as a function of physiological age using a Weibull distribution (R^2=0.88). This model provides a stochastic desciption of the age specific natality rate (m_x). Oviposition rate was modeled as a function of temperature (R^2=0.68). The combination of the fecundity and oviposition rate models can be used to predict both the onset of the chigger season and changes in the larval population during the season.

The integration of development and reproductive models provides a definitive technique for the investigation of the ecology of a species. These temperature driven models when combined with soil temperature profiles can predict and explain the dynamics of the natural populations of E. alfreddugesi. The proposed regulation of deutonymph development by a secondary enzyme system provides a mechanism to produce a large pulse of young adults just prior to the time when larval production should be maximized. This adaptation synchronizes the life cycles of E. alfreddugesi and it's prefered hosts, iguanid lizards so that the parasitic larval stage is most abundant only during periods when lizards, the prefered hosts are also plentiful and available to the chigger. The geographical distribution of the species is explained by the interaction of the range of developmental temperatures and the position of the optimum temperature for development.

Five methods for recovering deutonymph and adult stages of E. splendens were compared. Three involved soil and litter floatation in magnesium sulfate solution or tap water; one used a modified Ladell apparatus. Two extraction methods utilized Tullgren funnel extractors, with or without lights. Magnesium sulfate and tap water floatation, and Tullgren funnel extraction with lights resulted in greater than 90% recovery of the mites. Tullgren funnel extraction with lights, having lowest mortality rates and requiring the least labor, was the most efficient method. A calculated "extraction half-time" is proposed for estimating recovery times for postlarval chiggers from Tullgren funnels.

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CHAPTER I

INTRODUCTION

This study was undertaken to address questions about the ecology of freeliving stages of chigger mites. The chigger species, Eutrobicula alfreddugesi (Oudemans), was chosen as the principle species for study because it has the widest geographic range of all American species encompassing both tropical and temperate environments (Jenkins 1947) and a wide diversity of acceptable hosts including mammals, birds and reptiles. The combination of these factors provide the maximum potential for transfer of models and insights to other species that are constrained by more restrictive environmental requirements which may be considered subsets of E. alfreddugesi's niche parameters.

The contributions made by this project to our understanding of Trombiculid mite biology may be divided into several catagories: (1) Comparison of microhabitats for pest chigger abundance, (2) Detailed taxonomic description of the biotic associates of chigger infested sites and (3) A comparison of the soil fauna from ecologically-similar, chigger-free and chigger-infested sites, (4) Development of temperature driven development models for each of the seven life stages and, (5) Analytic models of physiological time for the eclosion/emergence of each stage, (6) Development of fecundity model on a physioilogical time scale and a temperature-dependent oviposition rate model, (7) Improvement of field and laboratory

techniques necessary for the ecological and bionomic analyses used for categories 1-6.

The habitat analysis phase of this study involved identification of postlarval E. alfreddugesi and E. splendens Ewing microhabitats (Chapter II). Microhabitats of E. splendens were investgated because this is the common pest chigger along the Georgia coast. Low numbers of postlarvae found in these microhabitats led to questions regarding the effectiveness of extraction methods. Evaluation of extraction methods (chapter VII) confirmed that postlarvae were being extracted from samples efficiently and that low numbers in collections were due to low abundance of postlarvae in the field. Consequently, analysis of biotic associations of E. alfreddugesi postlarvae, specifically the associated soil arthropod communities, was conducted at sites with chigger larvae, for where unfed larvae occur, adults must be in close proximity. Comparisons of arthropod communities were then made from sites with and without chigger larvae (chapter III).

The developmental rates of each stage, from the egg to the tritonymph, will be the focus of chapter V. The analysis of larval development is confined to the time from detachment after feeding until development to the protonymph is completed. This decision to consider the post detachment period of larval development was based on two points: The first is the developmental bottleneck caused by the parasitic nature of the larval period. As in other parasites, e.g., ixodids, the chigger's developmental processes are arrested until a host meal

is obtained, ,after which, development proceeds without need of additional nutrition (Balashov 1972). Secondly, because the development of the larva is rapid after feeding, the differences induced by the variability in chigger attachment and feeding rates at different sites on the host, and the variability resulting from physiological differences between each host would be sufficient to "swamp out" the differences in development at the warmer temperatures. The models used in chapters IV and V of development rate response to temperature and distribution of development times as a function of physiological time are based on the thermodynamics of absolute reaction rates in biological systems. This provides the foundation on which new hypotheses can be built and strategies for their evaluation.

The influence of temperature on the rate of reproduction is the topic of chapter VI. This is the first experimental analysis of ovipositional response to change in temperature reported for any chigger species. Changes in larval population in the field may be considered an indirect measure of reproductive rate. The literature has numerous reports of larval abundance for many species (Wharton and Fuller 1952, Wharton 1946, Jenkins 1947, Jones 1950, Richards 1950, Loomis 1956, Daniel 1958 and 1961). All observed that species occur in an annual seasonal cycle and hypothesize a relationship between temperature or precipitation as the environmental factor responsible for the boundries of the cycle. The statistical analysis of the oviposition rate models used in chapter VI provide an estimate of the extent to which temperature

determines the oviposition rates indicated by larval population changes in the field.

Equally important to the understanding of chigger population dynamics is the changes in fecundity rates as the adult population ages. This is represented in life tables as the age specific natality rate (m_x). Fecundity rates are not temperature dependent as are daily oviposition rates but are determined by the physiological age of the female. Life tables describe the natality rate as the average offspring production per age interval. The accuracy of this practice is limited due to the descrete values placed on a stochastic process. A far more accurate and meaningful description utilizes a distribution curve which is able to show the changes in reproductive ability as a continuous population variable (Sokal and Rohlf 1981). The stochastic model of fecundity defines the characteristic distribution of the reproductive potential of a population of E. alfreddugesi as a function of physiological age in the same way as the deterministic rate curves described earlier define physiological response attributes.

The integration of the eco-physiological and community composition studies provides a holistic discription of the ecology of trombiculid free living stages. These studies have advanced our understanding of chigger bionomics sufficiently that predictive models can be generated which function both as the basis for decision making in control programs and as a source for the construction of meaningful hypotheses concerning the structure and function of soil microarthropod systems.

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CHAPTER II

HABITAT SELECTION OF POSTLARVAL *EUTROMBICULA ALFREDDUGESI* AND *EUTROMBICULA SPLENDENS* FROM EIGHT MICROHABITATS

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INTRODUCTION

Postlarval Trombiculidae are free-living predators in soil and litter habitats (Krantz 1978), but are rarely collected in the field (Farner 1946, Brown 1952, Crossley 1960). Hirst (1926) hypothesized that postlarval chiggers would be found in nests of their vertebrate hosts. However, Andre (1928) and Keay (1937) investigated nests of bank voles (*Clethrionomys gloreolus*) and rabbits (*Oryctolagus cuniculus*) that were infested with chigger larvae, and failed to find postlarvae. A number of authors have collected postlarval chiggers from various habitats. Sasa 1960, reports Kawamura and Ikeda (1936) as collecting adults of *Trombicula akamushi* Nagayo *et al*. from soils in Japan. They reported that postlarvae were most abundant in the upper 3 cm of the soil, and that some adults were recovered as deep as 18 cm. Cockings (1948) and Jones (1950) collected adults of the "Harvest mite," *Trombicula autumnalis* Shaw, from soils, but the depth at which postlarvae were found depended on temperature and soil moisture. Cockings

(1948) reported that T. autumnalis migrates upward to within 10 cm of the soil surface during summer when soil is moist, and maximum soil

surface temperature reaches 26.6°C. However, the majority of adult T. autumnalis were found between 10-20 cm below the soil surface and usually within 4.6 meters of rabbit burrows. Cockings (1948) also reported that adult T. autumnalis go deeper in the soil following heavy, continuous rains, irrespective of temperature, or during prolonged droughts. Adults of T. autumnalis have been collected at depths of 30.5-45.7 cm (Cockings 1948), and Richards (1950) reported collecting adults as deep as ca. 1 meter. Jones (1950) reported that adult Eutrombicula batatas L. and Trombicula scutellaris Nagayo et al. are abundant on the soil surface in tropical areas, especially during the wet season. Nadchatram (1970) collected postlarval stages of chiggers (Leptotrombidium akamushi Nagayo et al.) from soils. Loomis (1954) collected nymphs and adults of Eutrombicula alfreddugesi (Oudemans) from soil underneath large flat limestone slabs, and in decaying logs, just beneath the loose bark and in the decomposing wood. Wolfenbarger (1952) collected deutonymphs and adult E. alfreddugesi under rocks in wooded areas immediatelv after rains, and on warm sunny days, in open pastures a few centimeters beneath the soil surface in cracks and crevices made by grass roots.

The purpose of this study was to investigate habitat

selection of postlarval stages of Eutrombicula alfreddugesi and E. splendens (Ewing). This information may contribute to our understanding of chigger mite infestations and control.

MATERIALS AND METHODS

Eight microhabitats were sampled for active postlarval stages (deutonymph and adult) of Eutrombicula spp., over a two year period. Microhabitats examined were soil, surface litter, tree holes, tree stumps, Spanish moss (Tillandsia usnoides L.), logs, nests, and tree bark. Forests, fields and disturbed habitats, were sampled on the Piedmont in Athens, Clarke County, Georgia. Sand dunes and coastal woodlands were sampled on the coastal plains at St. Simons Island and Jekyll Island, Glynn County, Georgia.

Soil habitats examined in this study were sampled by taking ca. 5 x 5 cm and 5 x 15 cm soil cores, and by using a 20 x 20 x 5 cm square soil sampling device. Soils examined ranged from nearly pure sands from the Jekyll Island sand dunes to heavy clay soils of the Georgia Piedmont.

Surface litter microhabitats consisted of coniferous and deciduous leaf litter and other organic debris in various stages of decomposition. An average of 359.7 grams of surface litter per sample was collected for extraction. Tree stumps examined in this study were all Pinus spp. in advanced stages of decay, and could easily be torn apart by hand. Much of the wood in

decomposing tree stumps was soil-like in texture. An average of 707.6 grams per sample of stump material was collected for extraction. Tree holes examined in this study were from Live Oak (Quercus virginiana L.) and were located on the ground at the base of trees, or were from one to five meters off the ground. Material examined from tree holes consisted of accumulated soil and other organic debris. Samples of Spanish moss were collected from the ground and trees. Collections of nests and nest materials were made from recently abandoned bird and mammal nests. Tree bark, from live and dead trees, and logs were examined visually, usually in the field. Only instances when postlarvae were found from logs or bark were recorded.

"Total habitat" is defined here as the total amount of microhabitat examined, and "positive habitat" is the portion of respective microhabitat in which postlarve were found.

Funnel extraction or flotation methods were used to extract postlarval chiggers from soil, tree hole, tree stump, surface litter, nests, and Spanish moss habitats (Mallow and Crossley 1984). Postlarvae collected alive were kept alive for laboratory cultures. Other postlarvae were preserved in 90% ethyl alcohol or mounted on slides.

RESULTS

A total of 94 postlarval Eutrombicula were collected from the various microhabitats. All postlarvae collected from the

Georgia Piedmont were identified as E. alfreddugesi and all postlarvae from the coastal plain were E. splendens. Active postlarval chiggers (deutonymphs and adults) were collected in five microhabitats (soil, surface litter, tree stumps, tree holes, and logs). No postlarvae were found in Spanish moss, vertebrate nests, or tree bark. Results of the postlarval collections are summarized in Table 1.

The highest number of postlarvae (46) was collected from rotting tree stumps. This habitat also contained the highest percentage of samples with postlarvae (25.4%), and the most postlarvae per 100 grams of positive and total habitat (3.5 and 1.0 respectively). Soil yielded the second highest number postlarvae (26). However, soil had the lowest percent of samples with postlarvae (1.8%), and the lowest number of postlarvae per 100 grams of positive and total habitat (1.9 and 0.1 respectively). Tree holes contained the third highest number of postlarvae collected (14) and percent of samples with postlarvae (7.7%). Tree hole microhabitats also contained the second highest number of postlarvae per 100 grams of positive habitat and total habitat (1.6 and 1.0 respectively). The fewest postlarvae were collected from surface litter (8), which also contained the lowest number of postlarvae per 100 grams of positive habitat (1.9). Surface litter had the second highest percent of samples with postlarvae (15.4%), and the third lowest number of postlarvae per 100 grams of total habitat. Nine

postlarval Eutrombicula were collected from logs.

DISCUSSION

The collection of only 94 individual postlarval Eutrombicula (E. alfreddugesi, E. splendens) from over 1400 samples confirms reports by Farner (1942), Brown (1952) and Crossley (1960) that postlarval stages of trombiculid mites are rarely collected. It was feared that the low number of postlarvae collected was due to low efficiency of extracting deutonymph and adult chiggers from environmental samples. However, Mallow and Crossley (1984) showed that postlarvae could be extracted from soil and litter habitats with greater than 90% efficiency.

The absence of postlarvae in vertebrate nests is in agreement with Andre (1928) and Keay (1937). Contrary to reports by Loomis (1954), no postlarvae were collected within or underneath bark, from either live trees or dead and decaying logs. Also, contrary to popular folklore, no chiggers, either larvae or postlarvae, were collected from Spanish moss.

Most published reports of postlarval habitat preference indicated soil to be a favored habitat. However, my data failed to show this. Significantly more soil samples were taken than from any other positive postlarval microhabitat (litter, tree stumps, tree holes, logs), yet the soil habitat yielded only the second highest number of postlarvae, the lowest percent of

samples with postlarvae, and the lowest number of postlarvae per 100 grams of positive and total habitat. Once again concern arose over whether our methods were effective, specifically whether soil samples were taken deep enough, comparable to depths reported by Cockings (1948) and Richards (1950) (30.5-45.7 cm, ca 1 meter, respectively). However, more than 95% of all soil samples taken were from the Georgia Piedmont, where the soil has a heavy clay dead pan approximately 7-10 cm below the soil surface. It is unlikely that many microarthropods, particularly those as large as postlarval trombiculids could penetrate beyond this depth. Over 58% of all postlarvae recovered from soil were collected from the Georgia Piedmont. The remaining postlarvae were collected from soils on the Georgia coastal plain (42% of total postlarvae from soil, from 5% of total soil samples). Soils from the Georgia coast are very sandy, and consequently porous, permitting even large microarthropods to migrate down to deeper soil layers. Although soil samples were not taken deeper than 15 cm in this porous coastal soil, I feel the efficiency of collecting postlarvae from this habitat was not compromised for two reasons. First, a relatively high number of postlarvae were collected from a small number of samples, compared with soil samples from the Piedmont. Secondly, a much larger number of postlarval E. splendens were collected from tree stumps and tree holes than from soils on the coastal plain. This suggests that soil is not a preferred

habitat for E. splendens in coastal habitats.

Tree stumps in advanced stages of decomposition yielded the highest number and greatest percent of total samples with postlarvae. However, only tree stumps from the coastal plain (77.8% of total tree stump samples) yielded postlarvae (E. splendens). No postlarvae were found from tree stumps on the Georgia piedmont. Tree stumps also yielded the highest number of postlarvae per 100 grams of positive and total habitat. Tree holes were only sampled from the coastal plain and all postlarvae recovered from this microhabitat were E. splendens. Deciduous trees on the Piedmont which had tree holes were devoid of chigger larvae and therefore were not sampled.

Surface litter yielded the lowest number of postlarvae, but was still apparently a preferred postlarval habitat over soil because litter contained a greater percent of samples with postlarvae and larger number of postlarvae per 100 grams of habitat. More than 62% of all postlarvae recovered from surface litter were collected from the coastal plain from only 36.5% of all litter samples examined.

Over 30 postlarvae were collected in the field by direct observation. Of these, nine were from logs. The remainder were from rotting tree stumps. However, it should be noted that the ratio of postlarvae found to time spent examining logs and stumps was low. Therefore, it is recommended that postlarvae be collected by passive extraction techniques such as funnel

extraction or flotation.

In conclusion, the information gained from this study serves as a first attempt to quantify the distribution of postlarval pest chiggers. Through an understanding of habitat preference and other ecological parameters, new methods of control may be directed at these postlarval stages. Because postlarvae occur in such low numbers, control methods may be more effectively directed at these life stages than at the more ubiquitous parasitic larvae.

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Table 2-1. Summary of habitat selection by postlarval *Eutrombicula alfreddugesi* and *E. splendens* recovered from microhabitats in Georgia.

	Soil	Litter	Tree Stumps	Tree Holes
Total samples examined:	1255	52	63	39
Mean weight per sample (grams):	230.4	359.7	707.6	353.0
Number of postlarvae collected:	26	8	46	14
Percent samples with postlarvae:	1.8%	15.4%	25.4%	7.7%
Number of postlarvae per 100 grams positive habitat:	1.9	1.9	3.48	1.64
Number of postlarvae per 100 grams total habitat:	0.08	0.48	1.03	1.02
Number of samples with postlarvae:	22	8	16	3

CHAPTER III

BIOTIC ASSOCIATIONS OF EUTROMBICULA ALFREDDUGESI

Submitted: Pedobiologia (1985).

INTRODUCTION

The family Trombiculidae is comprised of mites collectively known as chiggers, the larval stages of which are obligatory vertebrate parasites. Eutrombicula alfreddugesi, the common pest chigger on the Georgia Piedmont, is the species examined in this investigation. After attaching to a host, E. alfreddugesi larvae feed up to four weeks (Sasa 1960). Once engorged, the larvae fall to the ground, and pass through the remainder of their life cycle in the soil ecosystem.

No apparent environmental cue is known that determines where engorged larvae will drop off their hosts. Once engorged larvae enter the soil ecosystem, their ability to survive, successfully metamorphose into adults, and consequently produce more larvae may be dependent on biotic and/or abiotic soil conditions. As a result, E alfreddugesi larvae may or may not occur in habitats that are of similar appearance. Even within a given area, populations of chigger larvae will occur at some sites and not at others.

The purpose of this study was to determine whether biotic conditions specifically soil arthropod communities, differed at sites with and without populations of E. alfreddugesi. Owing to the infrequent occurrence and low abundance of chigger

postlarvae, comparisons of soil arthropod communities are made between sites with and without larval chiggers, for where the unfed larvae occur, postlarvae must have occurred at some point in time (Farner 1946, Brown 1952, Crossley 1960).

It is hypothesized that soil arthropod community structure influences the distribution of E. alfreddugesi through predatory and competitional effects. Predation and competition are prominant among many factors influencing structure and composition of biotic communities. Laboratory and field studies investigating the influence of predation and competition on community structure, or on the presence or absence of their component parts, are numerous. Reise (1977) found that predatory pressure affected benthic community structure. Presence of even a single predatory species has been shown to directly affect population dynamics of sympatric species. For example, Wurtzian (1977) reported that the presence of a predatory crab Pilumnus hirtellus (Leach) prevented settlement, and thereby the distribution of the brittle star Ophiothrix quinquemaculata (D. Chiaje). The predator's role in governing community compositon and structure may also be a result of their regulatory control of competition. Paine (1966) stated that removal of a predator ("keystone predator") on intertidal rocks increased interspecific competition, greatly reducing herbivore diversity to the point of exclusion.

Woodin (1974) stated that predatory pressure was not entirely responsible for establishing species abundance patterns. Instead, biological interaction, in the form of

competition, was of primary importance. Interspecific competition can arise through a multitude of factors in the niche hypervolume. Of these factors, competition for space and food have been rigorously investigated (Gause 1932, Beauchamp and Ullyott 1932, Frank 1952, Connell 1961a,b, Park 1962, Gordon 1972, Jackson 1977, Eagle and Hardiman 1977). Nicol (1961a,b) has found evidence to suggest that biotic competition may also be responsible for some extinctions.

Soil arthropod communities are very complex, consisting of individuals from all trophic levels (Wallwork 1981). It is inevitable that chigger postlarvae interact with the soil arthropod communities in some capacity. For example, deutonymph and adult stages are predatory on a variety of arthropods and their eggs (Lipovsky 1954). Competition for prey among deutonymphs, adults and between other predatory soil arthropods is likely (Crossley 1960, Dindal 1973). Also, proto- and tritonymphal stages lying quiescent in the soil may be a potential nutrient source succumbing to mortality by a variety of predatory soil arthropods. Likewise, deutonymphs, adults, eggs and deutova of trombiculid mites may also be preyed upon. Therefore, soil arthropod communities found at sites with and without populations of Eutrombicula alfreddugesi (Oudemans), were investigated to determine the following:

1) Are certain soil arthropod taxa present where chigger populations occur?

2) Are chigger populations absent from areas where certain soil arthropod taxa occur?

3) Are there differences in soil arthropod communities with respect to species diversity that may influence the presence or absence of chigger populations?

SITE DESCRIPTION

This study utilized three areas located in Clarke County, Georgia. The Simonton Bridge Road (SBR) area is located at the University of Georgia School of Forestry research area in Whitehall Forest. The specific sampling area was located 1.13 km west of the main entrance to Whitehall Forest. A transect starting 12.9 meters off Simonton Bridge Road extended southward into the sampling area. Twelve wooden stakes were placed four meters apart along the transect. The transect was elevated slightly when proceeding from stakes one to six and was angled 90° right, two meters past the sixth stake. The SBR area consisted of deciduous and coniferous hardwoods, and open areas of grass, weeds, and shrubs. Dominant species of hardwoods were Water Oak, (Quercus nigra L.), Southern Red Oak (Q. falcata Michaux), Dogwood (Cornus floridana L.), Red Cedar (Juniperus virginiana L.), Loblolly Pine (Pinus taeda L.), and Hawthorne (Crataegus sp.). Shrubs consisted predominantly of Vaccinium sp. and Lespedeza sp. Numerous grasses were present (Panicum sp. and other Gramineae spp.), as well as the grape vine, Vitis rotundifolia L. Litter descriptions are based on Heatwoles (1961) classification. Surface litter at the SBR area was comprised chiefly of pine needles lying flat upon each other, resulting in small interstitial spaces in the leaf litter.

Numerous logs occurred randomly scattered on the ground.

The remaining two areas were located 33.7 meters north of the rose garden in the University of Georgia Botanical Gardens. A single transect comprised of 12 stakes, three meters apart, crossed both sampling areas. The first six stakes of the transect crossed through an old field which ran parallel with overhead electric power lines. Vegetation primarily consisted of numerous shrubs, grasses and herbaceous growth. The dominant species of shrub was Privet (Ligustrum sinense L.). Herbacious growth consisted of Goldenrod (Solidago spp.), Camphorweed (Heterotheca subaxillaris (Lam.) Brittan and Ruby), Ragweed (Ambrosia artemisiifolia L.), Sunflower (Helianthus hirsutus Raf.), Ruellia carolinensis (Walter) Steudel, Prunella vulgaris L., Rubus sp., and Verbesina sp. Various grasses (Triodanis perfoliata (L.) A. DC., and other Gramineae spp.). Grape vines (Vitis rotundifolia) and several small Post Oak trees (Q. stellata Wang) were also present. Ground cover in the Botanical Garden Field (BGF) area was composed chiefly of dead Rubus sp. stems, which formed a nearly continuous carpet. However, the ground cover around stake six, which was on the border between the old field area and the Botanical Garden Woods (BGW) area was composed primarily of curled and bent leaves forming discontinuous, randomly-distributed heaps.

The remainder of the Botanical Garden transect (stakes 7-12) crossed through a mixed deciduous woods (BGW area), with very little surface vegetation. Dominant tree species were Red Oak (Q. rubra Rich.), Black Oak (Q. velutina Lam.), Hickory (Carya

sp.) and Winged Elm (*Ulmus alata* Michaux). Holly (*Ilex opaca* Aiton), the dominant surface vegetation, was randomly scattered throughout the woods. Surface litter varied between areas with curled, bent leaves having large interstitial spaces imparting a loose structure to the litter layer; areas with thick and thin leaves lying flat upon each other leaving small interstitial spaces, and areas of litter composed of woody materials.

The three areas investigated in this study were chosen for two main reasons. First, all three sites were known to contain chigger populations for at least three years prior to this study. The second reason is that the existence of chiggers in the BGF and BGW areas represent sharply contrasting habitats in which to study the biotic associates of chiggers. These two sites not only represent contrasting habitats with regards to vegetational and structural complexity, but also between a disturbed habitat, (BGF), which is maintained as a field for easy access to the electric power lines that run above it, and an undisturbed habitat, the BGW area. The SBR area represents a habitat that is intermediate between the BGF and BGW areas. The SBR area not only incorporates the dichotomy of field and wooded habitats, but also contains an area at the beginning portion of the transect nearest Simonton Bridge Road that is subject to mowing.

MATERIALS AND METHODS

Soil cores, ca. 5 cm in diameter by ca. 6 cm deep, were taken from a square meter area around each stake at each study

site. A single soil core was taken every two weeks for one year. Soil cores were wrapped in aluminum foil, taken to the lab, weighed, then placed on modified Merchant-Crossley high gradient extractors (Merchant and Crossley 1970). Soil arthropods were collected in vials containing 90% ethyl alcohol, 10% glycerine.

Acarina and Collembola were sorted and identified to genus whenever possible. All other arthropods were identified to class or order.

Designation of positive and negative chigger sites was based on frequency of positive ocurrences of larval chiggers during eight sampling dates of the chigger season (June-September). Three black vinyl chigger samplers (modified from Crossley and Proctor 1970), 9 cm x 14 cm x 0.15 cm, were placed around each stake for a two minute period, and the presence or absence of chigger larvae was recorded. Frequency of positive chigger occurrences over the chigger season is shown in Figure 3-1. Stakes were designated as "positive chigger sites" if chiggers were present on samplers seven or more dates during the chigger season. Likewise, stakes were designated as a "negative chigger site" if chiggers were present on the samplers two or fewer dates. Stakes with positive responses to three to six dates were eliminated from analysis.

Quantitative and qualitative analysis were performed on the soil arthropod data from both positive and negative chigger sites. Quantitative analysis utilized four nonparametric tests; Wilcoxon, Newman-Keuls, Mann-Whitney and Kruskall-Wallis. Data

were not transformed because nonparametric analysis does not require assumptions of normality (Zar 1980). Several significant differences are reported at the $p < .10$ level. The significance levels are accepted at larger alpha levels because a-posteriori nonparametric analysis utilized in this study inflates the alpha level thus increasing the chance of making Type I errors in the multiple comparisons (Gibbons 1976). The second reason is the large variance inherent in soil arthropod data (Hughes 1962, Nef 1962).

Owing to the low numbers of astigmatid mites collected in this study, they were eliminated from any order-suborder quantitative analysis. Also, because the group collectively designated as "miscellaneous" encompasses such a wide diversity of arthropods, quantitative analysis of this group were also eliminated.

Qualitative analysis involved comparisons of soil arthropod genera from positive and negative chigger sites, utilizing various indices of species diversity. Comparisons of soil arthropod diversity were made between the three study areas and between positive and negative chigger sites using Margalef (1958) and Pielou (1966) indices. Margalef indices were statistically compared using Kruskal-Wallis, Newman-Keuls and Mann-Whitney tests (Hutcheson and Slenton 1974, Zar 1974 and Sokal and Rohlf 1981).

RESULTS

By using vinyl chigger samplers, positive sites (with

chiggers) and negative sites (without chiggers) were identified (Table 3-3). The percent of positive chigger occurences was calculated for all three sites independently, from all locations on their respective transects, over the entire chigger season (June-September). The SBR area exhibited positive chigger occurrences 72.2% of the time, BGF area 66.7% and the BGW area only 35% of the time.

Table 3-2 shows the dates when significant differences occurred between major microarthropod groups from positive and negative chigger sites, when data from all three study areas were pooled. On the 4 March 1983 sampling date, negative chigger sites were significantly higher ($p < .05$) than positive sites for all groups including total microarthropods (Collembola and Mesostigmata significantly higher at $p < .10$ level).

Pooling data from all sample dates, for each area independently (Table 3-3), shows several significant differences between the major orders and suborders from positive and negative chigger sites. Prostigmata were significantly higher at positive sites in the BGF ($p < .05$) area, and Mesostigmata were significantly higher at negative sites in both the BGF and BGW areas ($p < .05$). Collembola were significantly higher in negative sites in the BGW area ($p < .05$). Both total microarthropods and Acarina were significantly higher at negative sites in the BGW area only ($p < .05$, $p < .10$ respectively).

A total of 198 soil arthropod genera were collected during this study (Appendix A). Of this total, 24 genera were not

"microarthropods" (mites or Collembola) but are considered "mesoarthropods". Mesoarthropods are included in the qualitative analysis because they are part of the soil ecosystem, and interact with biotic communities at least for some part, if not all their life cycle.

Several genera of soil arthropods were collected exclusively at positive or negative chigger sites. However, the number of individuals collected in each of these genera was too low to make any conclusions regarding their importance in influencing the presence or absence of chiggers.

Statistical comparisons using Newman-Keuls and Mann-Whitney nonparametric tests, were made between genera found in both positive and negative chigger sites (genera from all three study areas pooled) which comprised greater than 1.0% of their respective totals. The Oribatid genera Ceratozetes sp. and Peloribates sp., and the astigmatid "Acaridae sp. II" were significantly higher ($p < .05$) in negative chigger sites than positive chigger sites.

The Oribatid Tectocepheus sp., the prostigmatid Nanorchestes sp. and Cunaxidae III group (Cunaxoides sp. and Neocunaxoides sp. combined) as well as the collembolan Folsomia sp., were all significantly higher ($p < .05$) at positive chigger sites than negative sites.

Table 3-4 shows the results of comparing soil arthropod diversity from the three study areas (all dates and positive and negative chigger site genera combined). The SBR area had significantly higher soil arthropod diversity, in the form of

higher species richness, than both the BGF and BGW areas. The BGF area exhibited the highest evenness component of species diversity, followed by the SBR and BGW areas respectively.

Species diversity comparisons between positive and negative chigger sites, from each study area (Table 3-5) showed positive chigger sites at the SBR and BGF areas had significantly higher arthropod species diversity than their respective negative chigger sites. However, negative chigger sites at the BGW area had significantly higher species richness than positive chigger sites.

The results of comparing soil arthropod diversity from positive and negative chigger sites, pooling data from all three study areas and all sampling dates are shown in Table 3-6. Both Margalef and Pielou diversity indices were higher at positive chigger sites than negative chigger sites.

DISCUSSION

The randomized design of transects through chigger infested areas, and the designation of positive and negative chigger sites along these transects by use of chigger samplers showed that chigger larvae consistently occur at some sites and not at others, even within seemingly homogeneous habitats. Abiotic factors such as humidity, temperature and photointensity may partly explain why chiggers at all positive sites did not test positive 100% of the time (Cockings 1948, Sasa 1960). Likewise, negative chigger sites did not test negative 100% of the time possibly due to relatively rare occurences of

horizontal dispersal of a few larvae away from positive sites. Chigger larvae are negatively geotropic (Sasa 1960) and migrate vertically upwards which improves their opportunity of host attachment. However, the actual degree and frequency of horizontal dispersion by chigger larvae has yet to be quantitatively determined.

The results of testing the three study areas for the presence of chigger larvae have shown that the SBR area yielded the highest percent of positive responses. This finding indicates that mixed habitats may be more suitable as chigger habitats. The heterogeneity of vegetational types (grasses, shrubs, trees) and diversified structural complexity of the SBR area is condusive to supporting a wide variety of potential vertebrate hosts for chigger larvae to feed on. Since E. alfreddugesi will engorge on most terrestrial vertebrates (Wharton and Fuller 1952), availability of a large selection of vertebrates will insure that a greater percentage of larvae will make it to some postlarval stage.

Predatory soil arthropods found in chigger habitats play a double role in influencing chigger presence or absence. The first role is that of competitors. Competition for prey between chigger deutonymphs and adults, and other predatory soil arthropods will occur to some degree. Deutonymph and adult chiggers are among the slower soil microarthropod predators (personal observation). Consequently, they may not be as efficient as other predatory species in areas of limited prey abundance. Also, many predatory species of soil microarthropods

are similar in size and other morphological features. This may cause competition to arise between members of this trophic level for other dimensions in the niche hypervolume such as shelter, moisture regimes, and vertical distribution in the soil strata. Therefore, chigger postlarvae may be subject to competitive exclusion.

The second role predatory soil arthropods may play regarding chigger presence or absence is the degree of predation they exert on the chiggers. While competition between predatory species affects only deutonymph and adult stages of chiggers, predation may impact on all stages of the chigger life cycle. For these reasons, analysis of the predatory components of soil arthropod communities found in sites with and without chiggers is important. The two prevalent soil microarthropod groups containing predaceous species are the Mesostigmata and Prostigmata (Wallwork 1967). The majority of soil inhabiting species in the Mesostigmata are free living predators (Karg 1976). This group feeds on a variety of arthropods and their eggs. Quantitative analysis of this suborder showed that sites devoid of chigger larvae had significantly higher populations of Mesostigmata than positive chigger sites. Under no circumstances, either for pooled dates, pooled sites, or individual dates and sites were Mesostigmata significantly higher at positive chigger sites than negative sites. The SBR area also failed to show any significant differences in Mesostigmata between positive and negative chigger sites. Lack of differences may be attributed to high prey abundance in the

vegetationally diverse habitat at the SBR area. This may reduce competition among predatory microarthropod species, permitting nearly equivalent predator abundance, in the form of Mesostigmata abundance, at both positive and negative chigger sites.

The Prostigmata are a very large and diverse assemblage of mites comprising both parasitic and free-living species. The free-living forms include fungivores, detritivores, phytophages and a large number of predatory species (Wallwork 1967, Krantz 1980). Prostigmata are an important suborder of mites with regards to chigger abundance because this suborder contains many species that are potential prey for the deutonymph and adult chiggers, and many species that are also predaceous. It is in the Prostigmata that competition between predator species may be most intense because several predaceous families in this suborder (Trombidiidae, Smaridae) are morphologically and ecologically similar to the Trombiculidae. Results from quantitative comparisons of Prostigmata population levels from positive and negative chigger sites are ambiguous. Analysis of data at the suborder level in such an ecologically diverse group of mites, may have obscur ed relationships.

Collembola are another important group of soil arthropods known to be directly related to chigger survivorship. Through studies involving the culturing of chiggers in the laboratory, Lipovsky (1954) found that Collembola were a preferred nutrient source. Studies by Hayes (Doctoral dissertation in prep., Department of Entomology, University of Georgia) have shown that

the deutonymph and adult stages of chiggers selectively consume some genera and refuse to eat other genera of Collembola, even genera from the same family. This selectivity may be an important mechanism by which soil arthropod predators partition their food base, thereby reducing competition. It was initially hypothesized that negative chigger sites would be more depauperate in Collembola than positive chigger sites. However, statistical analysis has led to the rejection of this hypothesis. Negative chigger sites were significantly higher in Collembola than positive sites on nine sampling dates, compared to only five significantly higher sample dates of Collembola from positive sites. More feeding studies on chiggers are clearly needed to determine if high populations of Collembola from negative sites are comprised of unpalatable genera.

The Acarine suborder Cryptostigmata is usually the most taxonomically diverse and numerically abundant microarthropod group in most soil systems (Wallwork 1983). The Cryptostigmata are exclusively free-living and are primarily detritivores or microphytophages (Luxton 1972, Behan and Hill 1978). In this study, the Cryptostigmata were significantly higher at negative sites for 80% of the time, whenever significant differences occurred between positive and negative sites. One reason for this trend may be as follows: many Cryptostigmata are relatively large, and heavily sclerotized with inflexible exoskeletons. This may be a reason why oribatid mites are found in high numbers in organic soils with a loose soil structure (Loots and Ryke 1967). Therefore, the presence of significantly

high numbers of oribatid mites at negative chigger sites may competively exclude some prey species for postlarval chiggers. As a result, soils high in organic matter may not be favorable for chiggers. This hypothesis may be validated pending analysis of the organic matter content of soil core samples taken from both positive and negative chigger sites.

On the 4 March 1983 sampling date, all major microarthropod groups, including total microarthropods, were significantly higher at negative chigger sites. The implications of this occurence are not understood. Possibly during this period of the year, after the winter freeze, soil microarthropods become active in large numbers. Postlarval chiggers, being somewhat slower than most other predatory arthropods (personal observation), may suffer severe mortality through competition or predation from other predatory soil arthropods.

Statistical comparisons of genera comprising greater than one percent of the total number of individuals collected from positive and negative chigger sites showed that one species of astigmatid mite, "Acaridae sp. II", had significantly higher populations at negative chigger sites. This acarid mite may be an important agent in contributing to the failure of chiggers to successfully colonize certain areas. Hayes (personal communication) found that chigger colonies contaminated by acarid mites failed to produce adults, and consequently future generations of larvae. She observed these mites feeding on the quiescent proto- and tritonymphal stages thus causing the demise of the colony. This find may have practical implications

regarding chigger control in the field. Since manures usually harbor large populations of acarid mites (Proctor 1970, (unpublished Masters Thesis), Krantz 1981), applications of manure in the field may reduce chigger infestations without the potentially harmful side effects of chemical biocides.

The prostigmatid mite Nanorchestes sp. and the collembolan Folsomia sp. were collected in significantly higher numbers at positive chigger sites. Folsomia sp. is known to be a palatable food source for postlarval chiggers (Hayes in prep). Whether Nanorchestes sp., a small, slow moving fungivorous mite, is palatable to deutonymph and adult chiggers is not known.

The relationship between the presence of chiggers and high soil arthropod diversity is seen when comparing diversity indice values between positive and negative chigger sites. Soil arthropod diversity was higher at positive chigger sites when data from all three sutdy areas individually showed the SBR and BGF areas both exhibited greater soil arthropod diversity at positive chigger sites. These two areas, being more vegetationally diverse than the BGW area, are able to support a higher soil arthropod diversity, thus reducing the probability that trombiculid mites will be competitively excluded. The BGW area has limited litter diversity entering the soil ecosystem. This will limit the diversity of potential prey that are available to postlarval chiggers and other predatory microarthropods.

In conclusion, it appears that the soil arthropod community does impact on the ability of trombiculid mites to successfully

colonize various habitats. The occurence of significantly higher populations of palatable or potentially palatable genera such as Folsomia sp. at positive chigger sites suggests that certain components of the soil arthropod community must be present at adequate levels for chigger populations to exist. The occurence of significantly higher populations of acarid mite "Acaridae sp. II" at negative sites suggests that chigger populations cannot exist sympatrically with certain taxa of the soil arthropod community. A predatory threshold that precludes the success of chigger colonization is suggested by the absence of chiggers from sites with significantly high Mesostigmata populations. Likewise, some threshold may exist based on the results which showed that chigger populations are found at sites higher in soil arthropod diversity. This high diversity is primarily the result of the large component of primary consumers, bacteriophages, fungivores or other trophic groups that function in the role of prey for many soil arthropod predators. Therefore, higher soil arthropod diversity, may reduce competition. It should be noted that the occurence of no one particular species or trophic group alone can be claimed as the regulatory agent in controlling chigger presence or absence. Clearly, existence in a complex environment such as the soil habitat depends on many factors, both biotic and abiotic.

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Table 3-1. Number of locations designated as positive and negative chigger sites from transects on Simonton Bridge Road (SBR), Botanical Gardens Field (BGF) & Botanical Gardens Woods (BGW)

	SBR	BGF	BGW
Number of positive locations:	4	3	2
Number of negative locations:	3	2	3

Table 3-2. Significant differences in microarthropod population data pooled the Simonton Bridge Road, Botanical Gardens Field, and Botanical Gardens Woods study areas.

Dates	Cryptostigmata		Prostigmata		Mesostigmata		Acari		Collembola		Microarthropo	
1983-4	+	-	+	-	+	-	+	-	+	-	+	-
7/6				A				B				B
7/20		A										
8/31		A										
9/14									B			
10/28									B			
12/10									B			
3/4		A		A		B		A		B		A

A's and B's denote significant differences between the respective microarthropod groups (A=p< .05, B=p< .10). Only dates when significant differences occured are shown.

Table 3-3. Significant differences in microarthropod population data pooled from all sample dates over one years sampling period.

Dates	Cryptostigmata		Prostigmata		Mesostigmata		Acari		Collembola		Microarthropo	
1983-4	+	-	+	-	+	-	+	-	+	-	+	-
BGF			A			A						
BGW						A		B		A		A
SBR												

A's and B's in the negative and positive columns denote significant differences between the respective microarthropod groups (A=p< .05, B=p< .10).

Table 3-4. Margalef, and Pielou indices of species diversity for the Simonton Bridge Road (SBR), Botanical Gardens Field (BGF) and Botanical Gardens Woods (BGW) habitats. (data from all sampling dates, and positive and negative chigger sites pooled).

	SBR	BGF	BGW
Margalef	325.5	285.6	278.1
Pielou	0.90	0.91	0.86

Table 3-5. Margalef, and Pielou diversity indices for soil arthropods collected from positive and negative chigger sites at the Simonton Bridge Road (SBR), Botanical Garden Field (BGF), and Botanical Garden Woods (BGW) habitats. Arthropod data from all sampling dates pooled.

	Positive Sites			Negative Sites		
	SBR	BGF	BGW	SBR	BGF	BGW
Margalef	181.68	164.30	131.60	167.75	143.11	166.92
Pielou	0.89	0.90	0.85	0.90	0.90	0.84

Table 3-6. Margalef, and Pielou diversity indices for soil arthropods collected from positive and negative chigger sites. Data from all sites and dates pooled.

	Positive Sites	Negative Sites
Margalef	428.23	426.17
Pielou	0.90	0.88

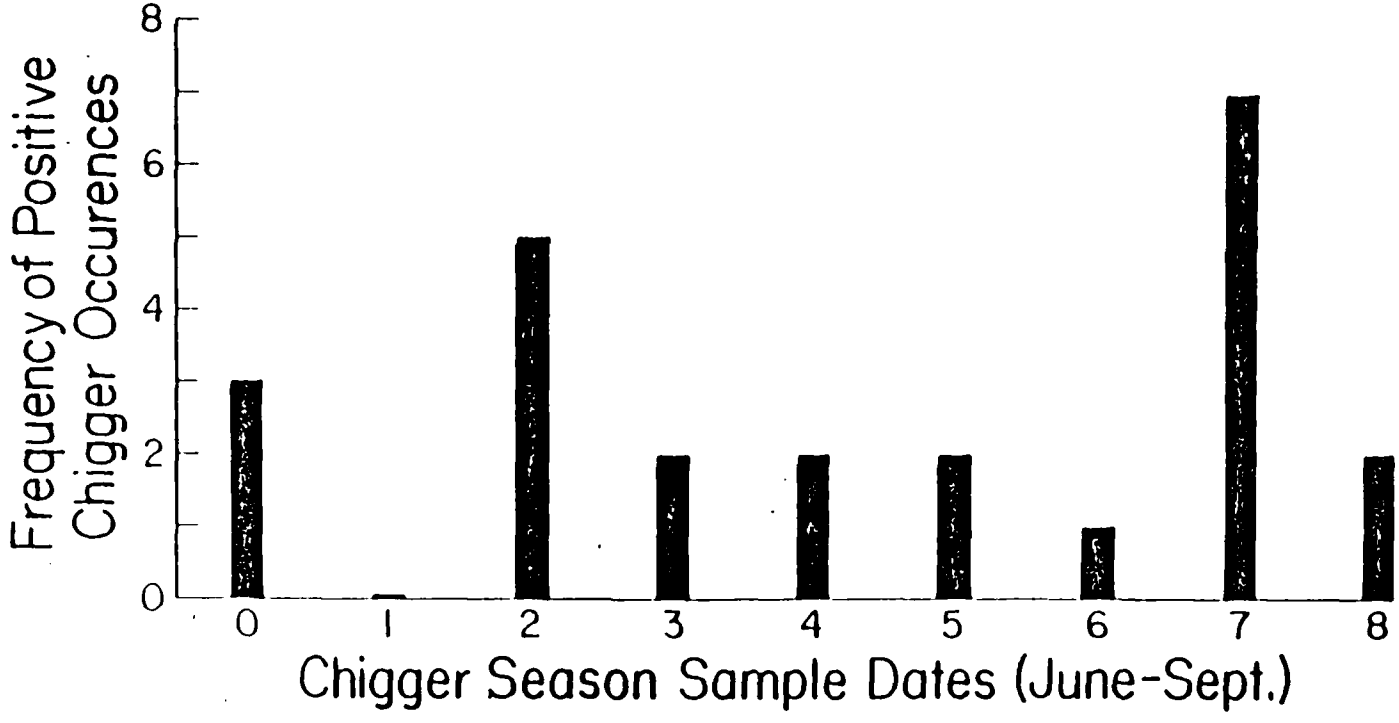


Figure 3-1. Frequency distribution of positive chigger responses over the eight sampling dates of the chigger season.

APPENDIX A:

List of Soil Genera

CRYPTOSTIGMATA

Achipteriidae
Anachipteria sp.

Astegistidae
Cultoribula spp.

Autognetidae
Eremobodes sp.

Belbodamaeidae
Dyobelba sp.

Brachychthoniidae
Brachchthonius sp.
Liochthonius sp.

Caleremaeidae
Caleremaeus sp.

Camisiidae
Camisia sp.

Carabodidae
Carabodes spp.

Ceratozetidae
Ceratozetes spp.
Propelops sp.
Trichoribates sp.

Ctenacaridae
Ctenacarus sp.

Damaeidae
Damaeus sp.
Epidamaeus sp.

Damaeolidae
Fosseremus sp.

Epilohmanniidae
Epilohmannia sp.

Eremaeidae
Eremaeus sp.

Eremobelbidae
Eremobelba sp.

Eremulidae
Eremulus sp

Euphthiracaridae
Microtritia sp.
Rhysotritia sp.

Galumnidae
Galumna spp.
Pergalumna spp.

Gehypochthoniidae
Gehypochthonius sp.

Gymnodamaeidae
Allodamaeus sp.
Gymnodamaeidae sp.
Jacotella sp.

Haplozetidae
Peloribates spp.
Rostrozetes sp.
Xylobates sp.

Hermaniellidae
Hermaniella sp.

Hypochthoniidae
Eohypochthonius sp.
Hypochthonius sp

Liacaridae
Liacarus spp.

Licneremaeidae
Licneremaeus sp.

Lohmaniidae
Lohmannia sp.

Malaconothridae
Malaconothrus sp.

Metrioppiidae
Ceratoppia sp.
M trioppia sp.

Microzetidae
Berlesezetes sp.

Nanhermanniidae
Nanhermannia sp.

Nehypochthoniidae
Nehypochthonius sp.

Nothridae
Nothrus sp.

Oppiidae
Oppia spp.
Oppiella sp.

Oribatellidae
Ferolocella sp.
Oribatella spp.

Oribatulidae
Oribatula sp.
Scheloribates spp.
Zygoribatula sp.

Parhypochthoniidae
Parhypochthonius sp.

Pelopidae
Pelopsis sp.

Phthiracaridae
Hoplophorella spp.
Phthiracarus sp.

Pterochthoniidae
Pterochthonius sp.

Spherochthoniidae
Spherochthonius sp.

Suctobelbidae
Suctobelbella sp.
Suctobelbila sp.

Tectocepheidae
Tectocepheus sp.

Trhypochthoniidae
Trhypochthonius sp.

Xenillidae
Xenillus spp.

Zetorchestidae
Zetorchestes sp.

PROSTIGMATA

Adamystidae
Adamystis sp.

Alicorhagidae
Alicorhagia sp.
Stigmalycus sp.

Alycidae
Alycus sp.
Bimichaelia sp.
Pachygnathus sp.
Petralycus sp.

Anystidae
Becksteinia sp.

Bdellidae
Bdella sp.
Cyta sp.
Spinibdella sp.

Caeculidae
Allocaeculus sp.

Cryptognathidae
Cryptognathus sp.

Cunaxidae
Cunaxa sp.
Cunaxoides sp.
Dactyloscirus sp.
Neocunaxoides sp.
Pseudobonzia sp.

Erythraeidae
Bocartia sp.
Erythraeidae sp.
Leptus sp.

Eupodidae
Cocceupodes sp.
Eupodes sp.
Linopodes sp.

Greanjeanidae
Greanjeanicus sp.

Labidostomatidae
Labidostoma sp.

Lordalycidae
Hybalicus sp.

Nanorchestidae
Nanorchestes sp.
Speleorchestes sp.

Oesherchestidae
Oesherchestes sp.

Paratydeidae
Neotydeus sp.

Penthalodidae
Penthalodes sp.

Pygmephoridae
Pygmephoridae spp.

Rhagidiidae
Coccorhagidia sp.
Rhagidia sp.

Rhaphignathidae
Rhaphignathus sp.

Scutacaridae
Scutacaridae sp.

Smaridae
Hirstiosoma sp.
Smaris sp.

Stigmaeidae
Eustigmaeus sp.
Ledermulleriopsis sp.
Stigmaeus sp.

Tarsonemidae
Tarsonemidae spp.

Tetranychidae
Bryobia sp.

Terpnacaridae
Alycomesis sp.
Terpnacarus sp.

Trombidiidae
Trombidiidae sp.

Trombiculidae
Eutrombicula sp.

Tydeidae
Lorryia sp.
Paralorryia sp.
Ricketydeus sp.

MESOSTIGMATA

Ascidae
Antennoseius sp.
Asca sp.
Cheiroseius sp.
Iphidozercon sp.
Protogamasellodes sp.
Ascidae spp. I+II

Laelapidae
Cosmolaelaps sp.
Gaeolaelaps sp.
Hypoaspis sp.
Pseudoparasitus sp.

Parasitidae
Pergamasus sp.
Vulgarogamasus sp.
Parasitidae sp.

Parholaspidae
Calholaspis sp.
Latinella sp.
Neoparholaspulus sp.
Parholaspulus sp.

Phytoseidae
Amblyseius sp.

Podocinidae
Podocinum sp.

Rhodacaridae
Rhodacarus sp.

Uropodina
Caminella sp.
Dithinozercon sp. (?)
Polyaspis sp.

Veigaiidae
Gamasolaelaps sp.
Veigaia sp.

Zerconidae
  Zercon sp.

ASTIGMATA

Acaridae
  Acaridae spp. I+II
  Tyrophagus sp.

COLLEMBOLA

Entomobryidae
  Entomobrya sp.
  Lepidocyrtus sp.
  Orchesella sp.
  Pseudosinella spp.
  Tomocerus sp.

Hypogasturidae
  Hypogastura sp.
  Odontella sp.
  Tetracanthella sp.

Isotomidae
  Anurophorous spp.
  Folsomia sp.
  Isotoma sp.
  Proisotoma sp.

Neelidae
  Arrhopalites sp.
  Neelus sp.

Onychiuridae
  Anurida sp.
  Morulina sp.
  Onychiuris sp.
  Tullbergia sp.

Sminthuridae
  Sminthuridae spp.

INSECTA

Coleoptera
  Aliculidae sp.
  Carabidae spp.
  Pselaphidae sp.
  Staphylinidae spp.

Diplura
  Campodia sp.
  Japyx sp.

Diptera
  Misc. spp.

Homoptera
  Misc. spp.

Hymenoptera
  Formicidae spp.
  Misc. spp

Isoptera
  Rhinotermitidae sp.

Lepidoptera
  Misc. spp.

Protura
Psocoptera
  Psocidae spp.

Thysanoptera
  Thripidae spp.

MYRIAPODA

Chilopoda
  Geophilus sp.
  Lithobius sp.

Diplopoda
  Polyxenus sp.
  Misc. spp.

Pauropoda
  Misc. spp.

Symphyla
  Misc. spp.

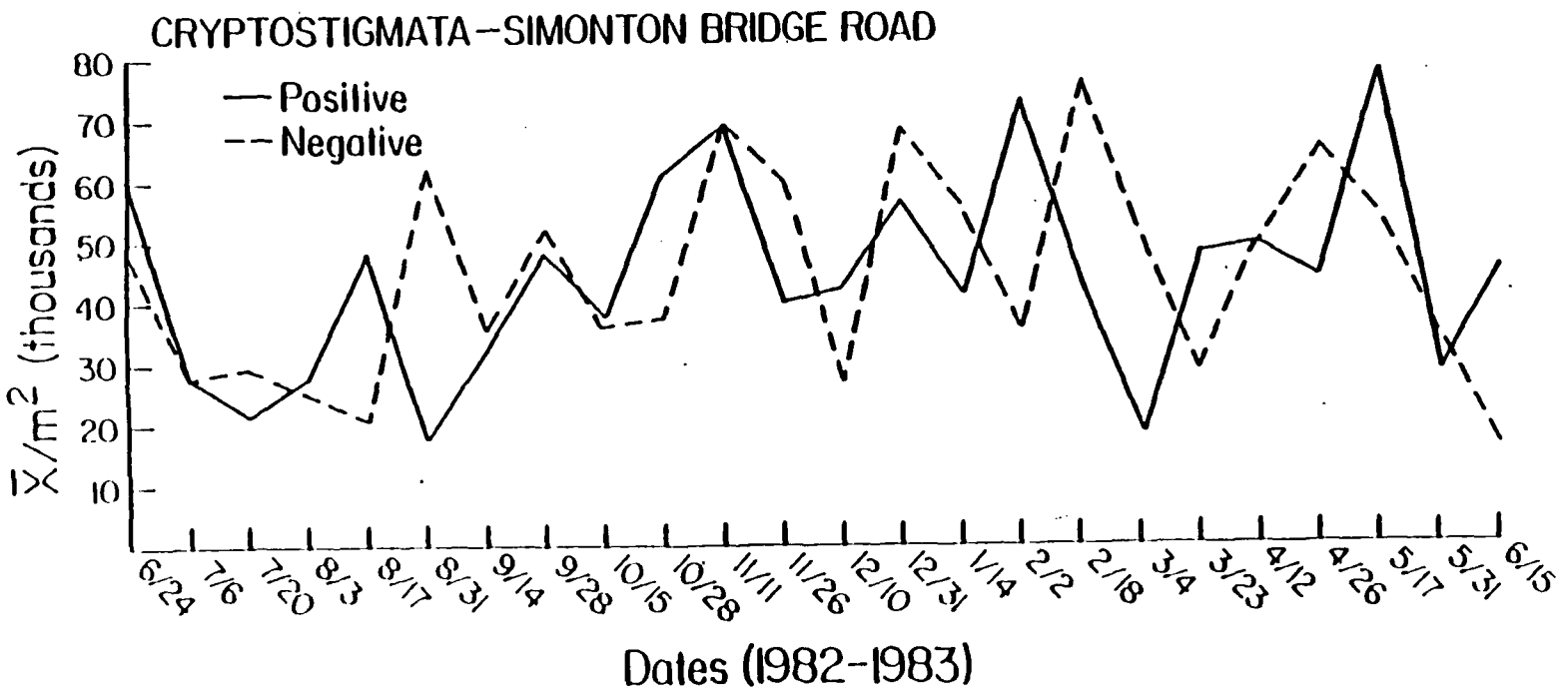
ARACHNIDA

Araneae
  Misc. spp.

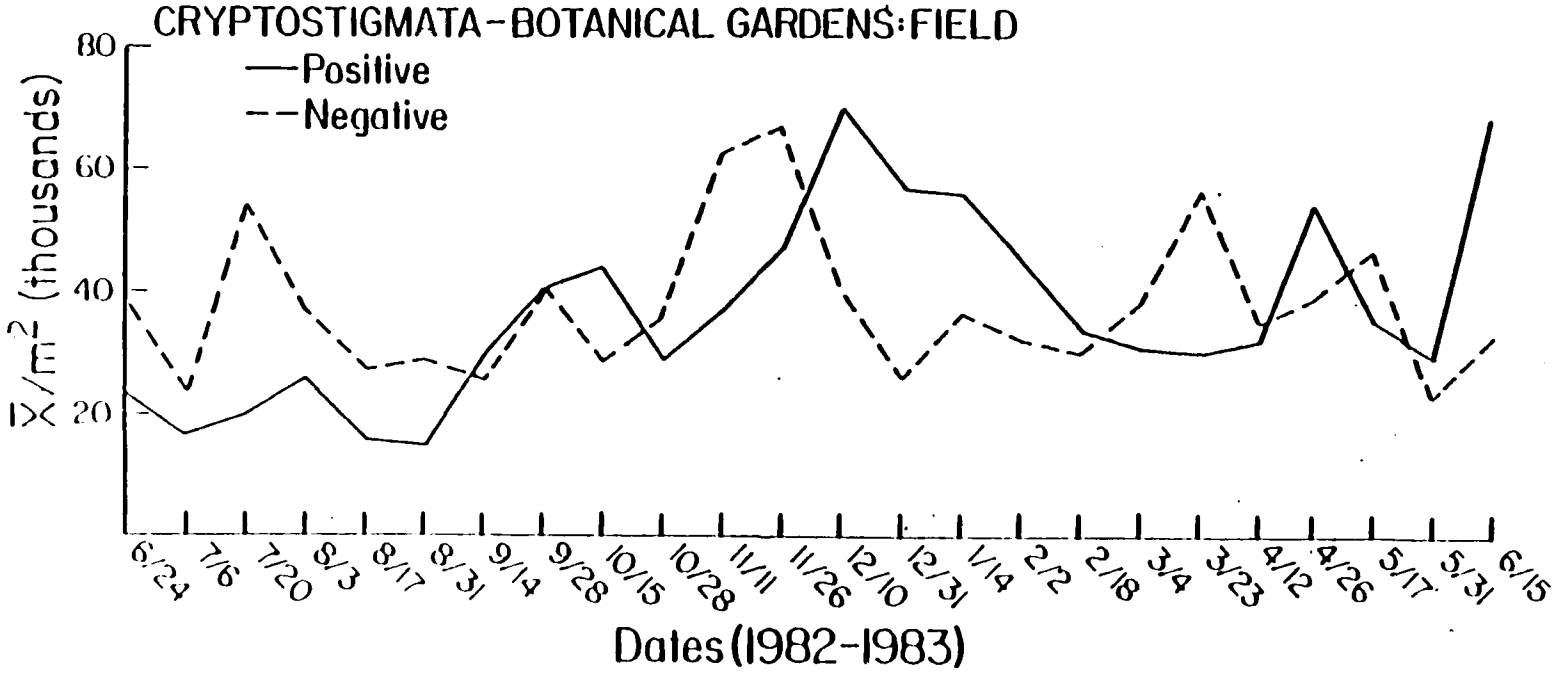
Pseudoscorpionida
  Misc. spp.

APPENDIX B:

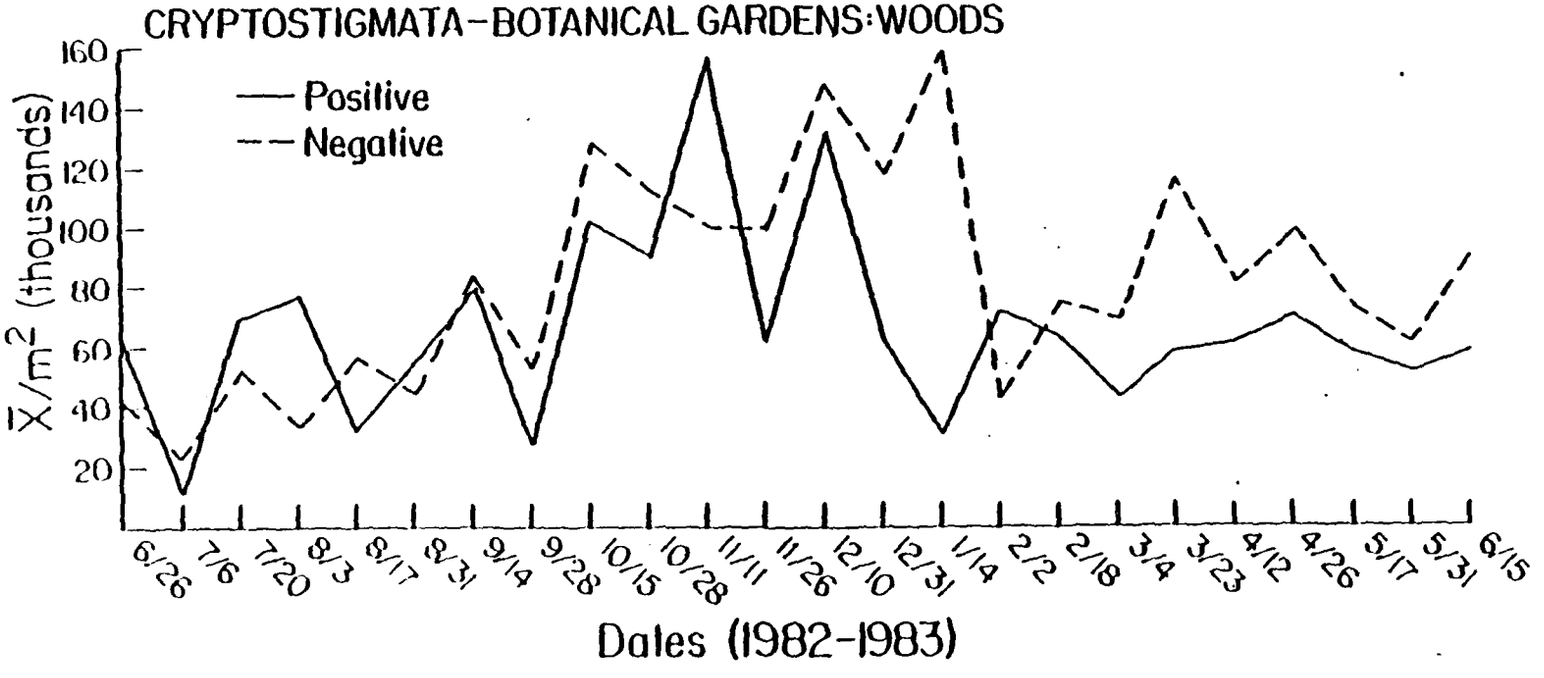
Figures of Soil Arthropod Population Levels



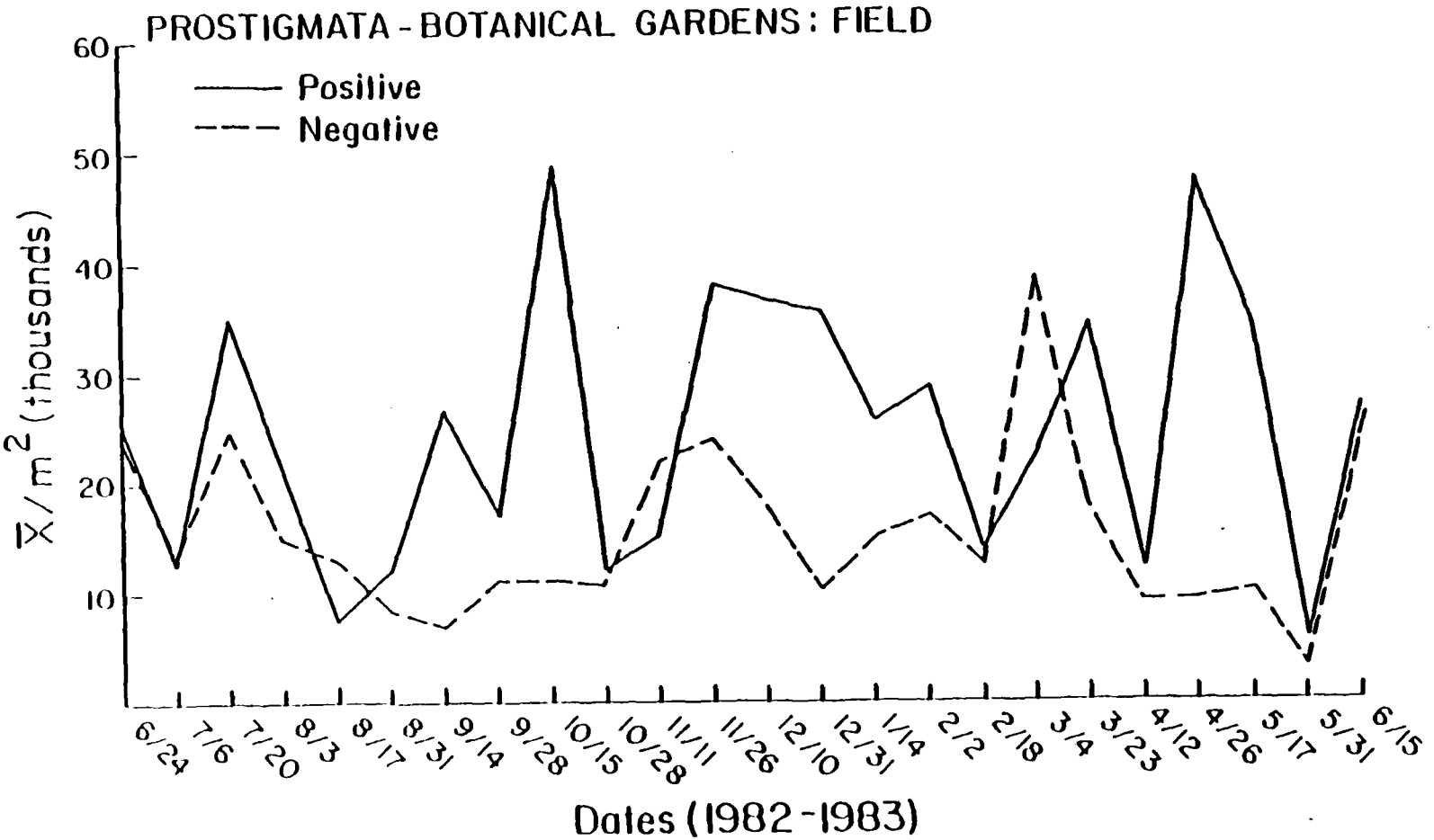
Populations of Cryptostigmata collected from positive and negative chigger sites sampled at the Simonton Bridge Road study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



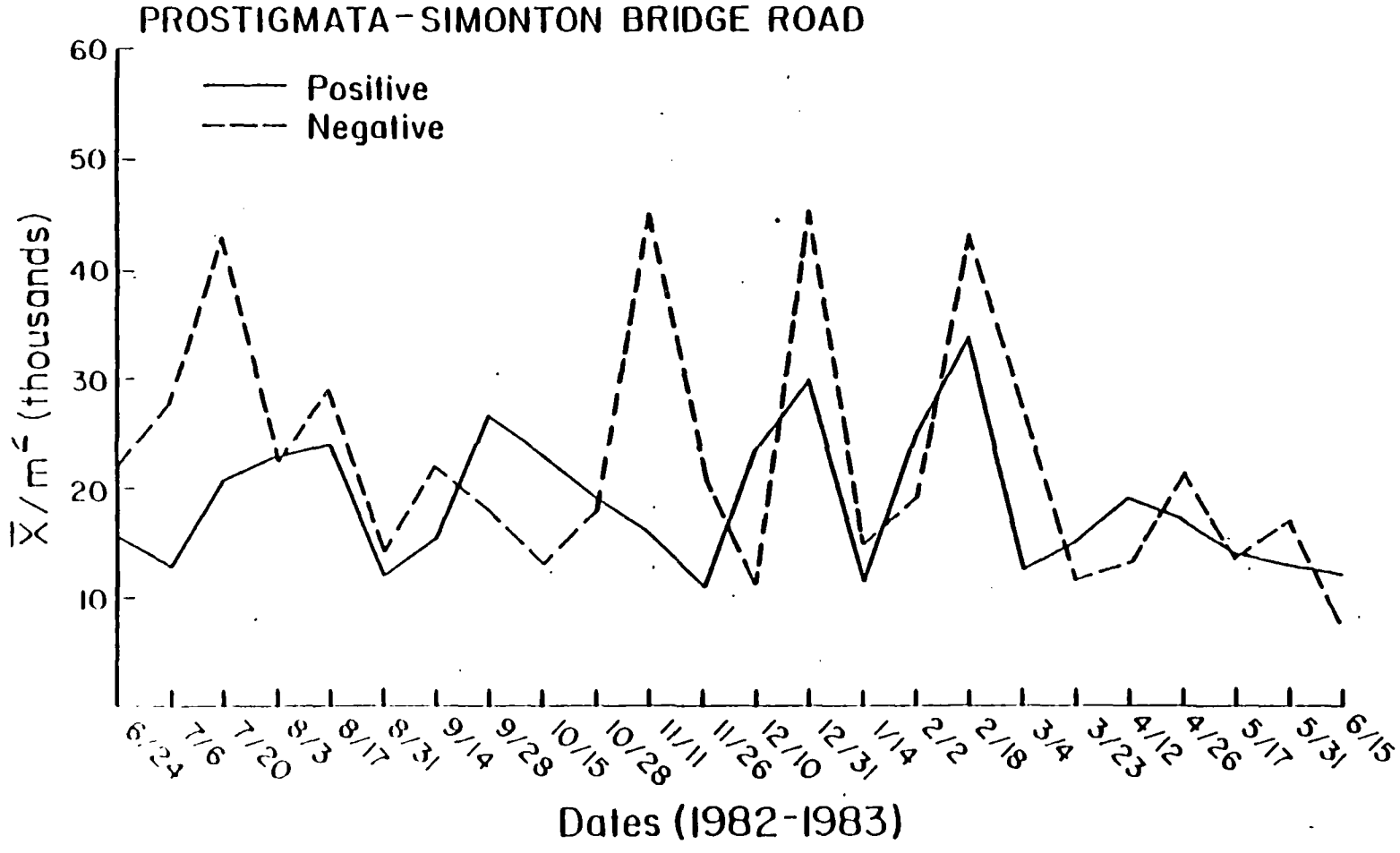
Populations of Cryptostigmata collected from positive and negative chigger sites sampled at the Botanical Gardens Field study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



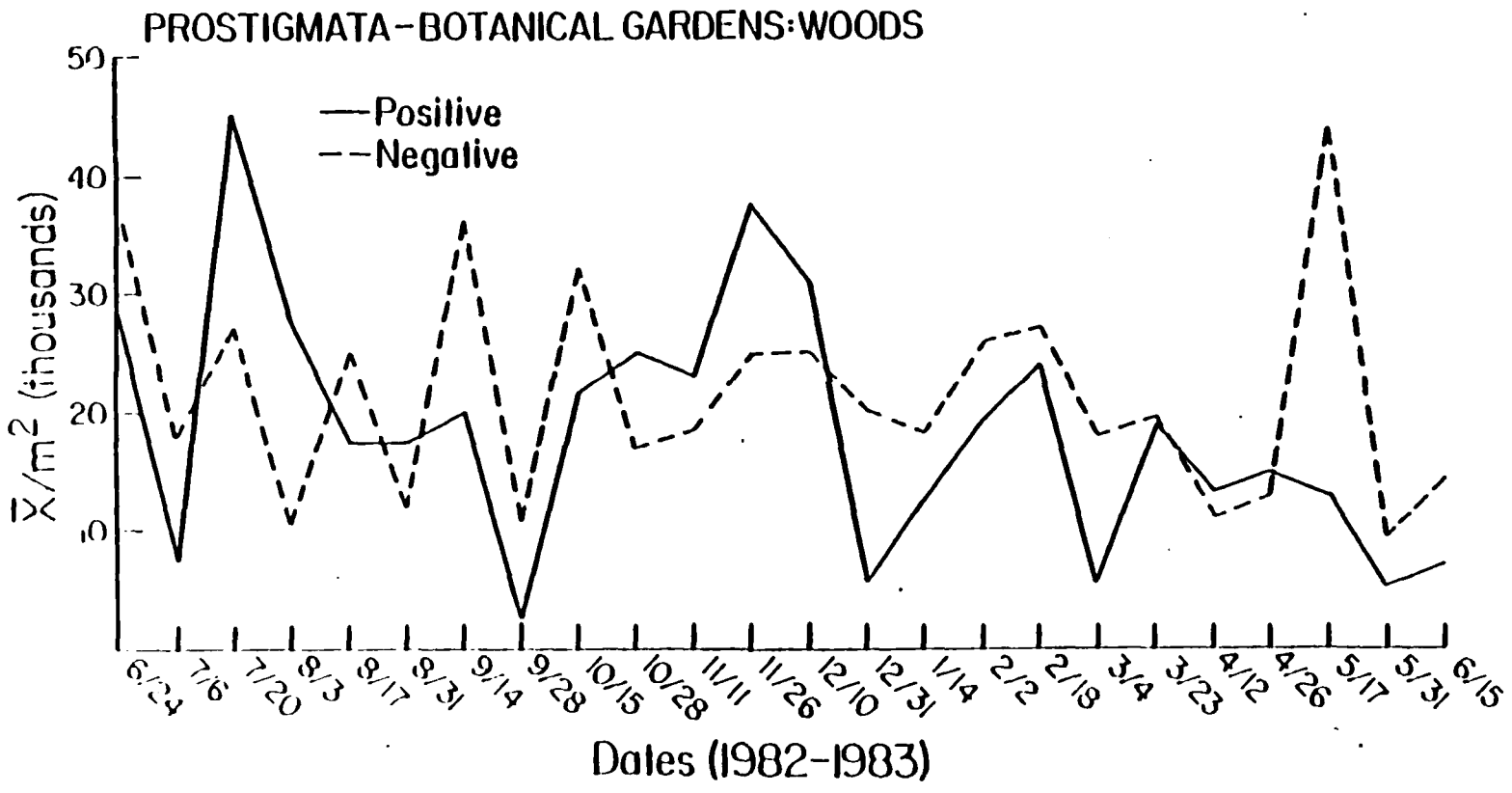
Populations of Cryptostigmata collected from positive and negative chigger sites sampled at the Botanical Gardens Woods study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



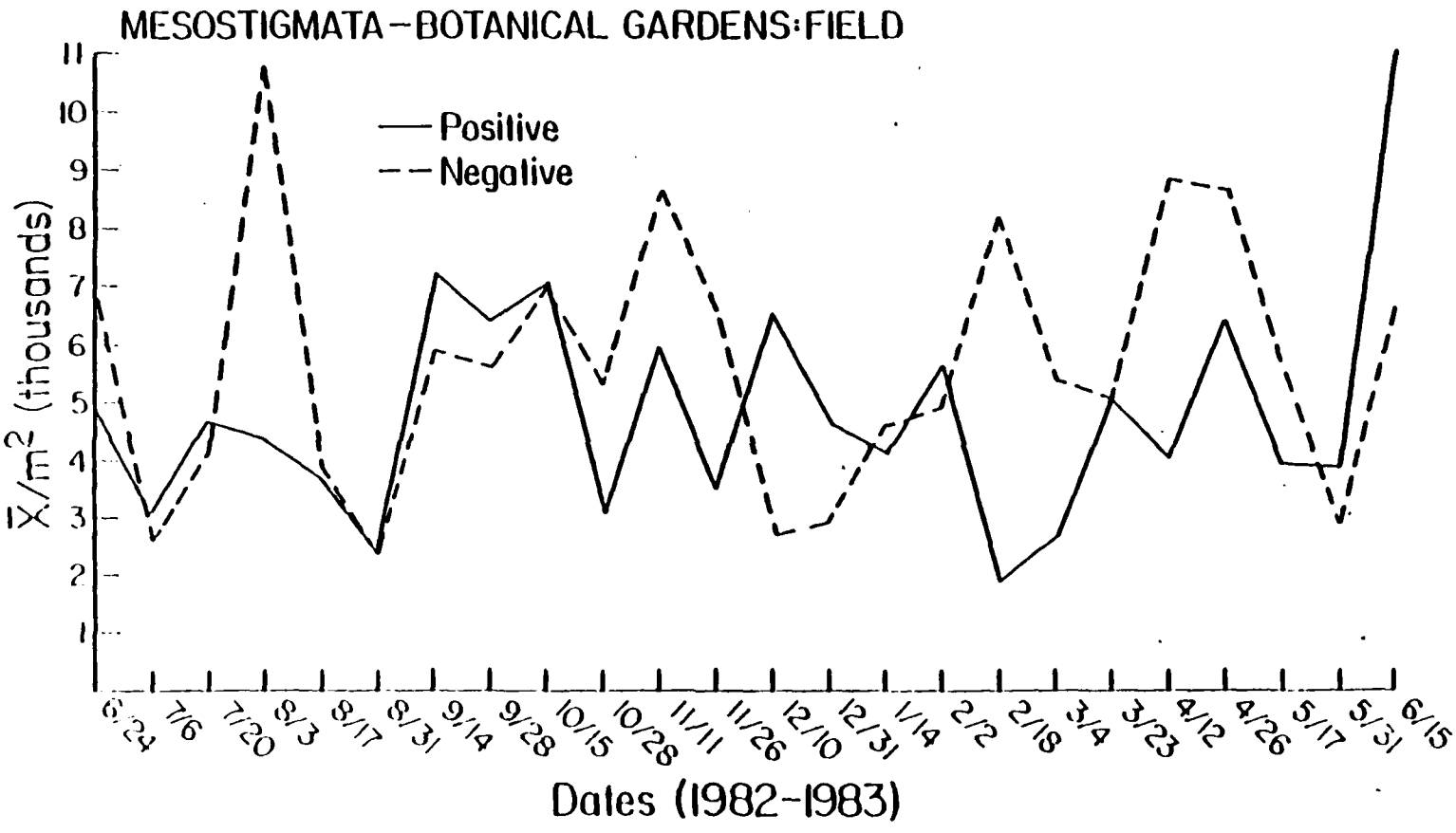
Populations of Prostigmata collected from positive and negative chigger sites sampled at the Botanical Gardens Field study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



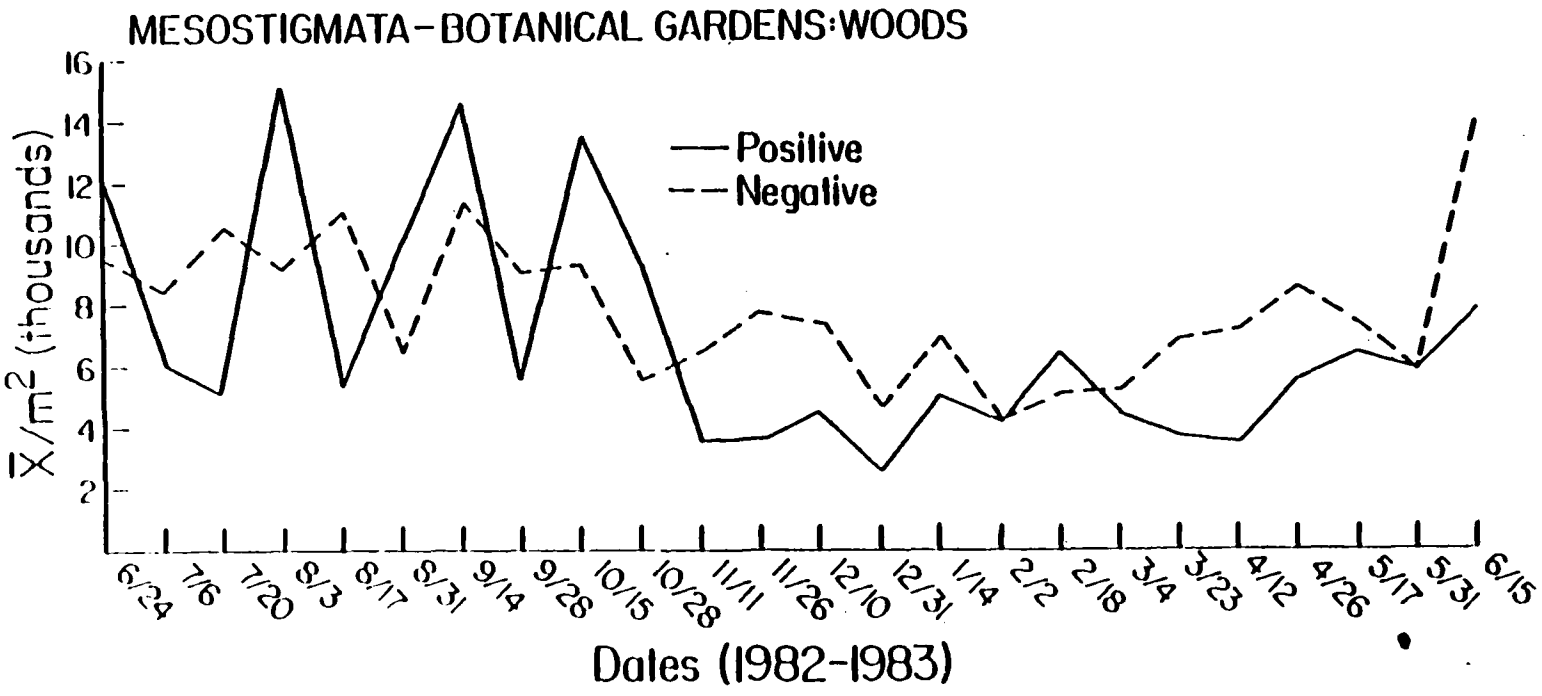
Populations of Prostigmata collected from positive and negative chigger sites sampled at the Simonton Bridge Road study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



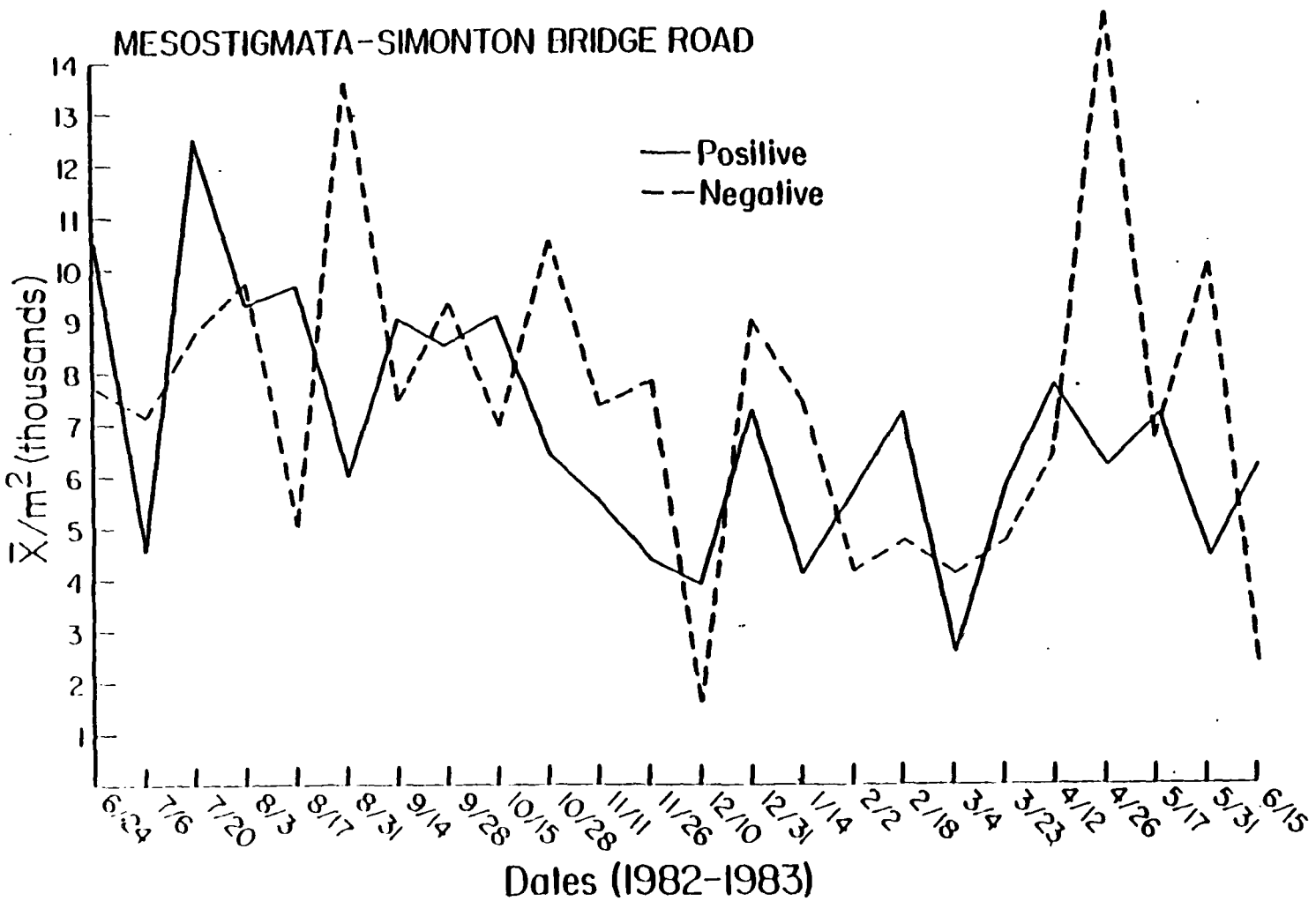
Populations of Prostigmata collected from positive and negative chigger sites sampled at the Botanical Gardens Woods study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



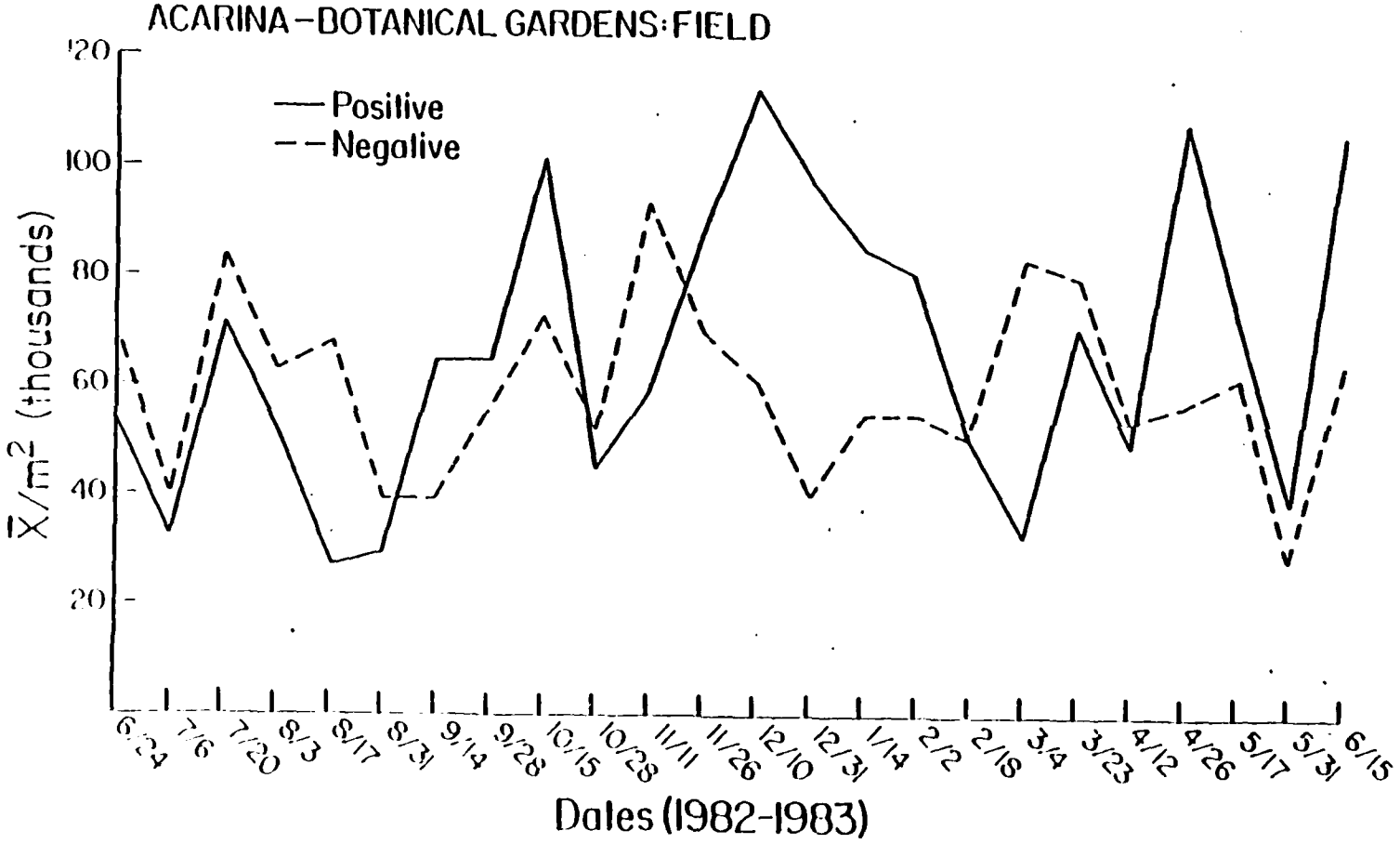
Populations of Mesostigmata collected from positive and negative chigger sites sampled at the Botanical Gardens Field study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



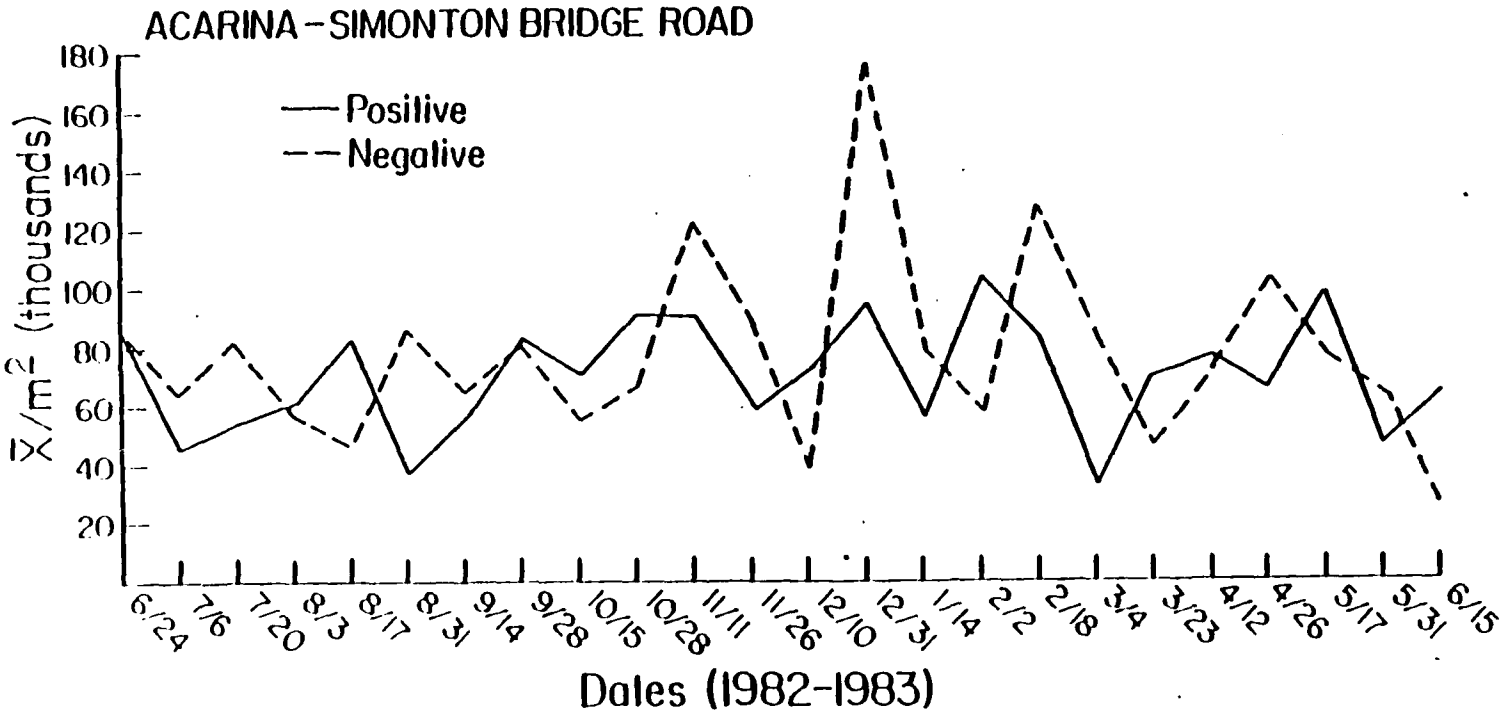
Populations of Mesostigmata collected from positive and negative chigger sites sampled at the Botanical Gardens Woods study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



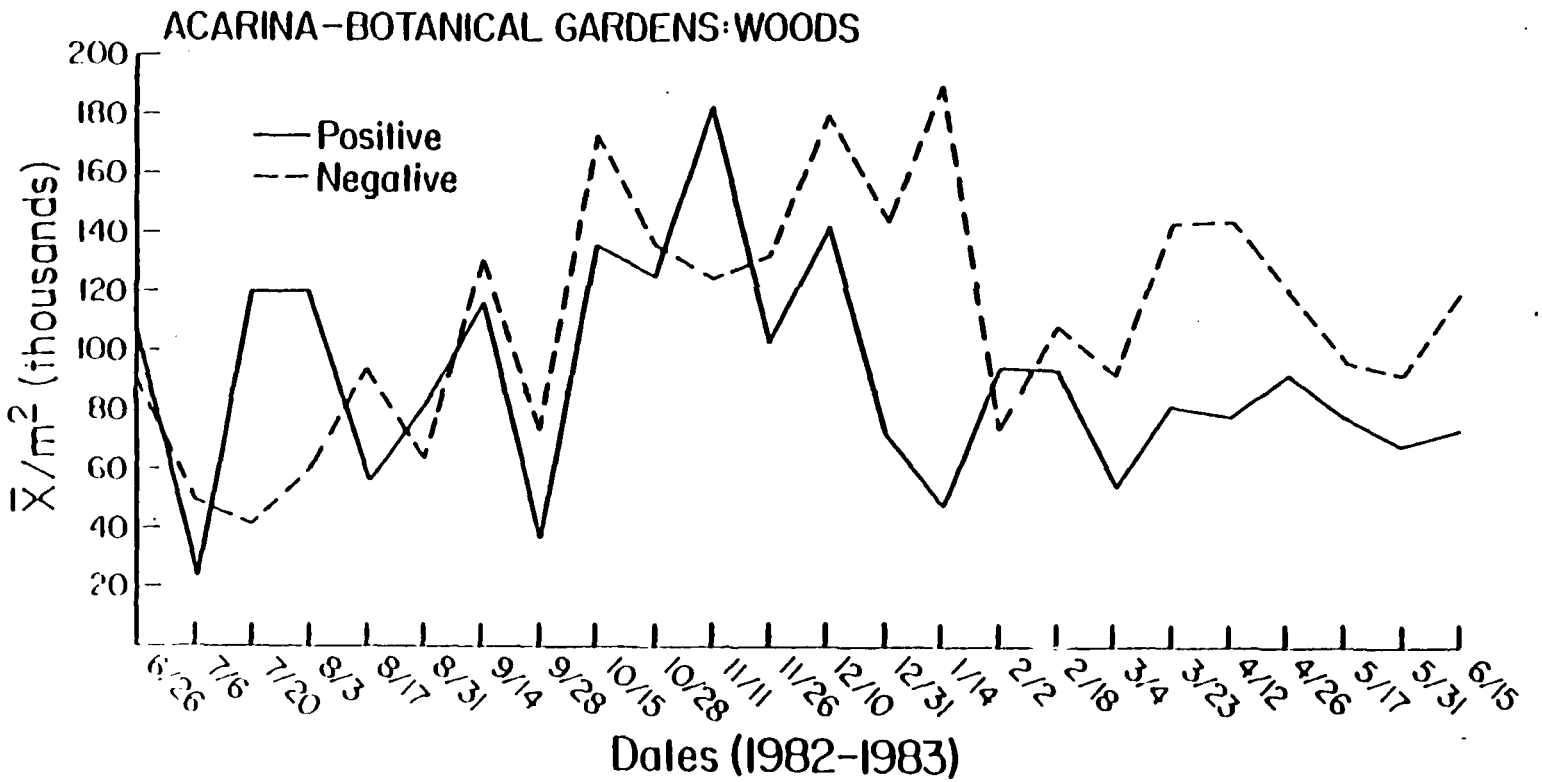
Populations of Mesostigmata collected from positive and negative chigger sites sampled at the Simonton Bridge Road study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



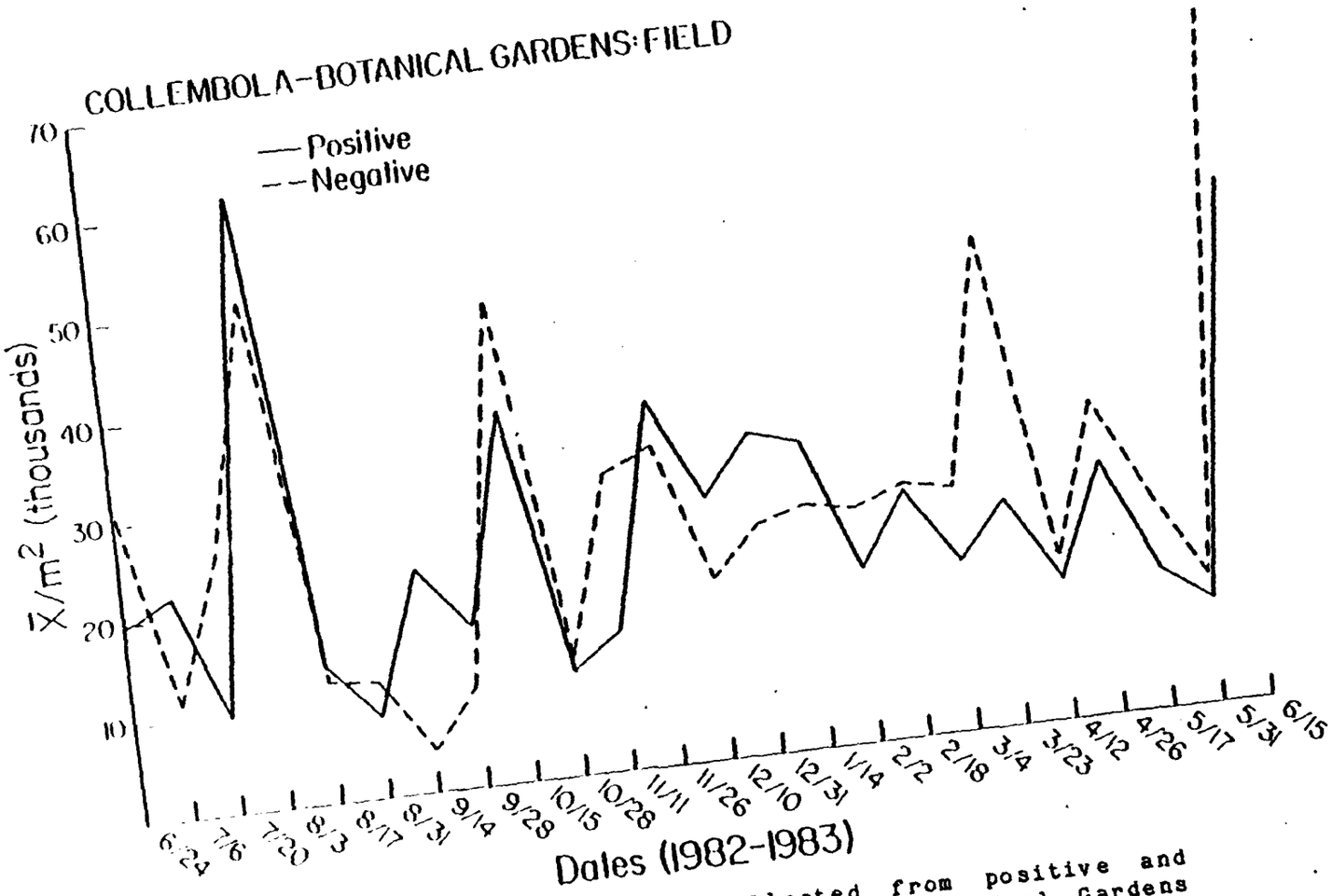
Populations of Acarina collected from positive and negative chigger sites sampled at the Botanical Gardens Field study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



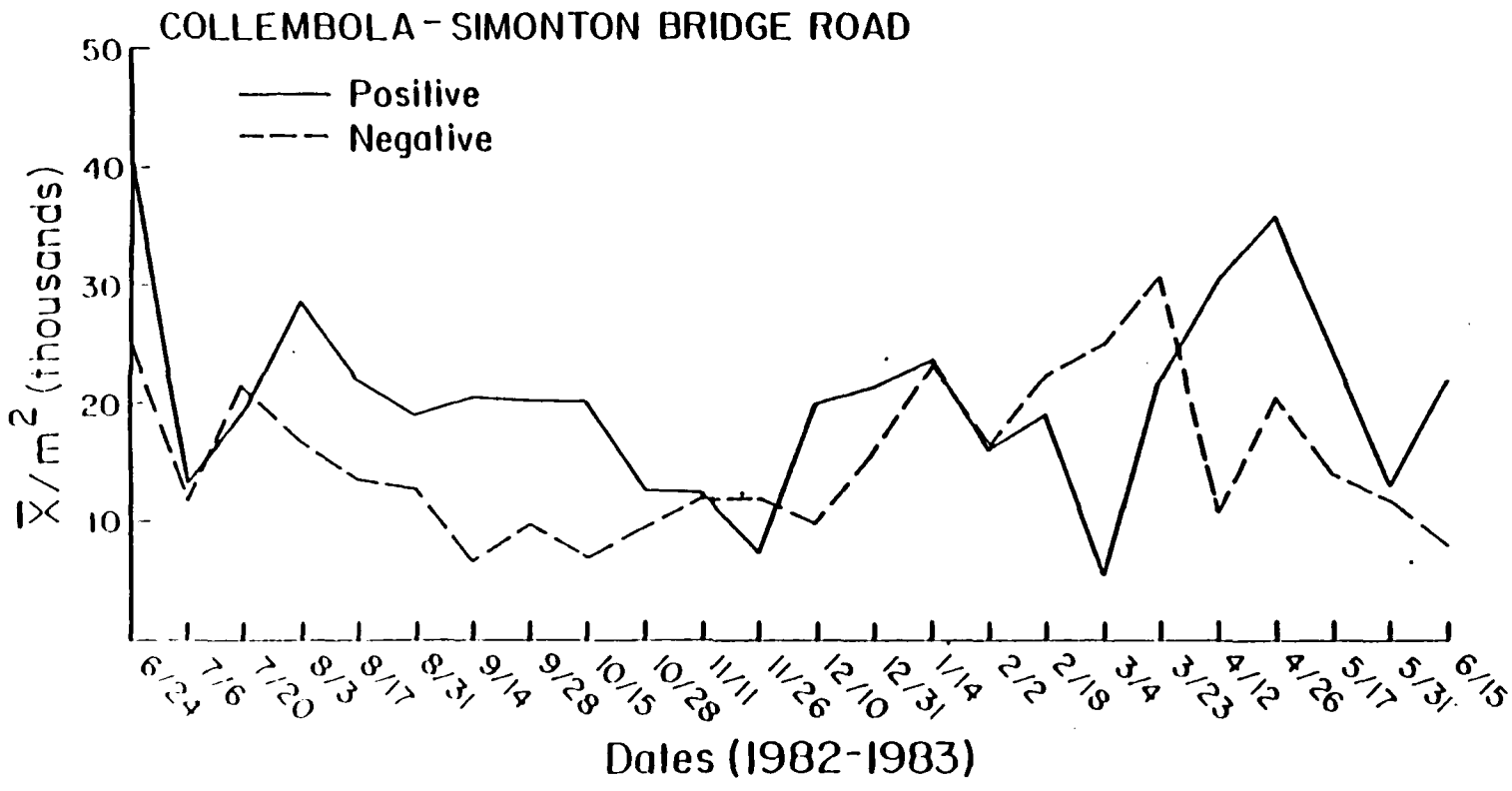
Populations of Acarina collected from positive and negative chigger sites sampled at the Simonton Bridge Road study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



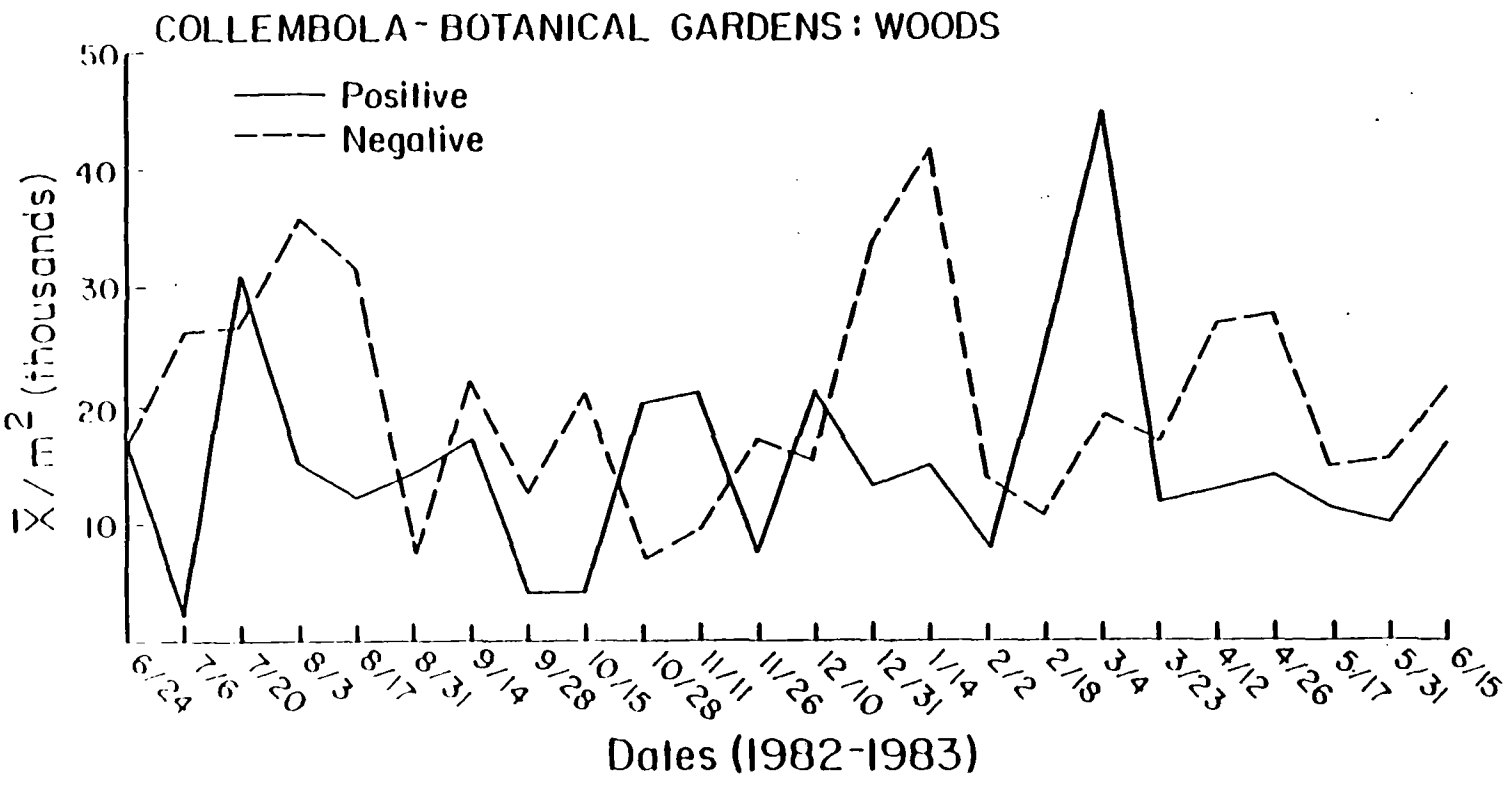
Populations of Acarina collected from positive and negative chigger sites sampled at the Botanical Gardens Woods study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



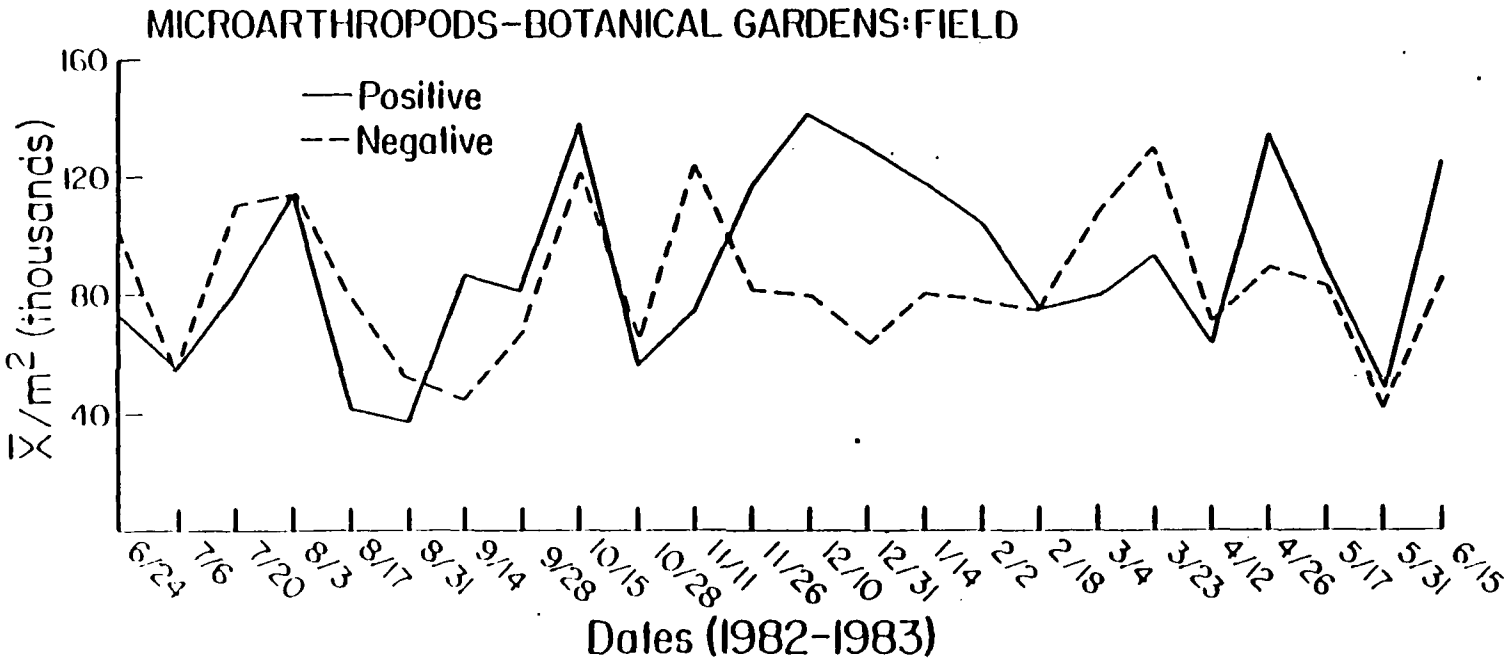
Populations of Collembola collected from positive and negative chigger sites sampled at the Botanical Gardens Field study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



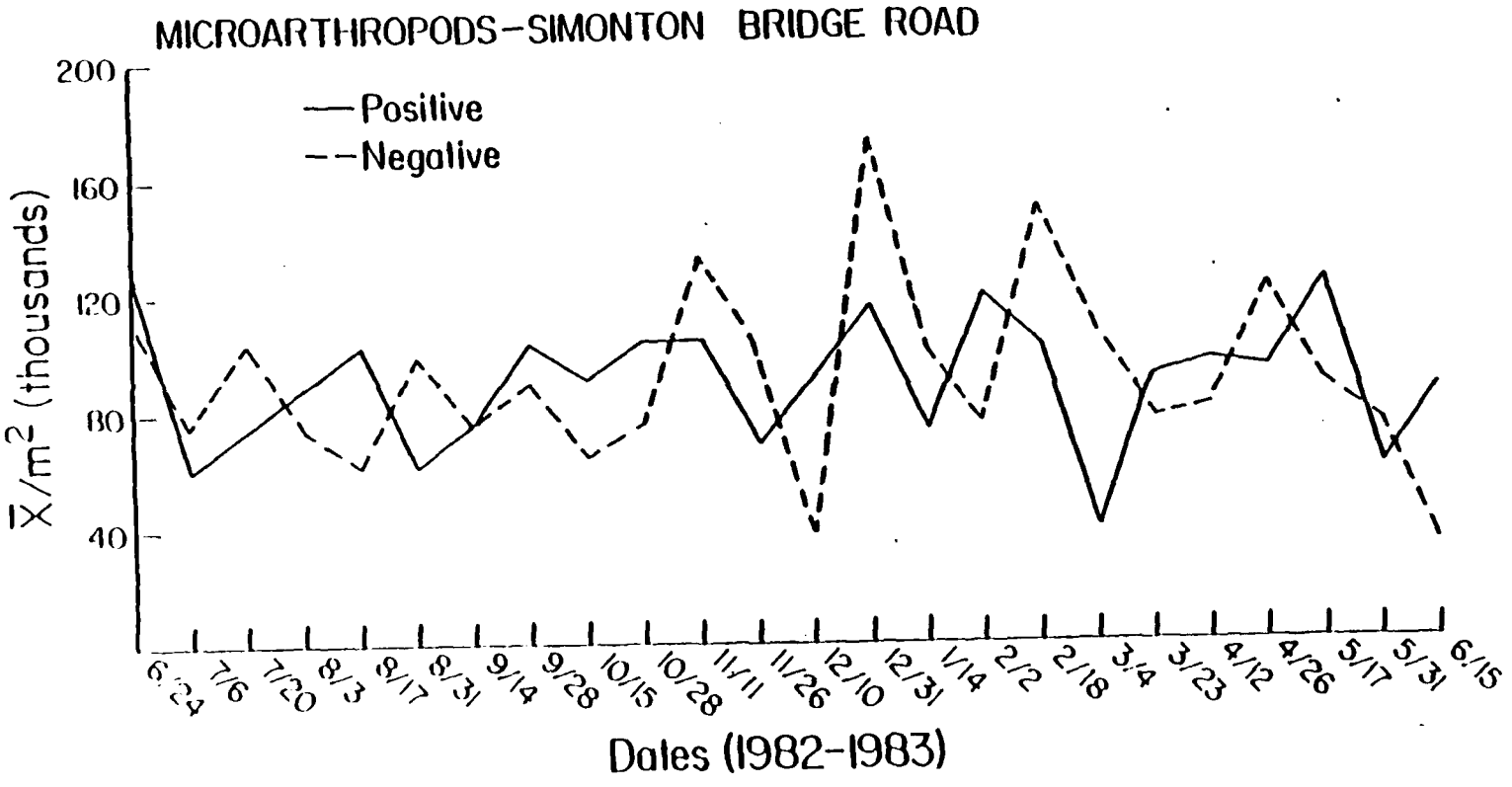
Populations of Collembola collected from positive and negative chigger sites sampled at the Simonton Bridge Road study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



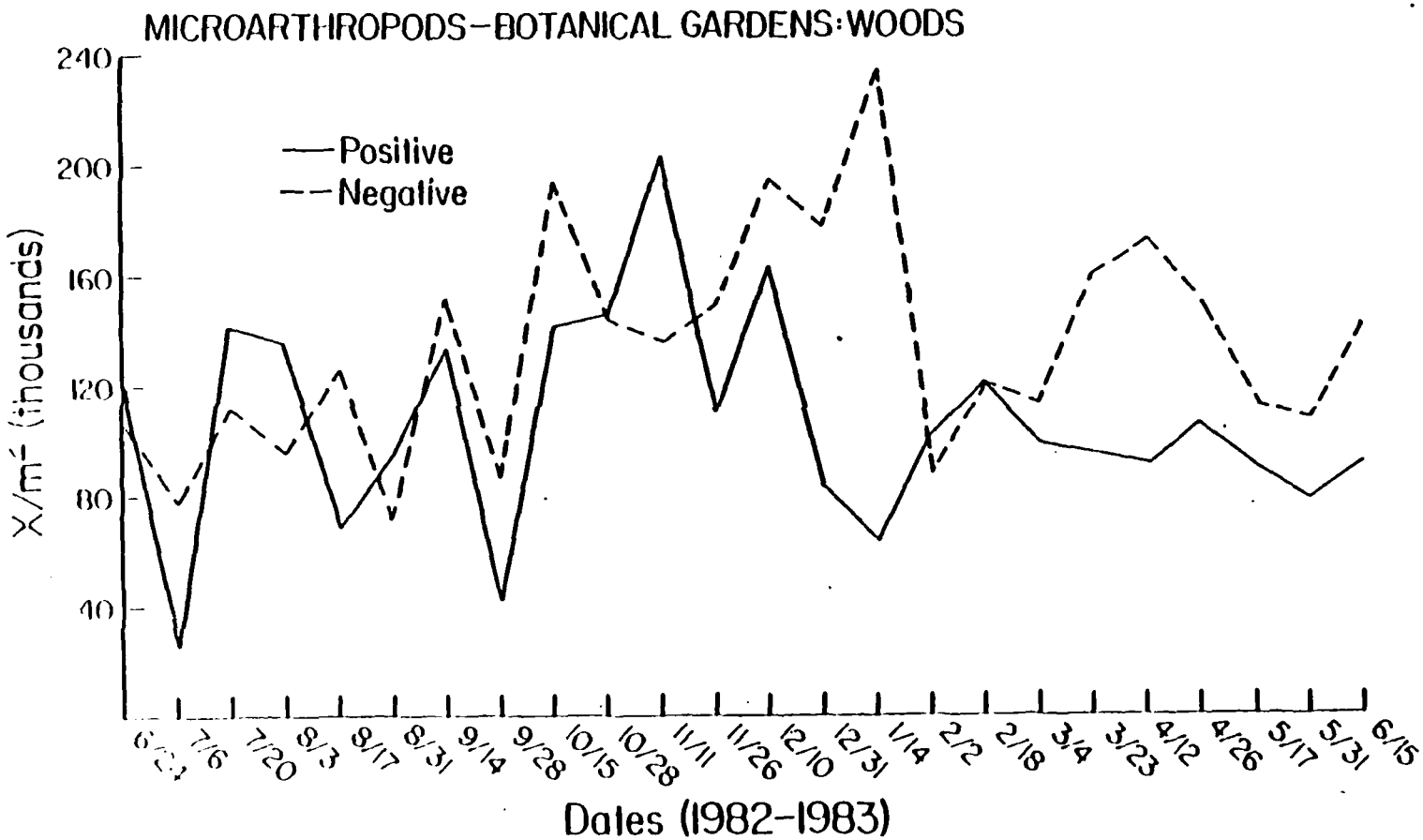
Populations of Collembola collected from positive and negative chigger sites sampled at the Botanical Gardens Woods study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



Populations of Microarthropods collected from positive and negative chigger sites sampled at the Botanical Gardens Field study area. All data points represent population estimates (mean per m^2), taken every two weeks fo a one year sampling period.



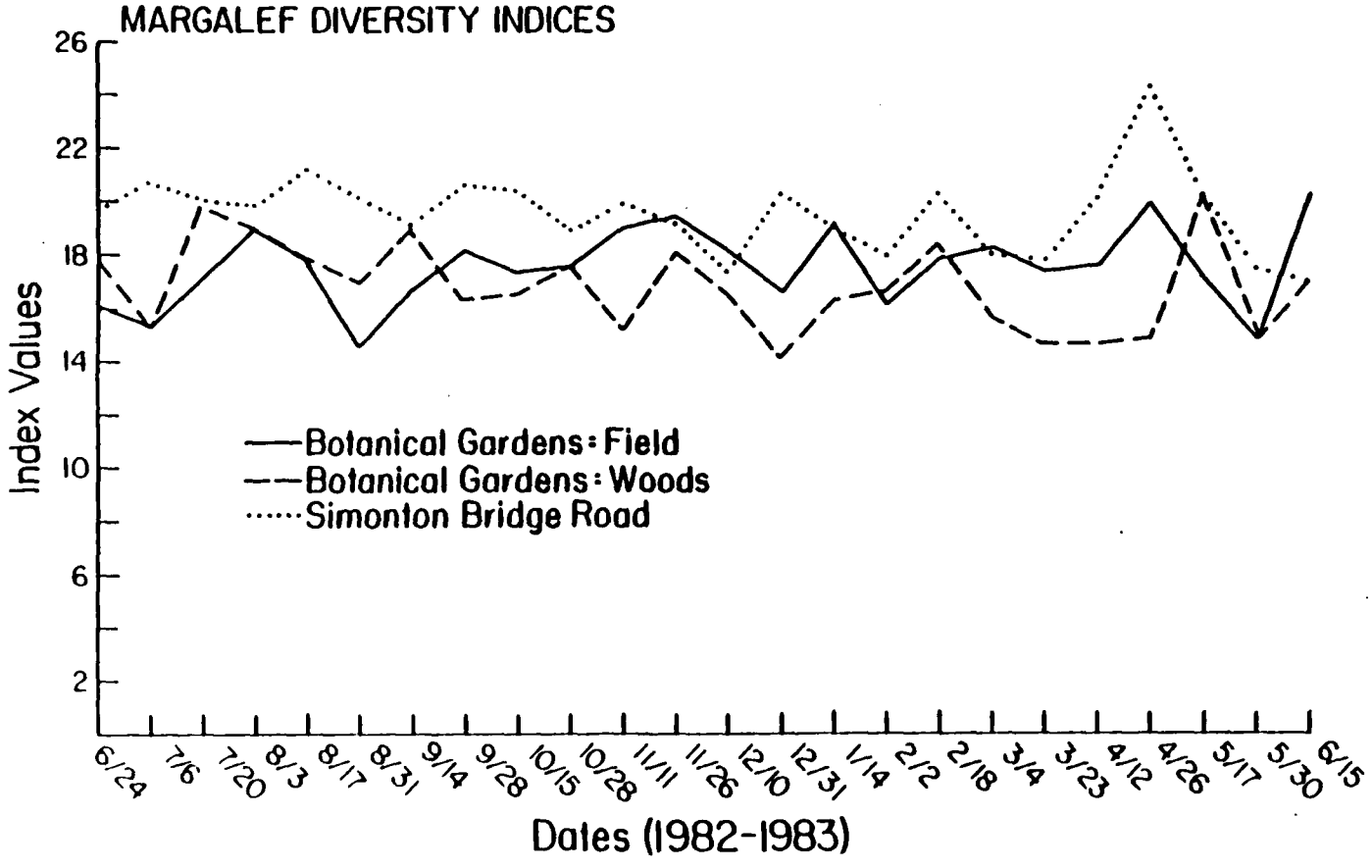
Populations of Microarthropods collected from positive and negative chigger sites sampled at the Simonton Bridge Road study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.



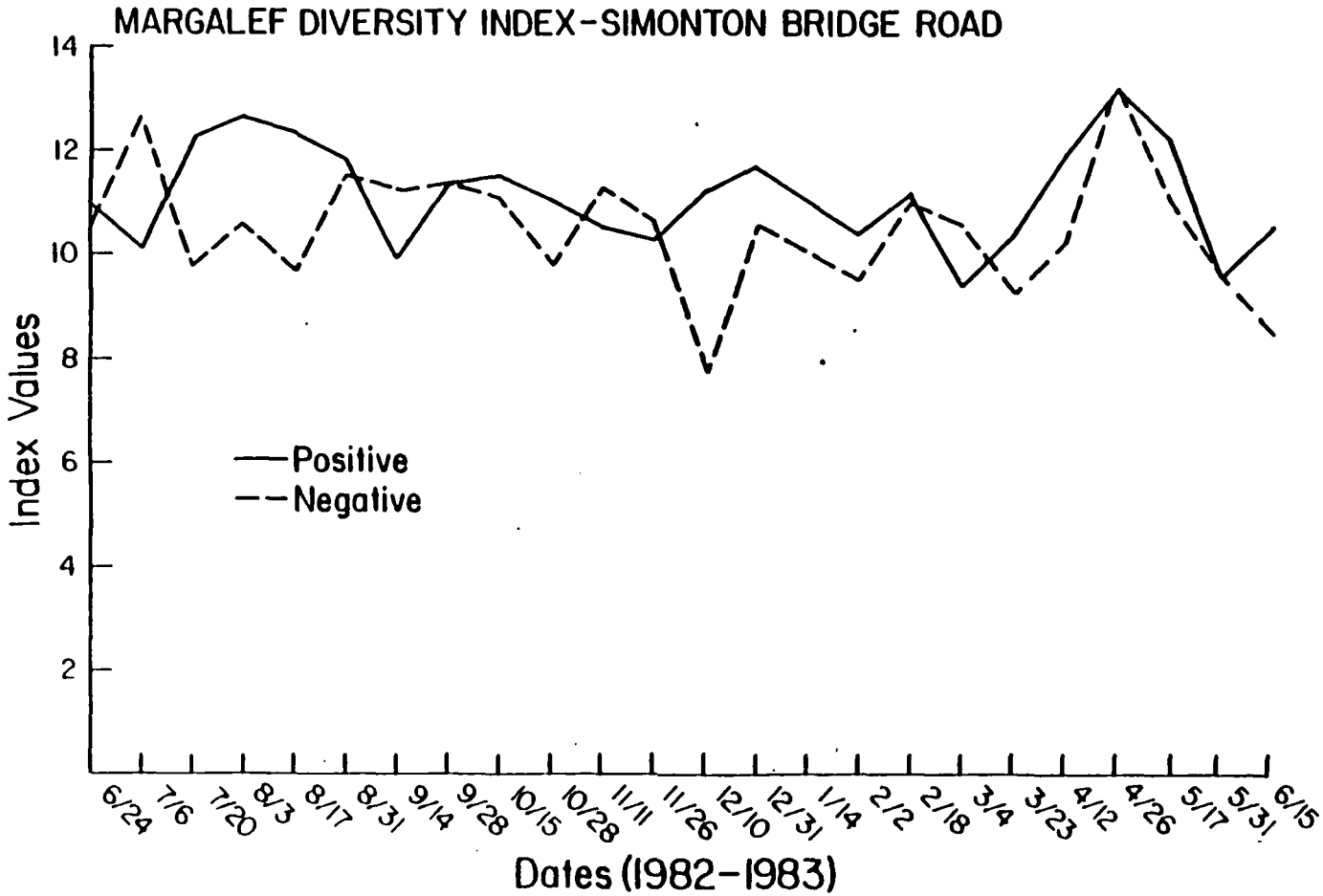
Populations of Microarthropods collected from positive and negative chigger sites sampled at the Botanical Gardens Woods study area. All data points represent population estimates (mean per m^2), taken every two weeks for a one year sampling period.

APPENDIX C:

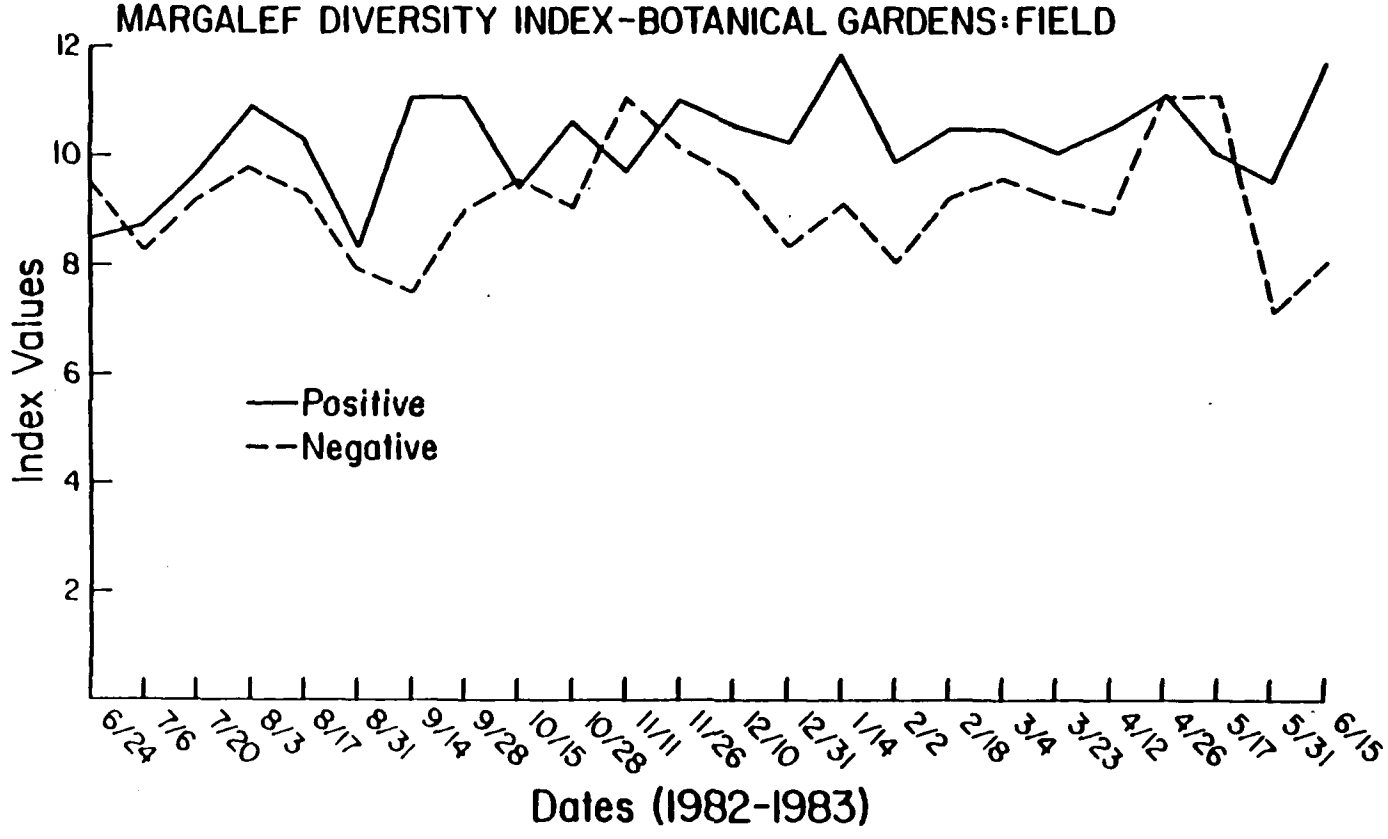
Figures of Soil Arthropod Diversity Index Levels



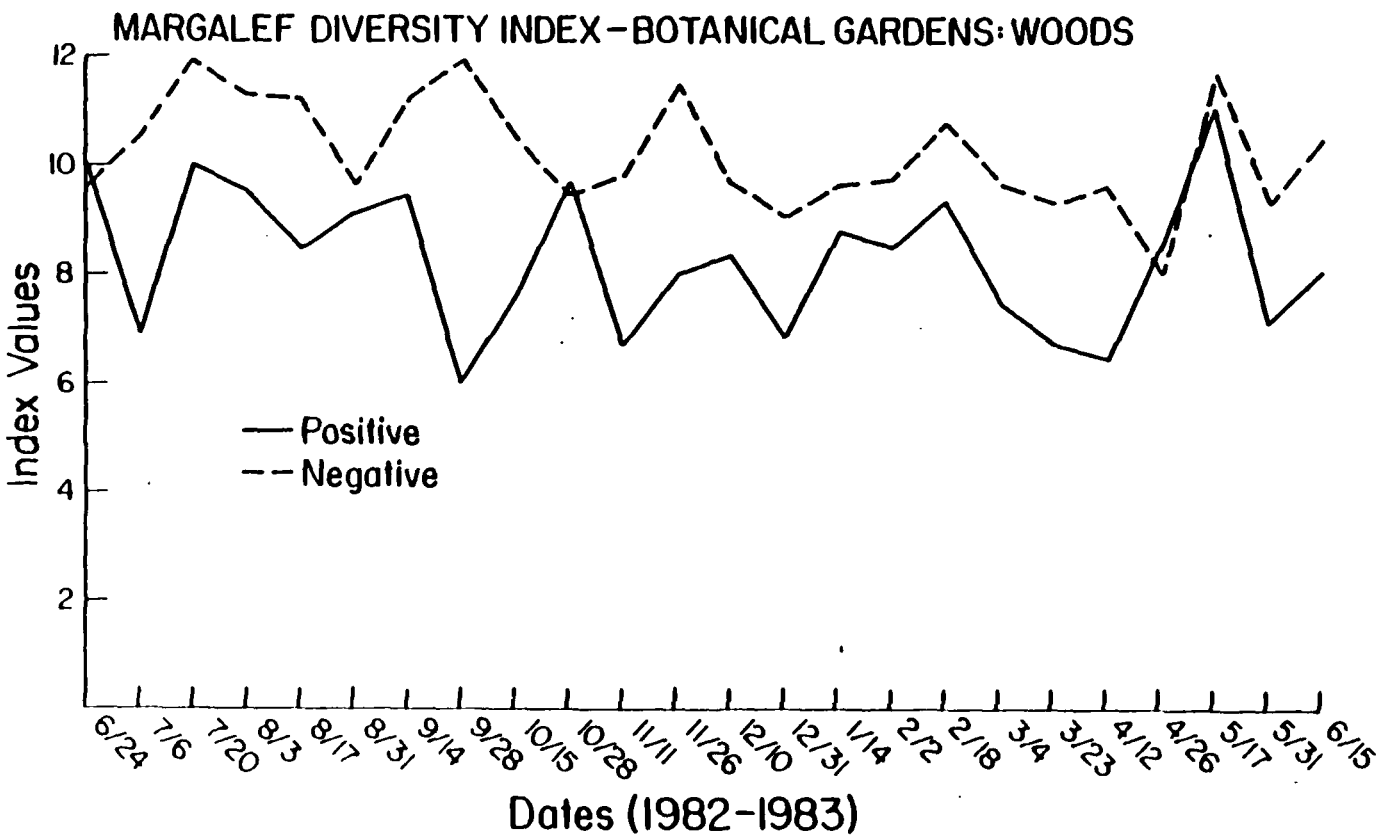
Comparisons of Margalef diversity indices for soil arthropods collected from the Simonton Bridge Road, Botanical Gardens Field, and Botanical Gardens Woods study areas. Data from positive and negative chigger sites pooled.



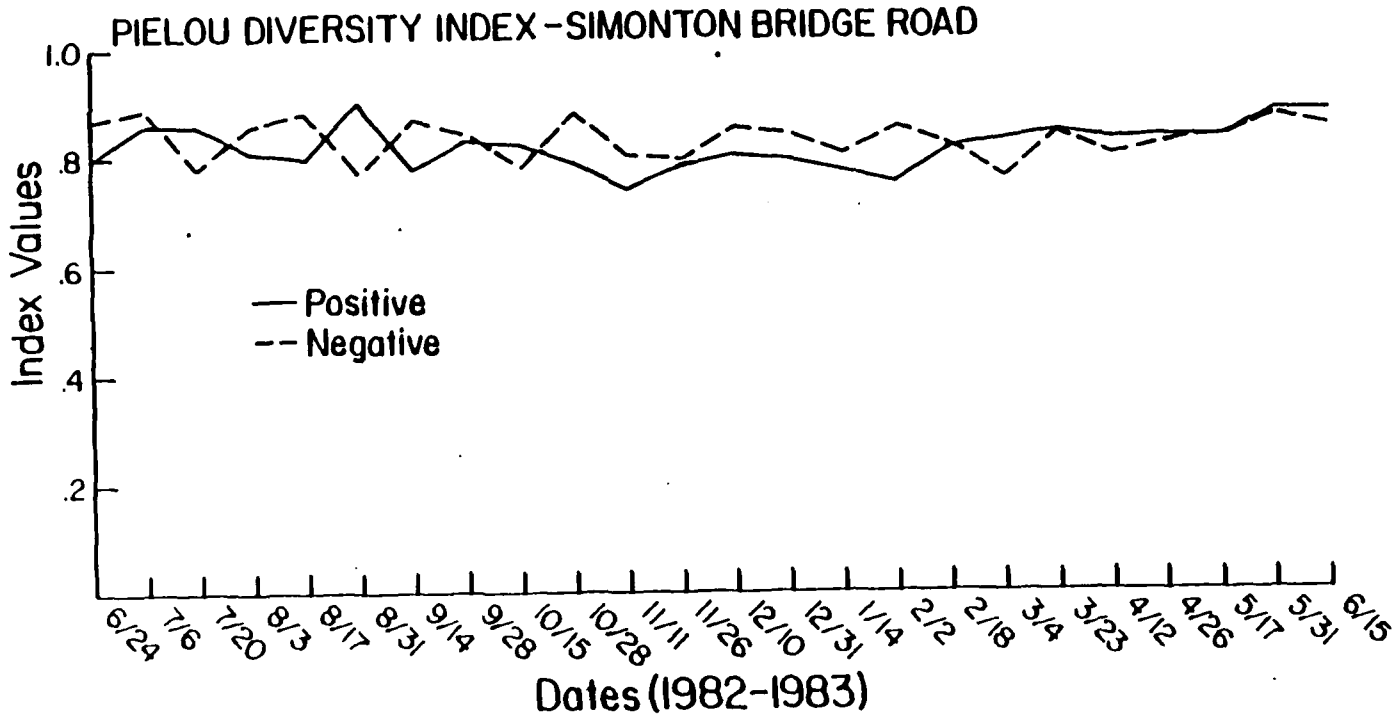
Comparisons of Margalef diversity values for soil arthropods collected from positive and negative chigger sites at the Simonton Bridge Road study area.



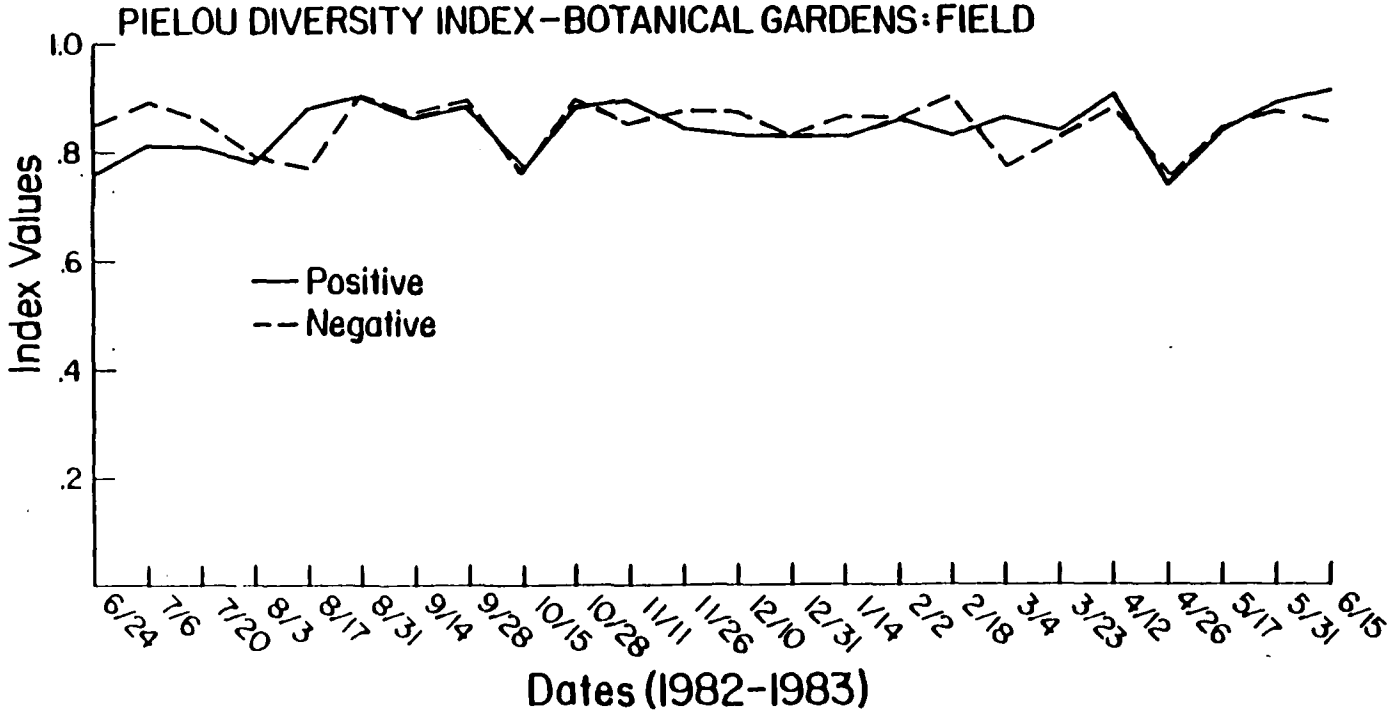
Comparisons of Margalef diversity values for soil arthropods collected from positive and negative chigger sites at the Botanical Gardens Field study area.



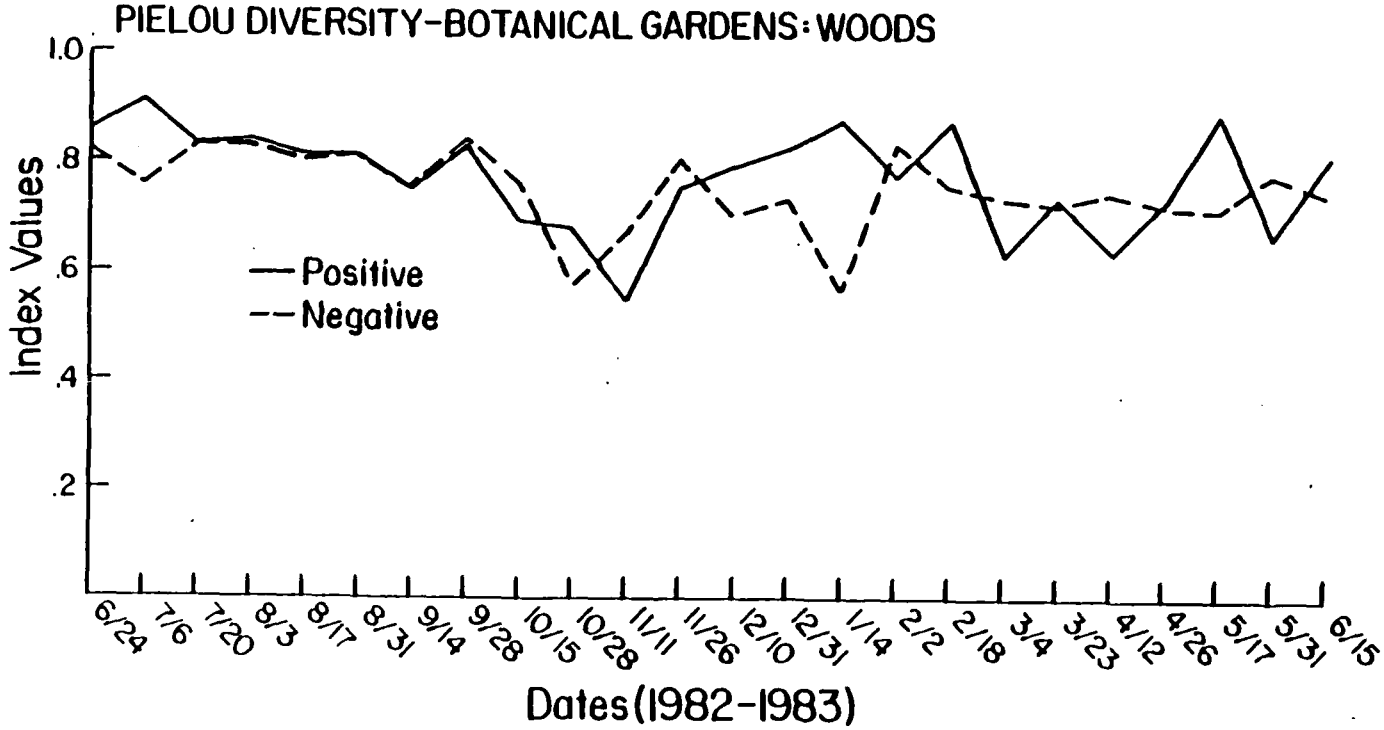
Comparisons of Margalef diversity values for soil arthropods collected from positive and negative chigger sites at the Botanical Gardens Woods study area.



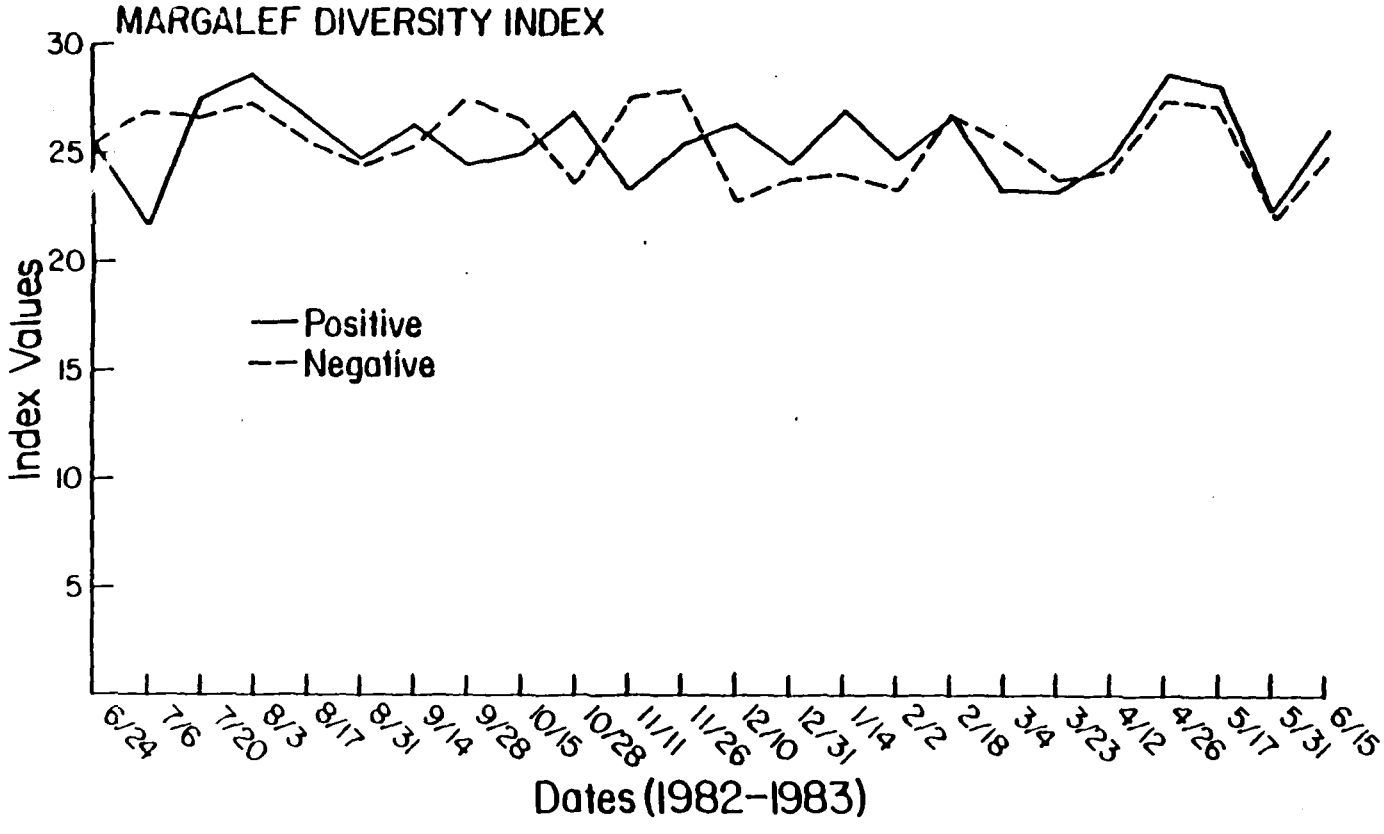
Comparisons of Pielou diversity values for soil arthropods collected from positive and negative chigger sites at the Simonton Bridge Road study area.



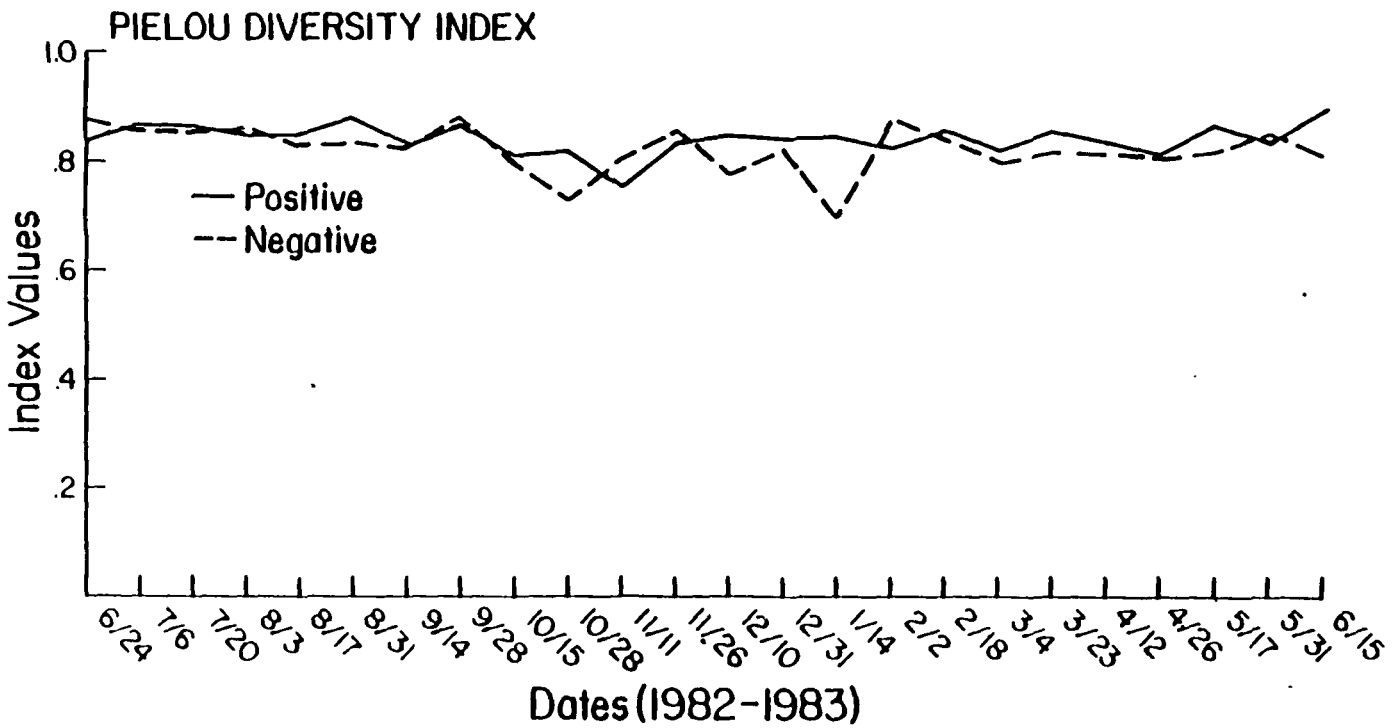
Comparisons of Pielou diversity values for soil arthropods collected from positive and negative chigger sites at the Botanical Gardens Field study area.



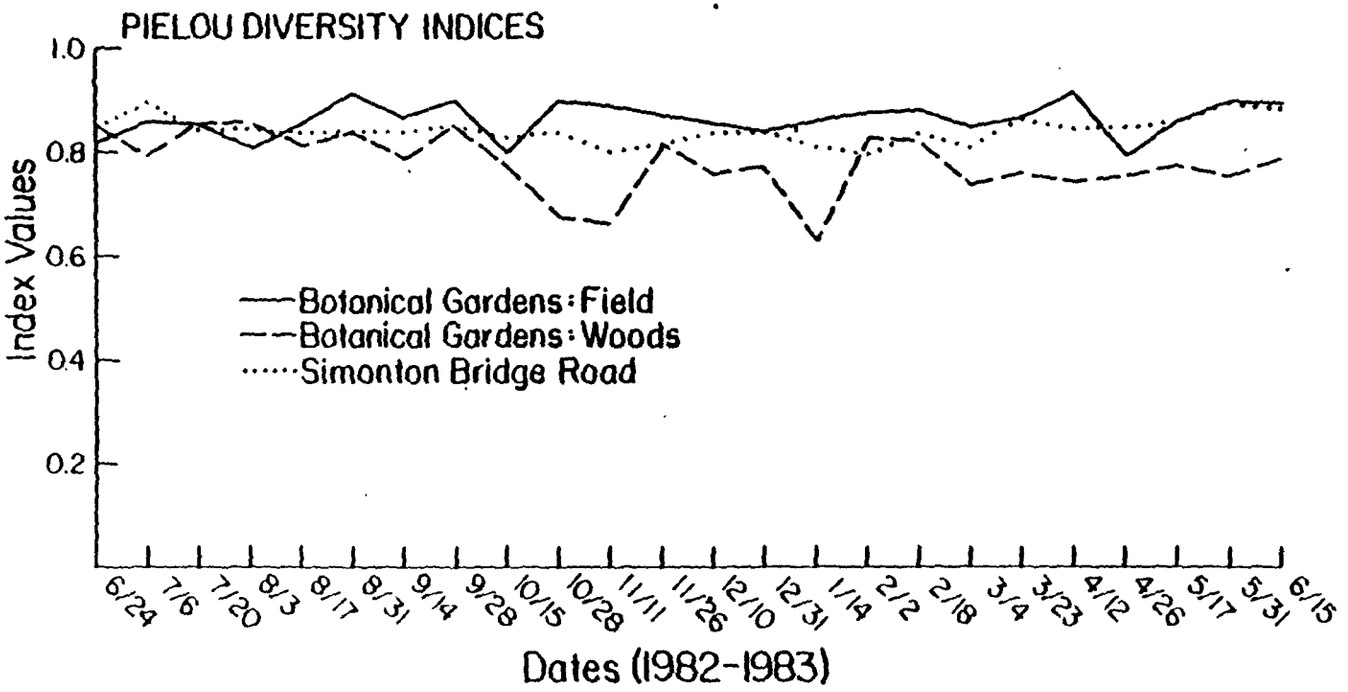
Comparisons of Pielou diversity values for soil arthropods collected from positive and negative chigger sites at the Botanical Gardens Woods study area.



Comparisons of Margalef diversity values for soil arthropods collected from positive and negative chigger sites (data from all three study areas pooled).



Comparisons of Pielou diversity values for soil arthropods collected from positive and negative chigger sites (data from all three study areas pooled).



Comparisons of Pielou diversity indices for soil arthropods collected from the Simonton Bridge Road, Botanical Gardens Field, and Botanical Gardens Woods study areas. Data from positive and negative chigger sites pooled.

CHAPTER IV

MODELS OF DISTRIBUTION TIMES FOR THE DEVELOPMENT OF EUTROMBICULA ALFREDDUGESI (OUDEMANS) (ACARINA:TROMBICULIDAE)[1]

Submitted: Annals of the Entomological Society of America. (1985).

INTRODUCTION

Insect development times have traditionally been reported as the averages of development time, e.g., degree days, but little attention has been accorded to the form of the distribution until recently (Wagner et al. 1984b). The enhanced accuracy achieved by the incorporation of variability into development rate studies was made evident in the 1970's as entomologists began to develop integrated pest management systems. This stochastic element can be incorporated into the developmental description by the use of the "same-shape" property model (Sharpe et al. 1977, Curry et al. 1978, Wagner et al. 1984b) to describe the distribution of development times. This model defines a cumulative distribution of emergence times in terms of physiological time which is independent of temperature. The cumulative distribution of development time provides a technique for thermal summation.

MATERIALS AND METHODS

LABORATORY TECHNIQUES

All mites used in this study were either collected from Whitehall forest, Athens, Georgia or were the first generation produced from laboratory colonies started from larvae collected from Whitehall forest. The experimental temperature range was 10.0+1°C to 40+1°C for all stages. The original evaluation was conducted at 5.0° increments begining at 10.0°C. Intermediate temperature data were then collected at 5.0° increments begining at 12.5°C during a second run in order to accomodate a limited number of environmental chambers. Only 17.5±1.0°C was omitted from this thermal sequence due to space limitations.

Observation chambers consisted of round plastic vials 30 mm (dia.) by 25 mm (ht.) which had 3 drainage holes drilled in the bottom covered with a 10 mm deep substrate of charcoal:plaster of Paris (1:9). The observation chambers were stored in 500 ml glass ointment jars with screw top lids. A layer of damp cellulose sponge in the bottom of the jar maintained a relative humidity near 100% which acted as a buffer against the possibility of dehydration within the observation vials. This was especially important in the upper region of the temperature range.

Eggs and Deutova

Eggs were collected hourly from individual females held at 25°C and transferred to damp filter paper in covered petri dishes. The petri plates were in turn stored over water in

sealed ointment jars similar to those described above for observation vials. Experimental groups ranged in size from 34 to 58 eggs. The resulting deutova were maintained at the same temperature they were derived from. Observations for both eggs and deutova were made approximately every 8 hours. For those temperatures at which eggs failed to develop, new deutova from 25°C were substituted in order to determine the complete developmental range of the deutovum.

Fed Larvae

Eutrombicula alfreddugesi unfed larvae were field collected on 2 day old chicks during the summer of 1983 and allowed to detach naturally from the hosts. Replete larvae were collected twice a day from beneath the chicks and stored in observation chambers which were placed immediately into the designated thermal environments. The fed larvae, which compose an experimental cohort, had all dropped from the hosts between 9 a.m. and 3 p.m. on the same day. The midpoint, noon, was used as the starting time for development and all groups were checked every 24 hours. Experimental group size varied from 40 to 105 fed chiggers.

Post-Larval Stages

As individual mites progressed to the next stage, they were moved to new observation vials and continued development at the same temperature. Larvae failed to develop at 12.5° and 40.0° C New protonymphs, from larvae which had developed at 25° C, were substituted to determine the full range of protonymphal development. This substitution process was repeated whenever a

stage was unable to complete development to the next instar. All substitutes had undergone their previous development at 25° C Each stadum was examined every 24 hours.

ANALYSIS OF DATA

The lengths of time required to complete development, for each stage, at each experimental temperature, were grouped into standard width classes. The mean, median, variance and skewness were determined for each temperature's distribution of development times with the univariate procedure from the SAS statistics computer program library.

A computer program of Wagner et al. (1984b) was used for the following distribution analysis. The developmental time distributions were converted to cumulative probability distributions by first summing the frequencies of successive classes and then standaridized by dividing the cumulative frequencies by the total frequencies. This eliminated variability within the distribution which results from differences in the length of the development period (i.e., the number of classes) due to temperature. The developmental distributions were then normalized for temporal displacement by dividing the standardized developmental times by the median time. This made the distributions independent of time and resulted in the overlay of distributions which all share the same median point. The time independent distributions, referred to as tau distributions by Wagner et al. (1984b), were then

multiplied by their mean rate to make them temperature independent as well. This generated standard tau curves which were evaluated for similarity of shape. The variation between the distributions was measured by the coefficient of variation calculated for 1%, 30%, 70% and 100% cohort development points. A mean standard tau distribution was then obtained by taking the average of each distribution's values which have been weighted for the total number of raw data points used to generate each value.

The mean standard tau distribution was fitted to a three parameter cumulative Weibull function with the form:

$$F(x) = 1 - \exp(-[(x-G)/E]^B)$$

where: F(x) is the probability of complete development at normalized

time x,

G (gamma) is the threshold value, i. e., expected complete development of first individual,

B (beta) is the shape parameter and

E (eta) is the location parameter.

Both "B" and "E" were estimated by transforming the Weibull distribution to the linear form: $\ln(-\ln[1-F(x)]) = B \ln(x-G) - B \ln E$, where "B" is the slope and the Y-intercept equals $-B \ln E$.

The correlation between the data and a Weibull distribution can be estimated by the coefficients of determination (R^2).

RESULTS

DEVELOPMENTAL TIME DISTRIBUTIONS,

EGGS

The frequency distributions of all stages tend to deviate from a normal distribution. For this reason the median rather then the mean was chosen as the best measure of central tendency to be used in correlation with temperature. The distributions of egg development times are all skewed (Fig. 4-1). The kurtosis of the development distribution at 30.0°C is strongly leptokurtic and has the smallest variability (CV=3.31). As temperatures decline, the frequency distributions become less peaked until. at 20.0°C and below, they become platkurtic. The coefficients of variance (CV) do not vary systematicly with temperature which demonstrates that the variances of the samples are independent of temperature.

DEUTOVA

The distributions of deutoval periods, like those of the eggs, deviated from the normal distribution. The freqency of emergence histograms were skewed to the right at higher temperatures but to the left at 15.0°C (Fig. 4-2). Both the 35.0° and 30.0° distributions are leptokuritic while the lower

temperatures are platykurtic. The magnitude of the peak is greatest at 30.0°C (55%)(Fig. 4-2). 20.0°C appears to lack a peak but if the width of the classes were increased from .33 day to 1 day then a low peak would be seen at 18 days.

FED LARVAE

The distribution of developmental time at 15.0°C is strongly skewed to the right while all other distributions of fed larvae above 15.0°C (Fig. 4-3) are near symmetrical in means and medians (Tables 4-1). The variances are independent of temperature throughout the range studied as indicated by the independence of the coefficients of variance from temperature. Like the previous developmental distributions, the fed larval distributions appear to be leptokurtic above 15.0°C The greatest precentage to complete development together, i.e., the strongest peak, was on the second day at 30.0°C. This temperature also has the narrowest range (3 days). The distributions of emergence times overlay each other on the time (X) axis, i.e., the entire range of the distributions for all temperatures is within the first 12 days (Fig. 4-3). The temperature-independent temporal homogeneity of fed larvae developmental times is not shared by the other stages where the position of the range of the developmental times distribution changes with temperature.

PROTONYMPHS

The frequency histograms of protonymph development are all

leptokurtic with all peaks containing at least 48% of the data (Fig.4-4). The strongest peak is associated with 25.0°C on the eighth day (65%). All distributions are slightly skewed except the 25.0°C distribution which is significantly skewed to the right. The variances of the distributions are independent of temperature as indicated by the random variability of the coefficients of variance. The range of the distributions associated with temperatures above 20.0°C are closely aligned between 0 and 12 days.

DEUTONYMPHS

The frequency distributions of deutonymph development times have a bimodal form which is most pronounced at 20.0°C where the 2 distributions are separated by a 190 day interval (Fig. 4-5). The bimodal character persists as temperature increases up to 32.5°C although the distance between the two populations decreases to 12 days. The proportion of deutonymphs in the rapid population increases with temperature (Table 4-2) until temperature reaches 35.0°C, where the histogram forms a single platykurtic distribution within the range of rapid development. A bimodal frequency reappears at 37.5°C with a separation of 9 days between the two distributions. The width of the range for both rapid and slow populations remained relatively narrow for all temperatures. The median range width for rapidly developing deutonymphs is 20 days and for slowly developing deutonymphs is 9 days (Appendix, Table A1). Range width does not decrease when temperature increases as is the case in other stadia development

distributions. The variances of the 2 deutonymphal development subpopulations appear to be independent of temperature as indicated by the non-systematic changes in the coefficients of variance.

TRITONYMPHS

The frequency distributions for development of the tritonymph are leptokurtic at all temperatures except 22.5°C and 15.0°C where they are platykurtic (Fig. 4-6). All leptokurtic distributions possessed strong peaks which represented 39% to 56% of the distribution's data points. The greatest concentration of data values is found in the 25.0°C distribution, 84% of the data is concentrated at the peak over days 9 and 10. The variances of the distributions do not correlate with temperature as demonstrated by the random changes in the coefficients of variance (Table 4-3).

ANALYSIS OF SAME SHAPE HYPOTHESIS AND WEIBULL DISTRIBUTION

In general, the ranges of variation is comparable to that found in other developmental data (Wagner et al. 1984b). Although the normalized cumulative frequency distributions do not conform to the theoretical same shape hypothesized by Sharpe et al. (1977), they do have similar shapes as shown by the moderate coefficients of variation.

The normalized distributions of each stage show the greatest variation at the extreme probabilities, i.e., 0.01 and 1.00 as

demonstrated by the coefficient of variations in Table 4-4. The relatively large coefficients of variation associated with the egg stage is primarily due to the small numbers of eggs which completed development and thus contributed to the distributions (Table 4-5). A similar problem exists for the two deutonymph developmental rate morphs; both high mortality and the a posteriori division of the deutonymph cohorts into rapid and slow developing subpopulations resulted in few data available for distribution analysis (Tables 4-2 and 4-6).

A small number of classes (2 in 27.5°C and 3 in 22.5°C, 25.0°C and 30.0°C) in the frequency distributions in the optimal temperature range is largely responsible for the large variation observed in the fed larvae. Insufficient number of classes also contributed to the variation in the distributions of the tritonymph. In addition, the impact of high mortality near the temperature extremes on the sample size was a second source of variation (Table 4-7).

The greatest absolute differences between the observed and expected values were all very small. The egg stage has the largest linear regression residual, 0.056 but these data also had a R^2 value of 0.995. These results are comparable to those reported by Wagner et al. (1984b) in his analysis of 23 data sets from the literature.

The normalized cumulative frequency distribution for each stage is efficiently modeled by a cumulative Wiebull function (Fig. 4-7, 4-8, 4-9, 4-10 and 4-11). How well the Wiebull function describes the transformed data can be determined by

plotting the Ln-Ln of the cumulative probabilities of the normalized distribution against the observed and expected values of the Ln of (the normalized cumulative frequency values minus the threshold value, i. e., gamma) (Appendix, Figs. A1 to A7). The coefficient of determination (R^2) for each stage is listed in table 4-4. With the exception of the slow deutonymph morph, all have a R^2 value greater then 0.99.

The values of the remaining two Wiebull parameters beta and eta (Table 4-8) are determined from the slope and Y-intercept respectively.

DISCUSSION

DISTRIBUTION MODEL AND MORTALITY

The variance of the cumulative frequency distributions of the developmental times must be independent of temperature if the same shape property is to apply. The coefficients of variance for each stadium do not correlate with changes in temperature. This independence provides the theoretical basis for the consideration of a single, biological time scale distribution to describe the developmental time distribution free of temperature considerations.

The greatest amount of relative variation occurs among the fed larvae cohorts. Variation in nutritional quality and quantity is a potential factor in the explanation of this variation. Complete engorgement was determined by detachment plus visual observations and was not quantified. The impact of host activities on the length of the attachment period and the possibility that nutritional quality may vary between sites of attachment have not been investigated. Variation in the individual chigger's ability to engorge fully and effectively utilize the host's nutrients may further compound the problem.

Variations among the normalized developmental distributions

(Table 4-4) follow the same pattern in which the variation among the distributions progressively increases as the distribution approaches its extremes. With the exception of fed larvae, the coefficients of variance for the extremes of the distribution (0.01 and 1.0 probabilities) fall within the range Wagner et al. (1984b) describes as small to moderate. These indicate that the cumulative frequency distributions used to estimate the standard normalized distribution are similar but not identical. Similar, but not identical, distributions were also found by Wagner et al.'s (1984b) review of data from the literature. They attribute this variation to four experimental design factors: insufficient number of class intervals, differences in sample size, inadequate sample size and selective mortality at temperature extremes. Intrinsic biologic factors may also play a role, e.g., variations in regional populations, interactions of unknown pathogens, population density, nutritional differences among cohorts and variations in other uncontrolled abiotic factors (Wagner et al. 1984b).

Several of the factors listed above may be responsible for some of the variation observed in this study. For example, the large variation among fed larvae cohorts is partially due to their rapid development which resulted in an insufficient number of observation intervals. Distributions should contain a minimum of ten classes for an accurate estimation of population parameters (Howe 1967), the fed larvae cohorts comprise nine classes at 15°C. and decrease to two classes at 27.5°C.. Nutritional differences, uneven sample sizes and the small

sample sizes of some cohorts also contributed to the variation. Reduction in variability due to experimental design, although always the goal, is diminished to the extent that the natural niche requirements of the organism being studied are compromised. The experimental necessity of colony produced cohorts resulted in a population reared under conditions not experienced by wild populations of E. alfreddugesi, which for most of its life, leads a very cryptic existance within the litter and soil. The ecological requirements of the postlarval stages have yet to be fully determined. These factors were also the source of problems in obtaining large cohorts for analysis. Additional variability is induced by the changes in behavior of a cryptic species forced into an exposed environment which is necessary for daily observations. The advantages provided by inclusion of stochastic aspects in the developmental rate models far outweigh the difficulties incurred in collecting the data.

The derived standard normalized distributions function as predictive models of the developmental distributions but with statistical reservations. The relative amount of variability in the distributions, as indicated by the coefficients of variation, changes as the probability for complete development of the cohort increases (Table 4-4). The coefficients provide relative measures of variability which, when incorporated into the model, define the statistical limits for the predictions of emergence times for each stage.

The accuracy of the Weibull function as a descriptive model of the distribution of development times of every stage of E.

alfreddugesi's development (Figs. 4-7, 4-8, 4-9, 4-10 and 4-11) is consistantly high (R^2 > 0.99 for all regressions). The combination of tolerable variability among the distributions of the experimental cohorts and accurate predictive models provide statistically reliable, simple mechanistic predictors of the proportions of the stadial cohort which complete development as a function of accumulating rates.

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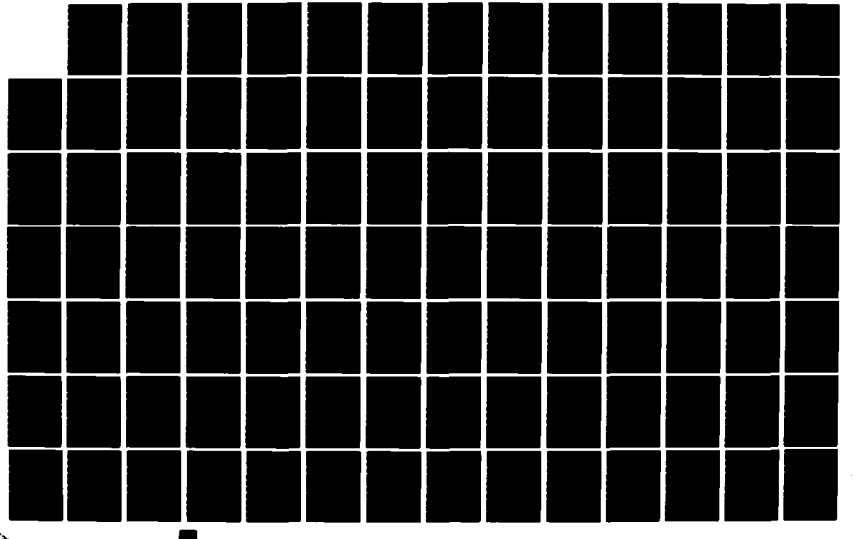

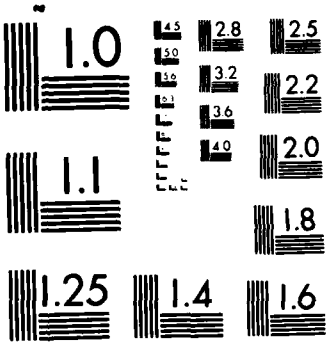

Table 4-1. Median development rates for the fed larvae of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0
15.0	4.3	0.2353	101	95.5
20.0	2.4	0.4192	97	75.8
22.5	3.0	0.3333	34	100.0
25.0	1.9	0.5185	103	98.1
27.5	1.8	0.5614	25	75.8
30.0	1.5	0.6707	100	100.0
32.5	2.0	0.5000	18	72.0
35.0	2.0	0.5000	24	77.8
37.5	2.6	0.3913	26	64.9*
40.0	N/D	---	0	0.0

N/D: No development occurs
* Significantly different (p=.05)

Table 4-2. Median development rates for the rapid development morph of the deutonymphs of Eutrombicula alfreddugesi

Temperature of population °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent surviving
12.5	N/D	---	0	0.0
15.0	N/D	---	0	0.0
20.0	19.5	0.0513	5	27.3
22.5	19.5	0.0513	10	58.8
25.0	11.0	0.0909	14	71.4
27.5	17.5	0.0571	12	80.0
30.0	17.0	0.0588	20	77.0
32.5	20.5	0.0488	18	93.7
35.0	17.5	0.0571	25	100.0
37.5	20.0	0.0500	14	77.8
40.0	N/D	---	0	0.0

N/D: No development occurs

Table 4-3. Median development rates for the tritonymphs of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development		Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0	
15.0	38.5		0.0260	11	55.0*
20.0	23.1	0.0433	20	95.2	
22.5	12.3	0.0811	20	100.0	
25.0	9.1	0.1103	21	100.0	
27.5	10.3	0.0976	22	100.0	
30.0	7.5	0.1333	23	100.0	
32.5	6.5	0.1538	19	95.0	
35.0	6.3	0.1587	22	100.0	
37.5	6.7		0.1493	13	48.2*
40.0	N/D	---	0	0.0	

N/D: No development occurs
* Significantly different (p=.05)

Table 4-4. Variation among the normalized developmental distributions of each stage of *Eutrombicula alfreddugesi*

	Coefficient of Variation(%) at Four Probabilities				R^2
	0.01	0.30	0.70	1.00	
Life Stage					
Egg	55.1	17.8	6.3	15.6	0.995
Deutovum	24.7	3.4	5.1	24.8	0.995
Fed Larva	124.1	12.7	10.5	24.8	0.998
Protonymph	19.6	5.4	5.1	19.0	0.999
Deutonymph (rapid)	18.7	18.6	13.3	10.3	0.993
Deutonymph* (slow)	4.9	5.1	16.6	19.1	0.965
Tritonymph	28.6	2.1	5.8	14.3	0.999

* 32.5°C. datum is omited because there was only a single observation.

Table 4-5. Median development rates for the eggs of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0
15.0	43.8	0.0228	14	46.7
20.0	18.9	0.0530	11	40.7
22.5	12.5	0.0803	17	56.7
25.0	10.9	0.0922	47	67.1
27.5	10.9	0.0922	23	63.9
30.0	7.1	0.1413	29	58.8
32.5	4.5	0.2205	17	53.1
35.0	5.5	0.1834	17	48.9
37.5	8.3	0.1200	35	54.7
40.0	N/D	---	0	0.0

N/D: No development occurs

Table 4-6. Median development rates for the slow development morph of the deutonymphs of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent of population
12.5	N/D	---	0	0.0
15.0	N/D	---	24*	100.0
20.0	228.5	0.0044	16	72.7
22.5	42.5	0.0235	7	41.2
25.0	42.0	0.0238	6	28.6
27.5	48.3	0.0207	3	20.0
30.0	55.0	0.0182	6	23.1
32.5	44.0	0.0227	1	6.3
35.0	N/A	---	0	0.0
37.5	43.5	0.0230	4	22.2
40.0	N/D	---	0	0.0

N/D: No development occurs
N/A: No data available
* Survived >220 days without development to the tritonymph

Table 4-7. Median development rates for the deutova of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0
15.0	36.5	0.0274	8	100.0
20.0	18.0	0.0555	11	100.0
22.5	12.5	0.0803	15	93.8
25.0	9.1	0.1102	16	100.0
27.5	9.2	0.1087	20	87.0
30.0	2.9	0.3509	30	100.0
32.5	6.3	0.1578	15	100.0
35.0	5.6	0.1802	17	100.0
37.5	5.06	0.2017	28	100.0
40.0	N/D	---	0	0.0

N/D: no development occurs

Table 4-8. Summary of Weibull distribution parameters for *Eutrombicula alfreddugesi*

Life Stage	Eta	Beta	Gamma
Egg	1.04565	6.14779	0.00000
Deutovum	0.35516	2.32462	0.70348
Fed Larva	1.13745	1.99863	0.04627
Protonymph	0.23258	2.10246	0.80426
Deutonymph (rapid)	0.59773	1.48348	0.51202
Deutonymph (slow)	0.14186	0.98405	0.92136
Tritonymph	0.40967	3.13734	0.63558

Table A1. Bimodal distribution characteristics of the rapid and slow deutonymph populations of Eutrombicula alfreddugesi

Temperature °C	Width of Subdistributions Rapid	Slow	Interval Between
12.5	N/D	N/D	---
15.0	N/D	N/D	---
20.0	15	24	190
22.5	20	9	12
25.0	14	28	26
27.5	18	7	12
30.0	20	16	25
32.5	22	1	12
35.0	22	N/A	---
37.5	21	6	9
40.0	N/D	N/D	---

N/D: No development occurs
N/A: No data available

Table A2. Developmental data for the deutonymphs of *Eutrombicula alfreddugesi*

Temperature °C	Mean # days for development ± Standard Error	Coefficient of Variance(%)	N*	Percent Survival
12.5	N/D	---	0	0.0
15.0	N/D	---	24#	48.0
20.0	172.7±20.5	55.53	22	52.4
22.5	29.2±3.2	44.39	17	54.8
25.0	23.9±4.6	85.74	21	41.2
27.5	23.6±3.4	55.14	15	65.2
30.0	27.6±3.6	66.62	26	65.0
32.5	20.1±2.5	48.92	16	88.9*
35.0	18.8±1.1	29.38	25	58.1
37.5	25.7±2.6	42.75	18	48.7
40.0	N/D	---	0	0.0

N*: Number surviving stadium
N/D: No development occurs
Survived >220 days without completing development
* Significantly different (p=.05)

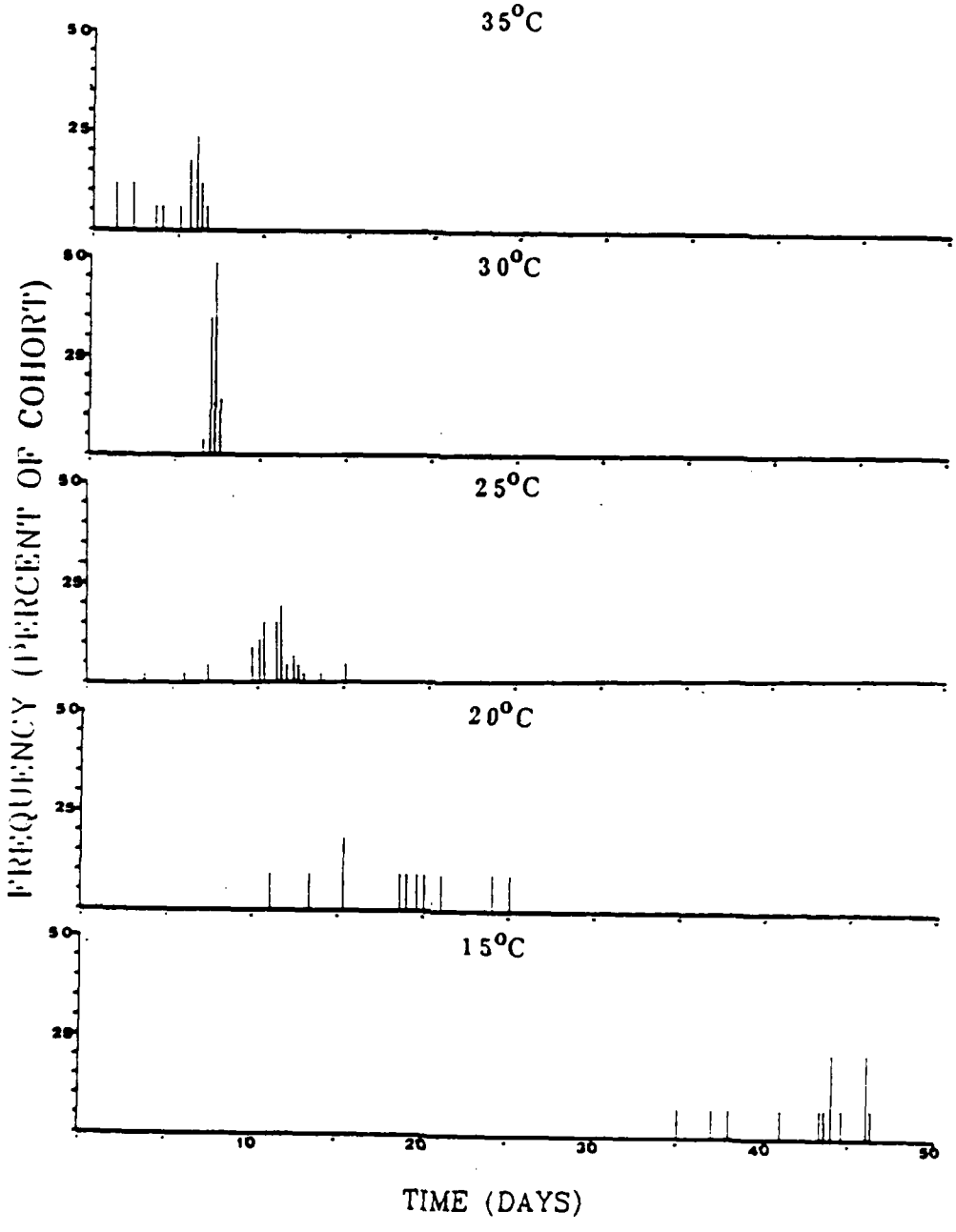

Figure 4-1. Frequency of eclosion times for the eggs of Eutrombicula alfreddugesi at 5C intervals within its developmental temperature range (15.0°C to 35.0°C).

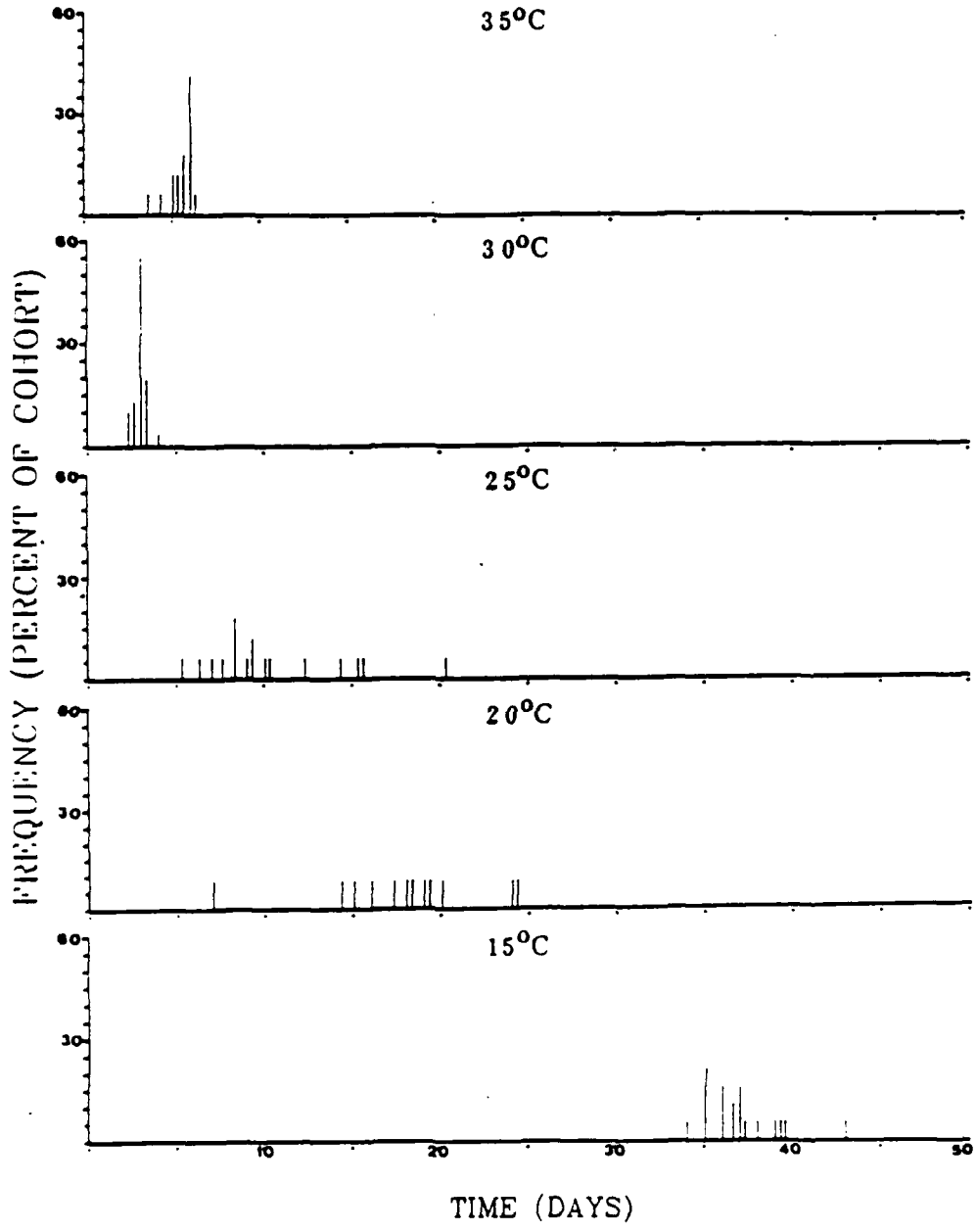

Figure 4-2. Frequency of emergence times for the deutova of Eutrombicula alfreddugesi at 5C intervals within its developmental temperature range (15.0°C to 35.0°C).

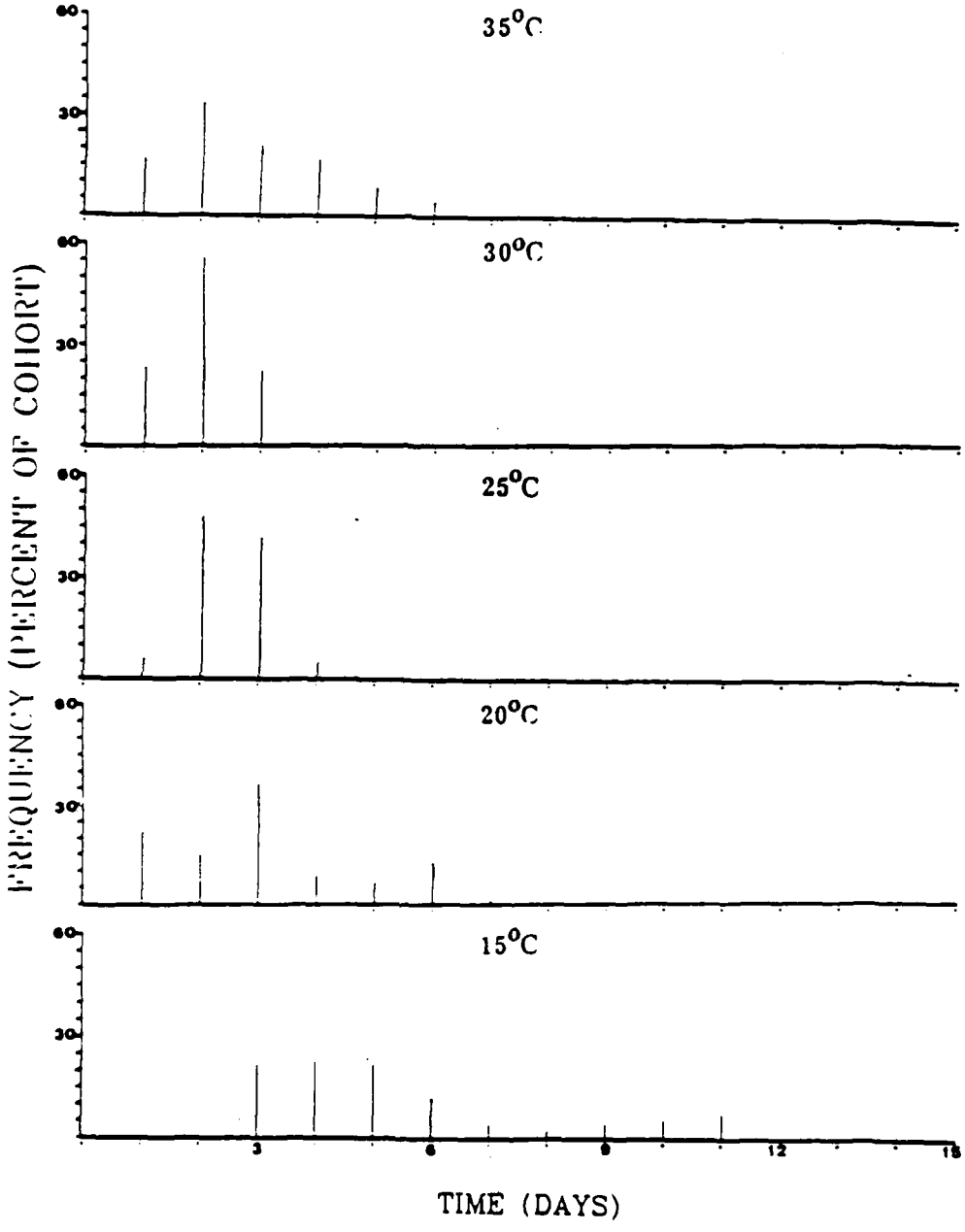

Figure 4-3. Frequency of emergence times for the fed larvae of Eutrombicula alfreddugesi at 5°C intervals within its developmental temperature range (15.0°C to 35.0°C).

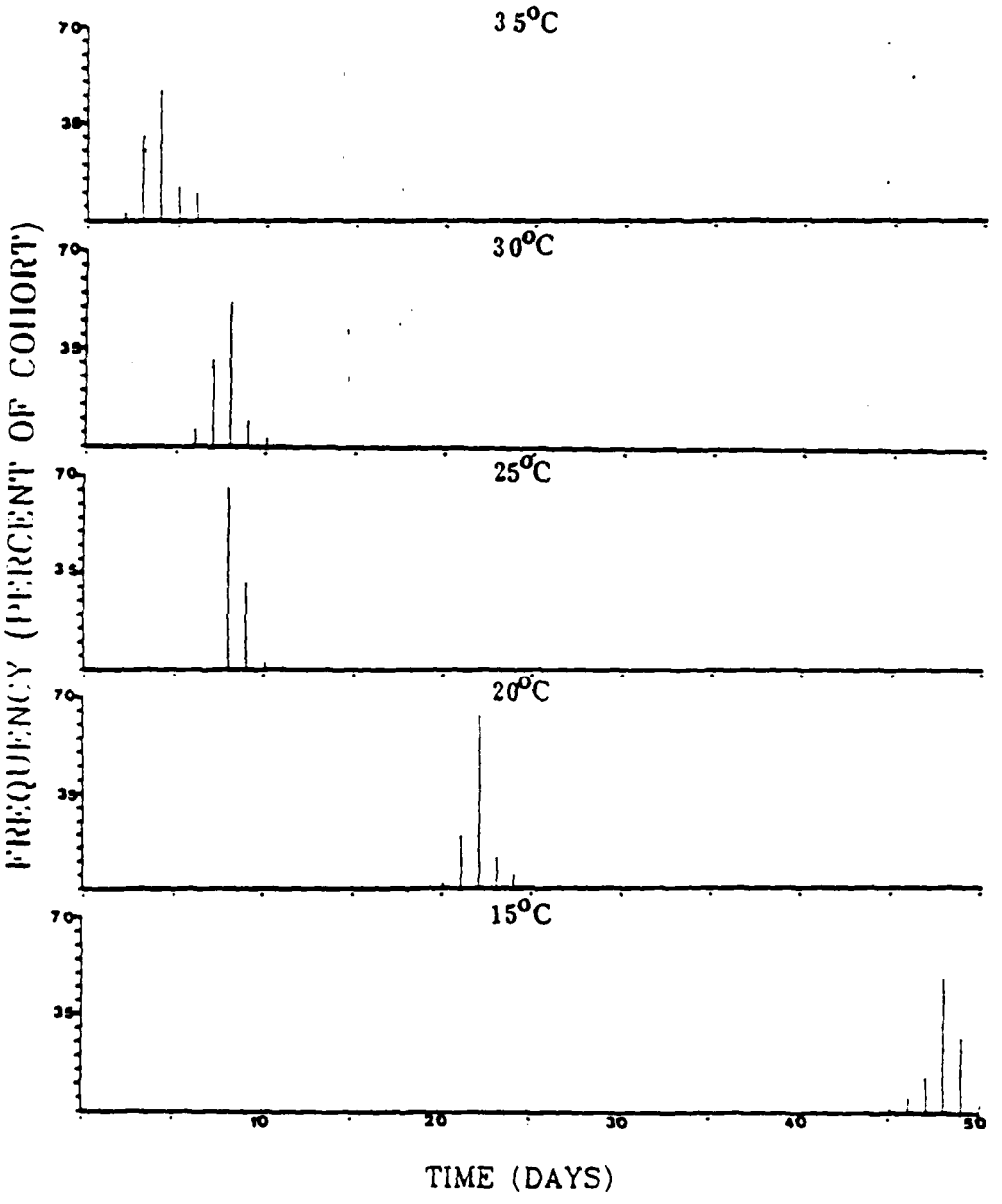

Figure 4-4. Frequency of emergence times for the protonymphs of Eutrombicula alfreddugesi at 5C intervals within its developmental temperature range (15.0°C to 35.0°C).

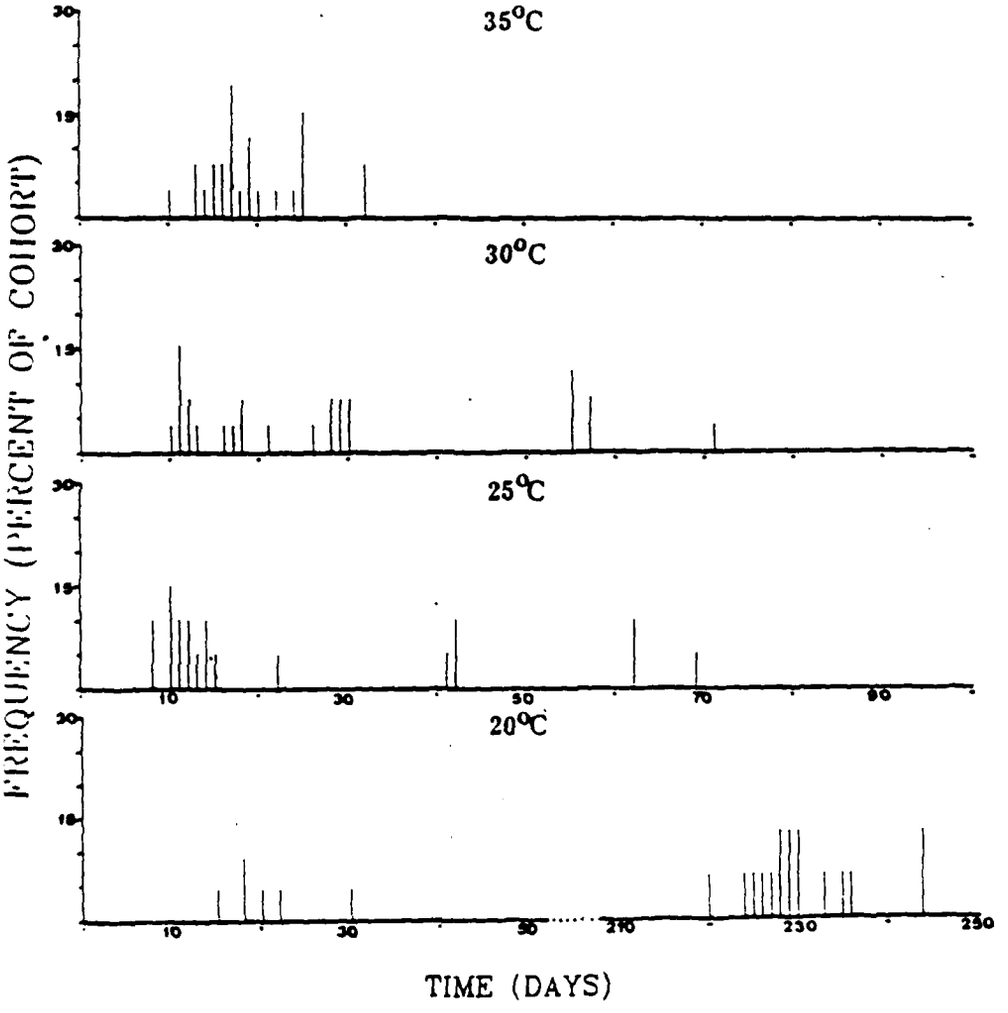

Figure 4-5. Frequency of emergence times for the deutonymphs of Eutrombicula alfreddugesi at 5°C intervals within its developmental temperature range (15.0°C to 35.0°C).

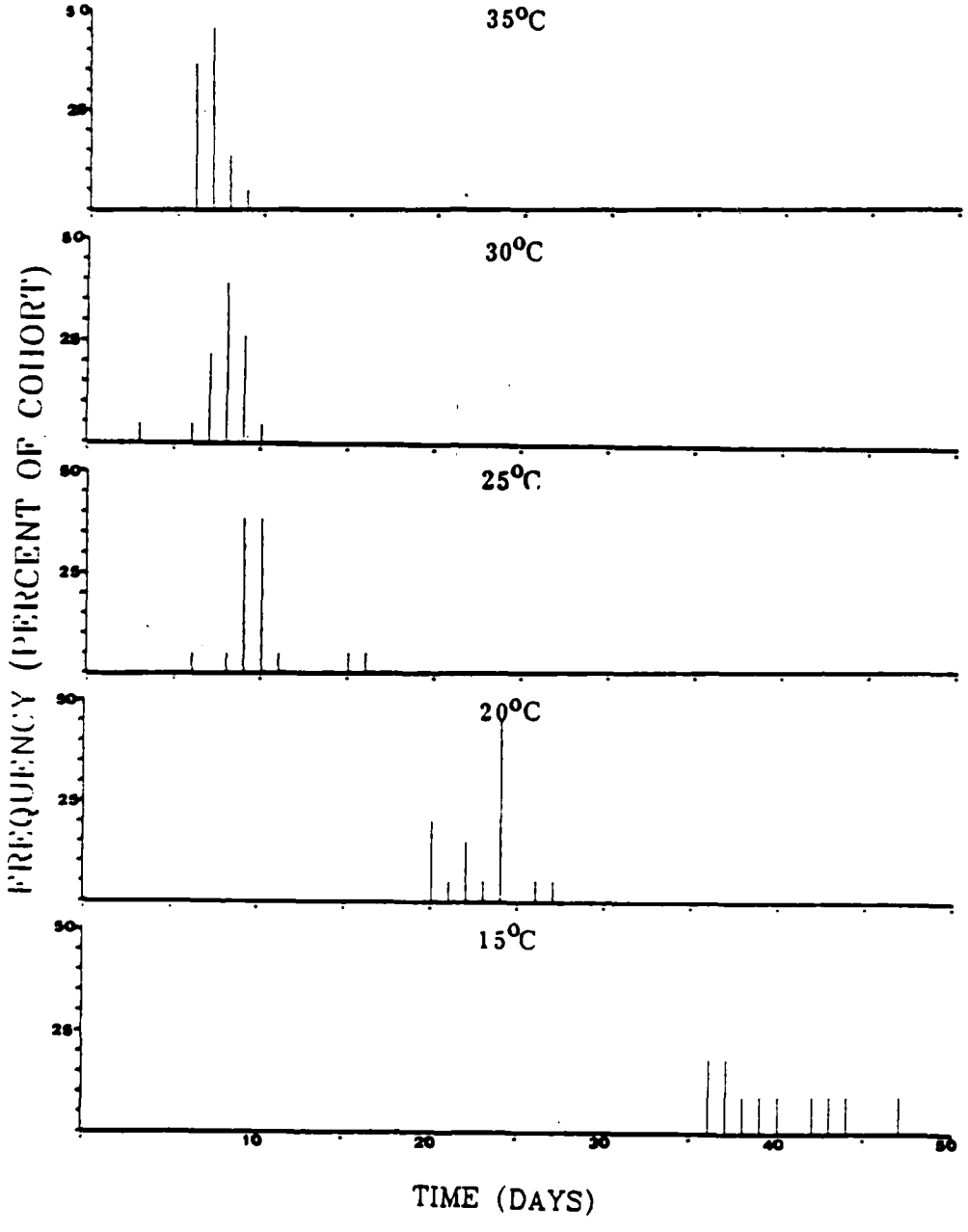

Figure 4-6. Frequency of emergence times for the tritonymphs of Eutrombicula alfreddugesi at 5°C intervals within its developmental temperature range (15.0°C to 35.0°C).

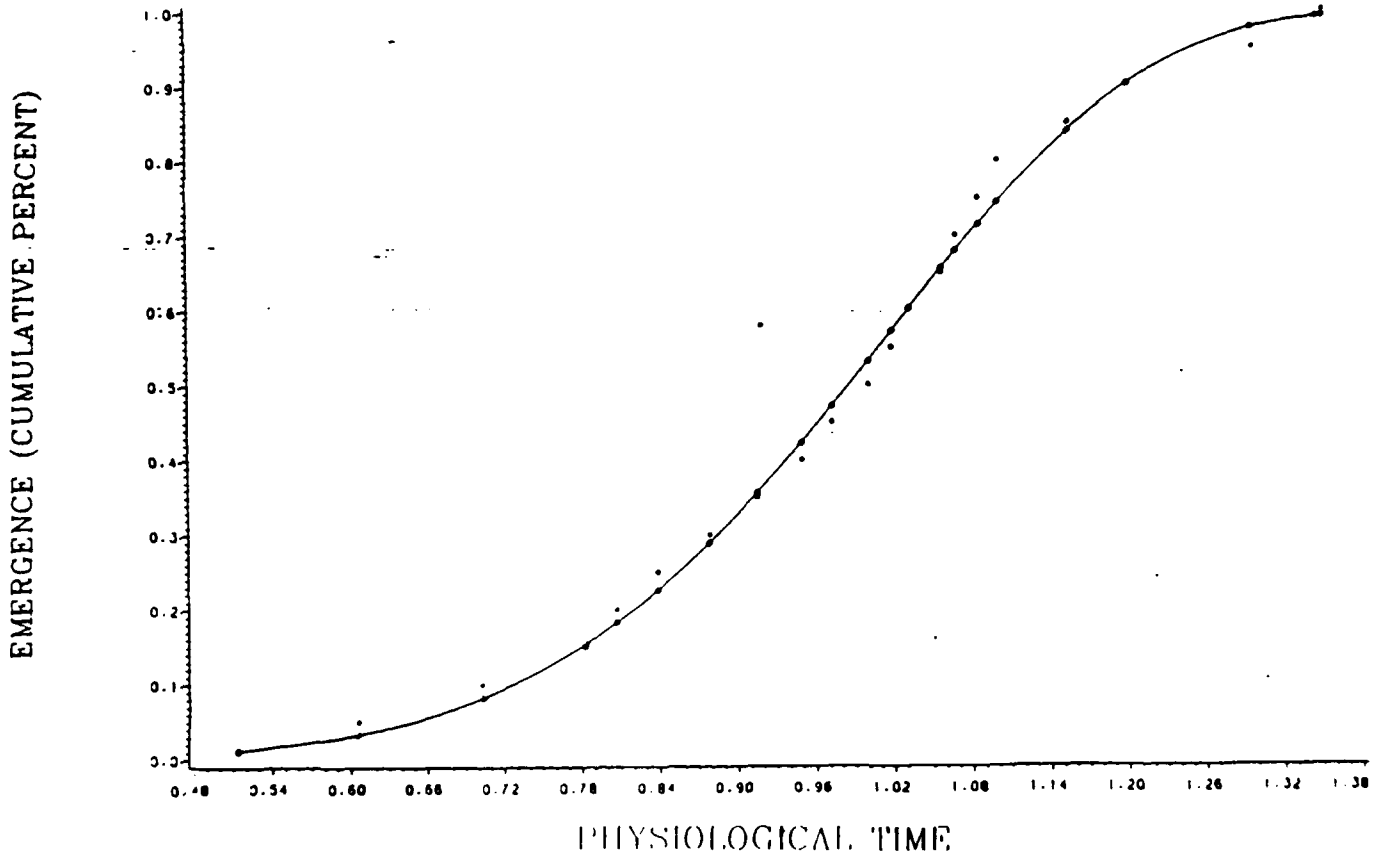

Figure 4-7. Model of the cumulative distribution of temperature-independent normalized development times for the eggs of Eutrombicula alfreddugesi compared with plot of observed data.

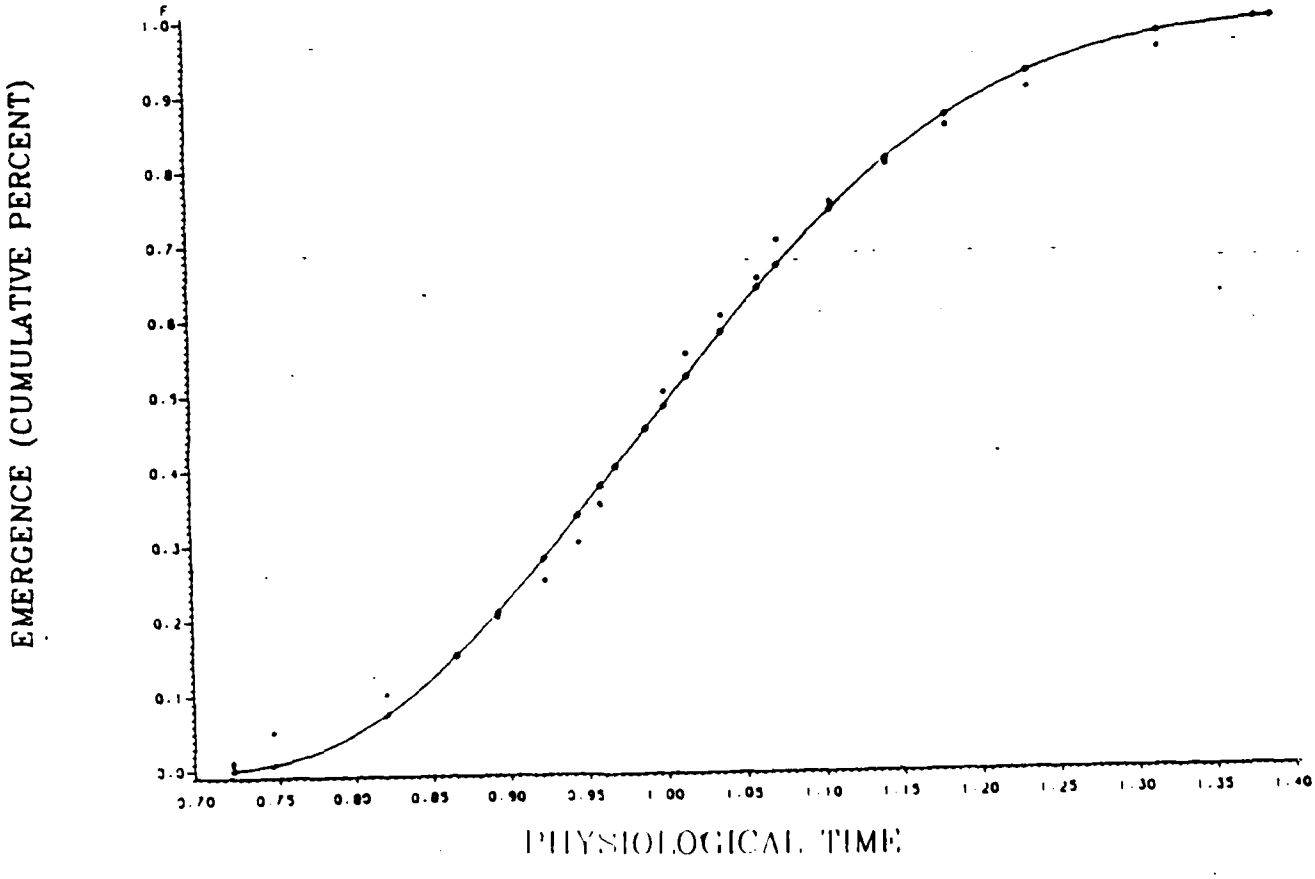

Figure 4-8. Model of the cumulative distribution of temperature-independent normalized development times for the deutova of Eutrombicula alfreddugesi compared with plot of observed data.

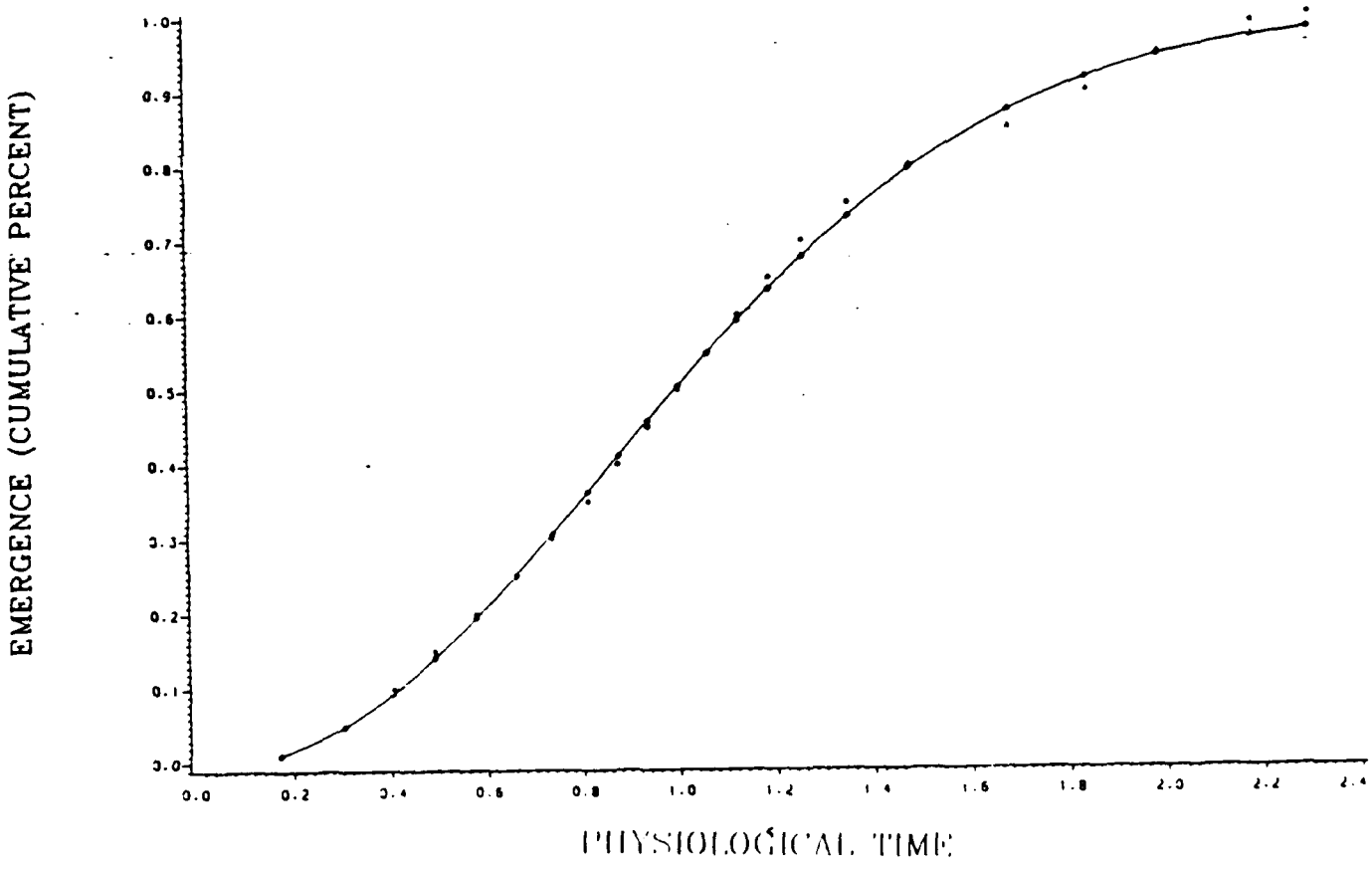

Figure 4-9. Model of the cumulative distribution of temperature-independent normalized development times for the fed larva of Eutrombicula alfreddugesi compared with plot of observed data.

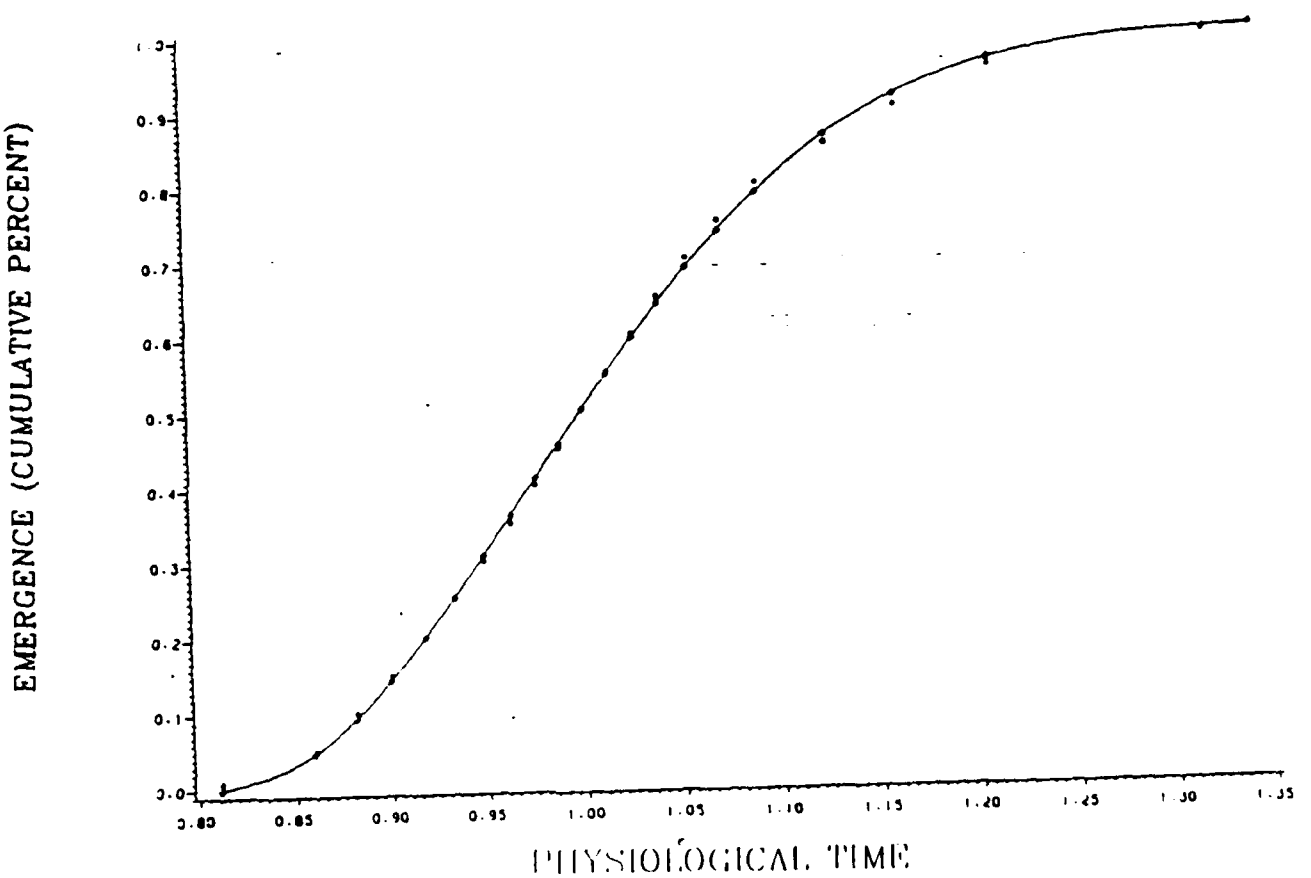

Figure 4-10. Model of the cumulative distribution of temperature-independent normalized development times for the protonymphs of Eutrombicula alfreddugesi compared with plot of observed data.

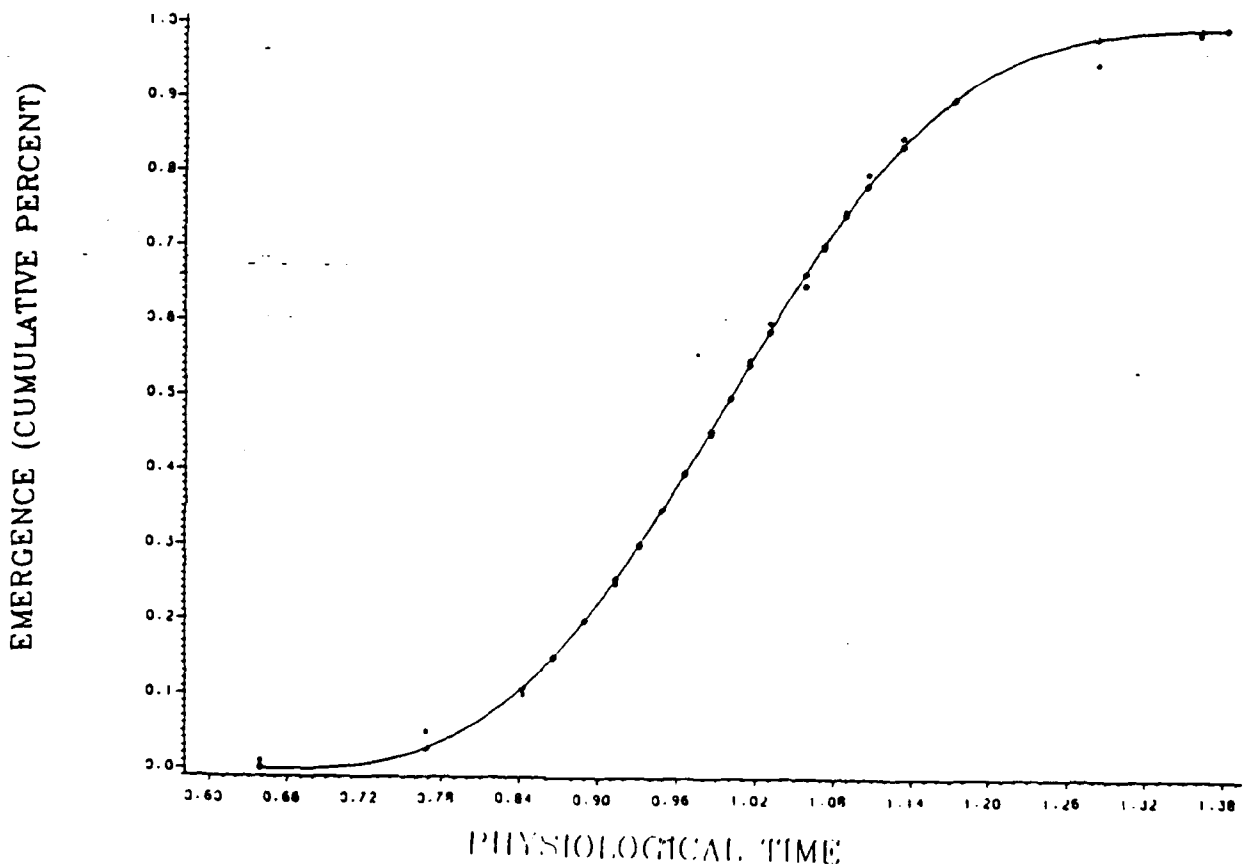

Figure 4-11. Model of the cumulative distribution of temperature-independent normalized development times for the tritonymphs of Eutrombicula alfreddugesi compared with plot of observed data.

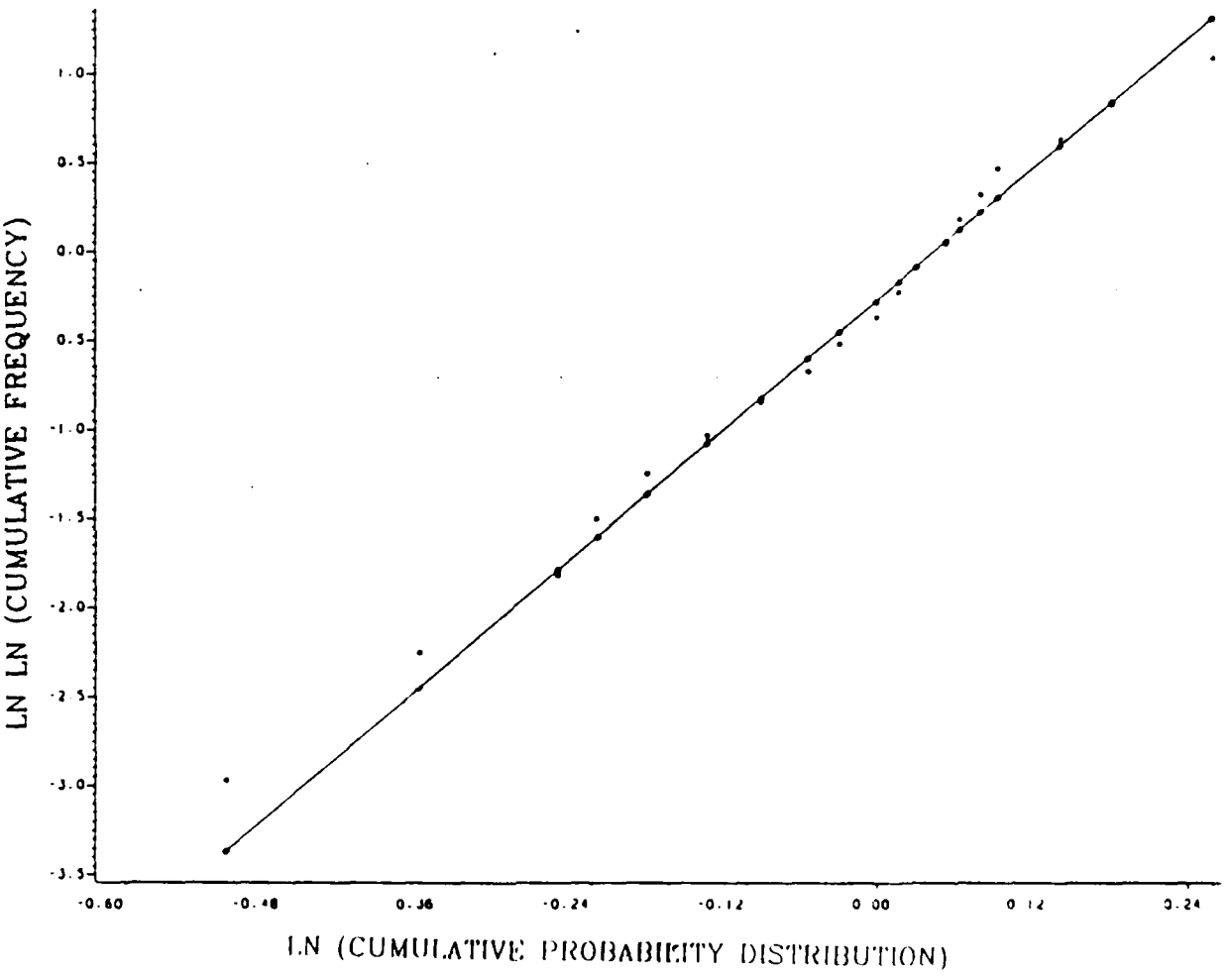

Figure A1. Linear regresssion analysis of the goodness of fit of the Weibull distribution to the model of developmental distribution times for the eggs of Eutrombicula alfreddugesi (parameter estimates: Beta = the slope, Gamma = threshold value and Eta = exp(-b/Beta), where b is the Y-intercept).

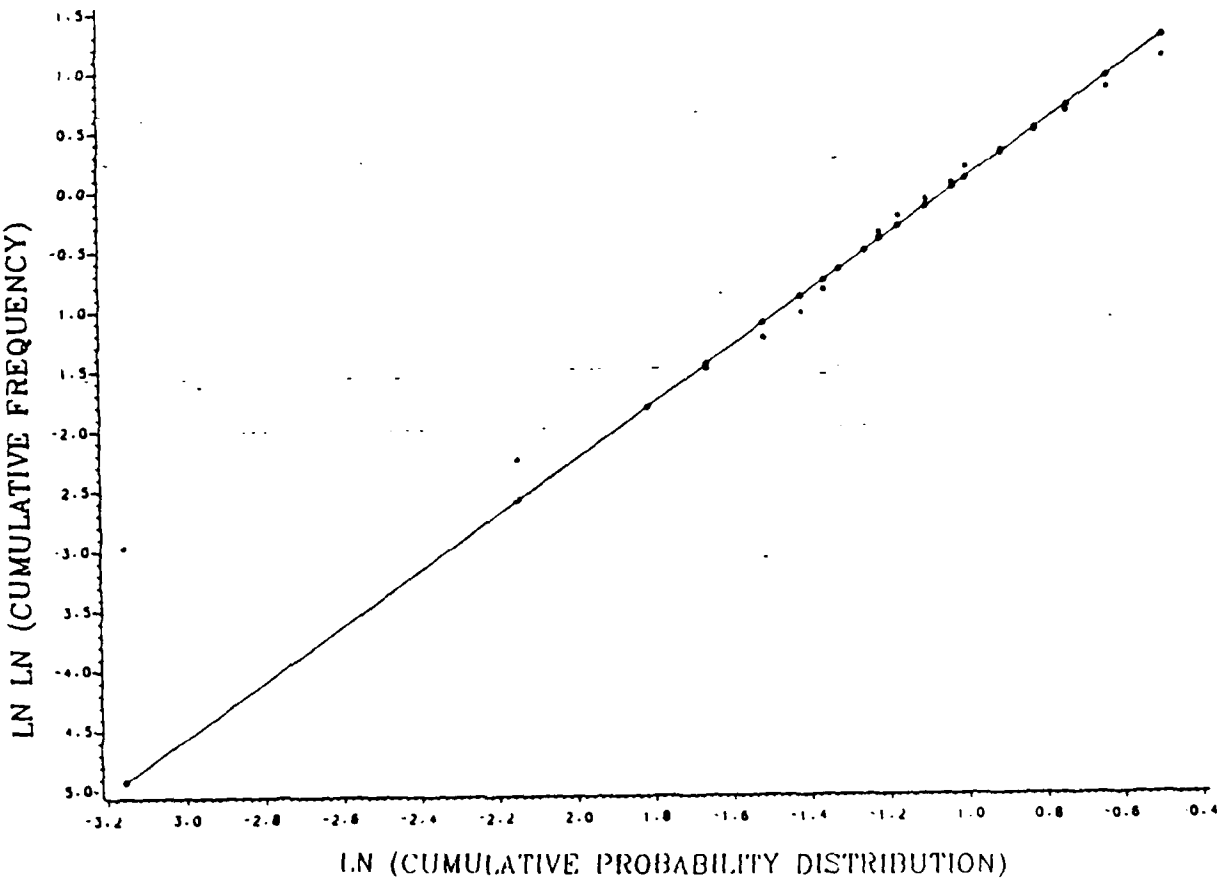

Figure A2. Linear regresssion analysis of the goodness of fit of the Weibull distribution to the model of developmental distribution times for the deutovum of Eutrombicula alfreddugesi (parameter estimates: Beta = the slope, Gamma = threshold value and Eta = exp(-b/Beta), where b is the Y-intercept).

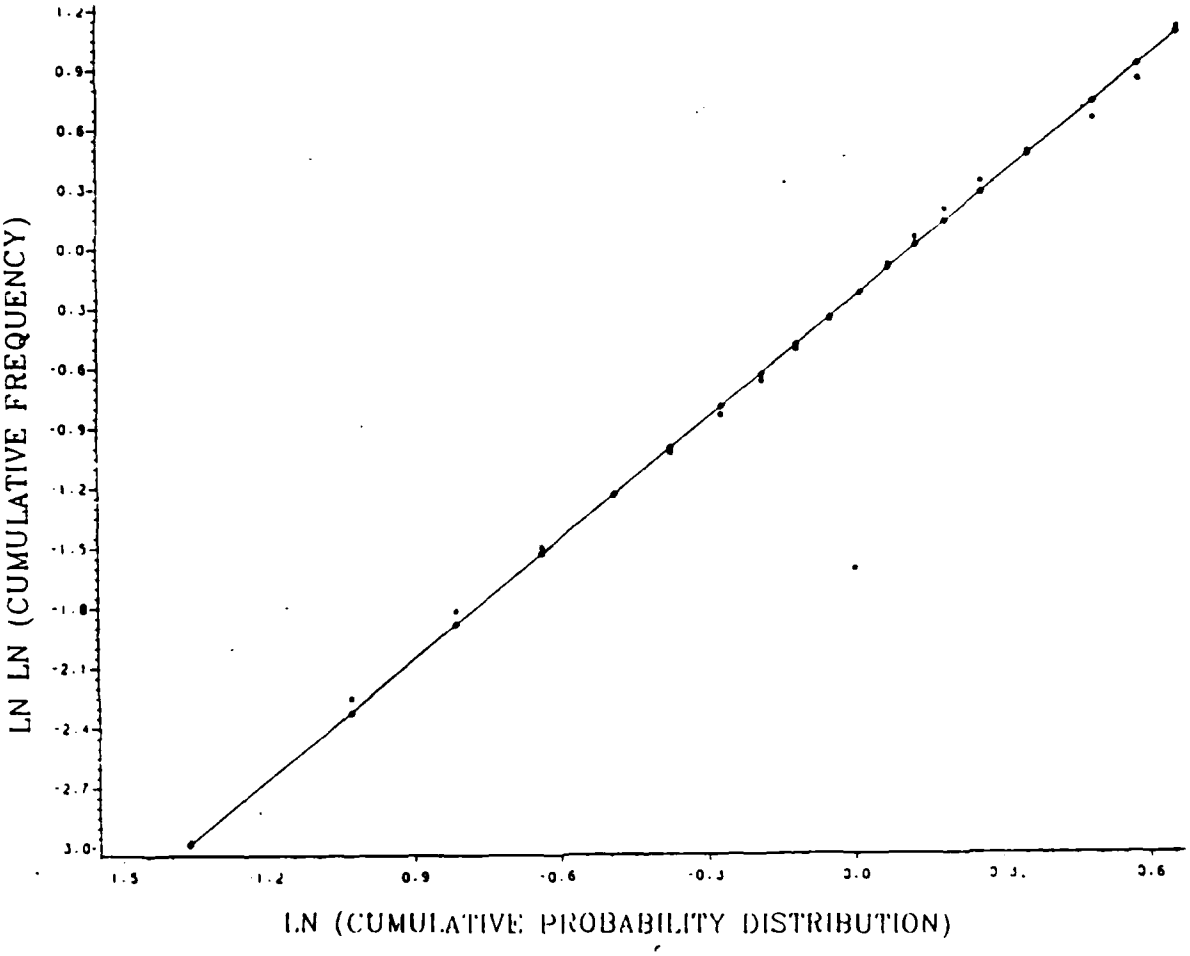

Figure A3. Linear regresssion analysis of the goodness of fit of the Weibull distribution to the model of devclopmental distribution times for the fed larvae of Eutrombicula alfreddugesi (parameter estimates: Beta = the slope, Gamma = threshold value and Eta = exp(-b/Beta), where b is the Y-intercept).

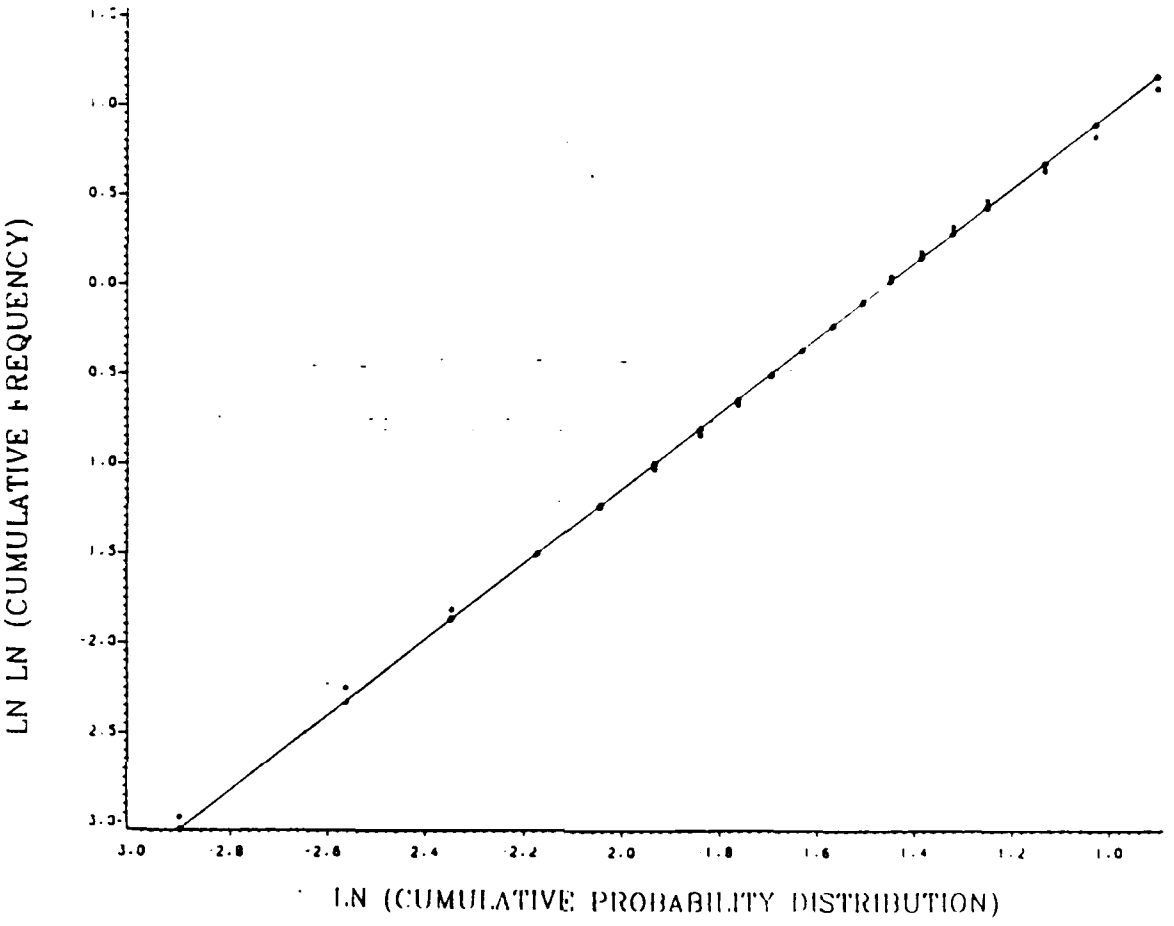

Figure A4. Linear regresssion analysis of the goodness of fit of the Weibull distribution to the model of developmental distribution times for the protonymphs of Eutrombicula alfreddugesi (parameter estimates: Beta = the slope, Gamma = threshold value and Eta = exp(-b/Beta), where b is the Y-intercept).

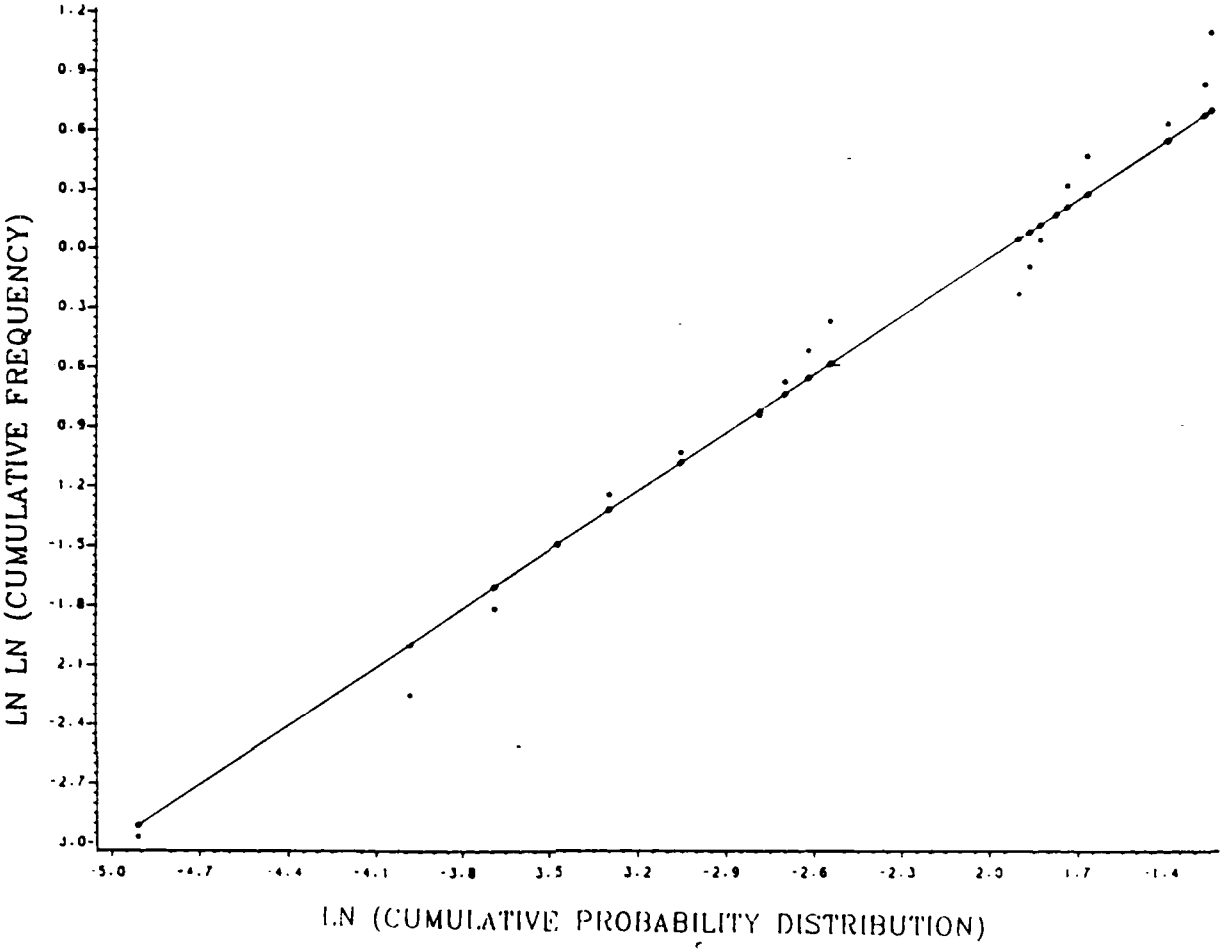

Figure A5. Linear regresssion analysis of the goodness of fit of the Weibull distribution to the model of developmental distribution times for the slowly developing morph of the deutonymphs of Eutrombicula alfreddugesi (parameter estimates: Beta = the slope, Gamma = threshold value and Eta = exp(-b/Beta), where b is the Y-intercept).

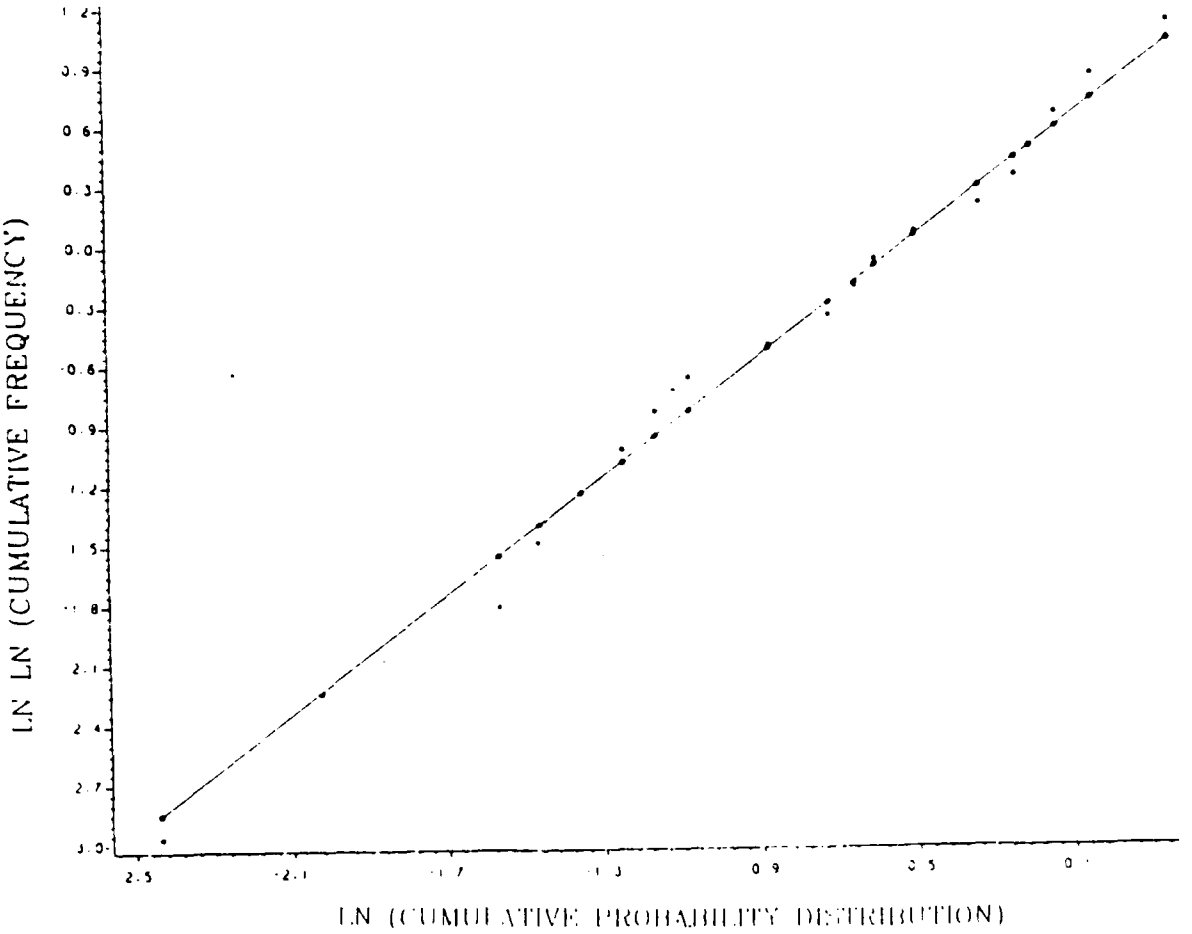

Figure A6. Linear regresssion analysis of the goodness of fit of the Weibull distribution to the model of developmental distribution times for the rapidly developing morph of the deutonymphs of Eutrombicula alfreddugesi (parameter estimates: Beta = the slope, Gamma = threshold value and Eta = exp(-b/Beta), where b is the Y-intercept).

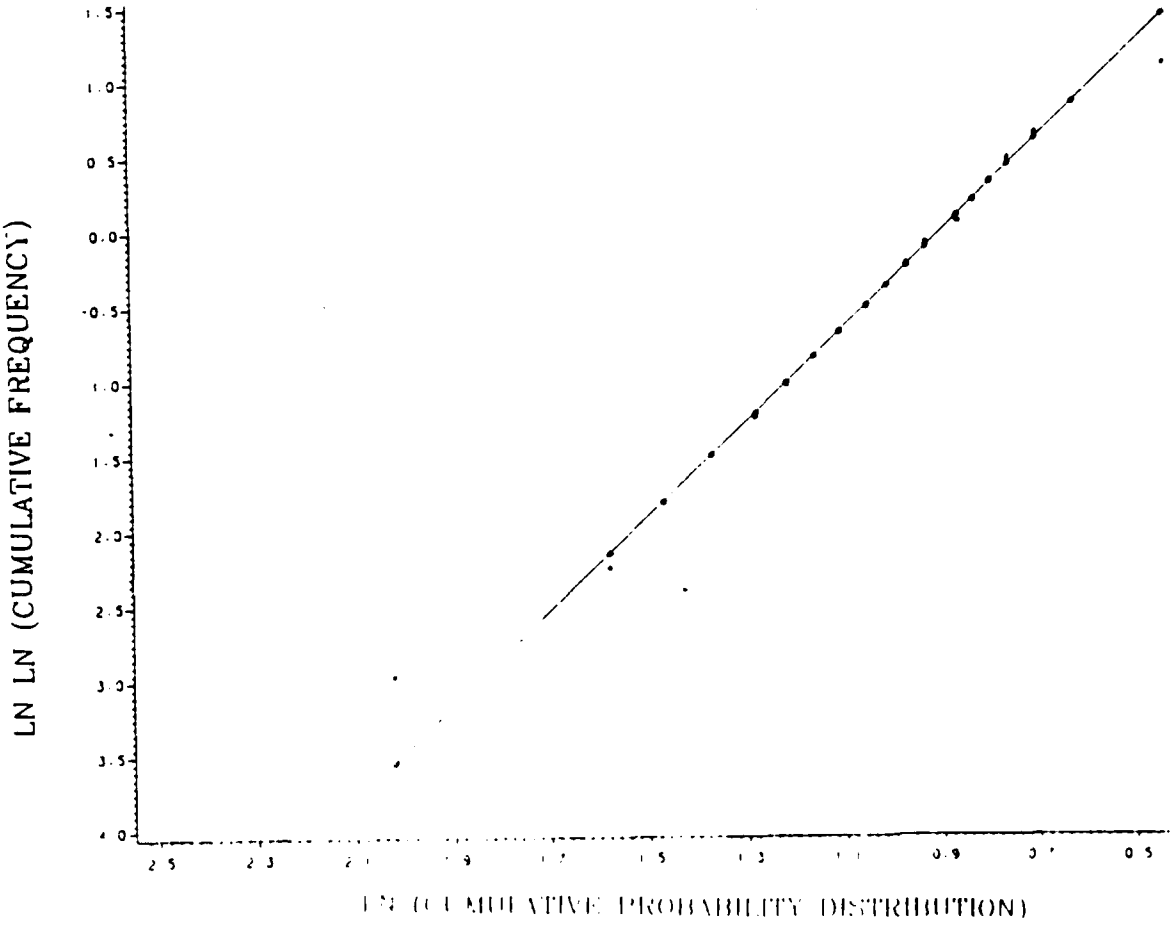

Figure A7. Linear regresssion analysis of the goodness of fit of the Weibull distribution to the model of developmental distribution times for the tritonymphs of Eutrombicula alfreddugesi (parameter estimates: Beta = the slope, Gamma = threshold value and Eta = exp(-b/Beta), where b is the Y-intercept).

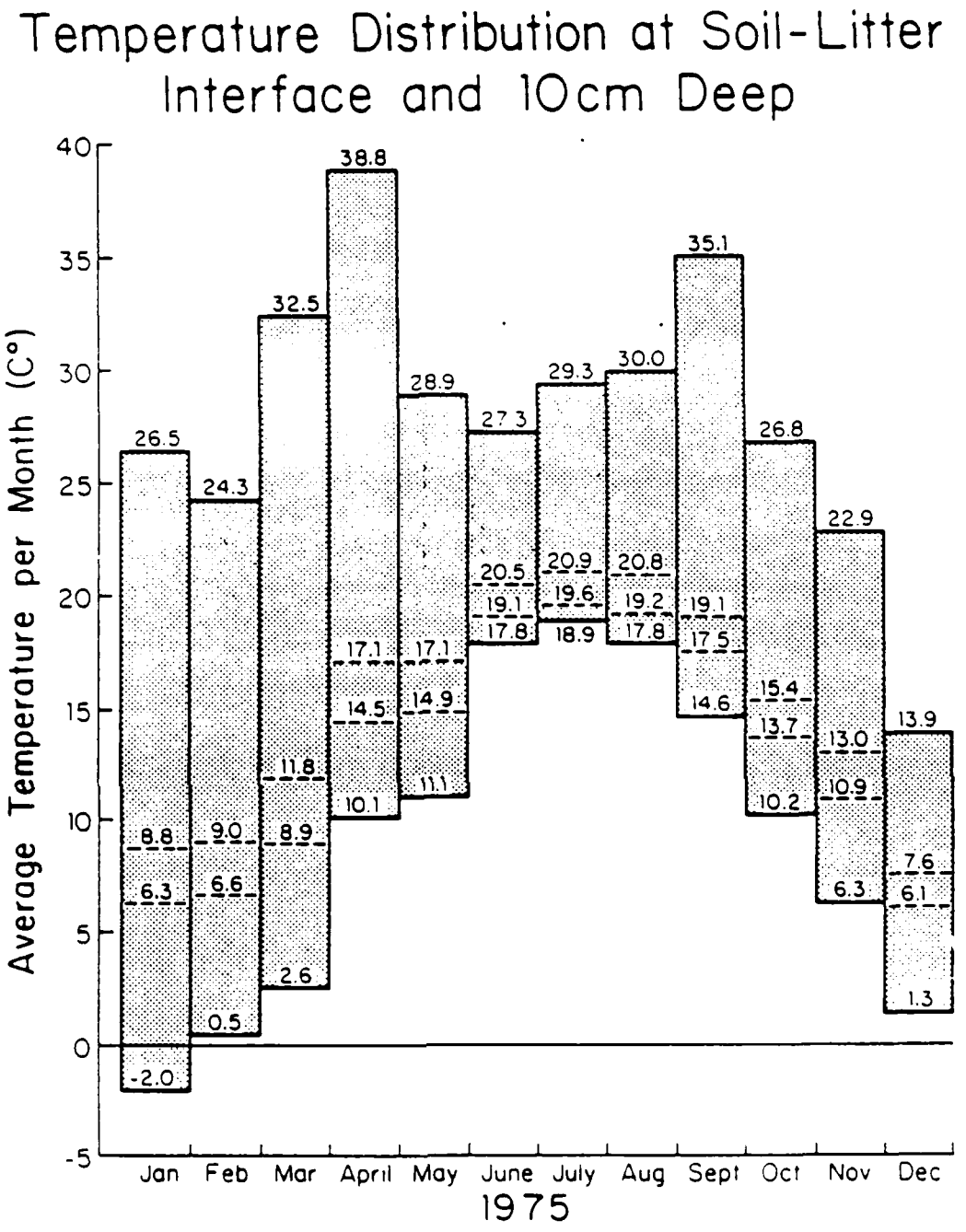

Figure A8. The range of temperature fluctuations at the soil-litter interface and at 10 cm soil depth (data from watershed 20, Coweeta Hydrologic Laboratory, Otto, N.C. 1975). The soil temperature extremes lie within the litter range throughout the year.

CHAPTER V

MODELS OF DEVELOPMENTAL RATES FOR THE IMMATURE STAGES OF EUTROMBICULA ALFREDDUGESI (OUDEMANS) (ACARINA:TROMBICULIDAE)[1]

Submitted: Annals of the Entomological Society of America. (1985).

INTRODUCTION

The larvae of trombiculid mites, or chiggers, are the only life history stage regularly observed in the field. The postlarval stages are difficult to study because of the cryptic nature of their soil/litter niche. The larvae appear at approximately the same time each year, although the season in which they are abundant varies for different species. The predictable cyclic recurrence of a chigger "bloom" each year suggests that the life cycle may be orchestrated by external cyclic phenomena. Jameson (1972) points out that the most obvious exogenous factors to consider are temperature, humidity and photoperiod. In the tropics, the amount of precipitation appears to be correlated with chigger appearance (Sasa 1961). In temperate regions, experimental evidence suggests that temperature is the controlling factor (Sasa 1961, Jameson 1972).

The ability to describe accurately the changes in the population characteristics of a pest species through the course of the year is imperative for formulating effective control methods. The need for basic population biology has been

demonstrated by mosquito control programs (Haile and Weidhass 1977, Greever and Georghiou 1979) and a fall armyworm control program (Barfield et al. 1978). The goal of this study is to construct a usable model for the development of the common pest species, E. alfreddugesi, which can serve as a foundation for an integrated pest management program. There are many developmental rate models available today. They have been thoroughly reviewed by Watt (1968), Laudien (1973) and Wigglesworth (1972). Few have a theoretical basis or are able to describe accurately the data throughout the viable temperature range. Watt (1968) concluded that the absolute reaction rate model based on work of Eyring is closest to having a theoretical basis and also adequately describing the data. Most recently Sharpe and DeMichele (1977) extended Eyring's work into a bio-physical, absolute reaction rate model which has been shown to be applicable over the complete developmental temperature range and is versitile enough to adequately describe both ascending and decending developmental rates for a wide variety of data (Wagner et al. 1984a).

MATERIALS AND METHODS

LABORATORY TECHNIQUES

All mites used in this study were either collected from Whitehall forest, Athens, Georgia or were the first generation produced from laboratory colonies started from larvae collected

from Whitehall forest. The experimental temperature range was 10.0+1°C to 40+1°C for all stages. The original evaluation was conducted at 5.0° increments begining at 10.0°C. Intermediate temperature data were then collected at 5.0° increments begining at 12.5°C during a second run in order to accomodate a limited number of environmental chambers. Only 17.5±1.0°C was omitted from this thermal sequence due to space limitations.

Data for the analysis of developmental rates were derived from the data set generated by the study of the distributions of developmental physiological times described in chapter IV; the experimental design is therefore the same as described in chapter IV.

ANALYSIS OF DATA

Mortality

Differences in mortality rates were evaluated with the Chi-Square test in the Commodore statistical package. Significance was determined at the .05 level.

Thermal Summation

The median rates for development for each stage and for the summed life cycle, which fell within a region of strong linear correlation, were used to estimate developmental zero through linear regression. The thermal constant (K) was estimated as the slope of the linear regresssion of developmental rate data for the region of strong linear relationship and developmental zero was estimated as the x-intercept of the rate data.

Distribution of Development Times

The lengths of time required to complete development, for each stage, at each experimental temperature, were grouped into standard width classes. The mean, median, variance and skewness were determined for each temperature's distribution of development times with the univariate procedure from the SAS statistics computer program library.

Modeling Development Rates

A computer program of Wagner et al.(1984a) was used to fit the median rate data, of each stage and the summed life cycle, to a modified version (Schoolfield et al. 1981) of the biophysical model of Sharpe and DeMichele (1977). The program first determines the existance of either low and/or high temperature inhibition in the data and selects the appropriate variation of the model which best fits the data. An Arrhenius plot of the data is then divided into regions of inhibition and non-inhibition which are used to estimate the parameters associated with inhibition (HL, TL, HH AND TH) and non-inhibition (HA and RH025). The low temperature inactivated enzyme system is thermodynamicly defined by the differences between the active and cold-inactivated systems, at equilibrium in terms of both the change in enthalpy "HL" and the temperature when the enzyme is half active/half inactive "TL" of activation. The descriptors of the high temperature inactivated enzyme system "HH" and "TH" are defined in anologous terms. These estimates are then used as starting values for the SAS Marquardt method of nonlinear regression to obtain a least squares

estimate of the model's parameters. The model is defined in these terms by the equation:

$R_D = T[e^{(RHO25 - H_A/T)/R]} / 1+e^{[(T_{1/2L} - H_L/T)/R]} + e^{[(T_{1/2H} - H_H/T)/R]}$.

Three physical constants are also used: Boltzmann's constant (K), Plank's constant (h) and the gas constant (R).

RESULTS

THERMAL SUMMATION AND MORTALITY

EGGS

The longest period of embryogenesis occurred at 15.0°C and decreased rapidly at 20.0°C The relationship between median development times and temperature forms a linear relationship between 20.0°C and 32.5°C with a linear correlation of -0.95. The developmental zero is 18.18°C and the thermal constant (K) for this temperature range is 71.30 degree-days. After 32.5°C hatching time increased.

Eggs held at 12.5°C did not hatch or undergo any change in color typical of embryogenesis. These eggs were moved to 25°C after 150 days. Of the original 55 eggs, 6 proceeded to undergo embryogenesis and 5 produced deutova. Embryogensis required an average of 13.95 days (s=7.08) and was significantly longer ($p>.001$) then the developmental times observed for eggs placed directly into 25°C (Table 5-1). Of the 5 deutova, only 2 completed development to the larval stage. This transition

required 7.18 and 8.25 days. These data are within 1 standard deviation of the mean development time for deutova whose entire development occured at 25°C (Table 5-2). These deutova also experienced a dramatic reduction in survivorship (40%) when compared to all other temperature groups (x=97.85%).

Within the viable temperature range (15.0° to 37.5°), mortality was not found to be significantly different (p=.05) (Table 5-1), although a trend does exist as indicated by the greatest mortality at temperatures near the extremes and the lowest mortality associated with the middle region (22.5° to 30.0°C). The average survivorship was 54.51%. The extreme temperatures are defined as those that resulted in 100% mortality. At the high extreme, 40.0°C, eggs were destroyed within 24 hours as evidenced by collapse of the chorion and discoloration due to fungal and/or bacterial growth. At the low extreme, 12.5°C, which proved insufficient for growth, was not immediately or completely fatal. This was demonstrated by the eggs transferred to 25.0°C after being held at 12.5°C for 5 months described above.

DEUTOVA

Deutoval development was slowest at 15.0°C and speeded up rapidly by 20.0°C (Table 5-2). There is a strong linear relationship between developmental times and temperature between 20.0°C and 27.5°C (r=-0.92). The developmental zero is 13.4°C and the thermal constant within this range is 116.4 degree-days. Development times are comparable to those exhibited by the eggs

(Table 5-1) at similar temperatures except at 30.0°C where the deutoval stadum is significantly abbreviated (Table 5-2). The median developmental period, estimated for this temperature by linear regression, is 4.7 days which represents a 40% decrease from the observed value. The range of the distributions of development times above the optimum differs from the other stadia, in that, the length of the development period continues to decrease until the temperature reaches 40.0°C, the lethal temperature. The distributions of development time of all other stages expand as temperature increases above the optimum. The variances of the developmental times for each temperature treatment group do not correlate with changes in temperature as indicated by the random fluxuations of the coefficients of variance (CV).

Low mortality was a consistant feature throughout the entire viable temperature range (15.0 ° to 37.5°C) (Table 5-2). Survivorship averaged 97.9% and showed no correlation to temperature.

FED LARVAE

The fed larvae placed at 12.5°C never became immobile and the majority were always found at the top of the storage vial. Their appearance remained that of a freshly detached larva for 4 days beyond which they began to appear progressively more shriveled. Ten percent had died after 21 days and 50% were dead by 28 days. One hundred percent mortality occured after 40 days.

Fed larval transformation is slowest at 15.0°C but achieves

a linear relationship with temperature at 20.0°C which persists to 30.0°C (r=-0.81). Developmental zero is estimated as 11.46°C and developmental constant as 27.05 degree-days. The shortest median developmental period occured at 30.0°C, above which, development took slightly longer as temperature increased.

Mortality was significantly larger at 37.5°C then at any other temperature (p=.05) (Table 5-3). There was no correlation between mortality and the viable temperatures below 37.5°C where survivorship averaged 86.11%.

PROTONYMPHS

Some development occurred in protonymphs held at 12.5°C. Distinct leg buds appeared in 10 of the 23 protonymphs. After 14 days, the appearance of their cuticle began to change from shiny and expanded to pubescent and finally shriveled after 28 days.

Protonymph development required over twice as long at 15.0°C (47.7 days) as compared to development at 20.0°C (21.5 days) (Table 5-4). The middle temperature region between 20.0° and 35.0°C, inclusive, posesses a linear correlation with temperature (r=-0.86). The best linear regression estimates of developmental zero is 18.5°C and of the developmental constant is 62.6 degree-days. The shortest developmental period is achieved at 35.0°C (3.4 days) above which there is a rapid increase in time (7.0 days at 37.5°C) (Table 5-4).

The protonymphs held at 37.5°C experienced a significantly greater mortality then did those maintained at lower

temperatures (p=.05) (Table 5-4). All other groups had an average survivorship of 79%. No apparent relationship exists between mortality and temperature.

DEUTONYMPHS

The median number of days required for rapid completion of the deutonymphal stadia does not correlate with temperature (Table 5-5) nor is there a significant difference between the medians of the developmental times for each temperature (p=.05) (x=17.8 days). The same is true for deutonymphs requiring an extended development period. The average median number of days needed for development by slow developing deutonymphs is 45.9 days (Table 5-6).

Deutonymphs held at 12.5°C lost mobility after the first week. They were never able to recognize and feed upon collembola eggs. After 58 days, 80% were alive, after 85 days, 50% still survived and 100% mortality was realized after 110 days.

None of the deutonymphs held at 15.0°C had completed development after 220 days; however, twenty-four of the original 50 had survived. The weights of these 24 were compared with the weights of deutonymphs from other temperature groups weighed within 48 hours prior to their completion of the deutonymphal stadum (n=32). Both populations were skewed to the right and leptokurtic therefore, nonparmetric analysis was used to compare the weights. Both the Wilcox 2-sample test and the Kruskal-Wallis test found that the deutonymphs maintained at 15.0°C were significantly heavier then their counterparts at

other temperatures (p=0.0006).

Twelve of the 15.0°C deutonymphs were moved to 35.0°C. They completed development between 6 to 12 days after being moved. Their median development time was 7.8 days, which is less then half the median time observed for deutonymphs maintained at 35.0°C for their entire development (Median=17.5 days). The nonparametric Wilcox 2-sample test and the Kruskal-Wallis test found the transfered group's development period in 35.0°C signifcantly shorter then that of the 35.0°C group (p=0.0001).

Mortality cannot be determined for the rapid and slow deutonymph populations since it is impossible to determine the membership of these groups beforehand. If the effect of temperature on the mortality of the total deutonymph cohort is considered (Appendix Table A2): Those deutonymphs held at 32.5°C had a significantly greater survivorship (88.9%) then deutonymphs held at any other temperature (x=54.2%).

TRITONYMPHS

The tritonymphs held at 12.5°C showed signs of development through the deutonymphal skin. The mites took on the elongated form with an anterior point and distinctly segmented legs as is typical of tritonymphal development; they gradually began to shrivel over a period of months. Ninety percent appeared to be alive after 55 days, 50% still appeared viable after 95 days. The last survivor was lost after 135 days. Subsamples were not taken to determine the probabilities of successfully completing the tritonymphal stadia. The mites were counted as living if

they maintained the customary color, cuticle trugidity and showed no signs of fungal growth.

The medians of tritonymphal development times (Table 5-7) associated with the lower temperature range from 15.0°C to 22.5°C possess a strong linear relationship (r=-0.98). The middle temperature region from 22.5°C to 35.0°C also has a strong correlation with tritonymph stadial length (medians) (r=-0.92). The developmental zero is 13.6°C and the developmental constant (K) is 125.4 degree-days. The shortest average developmental period was achived at 35.0°C (x=6.4 days) above which developmental time increased (Table 5-7).

Tritonymphs held near both extreme temperatures, i.e., 15.0°C and 37.5°C, had a significantly greater mortality then did the middle temperature range groups (p=.05) (Table 5-7). The mortality at all other temperatures is not significantly different and averages 98.6%.

ENTIRE DEVELOPMENT CYCLE

Chiggers were not reared continuously from egg to adult but some insight may be gained by the accumulation of median development times and survivalship data for each temperature. A summary of developmental time data is in the appendix, Table A3. Table 5-8 contains the summations of developmental periods and rates for the complete development of *E. alfreddugesi*. The impact of the two different deutonymph developmental time populations on total development time is most noticeable. At 20.0°C there is over 6 months difference between the rapid and

slow populations.

The correlation coefficient (r) for the linear regression of the rapid population's median development times on the temperature range from 20.0°C to 35.0°C is -0.85. The developmental zero is estimated to be 7.15°C and the developmental constant is 1084.40 degree days.

A correlation (r=0.90) also exists between the slow population's median development times and the temperature range from 22.5°C to 35.0°C. The developmental zero is predicted to be -9.1°C and the developmental constant is 2,974.3 degree-days, which is 2.7 times larger then that of the rapid population

Chiggers which develop at temperatures near the extremes, i.e., 20.0°C and 37.5°C suffer significantly greater mortality then do those mites maintained at temperatures within the middle region, i.e., 22.5°C to 35.0°C (p=.05) (Table 5-8). The average percentage of survival in the middle temperature range is 23.7% (s=2.6).

MODELS OF DEVELOPMENTAL RATES

The developmental rates used in the calculation of the biophysical model were computed as the inverses of the median developmental times for each temperature. The plots of the observed rates and model generated curve for each stage, except the deutonymph, comprise figures 5-1 through 5-5. Parameter estimates for each non-linear regression are listed in table 5-8.

The data and curve are in good agreement for the eggs, fed larvae, protonymphs and tritonymphs (Figs. 5-1, 5-3, 5-4 and 5-5). The coefficients of determination (R^2) for these comparisons of observed to expected is greater the 0.92 (Table 8). The peak temperature for the eggs, protonymphs and tritonymphs is 35.0°C while for the fed larvae it is 30.0°C

The coefficient of determination (R^2) for the model of deutovum development (Fig. 5-2) is 0.477. This correlation is much smaller then the R^2 for all the models of the other life stages, and is due to an unexpected high value at 30.0°C All other data points fall close to the predicted values of the curve. The 30.0°C cohort forms a tight distribution and had no mortality to bias the data (Table 5-2) suggesting the possibility that the data was biased by an unknown external factor or a statistical fluke. Due to the consistant rise of the following 3 rates (32.5°C to 37.5°C), it is unlikely that the observed unusually quick development rate at 30.0°C is a real phenomen. If the data point at 30.0°C were eliminated from the analysis, the coefficient of determination becomes 0.991. The deutovum curve also differs from the others in that it lacks high temperature inhibition prior to the plummet at 40.0°C, the lethal high temperature.

Neither of the deutonymphal development time morphs correlate with temperature. The coefficient of determination for rapid deutonymphs is only 0.325 while for the slow deutonymphs it is 0.017. Due to the low R^2 values associated with the deutonymph development, it was not appropriate to

describe developmental rates with model parameters and curves.

When the median developmental rates for the slow development morph were ploted (Fig. 5-6), a rapid rise in development rate occurs between 20.0°C and 22.5°C, after which it appears as if developmental rate is not affected by changes in temperature. The average median developmental rate, excluding the 20.0°C value, is 0.01947 day^{-1} (S.E.=0.00262) which is equivalent to 51.4 days.

The plot of median developmental rates for the rapid development morph (Fig. 5-7) shows an entirely different pattern. A single strong peak in rate occurs at 25.0°C where the rate is 0.0909 day^{-1} or 11.00 days, which is nearly twice as fast as noted at other temperatures. At all other temperatures, the rate varies only slightly around the average median rate of 0.0582 day^{-1} (S.E.=0.00152) or 18.7 days. Above 20.0°C, the rapid morph's development rate is 2.75 times faster then that of the slow morph and at 25.0°C, the fast morph's rate is 4.7 faster then the slow morph's. The plots of the 2 deutonymph development forms (Fig. 5-6 and 5-7) are not to the same scale and can not be compared directly.

The approximated median rates for the entire life cycle, incorporating either the rapid or slow deutonymph rates (Table 5-8) were also modeled. A slightly better fit is obtained with the slow phase data (R^2=0.953) (Fig. 5-9) then with the rapid phase data (R^2=0.911) (Fig. 5-10 and Table 5-8). The slow population is described by a 4 parameter model which lacks high temperature inhibition. The rapid development model requires 6

parameters because of both high and low temperature inhibition. Both curves are characterized by a long period of gradual rate increase. The straight line region extends from 22.5°C to 37.5°C for slow development and from 22.5°C to 35.0°C for fast development. The high coefficient of determination values, in both cases, prove the model has good accuracy. The peak development rate in both morphs corresponds to 35.0°C.

The slightly greater accuracy of the slow phase model which is most evident when the percent rate errors of the 2 phases are compared (Table 5-10) is due, in part, to the buffering of the non-predictive, vacillations in the deutonymphal development data which is inferred by the larger numbers involved in the calculations. In general, the model tends to overestimate the observed development rates. It has greater efficiency at the two extremes then at the peak temperatures. The greatest underestimate (error rate=-14.2%) occured in the rapid phase at 25.0°C This was primarily due to the strong peak in development rate noted in the deutonymph stage (Fig. 5-7). Without that developmental pulse, the expected would have only overestimated the observed value by 1.15%.

The accuracy of these models to predict development rate throughout the entire viable temperature range is three fold greater then that which is achieved with thermal summation. The average of the absolute percent rate error for the rapid phase model is 5.67% and for the slow phase model is 4.97% whereas, thermal summation averages a 20.21% rate error for the rapid phase and a 13.84% rate error for the slow phase (Table 5-11)

As expected, the accuracy of thermal summation predictions is greatest in the middle region, but even here, the biophysical model of Sharpe and deMicheal is generally a more accurate predictor of observed development data (Table 5-9 and Appendix Table A3).

DISCUSSION

DEVELOPMENTAL RATE MODEL

The biophysical model of Sharpe and DeMichele (1977), because of its biochemical basis, provides estimates of the enthalpy and indirectly, the entropy of the control enzyme's inactivation. High entropies of inactivation correlate strongly with large enthalpies of inactivation. Thus, a comparison of the enthalpy values of species provide as much information as a comparison of both enthalpy and entropy. Enthalpy values were chosen because they are consistantly reported by both the original model users and the modified model users in the literature and can therefore provide a wider data base for comparisons.

Empirical models of development have arbitrarily used the temperature at which maximum development occured as the "optimum" temperature for developmental processes. In the context of the biophysical model, the optimum temperature may be interpreted as the highest temperature within an optimum temperature range in which the maximum concentration of active

enzyme occurs. The increase in development rate, which occurs within the optimum range, can be explained by simple molecular kinetics as defined by the law of Arrhenius. The enthalpy of activation (HA) is the only thermodynamic parameter in the numerator of the model. The Arrhenius plot of the numerator of the equation is a straight line which coincides with the linear region of developmental rates. The slope can be estimated by dividing the enthalpy of activation by the gas constant (HA/R) (Schoolfield et al. 1981). This corresponds to the thermal conditions under which the probability of the control enzyme (or enxyme complex) being in the active state is greatest.

The enthalpy of activation for all stages of the chigger model (Table 5-8) fall within the range found in the literature for insects (5,360 to 21,600 cal/mol) (Sharpe and DeMichele 1977, Barfield et al 1977, Barfield et al. 1978, Sharpe et al. 1981, Schoolfield et al. 1981, McHugh and Olson 1982 and Wagner et al. 1984a). Like E. alfreddugesi, all of these insects are summer active species, which live in temperate and tropical environments. This provides the underlying explanation for the relatively narrow range of optimum temperatures and suggest that, for arthropods evolving under similar conditions, convergence to similar optimum thermodynamic properties have occurred.

Temperature extremes are of greater interest, because as Sharpe and DeMicheal (1977) point out, ecophysiological adaptations will occur most frequently under thermal stress and biotypes are most easily recognized by their response to

temperature extremes. In an Arrhenius plot, the enzyme deactivation of the thermal extremes are represented by the two downturned arms of the developmental rate plot. The region of the plot depicting the decreasing rate at low temperatures can be described, in terms of the model, as the numerator divided by the portion of the denominator defining enzyme inactivation at low temperatures (HL and TL). The enthalpy of inactivation for low temperatures (HL) is an indicator of the stability of a protein as temperature decrease. In a similar fashion, the region associated with decreasing rates at high temperatures is an interpretation of the numerator devided by the part of the denominator ascribed to enzyme inactivation at high temperatures (HH and TH). Like its counterpart, "HL", the enthalpy of inactivation for high temperature (HH) describes the stability of protein under high temperature stress.

The enthalpy values for both high and low temperature inactivation (Table 5-8) of the control enzymes of E. alfreddugesi fall in the high end of the range of enthalpy values reported in the literature (HH: 51,213 to 117,420 cal/mol and HL: -6,603 to -168,140 cal/mol). This indicates an enzymatic tolerance to a wide spread of temperatures under which development can continue. As inferred by the large enthalpy values, the temperature ranges of all stages of chigger development is slightly greater the the average for insects (Taylor 1981). Taylor (1981) concluded from computer simulations, in which he compared the impact of optimum temperature and size of the range of temperatures in which

development occurs, that decreases in optimum temperature and/or increases in size of the temperature range operated to increase accumulation under natural temperature conditions. The width of the developmentally active temperature range is directly related to the speed at which development accumulates, i.e., the passage of physiological time. The impact of the width is most important at low elevations and in temperate latitudes (Taylor 1981).

In regions where the annual thermal regime has extended periods of elevated temperature a low optimum temperature would prove deleterious. As noted earlier, the optimum temperature range is relatively narrow, as thermal conditions exceed this range, the rate precipitously drops as high temperature deactivation of development enzymes decreases the amount of active enzyme available. This could explain the preponderance of high optimum temperature species in the lower latitudes (Taylor 1981). The optimum temperature for fed larvae is 30°C which is the average optimum temperature for the 54 insect species used in Taylor's (1981) analysis. The chigger optimum temperature for all other stages is 35°C which falls near the upper limit of the optimal temperature range (22°C to 38°C) (Taylor 1981). These developmental characteristics lend credence to the hypothesis of Jameson (1972) that the genus of Eutrombicula originated in the tropics and have developed special adaptations that enabled them to invade new environments, e.g., the temperate regions.

One adaptation is developmental rates. Jameson (1972)

hypothesizes that winter chigger species evolved much higher developmental rates then summer species. This enabled them to colonize new niches which become available through temporal displacement. The developmental rates of comparable stadia of E. alfreddugesi are very similar to those reported for the protonymph and tritonymph of Eutrombicula belkini, a summer chigger species in California (Jameson 1972) and Leptotrombidium deliense, a tropical species of the Orient (Jameson 1968 as cited in Jameson 1972). At 20°C, the calyptostatic stages of these summer or tropical species require about twice the development time needed by 3 oriental winter species, Leptotrombidium fuji, L. palpale and L. pallidum (Jameson 1968 as cited in Jameson 1972). Thus, E alfreddugesi development data is consistant with the concept that two different developmental stategies have evolved among chigger species.

The differences occurs, not because of the development of an increased rate by winter species, but due to a displacement of the developmental rate curve toward cooler temperatures and a concomitant expansion of the developmental temperature range to lower temperatures. These adaptations are general characteristics of boreal insect species (Downes 1965). The protonymphs of the summer species, E. belkini, can not develop at temperatures below 20°C but the protonymphs of all three winter species completed development at 15°C and a few L. fuji developed at 10°C This combination of developmental features is clearly essential for any poikilotherm which must complete its life cycle under the thermal conditions experienced in the soil

during the winter months.

Leptotrombidium miyazakii, a oriental species found at high elevations (2,000 m), has a developmental rate with a thermal position similar to those of the summer species but a development temperature range which is extended down to 15°C (a few even developed at 10°C) like that of the winter species. The expansion of the developmental temperature range downward can appreciably increase the accumulation of development as demonstrated by Taylor (1981). This single adaptation apparently provides sufficient time on the physiological time scale for L. miyazakii to complete it's life cycle under the cooler temperatures which exist at higher elevations. E. alfreddugesi has a similar combination of development requirements; although its developmental rate is comparable to that of E. belkini, its developmental temperature range has also been extended downward, like that of the winter species, to 15°C for all stages except the deutonymph. This species is the most widely dispersed of all chigger species in the New World. Jenkins (1947) determined the distribution of this species; its northern limits extend to the southern margins of the northern tier of states and southward through Central America into South America as far as Argentina. The distributions of other Eutrombicula species found in the western hemisphere are limited to the tropical coastal regions of the southern-most states of the U. S., Mexico's coastal region continuing through Central America and into the Northern regions of South America (Loomis and Wrenn, 1984). The same developmental adaptation seen in E.

deliense, i.e., the inclusion of lower temperatures in the development range, now establishes the physiological milieu in E. alfreddugesi which has enabled the colonization of the higher latitudes.

The adaptation to cooler temperatures is not complete, however, since the deutonymph does not develop below 20°C and thus behaves like a summer species. The deutonymphs of E. alfreddugesi are immobilized at 12.5°C after 1 week, but are able to survive extended periods of time (50% survived 85 days). At 15°C, nearly half survived more then 220 days. The advantage gained by the rise of 2.5°C, which so notably increased their survival, is that they were able to locate, ingest and digest collembolan eggs. These deutonymphs were able to accumulate the essential nutrient stores necessary for metamorphosis but were unable to undergo the physiological changes associated with development. This is evident by their accelerated development when moved to 35°C It would seem that the first portion of the stadia is spent amassing sufficient provisions for the actual physiological process of development.

The development of the deutonymph is unusual in several ways. First, between 20°C and 37°C, the development rate for deutonymphs is independent of temperature (Figs. 5-6 and 5-7) and therefore cannot be described with a temperature-dependent model. Secondly, the timing of metamorphosis to the tritonymph has a bimodal distribution at all temperatures (except 35°C) (Fig. 4-5, Chapter 4) and Appendix Table A1). The plot of development rates for fast developing deutonymphs features a

single strong peak at 25°C which represents a development rate nearly twice as rapid as the rate at other temperatures. This peak in development rate at 25°C corresponds closely to the temperature regime observed in tropical soils where temperature at the surface fluctuates slightly (25±2°C) during the daily cycle and temperature at 10cm soil depth remains essentially constant at 25°C (Swift et al. 1979). This correlation between deutonymph development and tropical soil temperature is the basis for the hypothesis that, the fast morph is the more primitive form which evolved developmental rate control enzymes that capitalize on the thermal conditions in the soils of tropical environments before the species radiated northward.

Although the developmental rate is independent, the precentage of rapid developing deutonymphs in the population is dependent on temperature. The proportion of rapid developing deutonymphs increases as the temperature increases. The curve of the precentage of the rapidly developing morph in the population over temperature can be effectively described by the biophysical model (Fig. 5-8) (R^2=0.98). The accuracy of the model's fit to the data provides the basis for the speculation, that a secondary level of control enzymes, which is responsive to temperature, is regulating development. The regulation function may act as a switch to turn on the production of the developmental control enzyme. In which case, the switch would only be operable during two intervals in the life of the deutonymph. These intervals are not measured by physiological time since there is no correlation between the interval which

separates development modes and temperature (Table A1). The secondary control enzyme experiences significant high temperature inactivation above 35°C and low temperature inactivation below 22.5°C (Fig. 5-8). The linear region between 22.5°C and 35°C represents a range in which the probability of the secondary control enzyme being in an active state is directly proportional to temperature increase.

What selective advantage is gained by E. alfreddugesi by the addition of this temperature sensitive switching mechanism for rapid or slow development of the deutonymphs? For an obligate parasite, the criterion for fitness is not necessarily how fast they can develop but how closely they match the timing of their host's life cycle (Taylor 1981). Lizards appear to be the prefered hosts of Eurombicula species in both Central and North America (Wrenn and Loomis 1984). In temperate latitudes, reptiles brummate (hibernate) during the cold months and are therefore not available to ectoparasites during the winter (Spellberg 1982). Host numbers increase in early and mid-summer because reptile reproduction is cued into the increasing day-length of late spring and early summer (Heatwole 1976). From the parasite's (chigger's) point of view, the production of larvae, the only stage whose survival depends on finding a suitable host, must be timed to take advantage of the increase in potential hosts available. Thus a seasonal cycle which produces a large pulse of chiggers during June, July and August would maximize the population's fitness.

In temperate regions, such as the piedmont of north Georgia,

rapid development of the deutonymph would dominate the life cycle during the warmest period, late June, July and August, but as soil temperatures decline in the fall, the slow development phase becomes the most common. During September and October, the temperatures, at 10cm soil depth, are sufficient to support development of both the fed larvae and protonymph which creates an accumulation of deutonymphs in the slow phase in the fall. By early November, soil temperatures have fallen below 22.5°C (Fig A8), the effective threshold for deutonymph development (Figs. 5-6 and 5-7). This means that only those deutonymphs present in the population in early September will have reached the point of metamorphsis into the tritonymph. The majority will remain deutonymphs throughout the winter months and metamorphose to the tritonymph in April and May. The tritonymph can complete development at the soil temperatures which prevail from April through September (Fig. 5-5 and A8). New adults will begin to emerge in the middle of May.

Over-wintering adult Eutombicula alfreddugesi have been found in Kansas (Loomis 1956) and in Florida (Jenkins 1947). Although the sex was not determined, it may be assumed that the great majority were females because males have a much shorter life expectancy then females (Jenkins 1947). During reproductive studies in which females were isolated, it was noted that oviposition ceased after a few weeks. The availability of new adult males in the spring may therefore be essential in order for the overwintered females to contribute to the next generation of larvae. An additional potential

advantage to overwintering in the deutonymphal stage is increased fecundity in the newly emerged adult females. This phenomenon has been observed in Spodoptera littoralis and is believed to be the result of the extended feeding period during the larval stages (Laudien 1973).

The thermal summation model is the oldest and most popular method for predicting poikilothermic development. The popularity of this predictive technique isdue to it's conceptual and mathematical simplicity. The ever increaseing use of microcomputers, and the access to powerful macrocomputers which they provide, has reduced this advantage to a minor point. The accuracy of the biophysical model' predictions for the development of E. alfreddugesi is over three times greater then what can be achieved with the thermal summation technique. Although the improved accuracy is important to an effective integrated pest management program, more important, the biophysical model, with its theoretical basis, provides a framework on which to base hypotheses for testing. Theoretical models provide a tool for the quantitative study of the ecological interactions within a population and between different poikilothermic species and their regulation by the environment.

This study has suggested numerous areas for additional investigations, for example: To what extent do other abiotic factors, e.g., soil pH, moisture, and composition, interact with temperature to regulate the growth rate and size of the population? Do biotypes of this wide spread chigger species

exists? The range of *E. alfreddugesi* extends far more northward then other *Eutrombicula* species. The intensity of selection pressures are not the same throughout the geographic range and thus, the developmental rates of populations from different areas within the range may vary accordingly. The resolution of these questions, and others, will enhance the ability of the present temperature driven development models to predict and explain the dynamics of this cryptic species.

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Table 5-1. Median development rates for the eggs of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0
15.0	43.8	0.0228	14	46.7
20.0	18.9	0.0530	11	40.7
22.5	12.5	0.0803	17	56.7
25.0	10.9	0.0922	47	67.1
27.5	10.9	0.0922	23	63.9
30.0	7.1	0.1413	29	58.8
32.5	4.5	0.2205	17	53.1
35.0	5.5	0.1834	17	48.9
37.5	8.3	0.1200	35	54.7
40.0	N/D	---	0	0.0

N/D: No development occurs

Table 5-2. Median development rates for the deutova of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0
15.0	36.5	0.0274	8	100.0
20.0	18.0	0.0555	11	100.0
22.5	12.5	0.0803	15	93.8
25.0	9.1	0.1102	16	100.0
27.5	9.2	0.1087	20	87.0
30.0	2.9	0.3509	30	100.0
32.5	6.3	0.1578	15	100.0
35.0	5.6	0.1802	17	100.0
37.5	5.06	0.2017	28	100.0
40.0	N/D	---	0	0.0

N/D: no development occurs

Table 5-3. Median development rates for the fed larvae of *Eutrombicula alfreddugesi*

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0
15.0	4.3	0.2353	101	95.5
20.0	2.4	0.4192	97	75.8
22.5	3.0	0.3333	34	100.0
25.0	1.9	0.5185	103	98.1
27.5	1.8	0.5614	25	75.8
30.0	1.5	0.6707	100	100.0
32.5	2.0	0.5000	18	72.0
35.0	2.0	0.5000	24	77.8
37.5	2.6	0.3913	26	64.9*
40.0	N/D	---	0	0.0

N/D: No development occurs
* Significantly different (p=.05)

Table 5-4. Median development rates for the protonymphs of *Eutrombicula alfreddugesi*

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0
15.0	47.6	0.0210	79	75.2
20.0	21.5	0.0466	62	63.9
22.5	11.2	0.0890	34	91.2
25.0	7.8	0.1278	83	80.1
27.5	7.9	0.1260	23	92.0
30.0	7.3	0.1378	68	68.0
32.5	5.5	0.1818	18	72.0
35.0	3.4	0.2963	43	89.6
37.5	7.0	0.1429	12	50.0*
40.0	N/D	---	0	0.0

N/D: No development occurs
* Significantly different (p=.05)

Table 5-5. Median development rates for the rapid development morph of the deutonymphs of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent of population
12.5	N/D	---	0	0.0
15.0	N/D	---	0	0.0
20.0	19.5	0.0513	5	27.3
22.5	19.5	0.0513	10	58.8
25.0	11.0	0.0909	14	71.4
27.5	17.5	0.0571	12	80.0
30.0	17.0	0.0588	20	77.0
32.5	20.5	0.0488	18	93.7
35.0	17.5	0.0571	25	100.0
37.5	20.0	0.0500	14	77.8
40.0	N/D	---	0	0.0

N/D: No development occurs

Table 5-6. Median development rates for the slow development morph of the deutonymphs of Eutrombicula alfreddugesi

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent of population
12.5	N/D	---	0	0.0
15.0	N/D	---	24*	100.0
20.0	228.5	0.0044	16	72.7
22.5	42.5	0.0235	7	41.2
25.0	42.0	0.0238	6	28.6
27.5	48.3	0.0207	3	20.0
30.0	55.0	0.0182	6	23.1
32.5	44.0	0.0227	1	6.3
35.0	N/A	---	0	0.0
37.5	43.5	0.0230	4	22.2
40.0	N/D	---	0	0.0

N/D: No development occurs
N/A: No data available
* Survived >220 days without development to the tritonymph

Table 5-7. Median development rates for the tritonymphs of *Eutrombicula alfreddugesi*

Temperature °C	Median number of days for development	Rate (day^{-1})	Number surviving	Percent survival
12.5	N/D	---	0	0.0
15.0	38.5	0.0260	11	55.0*
20.0	23.1	0.0433	20	95.2
22.5	12.3	0.0811	20	100.0
25.0	9.1	0.1103	21	100.0
27.5	10.3	0.0976	22	100.0
30.0	7.5	0.1333	23	100.0
32.5	6.5	0.1538	19	95.0
35.0	6.3	0.1587	22	100.0
37.5	6.7	0.1493	13	48.2*
40.0	N/D	---	0	0.0

N/D: No development occurs
* Significantly different (p=.05)

Table 5-8. Cumulative developmental rates for the rapid and slow phases of Eutrombicula alfreddugesi

Temperature °C	Median # days for development		Developmental Rate (d^{-1})		% Survival
	Rapid	Slow	Rapid	Slow	
12.5	N/D	N/D	---	---	0.0
15.0	N/A	N/C	---	---	N/C
20.0	103.3	312.3	0.0097	0.0034	9.8*
22.5	71.0	94.0	0.0141	0.0106	26.6
25.0	49.7	80.7	0.0201	0.0124	21.7
27.5	57.5	88.3	0.0174	0.0113	25.2
30.0	43.2	81.2	0.0232	0.0123	26.0
32.5	45.4	68.9	0.0220	0.0145	23.3
35.0	40.2	63.4	0.0249	0.0150	19.9
37.5	49.6	72.6	0.0201	0.0137	4.2*
40.0	N/D	N/D	---	---	0.0

N/A: No data available
N/C: Development not complete (deutonymph fails to development)
N/D: No development occurs
* Significantly different (p=.05)

Table 5-9 Summary of model parameters for Eutrombicula alfreddugesi

	Rho25 day^{-1}	HA cal/mol	TH ^{o}K	HH cal/mol	TL ^{o}K	HL cal/mol	R^2
Life Stage							
Egg	0.08793	18069.5	309.9	117166.3	287.7	-422987.3	0.931
Deutovum	0.12350	7627.5	---	---	291.1	-96997.9	0.977*
Fed Larva	0.08320	10112.3	309.1	61971.0	288.8	-581988.0	0.989
Protonymph	0.10094	16549.2	301.6	4807297.0	287.7	-68652.3	0.928
Deutonymph	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Tritonymph	0.10198	11078.9	312.5	72210.6	288.8	-39113.2	0.959
Cum.Life Cycle (rapid deutonymph)	0.01806	5123.0	310.9	903397.7	292.3	-108169.5	0.911
Cum.Life Cycle (slow deutonymph)	0.01175	2651.9	---	---	291.7	-263398.0	0.953

* If 30.0^{o}C. data are omitted then the data for deutova have a R^2 value of 0.991

Table 5-10 Model Predicted developmental rates for the rapid and slow phases of *Eutrombicula alfreddugesi*

Temperature °C	RAPID PHASE					SLOW PHASE				
	Median # Days for Development		Developmental Rate (d^{-1})			Median # Days for Development		Developmental Rate (d^{-1})		
	Obs.	Exp.	Obs.	Exp.	%Rate Error	Obs.	Exp.	Obs.	Exp.	%Rate Error
12.5	N/D	---	---	---	---	N/D	---	---	---	---
15.0	N/D	---	---	---	---	N/D	---	---	---	---
20.0	103.31	104.36	0.0096	0.0096	0.00	312.30	312.40	0.0032	0.0032	0.00
22.5	70.97	67.56	0.0141	0.0148	4.72	93.97	93.72	0.0106	0.0107	0.93
25.0	49.68	56.85	0.0201	0.0176	-14.20	80.68	85.22	0.0124	0.0117	-5.98
27.5	57.51	51.40	0.0174	0.0195	12.25	88.26	81.33	0.0113	0.0123	8.13
30.0	43.17	47.28	0.0231	0.0211	-9.47	81.17	77.76	0.0123	0.0128	3.91
32.5	45.38	43.74	0.0220	0.0229	3.93	68.88	74.39	0.0145	0.0134	-8.20
35.0	40.18	40.47	0.0249	0.0247	-0.81	66.43	71.22	0.0150	0.0140	-7.14
37.5	49.55	49.55	0.0202	0.0202	0.00	72.55	68.23	0.0138	0.0146	5.47
40.0	N/D	---	---	---	---	N/D	---	---	---	---

N/D: No development occurs

Table 5-11 Thermal summation estimates of developmental rates for the rapid and slow phases of Eutrombicula alfreddugesi

Temperature °C	RAPID PHASE: Median # Days for Development		RAPID PHASE: Developmental Rate (d^{-1})			SLOW PHASE: Median # Days for Development		SLOW PHASE: Developmental Rate (d^{-1})		
	Obs.	Exp.	Obs.	Exp.	%Rate Error	Obs.	Exp.	Obs.	Exp.	%Rate Error
12.5	N/D	---	---	---	---	N/D	---	---	---	---
15.0	N/D	---	---	---	---	N/D	---	---	---	---
20.0	103.31	85.07	0.0096	0.0118	18.64	312.30	97.92	0.0032	0.0102	68.75
22.5	70.97	76.25	0.0141	0.0131	-7.63	93.97	92.77	0.0106	0.0108	1.66
25.0	49.68	67.42	0.0201	0.0148	-35.81	80.68	87.62	0.0124	0.0114	-8.66
27.5	57.51	58.60	0.0174	0.0171	-1.75	88.26	82.47	0.0113	0.0121	6.82
30.0	43.17	49.78	0.0231	0.0201	-14.92	81.17	77.32	0.0123	0.0129	4.90
32.5	45.38	40.95	0.0220	0.0244	9.92	68.88	72.18	0.0145	0.0138	-4.68
35.0	40.18	32.13	0.0249	0.0311	20.01	66.43	67.03	0.0150	0.0149	-0.67
37.5	49.55	23.30	0.0202	0.0429	52.96	72.55	61.88	0.0138	0.0162	14.56
40.0	N/D	---	---	---	---	N/D	---	---	---	---

N/D: No development occurs

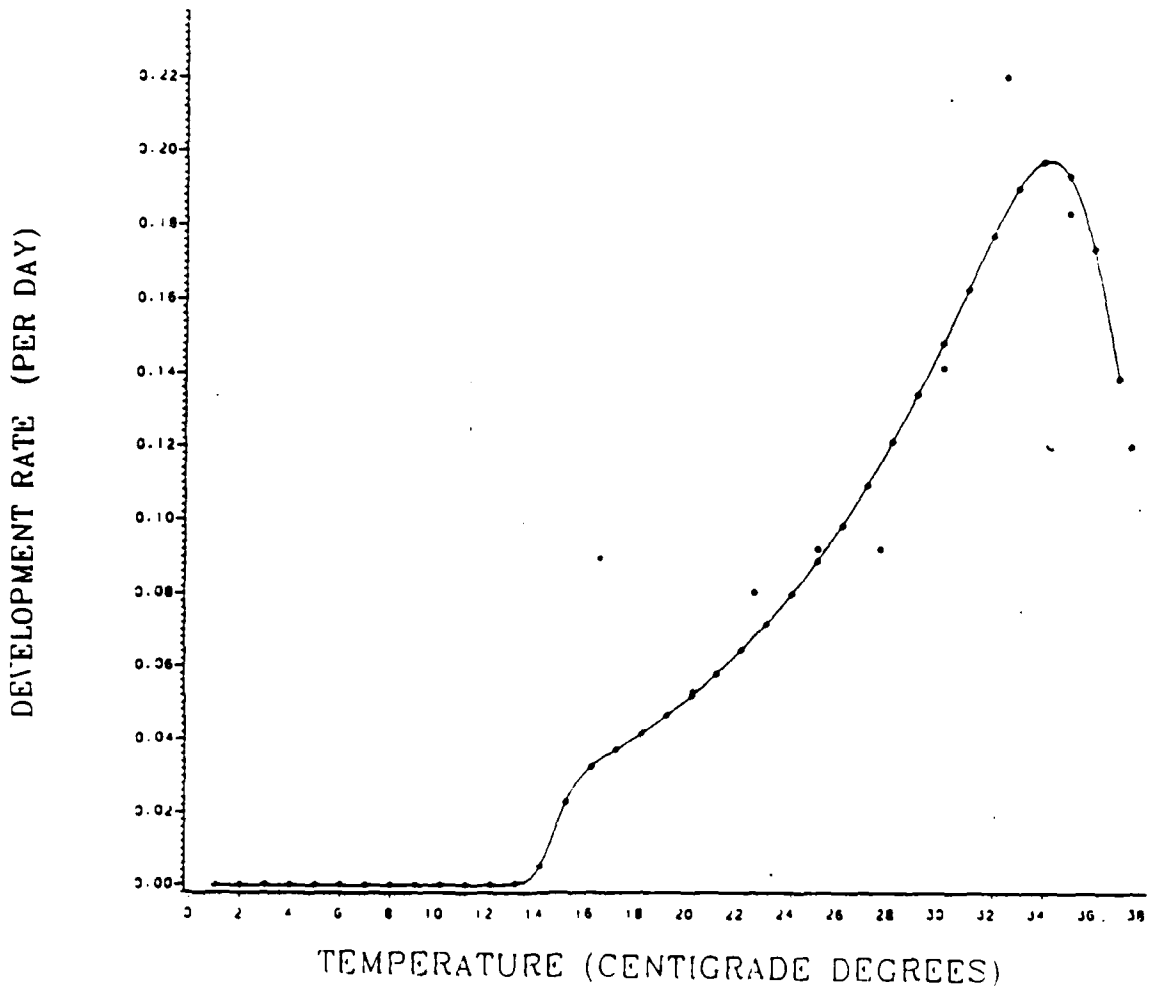

Figure 5-1. Model of the developmental rate as a function of temperature for the eggs of Eutrombicula alfreddugesi compared with plot of observed data.

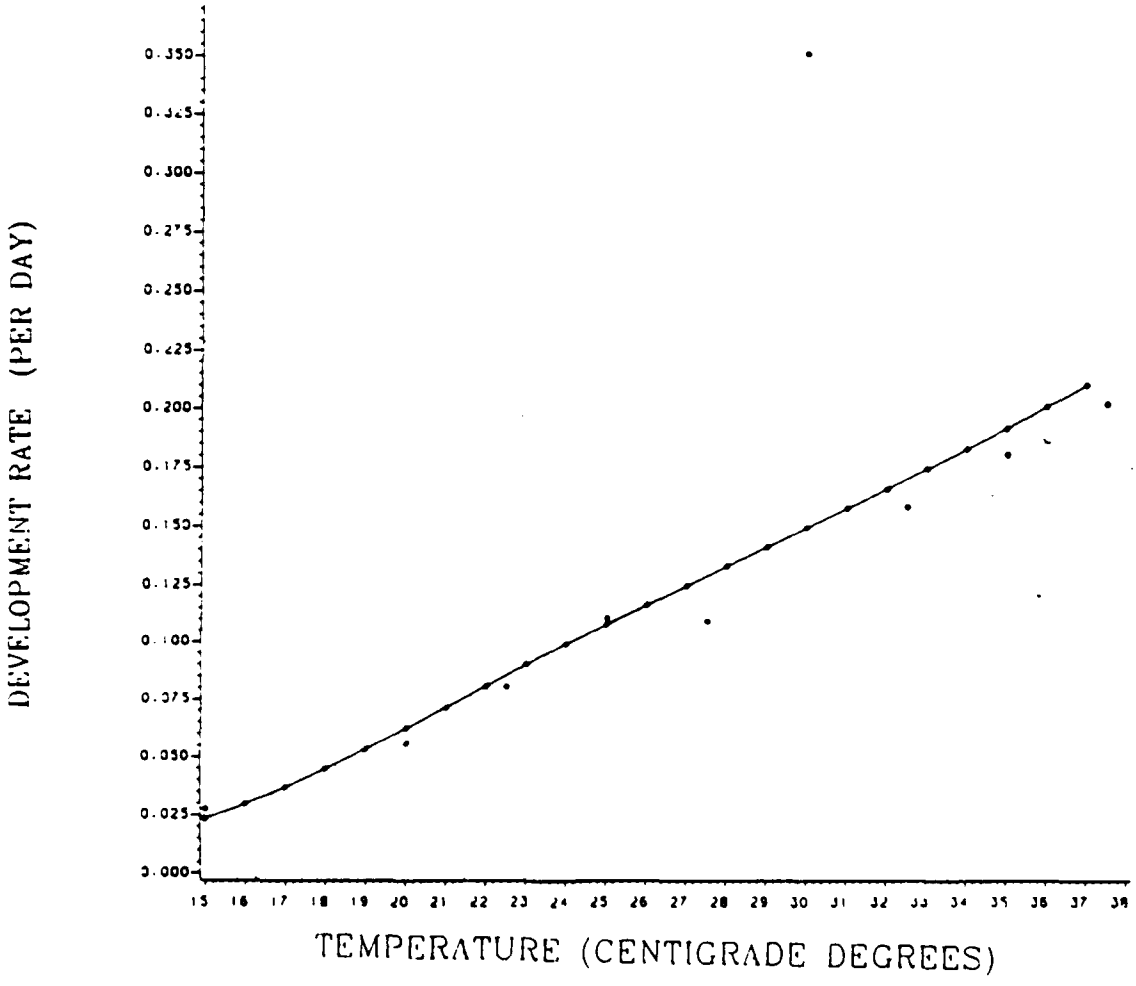

Figure 5-2. Model of the developmental rate as a function of temperature for the deutova of Eutrombicula alfreddugesi compared with plot of observed data.

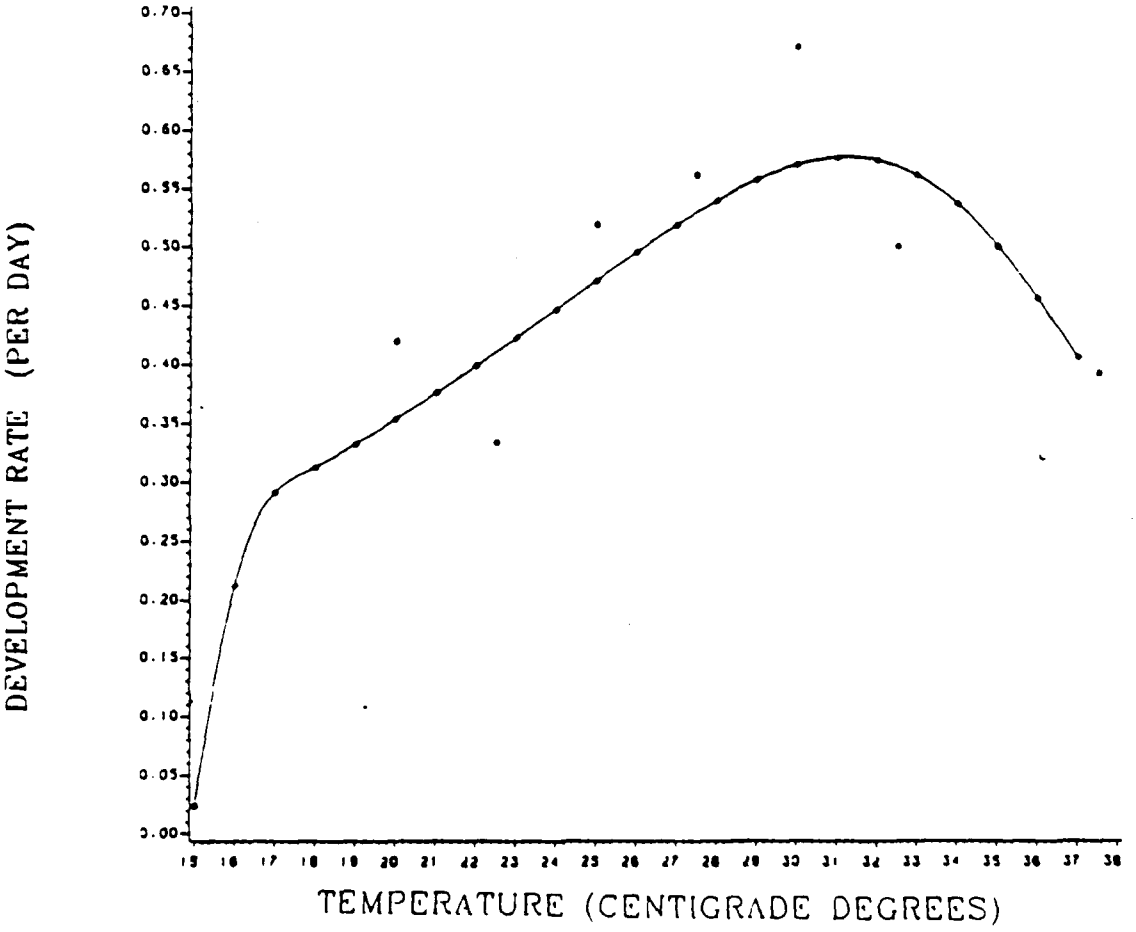

Figure 5-3. Model of the developmental rate as a function of temperature for the fed larvae of Eutrombicula alfreddugesi compared with plot of observed data.

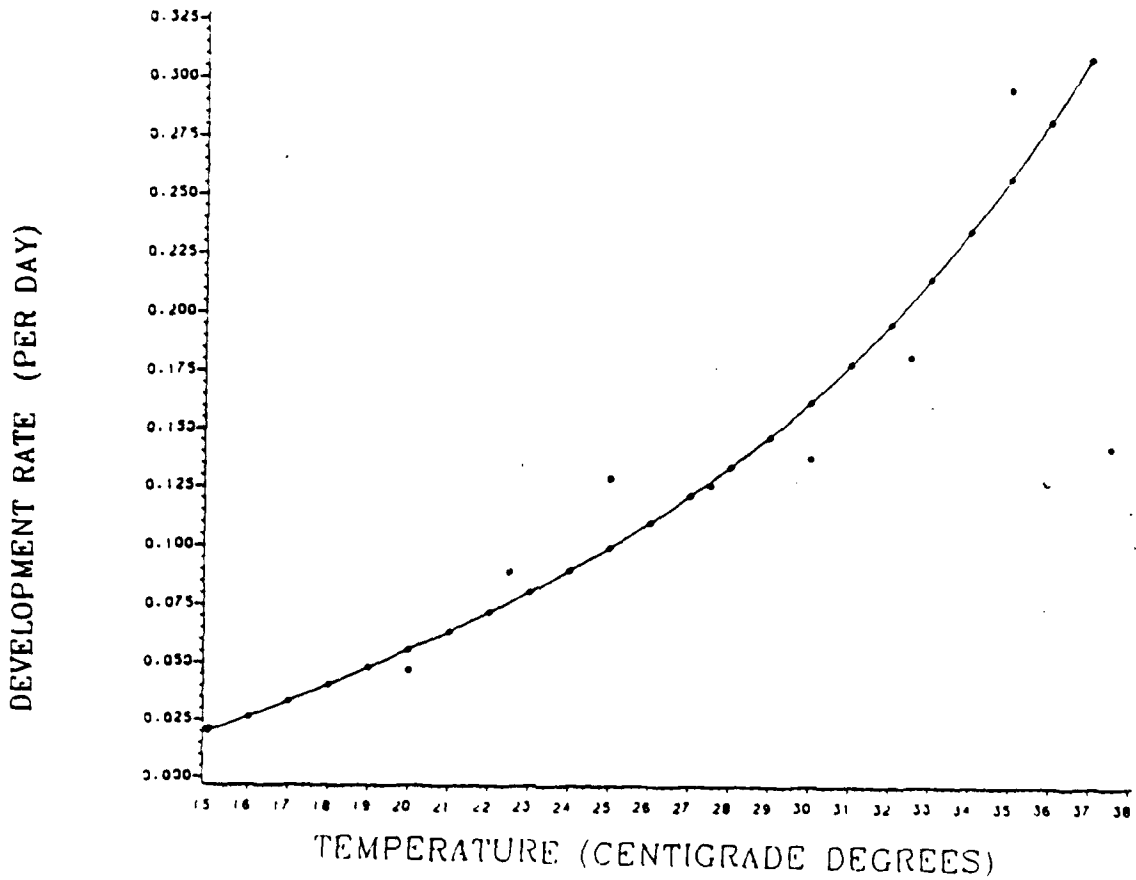

Figure 5-4. Model of the developmental rate as a function of temperature for the protonymphs of Eutrombicula alfreddugesi compared with plot of observed data.

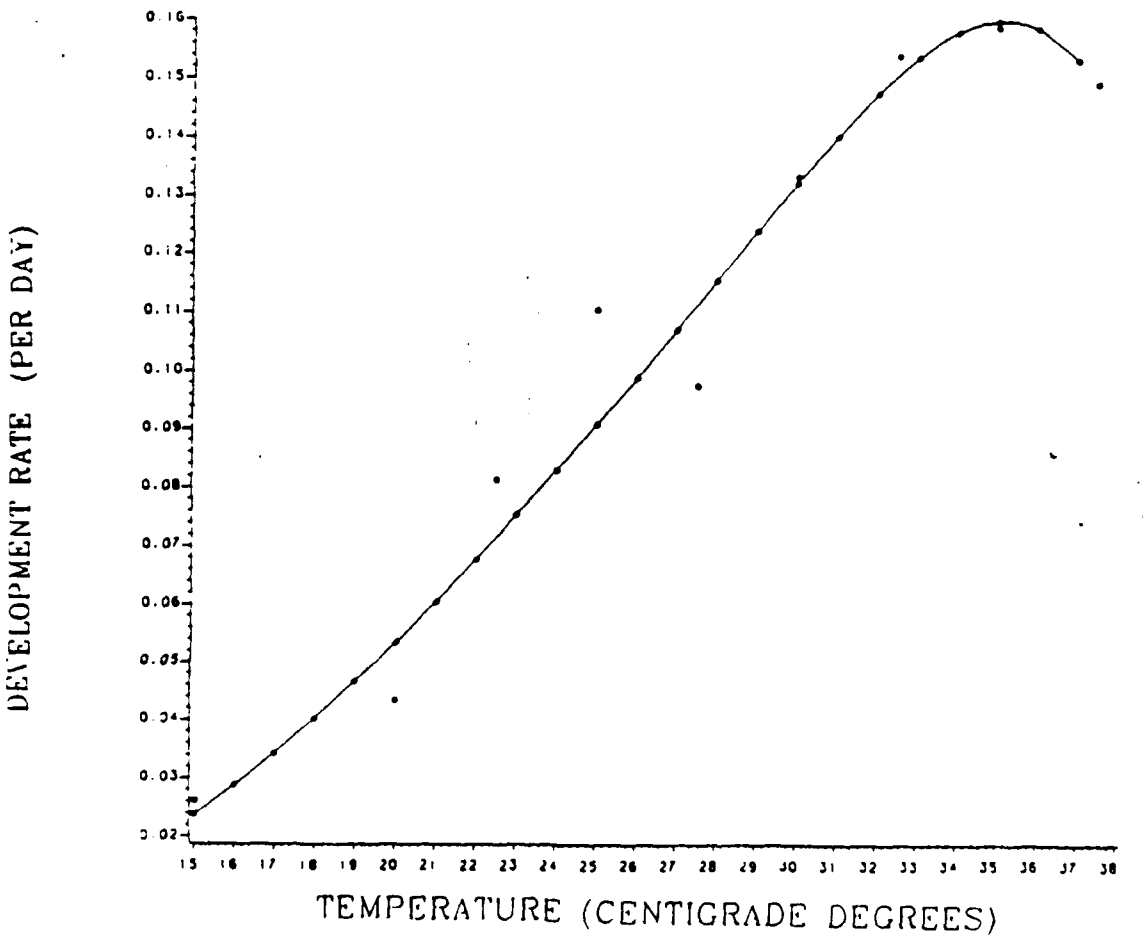

Figure 5-5. Model of the developmental rate as a function of temperature for the tritonymphs of Eutrombicula alfreddugesi compared with plot of observed data.

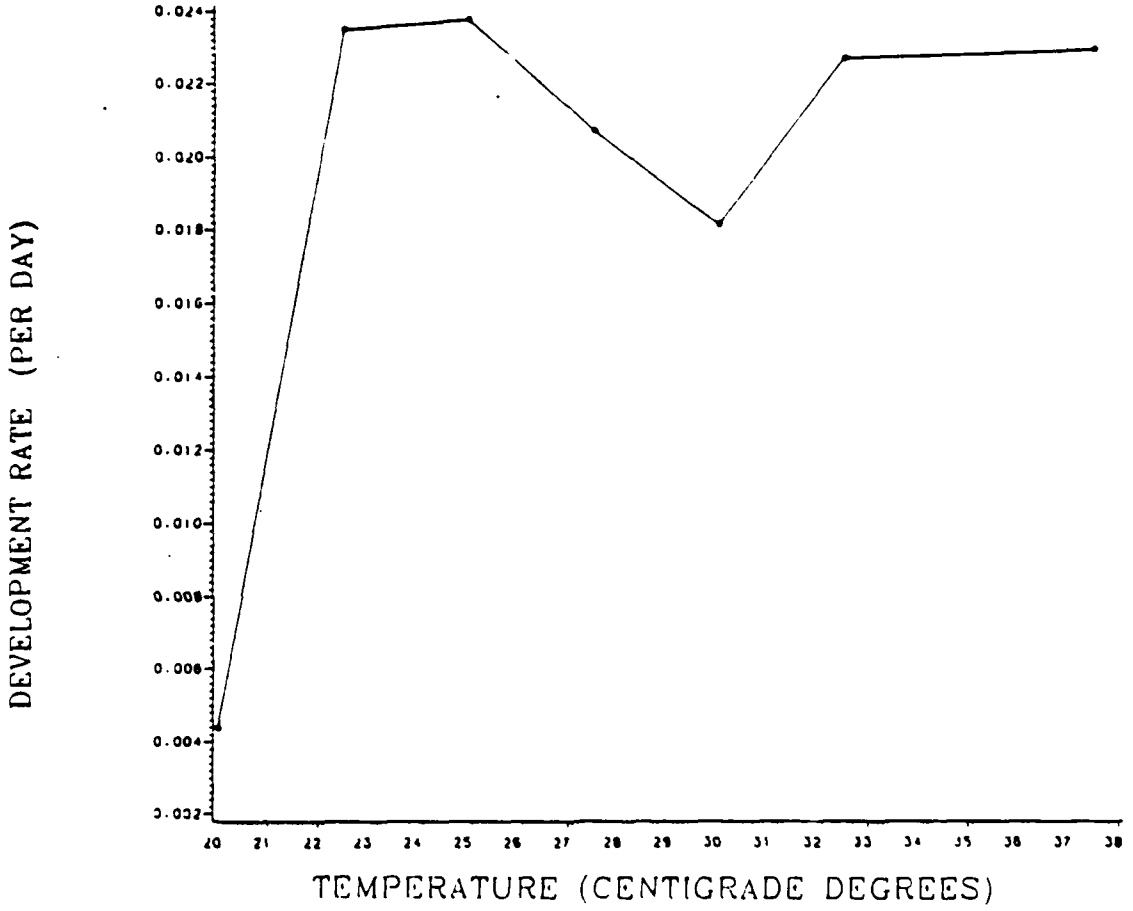

Figure 5-6. The developmental rate as a function of temperature for the slow development morph of the deuotnymphs of Eutrombicula alfreddugesi.

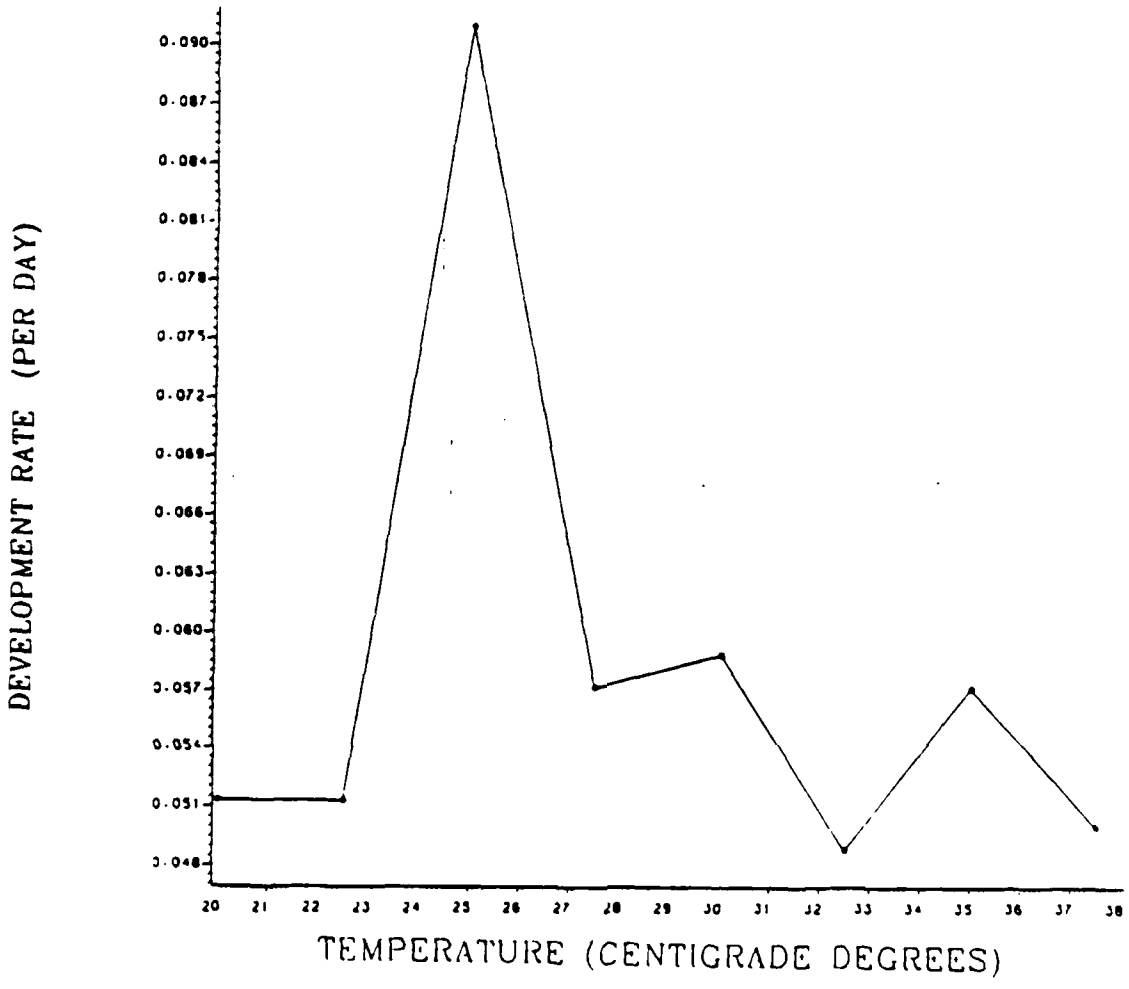

Figure 5-7. The developmental rate as a function of temperature for the rapid development morph of the deuotnymphs of Eutrombicula alfreddugesi.

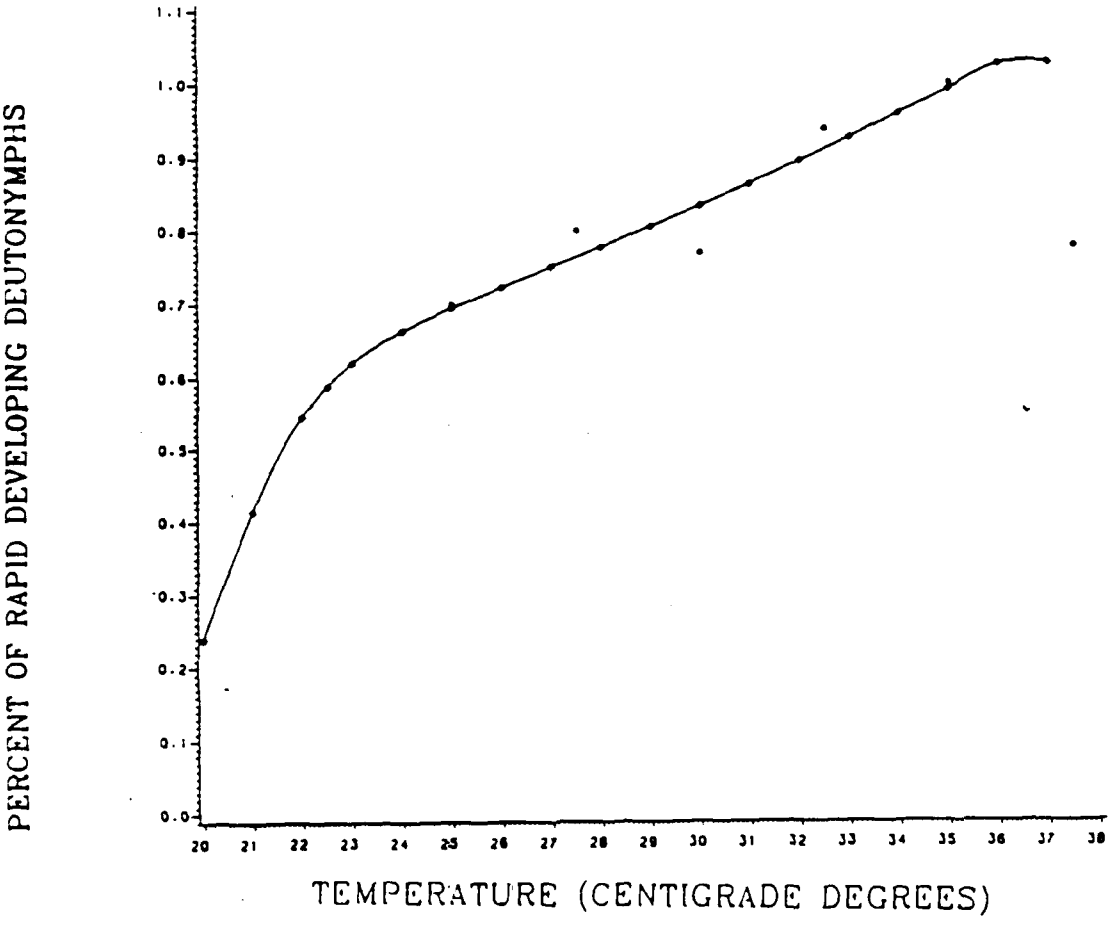

Figure 5-8. Model of the change in the proportion of the rapid development morph deutonymphs in E. alfreddugesi's population as a function of temperature compared with plot of observed data.

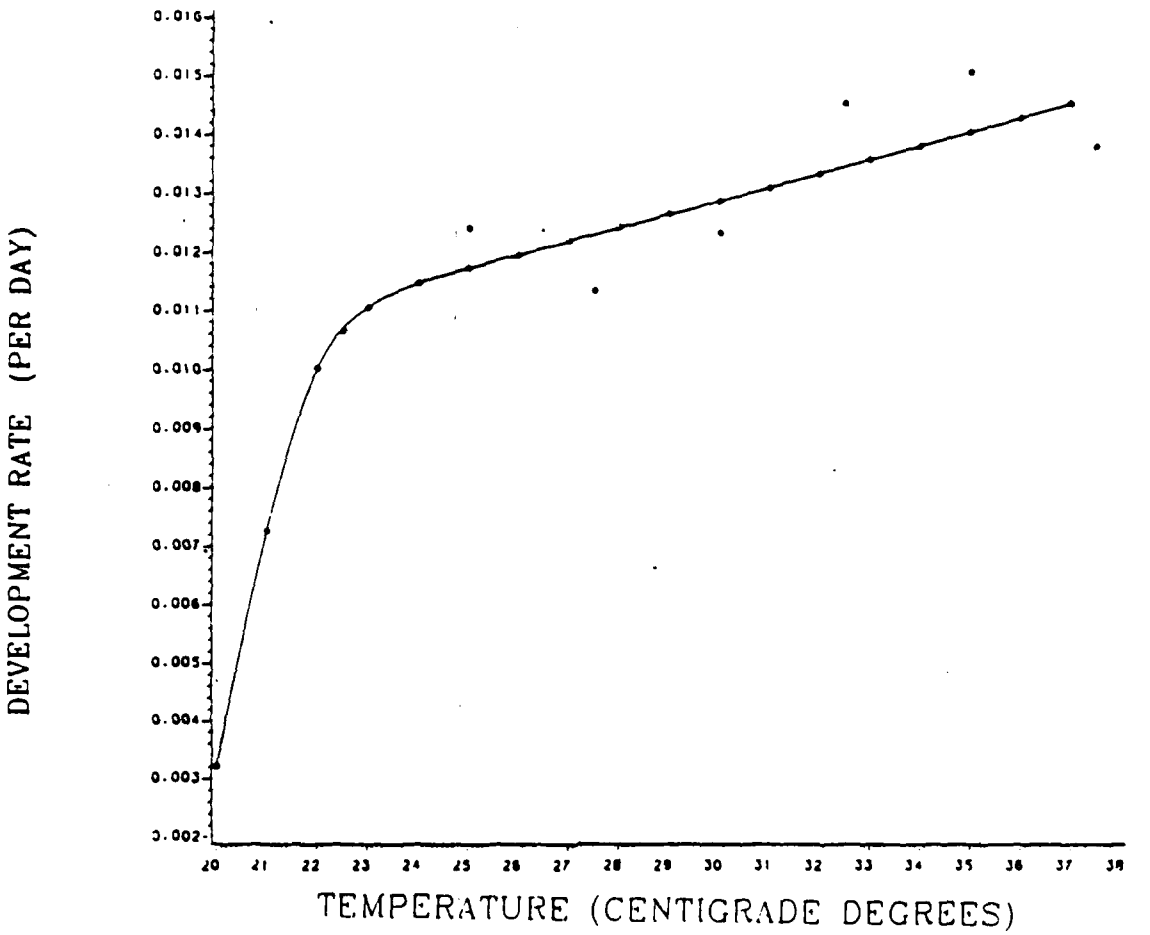

Figure 5-9. Model of the developmental rate as a function of temperature for the entire life cycle of Eutrombicula alfreddugesi (using slow deutonymph morph data) compared with plot of observed data.

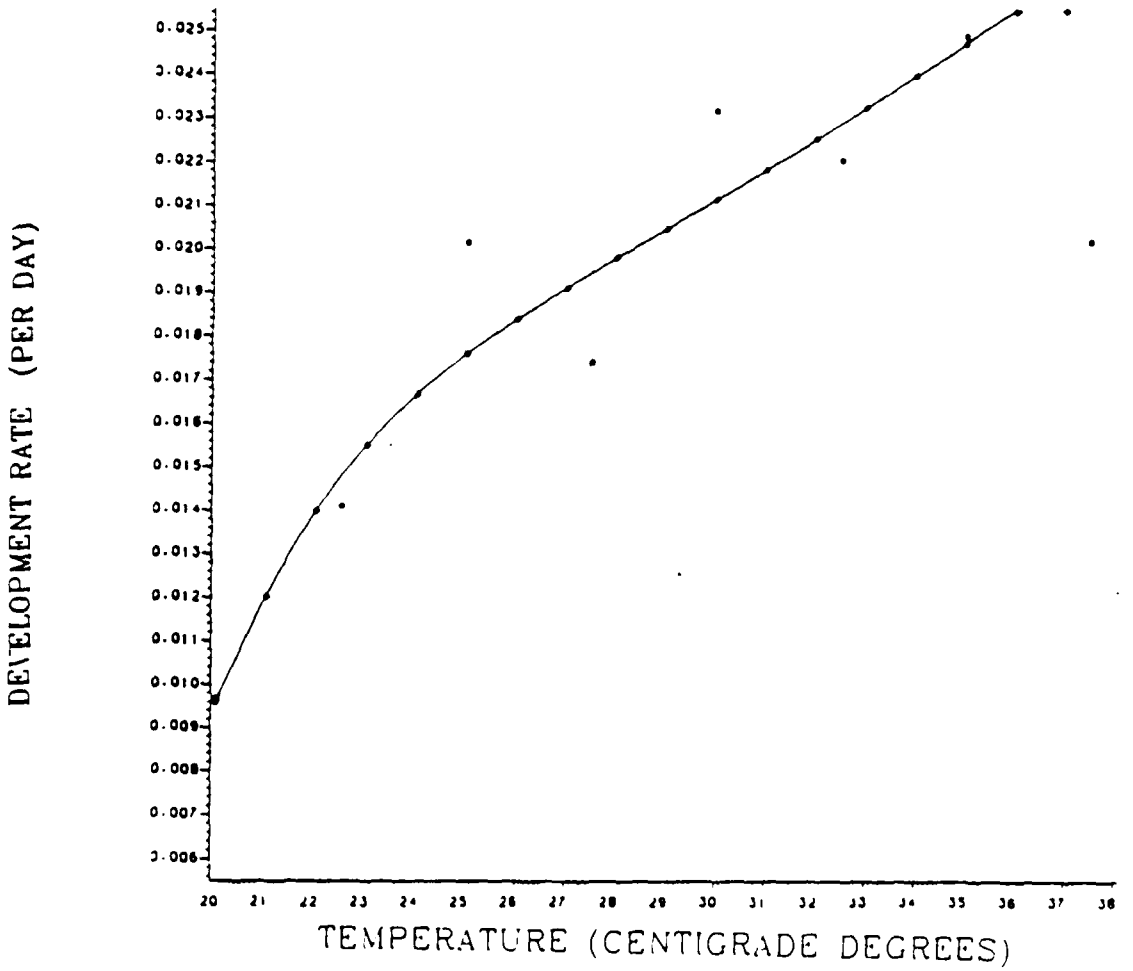

Figure 5-10. Model of the developmental rate as a function of temperature for the entire life cycle of Eutrombicula alfreddugesi (using rapid deutonymph morph data) compared with plot of observed data.

CHAPTER VI

MODELS OF OVIPOSITIONAL RATES AND FECUNDITY FOR EUTROMBICULA ALFREDDUGESI (OUDEMANS) (ACARINA:TROMBICULIDAE)[1]

Submitted: Annals of the Entomological Society of America (1985).

INTRODUCTION

The presence of chiggers, the parasitic larvae of trombiculid mites, is usually the only evidence that the adult mites are present in a given microhabitat. The obscurity of the post-larval stages is due to the cryptic nature of their life cycle in the soil/litter system. The appearance of the larvae occurs about the same time every year althrough the season of larval abundance varies from species to species. The larva is the result of two activities; adult reproduction and the successful completion of egg and deutovum development. The development rates for each stage of the life cycle is the subject of the previous paper (Chapter 2).

Fecundity of any organism is influenced by a number of factors. The most important factor in a predictive model of chigger population dynamics, of all the abiotic elements, is that which correlates best with the chigger "bloom". The factors which determine the timing of the chigger season

varies between the temperate and tropic zones. In temperate regions, temperature is the regulating factor while in the tropics it is precipitation (Sasa 1961). The difference in the source of regulation between regions demonstrates the need for a careful analysis of the physiological impact of each factor on Eutrombicula alfreddugesi populations which has a continuous geographical distribution from the northern tier of states in the United States south to northern South America (Loomis and Wrenn 1984) and could, therefore, be restricted by either rainfall or temperature. The genus Eutrombicula is believed to have evolved in the tropics of Central America and then invaded the temperate regions by developing special adaptations (Jameson 1972). Thermal regulation of the population would be one possible adaptation.

Fecundity, like many other metabolic processes, responds to the temperature of the environment (Laudien 1973). Temperature determines the actual number of offspring produced by an individual female (Tanigoshi et al. 1975, Curry et al. 1978). The plots of oviposition rates over temperature generate patterns which are similar to those of development rates. This similarity has led to the use of the same models to describe both development and fecundity.

The biophysical model of Sharpe and DeMichele (1977), which is an extension of Eyring's (1935) absolute reaction rate theory, is the only model available today which provides a theoretical basis for the description of both optimum

temperature and extreme temperature effects on metabolic processes. It is defined in terms of accepted biophysical laws as they apply to a hypothesized control enzyme that can exist in three distinct activity states. Absolute reaction rate theory has been effectively used in the discription of a wide variety of temperature sensitive biological activities (Johnson et al. 1974). Its wide applicability provides support for the use of the biophysical model to describe the fecundity of poikilotherms such as E. alfreddugesi.

Ecologically, a physiological model is somewhat misleading because the low rates associated with extreme ends of the oviposition temperature range are generally so low that the number of new individuals added to the population can not assure the continued existance of that population. For this reason, the practical thermal limits fall within the physiological limits (Das and Das 1967 as cited in Laudien 1973). This problem can be effectively dealt with by the inclusion of a stochastic component to the oviposition rate model. This increases the ability of the model to realisticly predict the changeing oviposition rates of a poikilotherm species. Realism is essential for the function of a predictive model both in ecological population models and in integrated pest management strategy models (Hardman 1976a, 1976b, Logan et al. 1976, Curry et al. 1978). Curry et al. (1978) point out that the reproductive rate of poikilotherms also depends on the individual's physiological age. This is the reason that the age specific natality rate

(m_x) is included in demographic studies of populations. A model of distribution converts this deterministic measure (m_x) of life tables to a stochastic descriptor. The plot of the proportion of the total offspring produced at each age generates a continuous estimator of natality which may then be integrated with the temperature driven oviposition rate model.

MATERIALS AND METHODS

TECHNIQUES

All mites used in this study were the first generation produced from laboratory maintained colonies descended from larvae collected from Whitehall forest, Athens, Georgia during the summer of 1983. The experimental temperature range was $12.5\pm1^{o}C$ to $40\pm1^{o}C$. The ovipositional response was evaluated at 2.5^{o} increments throughout the experimental range. Only $17.5\pm1.0^{o}C$ was omitted from this thermal sequence due to space limitations.

Observation chambers consisted of round plastic vials 30 cm (dia.) by 25 cm (ht.) which had 3 drainage holes drilled in the bottom covered with a 10 cm deep substrate of charcoal:plaster of Paris (1:9). The observation chambers were stored in 500 ml glass ointment jars with screw top lids. A layer of damp cellulose sponge in the bottom of the jar maintained a relative humidity near 100% which acted as a

buffer against dehydration. This was especially important in the upper region of the temperature range.

A total of 16 experimental groups was used. Each consisted of 5 adult mites taken from colonies which had been producing eggs for 1 week. The number of females in the group was determined at the end of the study by examining slide preparations of the mites mounted in Hoyer's mounting medium, with phase contrast microscopy. Groups of mites were used because isolated females frequently lay eggs for only one to two weeks after being separated from the colony. Any mortality within a group excluded that group from participation in the remainder of the experiment. The mites were provisioned with an excessive supply of fresh collembolan eggs (Sinella curviseta) on a daily basis.

Random number tables were used to assign the experimental groups to a different experimental temperature each week. The random reassignment was necessary because of the great variability among the oviposition rates of individual females. Differences in the number of experimental groups assigned to the constant temperature regimes resulted from a combination of a limited number of environmental chambers and the random assignment process. Every temperature regime had a minimum of 6 replicates. Data were collected on all but 1 of the 16 groups at 35.0°C to determine the level of variance within the population. To minimize the variance due to previous thermal experiences, the eggs collected on the first day after the transfer were not included in the data. Daily

egg counts were made on the following 6 days.

ANALYSIS OF DATA

A sample represents the 6 days of data collected for a group at a particular experimental temperature. Each sample was adjusted for the number of females present in the group. The adjusted sample data were then combined into groups based on temperature. The univariate procedure from the Statistical Analysis System (SAS) library (1982 edition) was used to determine that the data sets had a negative binomial distribution. A log(x+1) transformation was used to normalize the data; this was verified by the univariate program from the SAS library. An analysis of variance was performed using the GLM procedure from the SAS library to determine the variance due to group membership and due to temperature. The GLM procedure was then used to run an analysis of covariance to compensate for the variance due to group membership in the regression. The estimated means were then transposed with the antilog of $(x+1.15s^2)$ to determine the derived means.

Modeling Development Rates

This procedure provided estimated means which were then used to model the effect of temperature on oviposition rate. The computer program of Wagner et al. (1984a) was used to fit the mean oviposition rate data to Schoolfield et al.'s (1981) modified version of the biophysical model of Sharpe and

DeMichele (1977). The program first determines the existance of either low and/or high temperature inhibition in the data and selects the appropriate variation of the model which best fits the data. An Arrhenius plot of the data is then divided into regions of inhibition and non-inhibition. These regions are used to estimate the parameters associated with inhibition (HL, TL, HH AND TH) and non-inhibition (HA and RH025). These estimates are then used as starting values for the SAS Marquardt method of nonlinear regression to obtain a least squares estimate of the model's parameters.

Production data for 8 colonies of E. alfreddugesi were obtained from the U.S.D.A. Insects Affecting Man Laboratory in Gainesville, Florida. Larval production data were combined into 1 week intervals producing an average of 11 classes per colony (Std. Dev.=3.2).

Differences in fecundity distributions were analyzed with the computer program of Wagner et al. (1984b). The production distributions were converted to cumulative probability distributions by first summing the frequencies of successive classes and were then standardized by dividing the cumulative frequencies by the total frequencies. These mathematical manipulations eliminated variability within the distribution which results from differences in the length of the oviposition period (i.e., the number of classes). The fecundity distributions were then normalized for variation due to colony size by dividing the standardized oviposition rates by the median rate. The normalization process made the

distributions independent of the actual number of eggs produced per colony and resulted in the overlay of distributions which now all share the same median point. The production independent distributions, refered to as tau distributions by Wagner et al. (1984b), are then multiplied by their mean rate to make them colony independent as well. This generates standard tau curves which are evaluated for similarity of shape. The variation between the distributions was measured by the coefficient of variation calculated for 1%, 30%, 70% and 100% cohort fecundity points. A mean standard tau distribution is then obtained by taking the average of each distribution's values which have been weighted for the total number of raw data points used to generate each value.

The mean standard tau distribution is then fitted to a three parameter cumulative Weibull function with the form:

$$F(x) = 1 - \exp(-[(x-G)/E]^B)$$

where:F(x) is the probability of complete development at normalized

time x,

G (gamma) is the threshold value, i. e., expected complete development of first individual,

B (beta) is the shape parameter and

E (eta) is the location parameter.

Both B and E are estimated by transforming the Weibull distribution to the linear form: $\ln(-\ln[1-F(x)]) = B \ln(x-G) - B \ln E$, where B is the slope and the Y intercept equals -B

lnE. The correlation between the data and a Weibull distribution can be estimated by the coefficients of determination (R^2).

RESULTS

DISTRIBUTION OF OVIPOSITION DATA

The negative binomial distributions of the temperature treatment groups except 15.0°C are very similar to each other. The level of skewness is independent of class size where classes contain a minimum of 36 values. The skewness at 15.0°C is the largest (6) as measured by the univariate procedure of the SAS library. The skewness of the other experimental distribution are very similar (average= 0.92). Kurtosis has a similar pattern to skewness being greatest at 15.0°C (36) and very similar among the other distributions (average=0.82).

The ovipositional rate of nearly all females (n=90) used in this study was evaluated at 35.0°C to provide a large sample estimate of variance. Although the non-transformed data do not have a normal distribution as determined by the Kolmogorov-Smirnov D-statistic (p=0.05), it does approach closely to a normal distribution. Sample sizes of 36 are sufficient however as indicated by the distributions of data at 27.5°C and 30.0°C which are equally as close to a normal distribution as that of 35.0°C.

The log transformation converted the negative binomial distributions of the temperature treatment data to normal distributions for all treatments except 15.0°C and 20.0°C

(Table 6-1). The 15.0°C data had only one point of the 36 entries greater than 0, and thus may functionally be considered as below the ovipositional threshold. The data for 20.0°C had 9 zero counts of the 36 data points taken. Zeros are unaffected by log transformation and so the result is the normalization of the remainder of the data while the 0 counts are unaffected. The transformed data have a bimodal appearance with peaks at 0 and 0.69897 and a median of 0.46265 which was used in the remaining calculations instead of the mean as a more accurate measure of central tendency.

The removal of the variance due to group membership had a limited impact on the within treatment variability. The majority of variance in the analysis of variance is due to the effect of temperature; the variance associated with group membership constituted only 3.98% of the total variance among the transformed treatment temperature data.

MODEL OF OVIPOSITION RATE

The log transformed data (Table 6-1) were used in order to assure homoscedasticity in the samples, a basic assumption of the biophysical model. Figure 6-1 shows plots of the derived rates and model generated curve. The model approximately describes the ovipositional data (R^2=0.88). Parameter estimates are provided in Table 6-2. The derived means, which are obtained by an antilog function of the log rates used in the model (Table 6-3), are close to the averages of the original data (Table 6-1). The derived model

estimates (Table 6-3) show significant rate errors which seem incongruous in light of the high R^2 value. This apparent discrepency is the result of using log transformed data for the model but estimating the rate errors in terms of derived data. The model predicts a range of high reproductive rates between 27.5°C and 35.0°C (Table 6-3) with a peak rate at 30.0°C. It is within this region that the model seriously underestimates the oviposition rates at both 27.5°C and 30.0°C, the peak fecundity regions.

MODEL OF FECUNDITY DISTRIBUTION

The distributions of age specific natality rates for the colonies have similar coefficients of variance which average 34.81 (Std. Dev.=16.24). This represents the sum of the variation in ovipositional rates between females and within each female. Variations among the normalized fecundity distributions (Table 6-4) is greatest at the beginning and end of the reproductive period and progressively decrease as the distributions approach the median age. This trend in variation level relative to the physiological age is due to the statistical manipulations involved in forcing the distributions to overlap in order to generate the natality rate distribution model. The coefficients of variance for the normalized distributions fall within the range observed in developmental distributions which Wagner et al. (1984b) defined as moderate. This indicates that the cumulative frequency distributions used in the estimation of the

standard normalized distribution are similar but not identical. The extent to which the distributions differ can be attributed to differences in sample size (Wagner et al. 1984b). Density dependent factors may also be involved, e.g., the presence of pathogens, competitors and predators and the effect of population density on both the males and females.

The cumulative Weibull distribution accurately defines the standard normalized distribution model (Fig. 6-2). The quality of the distribution's fit to the data is measured by plotting the Ln-Ln of the cumulative probabilities of the normalized fecundity distributions against the observed and expected values of the Ln of (the normalized cumulative frequency values minus the threshold value, i.e., gamma) This regression has an R^2 value of 0.999 (Fig. 6-3). The values of the remaining two Wiebull parameters beta and eta (Table 6-4) are determined from the slope and Y-intercept.

DISCUSSION

The model's description of ovipositional rates within the biologically active temperature range (Fig. 6-1) identifies a wide temperature tolerance. The controlling enzymes of the reproductive process are especially resilient to high temperature deactivation as indicated by the moderate slope between 32.5° and 37.5°C. This ability to maintain high rates of reproduction at high temperatures allows the

extension of the rapid population build-up period into late summer, which for the soil temperature regime in north Georgia is August and September (Fig. 6-2 and Fig. A8). High reproductive rates are possible early in the spring by diurnal migration into the litter layer where the absorption of solar radiation produces daytime temperatures that often exceed the air temperature. This hypothesis is suggested by the behavior of another chigger species: Daniel (1961) observed vertical migration of Trombicula autumnalis nymphs and adults upwards in early spring and downwards in late fall.

Larval production drops during summer droughts which in turn indicates a reduction in reproductive rates. A possible explanation for this is provided by the oviposition rate model. Drying of the litter and top soil would drive the mobile post-larval stages deeper into the soil where the temperature is much lower. At 10cm depths, the temperature profile does not exceed 21°C. The model predicts an oviposition rate that is only 25% of the maximum potential. In addition, the eggs laid in this cooler region will require much longer periods of development. The combination of these two rate reductions would have the net effect of reducing the number of new larvae available for attachment to a small fraction of its potential predicted by litter or air temperatures.

The choice of the biophysical model to describe temperature's effect on reproductive rates provided a

theoretical mechanism with which to probe the interaction of temperature and the fundamental biochemical processes which result in the observed oviposition activity. Jones and Brown (1983) used multiple regression analysis to model the reproductive response of the broad mite, Polyphagotarsonemus latus to constant temperature and humidity regimes. Their model described the data well as indicated by their coefficient of determination (R^2) of 0.81. Although their accuracy is comparable to what was obtained in this study (R^2=0.88), the multiple regression analysis is an empirical model which does not provide the theoretical basis for biological interpretation.

The fecundity-physiological age model provides a temperature free stochastic description of specific age natality (m_x). Fecundity is very low during the first 14% and the last 23.5% of the ovipoition period (Fig. 6-2) During the middle 62.5% of the oviposition period, fecundity remains relatively constant. This differs from the fecundity pattern observed in Tetranychus mcdanieli (Tanigoshi et al. 1975), in that T. mcdanieli had a strongly depressed oviposition rate during the entire last half of the reproductive cycle. The ability to maintain maximal reproductive rate over the majority of the reproductive period allows E. alfreddugesi to maintain a large population of larvae throughout the early and mid-summer period. The flooding of the local environment with the parasitic stage during the season of maximum host abundance (a major limiting

resource in the life cycle) has a large adaptive value for a campestrous species where the probability of the larvae obtaining a host is low.

The contributions made by females which overwinter to the next season's larval population are unknown. Cunningham (1978) found that a single cohort of Neoschongastea americana could contribute to the larval population in 3 summers. The rate of egg production for the second and third season is not known but may be important in the rapid build up of larvae early in the summer.

The length of the chigger season in north Georgia is not believed to be lengthened by an unusually cool summer and may mean that the length of the oviposition period may not necessarily depend on the temperature regime. Independence of oviposition period length from temperature has been discovered in another acarine, T. mcdanieli whose oviposition period is not statistically different between females maintained at 18° and 35°C. (Tanigoshi et al. 1975). Moisture may be the determining factor for the cessation of oviposition in temperate regions as well as in the tropics. In labortory colonies, reproduction only occurrs within a restricted moisture range; the charcoal-plaster of Paris substrate must be maintained just damp but not wet to assure good larval production. Reductions in chigger counts in the field are believed to correlate with extended drought periods (Wharton and Fuller 1952).

The combination of models developed in this paper,

temperature-oviposition rate model and fecundity-physiological age model provide insight into the underlying physiological mechanisms which produce the population events observed in the field. In north Georgia, chiggers first appear about the first of June which means that the females must be mated and laying eggs by the end of April in order to allow sufficient time for egg and deutovum development to occur. The oviposition rate model shows that the females must be utilizing the warmth in the upper litter layer in order to raise the concentration of the control enzyme in an active state high enough to iniate oviposition. The rapid increase in larval populations that occurs in early June is the result of a combination of increased reproductive rate at the soil warms (Figs. 6-1 and A8) and the advancement of females in physiological age into the period of maximum fertility as indicated by the fertility model (Fig. 6-2). A small increase in initial larval numbers may also be due to the increasing development rates experienced by the egg and deutovum as temperature increases causing later laid eggs to developmentally catch up to earlier eggs.

In preliminary studies, the ovipositional rate varied enormously between females. It also varied to a lesser extent from day to day for each ovipositing female. Ovipositional variation is not uncommon among insects and other poikilotherms. The fertility X temperature studies of Kevan and Sharma (1963) for Tyrophagus putrescentiae, Ball's (1980) experiments with four species of predacious mites

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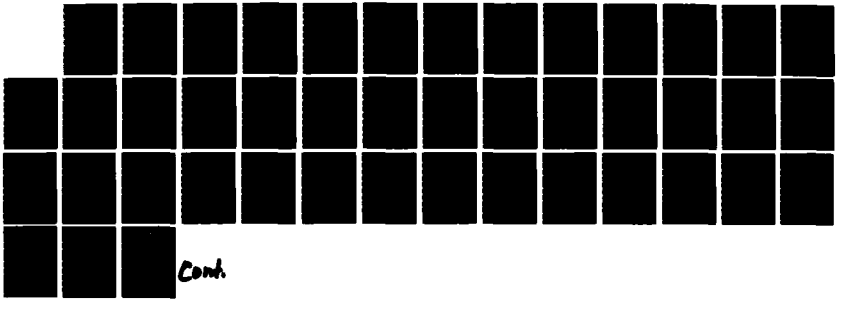

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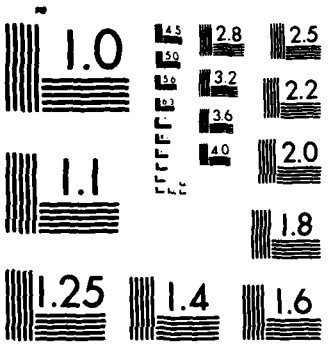

(Phytoseiidae) and Elsey's (1980) research on the pickleworm (Diaphania nitidalis) all demonstrate large variability both among females and from day to day for each female. Ball (1980) hypothesized that the variablity may be due to differences in feeding efficiency, genetic differences in fecundity potential and possibly an endogenous gynotrophic cycle.

Individual variability is partially masked by measuring the reproductive rates of more then one individual as was done in our study. The number of females per experimental unit ranged from 2 to 4 per unit (average=2.94 females/unit). The laboratory population had a sex ratio of 1.12 females/males. The significance of the masking effect should increase as the number of females per unit increases. However the standard deviation of experimental unit data does not systematically decrease as the female proportion in the exprimental sub-samples increased.

The length of the oviposition period depends on the ability of females to replenish their sperm stores ad libitum. The availability of spermatophores may also provide behavioral or physiological requirements which affect the oviposition rate as well as the length of the egg laying period. Kevan and Sharma (1963) fond that repeated matings are essential for continued egg production by T. putrescentiae. Isolated females of this stored product pest mite cease laying eggs after 5 weeks but resume oviposition if allowed to remate (Kevan and Sharma 1963). Ball (1980)

speculates that for phytoseiid mites the requirement of repeated matings for continued oviposition may play an important role in population dynamics. During periods of low food supply, reduced mating would act to preserve the reproductive potential of the females and reduce the energy requirements of females allowing available nutrition to be directed into maintenance activities. The impact of nutrition quantity and quality on spermatophore production by males could act as a population regulator.

Changes in the rate of spermatophore production during the chigger season may also explain why larval production ends with the first frost even though the soil may rewarm in the fall sufficiently to support oviposition. Exposure to a short period of cold has been shown to induce permanent sterility in males of the hymenopteran, Aphytis lingnanensis and to kill both the spermatozoids in the male and what is stored in the mated female (Laudien 1973). If sterility is permanent, this would require the production of new males in the spring prior to the reinitiation of oviposition by overwintering females. The function of temperature extremes as a terminator of reproductive activity among chiggers is demonstrated by Cunningham et al.'s (1977) study of the turkey chigger Neoschoengastia americana. Single cohort colonies maintained indoors continued to produce larvae for 18 to 31 months while comparable colonies kept outside exhibited the expected cyclic activity of that species. In this experiment, only adults from the founding population of

fed larvae were present in the colonies and it is unknown what the rate of mortality for the two sexes were. Jenkins (1947) describes the males of E. alfreddugesi as being relatively short lived compared to the females of this species, which could explain why larval production in colonies of E. alfreddugesi usually last for only about 3 months.

This study demonstrates the value of modeling in uncovering potential areas for further investigations. The extent to which temperature is the major regulator of the rate of oviposition is indicated by the fit of the model to the data (R^2=0.88). The study of the impact made by other factors, such as, changes in soil moisture, seasonal changes in the soil chemistry and, changes in the populations of prey species will provide the knowledge needed for increasing the accuracy of the model to predict changes in oviposition rate and to explain the nderlying mechanisms responsible for those changes.

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Table 6-1. The original and log transformed distributions of ovipositional data weighted for number of females of Eutrombicula alfreddugesi

Temperature °C	Original Data[1] Mean (eggs/day)	Variance	Log transformed Mean	Variance	N*	Normal Dist.
12.5	0.00	---	---	---	24	---
15.0	0.01	0.001	0.002	0.0002	36	-
20.0	2.73	6.33	0.463	0.107	36	-
22.5	5.30	22.43	0.641	0.168	54	+
25.0	3.76	12.17	0.559	0.117	24	+
27.5	12.87	24.80	1.115	0.025	36	+
30.0	14.07	50.24	1.129	0.046	36	+
32.5	7.56	11.57	0.904	0.025	24	+
35.0	9.79	17.14	1.000	0.030	90	+
37.5	9.69	14.21	0.900	0.034	36	+
40.0	N/S	---	---	---	12	---

1: Means adjusted for number of females in observation group
N*: Number of observations
N/S: Adults could not survive more then a few hours

Table 6-2. Model parameters for log transformed oviposition rates for *Eutrombicula alfreddugesi*

Parameters	Estimates
Rho25 (day^{-1})	0.7741563
HA (cal/mol)	17603.28
TH ($^{o}K.$)	307.8054
HH (cal/mol)	48860.47
TL ($^{o}K.$)	289.4303
HL (cal/mol)	-619955

Table 6-3. Derived ovipositional rates for *Eutrombicula alfreddugesi*

Temperature °C	Derived Means eggs/day	Derived Model Estimates eggs/day	%Rate Error
12.5	0.00	0.00	0.00
15.0	0.01	0.01	0.00
20.0	2.85	2.74	-4.01
22.5	5.82	4.87	-19.50
25.0	3.93	5.53	28.93
27.5	12.93	6.91	-87.12
30.0	15.20	10.13	-50.05
32.5	7.57	10.95	30.87
35.0	9.87	9.89	0.02
37.5	7.71	7.04	-9.52
40.0	N/S	---	---

N/S: Adults could not survive more then a few hours

Table 6-4. Fecundity model statistics for *Eutrombicula alfreddugesi*

Variation among the normalized fecundity distributions

Coefficient of Variation% at Four Probabilities			
0.01	0.30	0.70	1.00
58.82	14.81	16.99	36.51

Summary of Weibull distribution parameters for the fecundity model

Eta	Beta	Gamma
1.13994	2.23099	0.04249

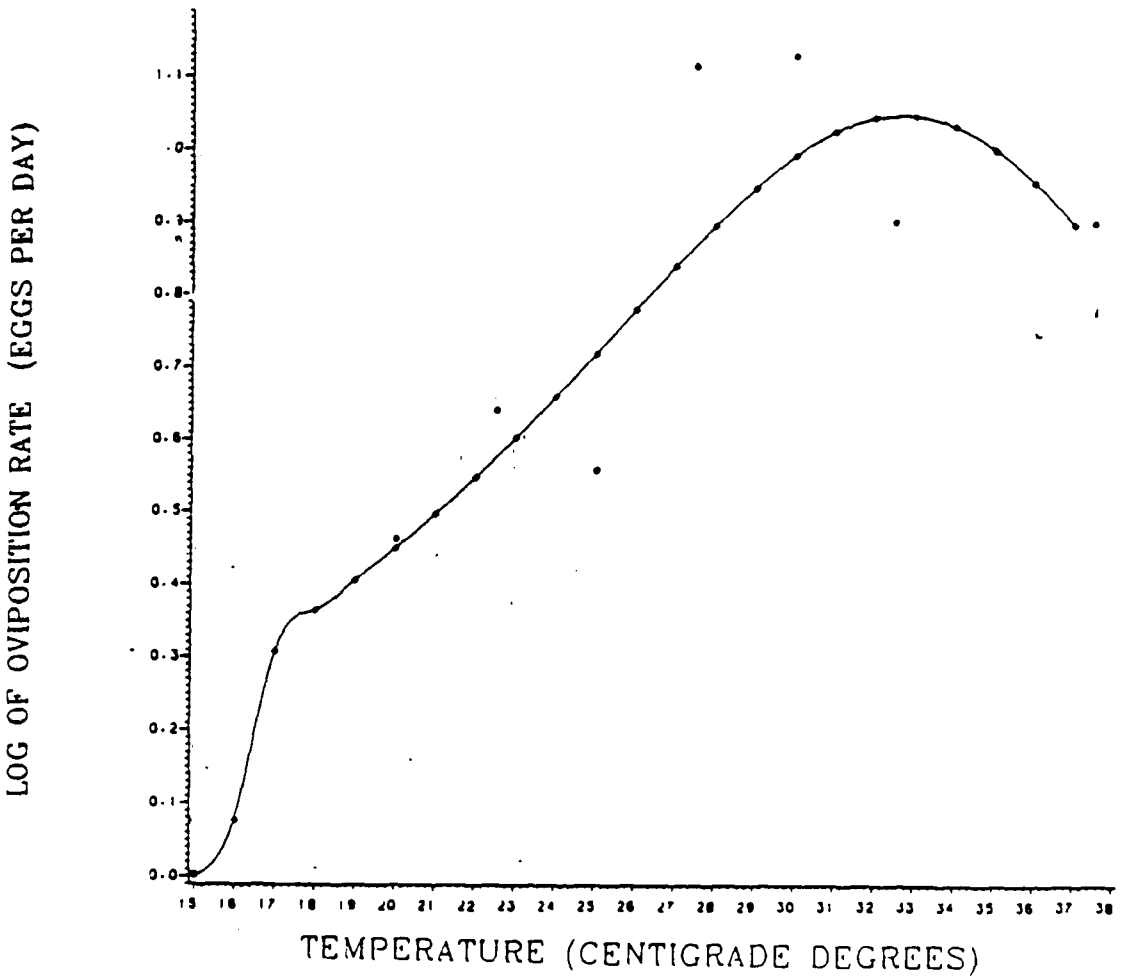

Figure 6-1. Model of the ovipositional rate as a function of temperature for Eutrombicula alfreddugesi compared with plot of observed data.

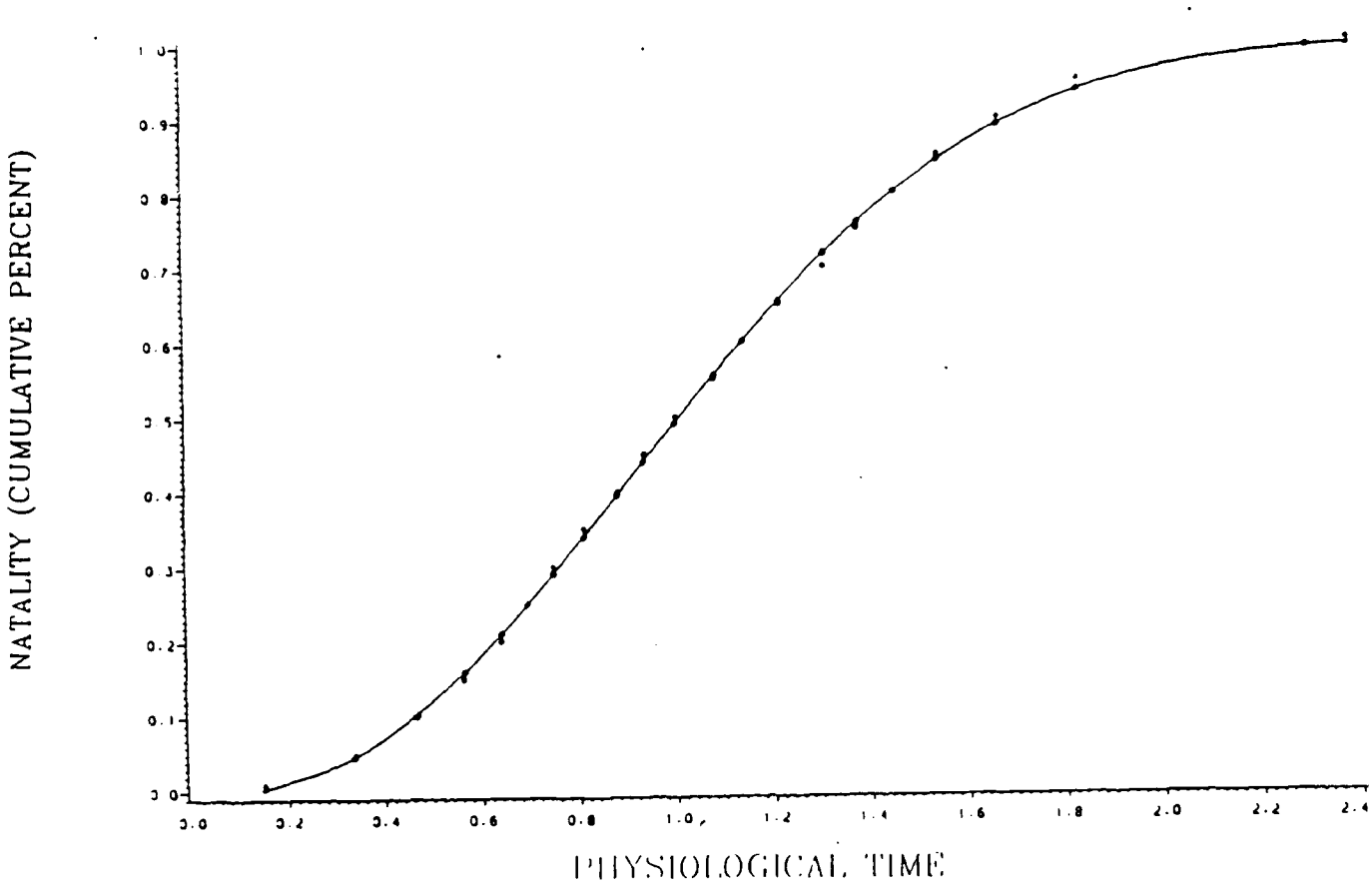

Figure 6-2. Model of the cumulative distribution of temperature-independent normalized fecundity of Eutrombicula alfreddugesi compared with plot of observed data.

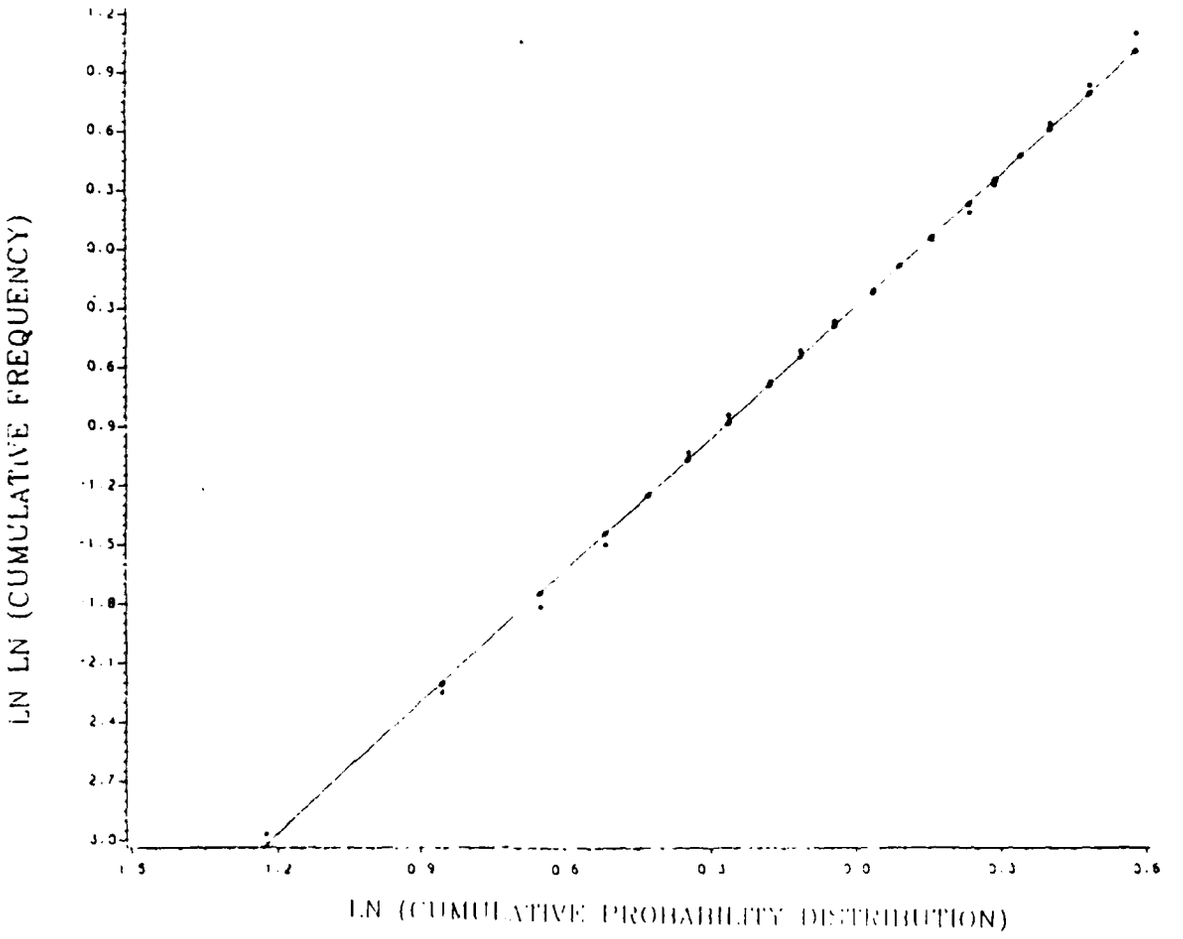

Figure 6-3 Linear regresssion analysis of the goodness of fit of the Weibull distribution to the model of fecundity as a function of physiological age for Eutrombicula alfreddugesi (parameter estimates: Beta = the slope, Gamma = threshold value and Eta = exp(-b/Beta), where b is the Y-intercept).

CHAPTER VII

AN EVALUATION OF FIVE TECHNIQUES FOR RECOVERING POSTLARVAL STAGES OF CHIGGERS FROM SOIL HABITATS

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INTRODUCTION

Postlarval stages of chiggers are rarely collected in the field (Farner 1946, Brown 1952, Crossley 1960). The difficulty in finding postlarvae for ecological studies has necessitated taking large numbers of soil and litter samples. For this reason, developing a productive time- and cost-effective technique for extracting postlarvae from large numbers of samples is important. The few reported attempts at extracting postlarval chiggers (Cockings 1948, Wolfenbarger 1952, Steffey 1976), specifically the deutonymph and adult stages, utilized floatation techniques. When placed into water, the hypertrichous body of the deutonymph and adult stages traps a layer of air between the setae and the body wall causing them to float on the water surface. Richards (1950) successfully floated postlarvae using a magnesium

sulfate (epsom salts) solution at a specific gravity of 1.18. Kawamura and Ikeda (1936, cited in Sasa 1961), Cockings (1948), Steffey (1976) and Wolfenbarger (1952) all floated post-larvae in tap water. Cockings (1948) recommended using tap water at 30°C. The warm water supposedly facilitates active movement of the postlarvae, enabling them to free themselves more easily from the soil and debris.

While floatation methods are effective, they are labor intensive. A possible alternative to floatation methods for extracting postlarvae is Tullgren funnel extraction. However, Richards (1950) and Loomis (1956) both reported that extraction of postlarval chiggers in funnels was not effective. They reported that heat and desiccation caused the deutonymph and adult to lose water too quickly, causing them to die and remain in the funnels.

This investigation compared the effectiveness of three floatation and two funnel extraction techniques in extracting the active postlarval stages of chiggers. Floatation extraction utilized a magnesium sulfate solution, tap water, and a modified Ladell apparatus (Lawson and Merrit 1979). Tullgren funnel extraction was done with and without a light source.

MATERIALS AND METHODS

All extraction techniques evaluated in this investigation involved placing a predetermined number of postlarval chiggers, Eutrombicula splendens Ewing, into plastic bags containing 550 grams of autoclaved soil and surface litter. Five postlarval chiggers were carefully placed into each bag. Five replicate bags of soil, litter, and postlarvae were used for each floatation method (25 postlarvae for each method), and eight replicates were used in each funnel extraction method (40 post-larvae for each method). Five hundred and fifty grams of soil per bag was used because this was the mean sample weight taken over a one-year period. Five postlarval chiggers per bag were used because this was the maximum number of postlarvae collected from any of the past year's samples. Postlarvae were left in the bags to disperse through the soil and litter for one hour prior to extraction.

Floatation with magnesium sulfate solution was performed as follows: two liters of magnesium sulfate solution (300 gms/liter, sp. gr. 1.16) was poured into a 13.4 liter basin. After an initial scan of the surface for floating postlarvae, the contents of the basin were stirred vigorously. Again the surface was scanned, and any postlarvae floating were removed using a camel hair

brush. This process was followed for 20 minutes. Floatation with tap water followed the same procedure, except that no magnesium sulfate was used.

The Ladell apparatus we used was constructed following the description of Lawson and Merrit (1979). The apparatus allows for reuse of the magnesium sulfate, and provides a sieving procedure for recovering macrofauna from soils. Our device consisted of a floatation chamber (25.4 cm dia by 35.4 cm high) with an agitator and bubbling mechanism, a collection basin with a 125 um sieve, a filtering apparatus and a 5-gal Nalgene^{R} aspirator bottle. Details of construction and operation were given by Lawson and Merrit (1979). Five replicate bags of soil, each containing 5 postlarvae, were extracted.

Tullgren extractions were done using a group of 16 funnels, each 28 cm dia by 30 cm high, constructed of stainless steel, without tubes on the ends. Each funnel was equipped with a 40-watt light source. On eight of the funnels, a rheostat was used to adjust the bulbs to a low heat level (5 ft-candles of light). On the other eight, lights were turned completely off. Collections were made into vials of tap water. Temperature probes were placed in the center of one soil sample in both the light and dark funnels. Ambient temperature was also monitored

inside the funnel extraction room. The vials and temperatures were checked every eight hours. Extraction continued for 208 hours.

Statistical comparisons between the five extraction techniques used the Kruskal-Wallis nonparametric test for intergroup differences (Zar 1974).

RESULTS AND DISCUSSION

Results of the five extraction methods are summarized in Table 7-1. Recovery of postlarval chiggers was greater than 90% in the epsom salt solution and tap water floatation methods. Tullgren funnels utilizing a light source were more than 90% effective in recovery of postlarvae. The Ladell apparatus and Tullgren funnels without lights were the least effective methods (56% and 63% respectively). Analysis of the five methods, using the Kruskal-Wallis test, showed that all techniques were not equally effective at extracting postlarval chiggers ($p<.05$).

Although postlarval recovery from the magnesium sulfate and tap water methods were as effective as Tullgren funnels with lights, floatation methods are labor intensive, requiring constant labor input by the investigator. Tullgren funnels, once set up, require very little labor input.

Another important consideration for selecting an extraction method is the success at which postlarvae are recovered alive. This is important since live postlarval chiggers are required for many ecological and behavioral investigations. Postlarvae extracted in the salt solution suffered greater mortality than those floated in tap water (Table 7-1). This high mortality may be due to crystallization of magnesium sulfate on the postlarvae, possibly clogging respiratory openings, or acute toxicity from ingestion. Although the Ladell apparatus had very low post-larval recovery success, 92% of those extracted were alive. No mortality was observed in postlarval chiggers extracted from Tullgren funnels. This method depends upon the animals' own activity.

Tullgren funnels without lights were evaluated because it was thought lights might be attractive to postlarvae as it is to larvae. However, no evidence of attraction to light was found. The temperature means and ranges for funnels with and without lights, and ambient temperature of the funnel extraction room, are shown in Table 7-1. Mean temperature for funnels with lights were only slightly higher than funnels without lights, and only slightly higher than the mean ambient temperature. Funnels with lights fluctuated 5.4°C in temperature, peaking at 112 hours. Funnels without lights fluctuated

2.8°C in temperature, peaking at 184 hours, and ambient temperature only fluctuated 1.9°C, also peaking at 184 hours. It is assumed, as others have (Edwards and Fletcher 1970), that desiccation is more important than temperature in extraction efficiency.

Figure 7-1 illustrates the temporal pattern of postlarval recovery from the funnels. In funnels with and without lights, postlarvae exhibited three main peaks of emergence. In both methods, postlarvae exhibited the first emergence peak at the 8-16 hour interval. This may be attributed to an advantageous positioning of postlarvae when the soil and litter samples are initially placed into the funnels. The Tullgren funnels with lights exhibited other emergence peaks at the 88-96 hour interval and at 200 hours. Tullgren funnels without lights exhibited other emergence peaks at 40 hours and 160 hours. Reasons for these latter peaks are not obvious for either funnel method, and may simply be the result of several individuals randomly moving out of the soil and litter at the same time.

When the individual emergence pattern shown in Figure 7-1 is summed and logarithmically transformed, a linear relationship is observed between the number remaining in the funnels and time (Figure 7-2). As a result of this linear relationship, it is possible to calculate an

"extraction half-time" for postlarval chiggers in Tullgren funnels. This is the time required for extraction of 50% of the individuals. When calculated for funnels with and without lights, the predicted extraction half-time is 73.9 and 141.6 hours respectively. The observed time taken for half the postlarvae to be extracted from both funnel methods was 72 and 136 hours respectively. For both the predicted and observed extraction half-times, funnels without lights took approximately twice as long to extract half the postlarvae as did funnels with lights.

The extraction effectiveness of funnels without lights was low (63%), possibly because the procedure was terminated too soon. If the extraction half times calculated above are accurate, then doubling this value for funnels without lights would indicate that at least 283 hours are required for adequate recovery from soil samples. The difference between funnels with and without lights would become a matter of differences in efficiency (number extracted through time) and not effectiveness (number extracted). Differences in initial moisture levels in the soil and litter may result in differential rates of desiccation taking place inside the Tullgren funnels. This may add to variability in extraction efficiency for different soil types under different conditions. It might prove desirable to moisten samples

before Tullgren extraction, to assure a predictable pattern of recovery for postlarval chiggers.

The results of this investigation have shown that floatation methods in both tap water and epsom salts are adequate methods for recovering postlarval chiggers from soil and litter. However, due to the high labor input required in these methods they are not time and cost effective. Contrary to reports by Richards (1950) and Loomis (1956) that extraction of postlarval chiggers in Tullgren funnels is not effective, this technique proved to be equal in effectiveness to floatation methods. Tullgren funnel extraction also combines the added advantages of zero mortality in recovered postlarvae, plus minimal labor.

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Table 7-1. Comparison of 5 methods for recovery of postlarval Eutrombicula splendens from soil samples

Methods	Number of replicates	Postlarvae per replicate	Mean[1] postlarvae recovered per replicate(±se)	Percent recovered	Mean number of postlarvae recovered alive	Percent recovered alive
			FLOTATION			
Magnesium Sulfate	5	5	4.6± 0.134^{A,B}	92	3.6	78
Tap Water	5	5	4.8± 0.089^{A}	96	4.6	96
Ladell Apparatus	5	5	2.8± 0.313^{B}	56	2.6	92
			FUNNEL EXTRACTION			
With Light	8	5	4.6± 0.18^{A,B}	93	4.6	100
Without Light	8	5	3.1± 0.69^{A,B}	63	3.1	100

[1]Means with same letter are not significantly different (Kruskall Wallis test, $P < .05$).

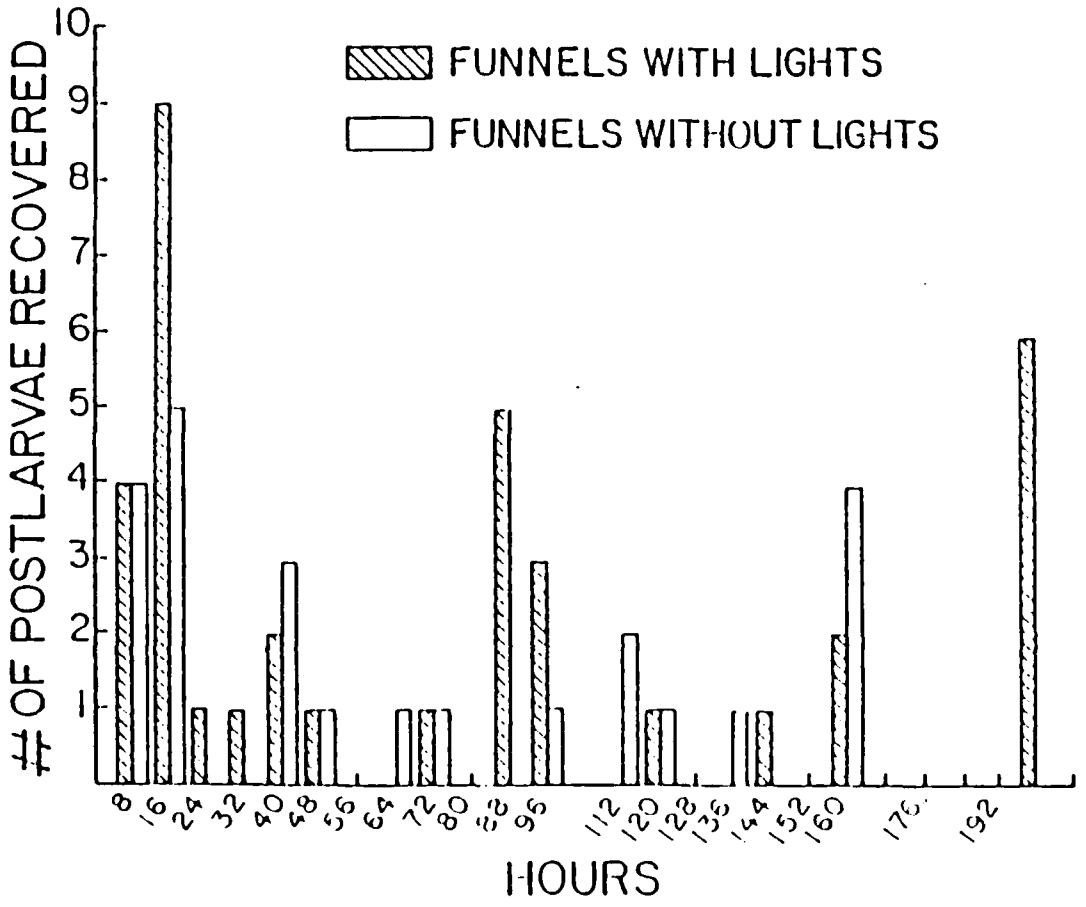

Figure 7-1. Patterns of recovery of postlarval E. splendens in Tullgren funnels.

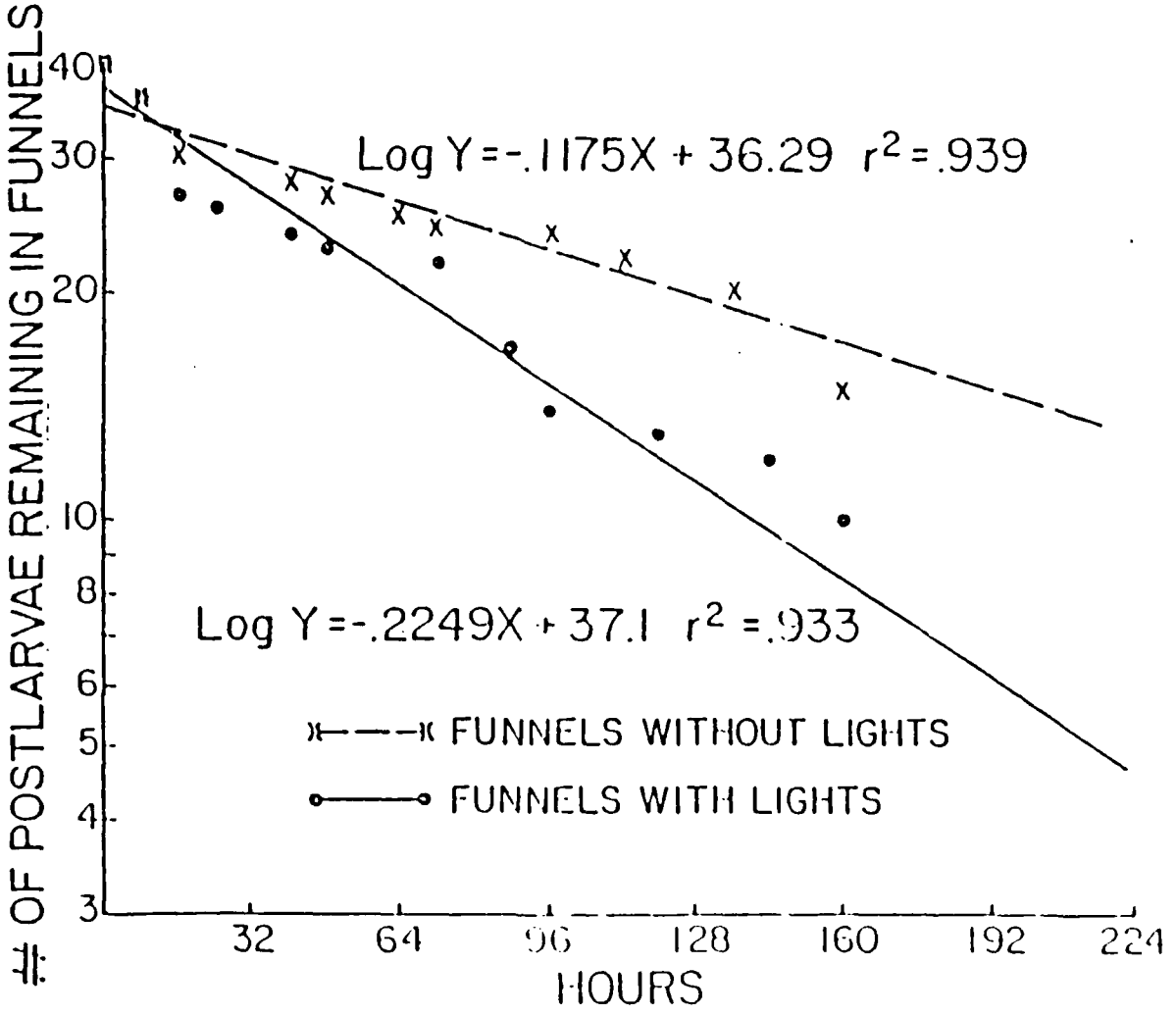

Figure 7-2. Numbers of postlarval E. splendens remining in Tullgren funnels during the extraction period.

CHAPTER VIII

SUMMARY AND CONCLUSIONS

This project was the first to address questions of the ecology of nymphal and adult stages of chigger mites directly. Knowledge of their abiotic requirements, their food and other biotic associations was limited to inferences made from host associations of the parasitic larval stage. Our approach was two-fold: 1. field studies employing modern ecological theory and techniques and 2. definitive quantitative analysis of species bionomics in the laboratory.

Eight microhabitats were sampled for postlarval Eutrombicula alfreddugesi (Oudemans) and E. splendens Ewing. Five microhabitats (soil, surface litter, tree holes, tree stumps and logs) yielded postlarvae. In the samples taken no postlarvae were found in Spanish moss, vertebrate nests or tree bark. Tree stumps yielded the most postlarvae, the greatest percent of samples with postlarvae, and the most postlarvae per 100 grams of habitat. Soil yielded the second highest number of postlarvae but contained the lowest percentage of samples with postlarvae, and contained the fewest postlarvae per 100 grams of habitat.

Five methods for recovering deutonymph and adult stages of E. splendens were compared. Three involved soil and litter

floatation in magnesium sulfate solution or tap water; one used a modified Ladell apparatus. Two extraction methods utilized Tullgren funnel extractors, with or without lights. Magnesium sulfate and tap water floatation, and Tullgren funnel extraction with lights resulted in greater than 90% recovery of the mites. Tullgren funnel extraction with lights, having lowest mortality rates and requiring the least labor, was the most efficient method. A calculated "extraction half-time" is proposed for estimating recovery times for postlarval chiggers from Tullgren funnels.

Soil arthropod communities were analyzed and compared between sites with and without chigger larvae in three habitats: old fields, woods, fields-woods combined. Sites significantly higher in Mesostigmata, a primarily predaceous suborder, were devoid of chiggers. Analysis of soil communities at the generic level showed positive chigger sites significantly higher in species diversity. Competitive exclusion is hypothesized to be acting on chiggers at less diverse sites. An undetermined genus of acarid mite, known predators on quiscent postlarval stages, was significantly higher at negative chigger sites. The collembolan, Folsomia, a known food source of postlarvae, and the mite Nanorchestes, a potential food source, were significantly higher at positive chigger sites.

Population and physiological models provide a definitve technique for the probing of the ecology of a species. It has special value for organisms such as trombiculid mites, which are difficult to study because of their cryptic nature. The use of Sharpe and DeMichele's (1977) biophysicial model to analyze the effect of temperature on the dynamics of Eutrombicula alfreddugesi populations has established a framework to which models of other regulating factors may be added. The theoretical basis created a foundation on which to construct hypotheses about the adaptations which have evolved in the life cycle of this poorly understood species.

The life cycle of a parasite, of necessity, contains many adaptations which enable it to utilize a highly specialized niche. The common pest chigger, Eutrombicula alfreddugesi is no exception to this rule. An expansion of its developmental temperature range downward has enabled this species to radiate further northward then any other member of its genus. A shift in its optimum temperature to cooler temperatures was not necessary for the invasion of temperate latitudes but would be an essential pre-adaptation for colonization of boreal regions (Downes 1965). The position of the optimum temperature is the limiting characteristic which prevents E. alfreddugesi from becoming established north of the Canadian border. In the genus Eutrombicula, these two parameters, spread of the developmental temperature range and position of the optimum

temperature for development seem to be more libile to selective pressure then the actual development rate (Jameson 1972). Shifts in these thermal characteristics were suggested by Taylor (1981) to be the simplest way selection could act to customize the development of an organism to its environment. The chemical changes associated with these two parameters do not require modifications at the control enzyme's active sites but rather small changes in conformational stability as simple as the addition of a methyl group or the addition of a single hydrogen bond. Conformational changes are not as likely to be deleterious to the organism as active site changes since they do not require concomitant changes in associated developmental enzymes to maintain the effective functioning of the system.

The unusual development strategy discovered in the deutonymphs contains several unique adaptations. The single strong development peak at 25°C. for rapid developing deutonymphs, provides strong circumstantial evidence for the early evolution of E. alfreddugesi in tropical soils where 25°C is the prevailing soil temperature year round (Chap. 1, Fig. 13) (Swift et al 1979). The similarity of the remaining developmental rates throughout the rest of the active temperature range (20.0° to37.5°C.) may mean that there are two developmental processes. An accelerated process which is only functional within a very narrow temperature range around 25.0°C. and a slower base process. The second process is

characterized by the thermodynamic combination of no high temperature inhibition and low temperature deactivation only below 20.0°C. which maintains a maximum activity rate across a relatively wide temperature range. The width of the active development range, in combination with vertical migrations to optimize thermal conditions, would allow continued development in north Georgia from April to October.

Continued development in the fall months to the adult stage would be deleterious to the population as a whole. The soil remains sufficiently warm enough to support complete tritonymph development in September and October. A portion of the highest fecundity period would be lost as the adults physiologicaly aged during the winter and spring months. Larval production is synchronized with the activities of their preferred and presumably original hosts, Iguanid lizards (Wrenn and Loomis 1984). This coordination is essential for the success of the parasite population's continued survival. Maximization of fecundity during the season, when the probability of finding a host is greatest, has provided the driving pressure behind the orchestration of the timing of the emergence of new adults. This is achieved by the inclusion of a secondary control system in deutonymph development which is responsive to temperature and acts to switch deutonymph development from a rapid summer form to a very slow winter form.

The deutonymph is the ideal holding stage in chigger development. It is able to actively feed during the cold periods, whenever the temperature rises above 15.0°C., and could therefore survive an extended period of non-development. The situation is considerably different for the calyptostatic stages which do not feed and therefore must complete development prior to the exhaustion of their stored energy reserves. The mobility of the deutonymph creates an additional advantage during overwintering. This stage is able to actively avoid predators and can seek favorable moisture and temperature locations. Complete development from the fed larva to the deutonymph can be achieved in less then 2 months at temperatures as low as 15.0°C. This is the result of the extension of the development temperature region downward as discussed above. The actual effect of this expansion on the population is to transform the fed larvae from the end of the summer season into the better equiped deutonymph stage.

Reproductive rate is carefully matched to the probability of the larva finding a host. In Clarke county, Georgia, lizards are completely free of chiggers in early September (D. Ludwig, pers. comm.). This means oviposition would have ceased about 2 to 3 weeks earlier. What causes this suspension of egg production is not clear. The oviposition rate model does not indicate temperature as the limiting factor since the soil temperature is high enough to allow

continued reproduction through October. Potential limiting factors which should be considered for further study include changes in male spermatophore deposition and availablity of sufficient acceptable nutritional resources. The alternative hypothesis must also be considered, that no factor becomes limiting, but rather the females and or males respond to annually recurring cues in the soil, such as, fluctuations in the soil temperature and changes in soil chemistry and moisture, which correlate with a decline in the probability of future offspring successfully completing development. The development of a comprehensive population model will provide both the means and the direction for future studies to answer these, and other questions, concerning the population dynamics of E. alfreddugesi.

The chigger ecology project, while providing answers to our original questions concerning the ecology of chigger mites, has also uncovered many more avenues of interest to be investigated. The integration of both field and laboratory data provides a solid foundation for the development of predictive ecological models that can function to both minimize the probability of human-chigger interactions and maximize the potential for control programs.

The unique life cycle of chiggers provides an ideal model for the development of generalized soil microarthropod populatior models. The obligatory parasitic nature of the

larval stage on vertibrates, is an easily monitored population index which can be maintained throughout the season without distruction of the habitat. At the end of the research period, microsporidian endoparasites were discovered in adult E alfreddugesi. Future research will examine the impact of endoparasitism on the timing of the life cycle stages and on the interaction of post-larval chigger interactions with their biotic associates.

Future research on chigger ecology will emphasize population interaction with the community. Trombiculid habitats are characterized by strong community diversity. The potential interactants have been identified; it now remains to quantitatify the relationships. As the relationships are clarified, additional submodels will be appended to the life cycle models building a single unified model of chigger ecology.

APPENDIX I

Publications, Dissertations and Presentations resulting from the current award.

1. PUBLICATIONS

Published

Wicht, M. C., Jr. and D. A. Crossley, Jr.. 1983. Optimal concentrations of detergent solutions used for recovery of chiggers (Acarina : Trombiculidae). from vertebrate hosts. Jour. Georgia Ent. Soc. 18:514-516.

In Press

Mallow, D. and D. A. Crossley, Jr.. Evaluation of five techniques for extracting the postlarval stages of trombiculid mites (Acarina : Trombiculidae). Jour. Econ. Ent.

Submitted for Publication

Hayes, M. J. and D. A. Crossley, Jr.. Food preferences on Eutrombicula splendens, Eutrombicula alfreddugesi and Fonsecia gurneyi (Acarina : Trombiculidae) among different species of collembolan eggs. Bull. Ent. Soc. Am.

Hayes, M. J., D. A. Crossley, Jr. and D. L. Ludwig. Effect of light intensity on spatial distribution of potential hosts and infective larvae of the common pest chigger, Eutrombicula alfreddugesi (Acarina : Trombiculidae). Jour. Med. Ent.

Ludwig, D. F., D. A. Crossley, Jr., M. J. Hayes and D. Mallow. Infestation of mammals by the common pest chigger, Eutrombicula alfreddugesi. Jour. Georgia Ent. Soc.

Ludwig, D. F., D. A. Crossley, Jr., D. Mallow and M. J. Hayes. Landscape, disturbance and parasitic processes. Bull. Ecol. Soc. Am.

Ludwig, D. F., D. Mallow, and D. A. Crossley, Jr. Ecosystem structure in chipmunk (Tamias striatus) burrows. Jour. Georgia Ent. Soc.

Mallow, D., D. Ludwig and D. A. Crossley, Jr. Microarthropod community structure in a coastal due ecosystem on Jekyll Island, Georgia. Pedobiologia.

Manuscripts in Preparation

Hayes, M. J. and D. A. Crossley, Jr. The phototypic response of post-larval Eutrombicula alfreddugesi (Acarina : Trombiculidae) to three regions of the light spectrum.

Hayes, M. J. The effect of temperature on the development of Eutrombicula alfreddugesi (Acarina : Trombiculidae).

Hayes, M. J. The effect of temperature on the fecundity of Eutrombicula alfreddugesi (Acarina : Trombiculidae).

Ludwig, D. F. Landscape attributes and distribution of parasitic organisms.

Ludwig, D. F. Ecology of parasitic larvae on Trombiculidae (Acarina : Prosigmata).

Ludwig, D. F., D. A. Crossley, Jr., D. Mallow and M. J. Hayes. The chigger mites of Georgia with a key to species.

Ludwig, D. F. and D. A. Crossley, Jr. Host-parasite evolution in the Trombiculidae (Acarina : Prosigmata): a multivariate study.

Ludwig, D. F. and D. A. Crossley, Jr. Ecologicallly divergent life history stages and hypothesis-testing in host-parasite evolutionary processes.

2. DISSERTATIONS

Hayes, M. J. 1984. A temperature driven model of development and fecundity in the common chigger, Eutrombicula alfreddugesi (Oudemans) (Acari : Trombiculidae). University of Georgia. (In preparation).

Ludwig, D. F. 1984. Host-parasite ecology of chigger mites, with parameter estimation for a model of larval abundance. University of Georgia (in preparation).

Mallow. D. 1984. Biotic associations of the common pest chigger Eutrombicula alfreddugesi (Oudemans). University of Georgia. (In preparation).

3. PRESENTATIONS & PUBLISHED ABSTRACTS

Ludwig, D. F., D. A. Crossley, Jr., M. J. Hayes, D. Mallow and M. C. Wicht, Jr.. 1982. Host-parasite relationships of chigger mites (Acarina : Trombiculidae). Presented at annual meeting of Ecological Society of America, University Park, PA.

Hayes, M. J. and D. A. Crossley, Jr.. 1983. Field evaluation of the photointensity response of unengorged chiggers, Eutrombicula alfreddugesi (Acarina : Trombiculidae). Presented at annual meeting of Georgia Entomological Society, Tifton GA.

Hayes, M. J., D. A. Crossley, Jr. and D. F. Ludwig. 1883. The behaviorial response of larval Eutrombicula alfreddugesi (Acarina : Trombiculidae) to photointensity under field conditions. Presented at annual meeting of Ecological Society of America, Grand Forks, ND.

Hayes, M. J. and D. A. Crossley, Jr.. 1983. The photoresponse of the postlarval stadia of Eutrombicula alfreddugesi (Acarina : Trombiculidae), a common pest chigger species. Presented at the annual meeting of the Southeastern Branch of the Entomological Society of America, Little Rock, AK.

Hayes, M. J. and D. A. Crossley, Jr.. 1983. The influence of temperature on the developmental rate and survivorship of the common chigger, Eutrombicula alfreddugesi. Presented at the annual meeting of the Entomological Society of America, Detroit, MI.

Ludwig, D. F., D. A. Crossley, Jr., M. J. Hayes and D. Mallow. 1983. Some simple parameters of chigger mite infestation. Presented at the annual meeting of the Southeastern Branch of the Entomological Society of America, Little Rock, AK.

Ludwig, D. F., D. Mallow and D. A. Crossley. Jr.. 1983. Arthropod community structure of chipmunk (Tamias stratus) burrows. Presented at the annual meeting of the Ecological Society of America, Grand Forks, ND.

Mallow, D., D. Ludwig and D. A. Crossley, Jr.. 1983. Microarthropods from a Jekyll Island sand dune. Presented at the annual meeting of the Southeastern Branch of the Entomological Society of America, Little Rock, AK.

Mallow, D., D. Ludwig and D. A. Crossley, Jr.. 1983. Microarthropods from a Jekyll Island sand dune: Biotic associations of trombiculid mites. Presented at the annual meeting of the Ecological Society of America, Grand Forks, ND.

Mallow, D., D. Ludwig and D. A. Crossley, Jr.. 1983. Microarthropods from a Jekyll Island sand dune: Roles in nutrient cycling and dune stabilization. Presented at the annual meeting of the Estuarine Research Federation, Norfork, VA

Mallow, D. and D. A. Crossley, Jr.. 1984. Biotic associates ofthe chigger mite Eutrombicula alfreddugesi (Oudemans), Acarina : Trombiculidae. Presented at the annual meeting of the Southeastern Branch of the Entomological Society of America, New Orleans, LA.

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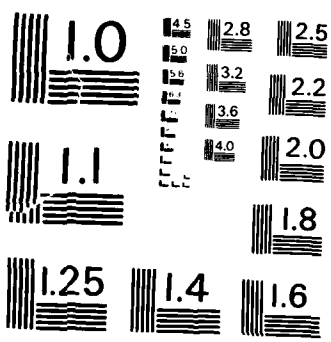

SUPPLEMENTARY

INFORMATION

Errata

AD-A160 [illegible]

Page [illegible] not numbered [illegible]
Should be numbered 43/44, 45/46, 47/48, & 49/50

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