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**STUDIES OF THE PARASITES OF THE JACK PINE BUDWORM:
LIFE HISTORY STUDIES; HYPERPARASITISM; AND THE APPLICATION OF
TIME SERIES ANALYSIS TO THE STUDY OF ADULT ACTIVITY PATTERNS**

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Entomology

1985

ABSTRACT

STUDIES OF THE PARASITES OF THE JACK PINE BUDWORM: LIFE HISTORY STUDIES; HYPERPARASITISM; AND THE APPLICATION OF TIME SERIES ANALYSIS TO THE STUDY OF ADULT ACTIVITY PATTERNS

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Aspects of the life history of the parasites Glypta fumiferanae Viereck, Apanteles fumiferanae (Viereck) and Apanteles morrisoni Mason were studied in populations in Michigan's lower peninsula. Host-parasite synchrony, spatial and temporal activity patterns of adult parasites, impact on jack pine budworm populations, and adult food relationships were studied. The results indicated that the activity of populations of adult parasites varied temporally and spatially in relation to budworm phenology, time of day, temperature, and vertical stratum within tree crowns. The three species exhibited consistent levels of parasitism in the cohorts studied. Honey was found to increase the longevity of G. fumiferanae and A. fumiferanae, but honeydew produced by an undetermined aphid species that was abundant in the study sites did not increase the longevity of adults over those not fed.

Mortality of Apanteles spp. pupae was studied in the field. Hyperparasites, predators, and unknown causes accounted for high levels of mortality in the cohorts studied. Mortality caused by one hyperparasitic species was found to be positively spatially dependent on the density of Apanteles spp. pupae.

A univariate ARIMA model was fitted to three years of daily trap catch records for adult female Glypta fumiferanae. The properties and problems

associated with the use of time series models fitted to population data of the type employed here were discussed. Multivariate (transfer function) models incorporating average daily temperature and total daily rainfall as input processes were fitted. The resulting models showed little improvement in predictability over the univariate model.

To Janice, David, Robbie,
and Christina; and to
Tabbatha too.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Gary Simmons for serving as my major advisor. I am particularly grateful for the intellectual stimulation, encouragement, and confidence he provided me during my program. Thanks also to Lal Tummala for serving as co-major advisor and providing insight on quantitative methodology. To my committee, Dean Haynes, Stuart Gage, and Roland Fischer I extend my appreciation for their guidance during my graduate training.

A number of people assisted in collecting data for this thesis. In particular, I thank Charley Chilcote, Ray Drapek, and Frank Sapio, each of whom took time out from their busy schedules to help me at critical times during my research.

Finally, I thank Susan Battenfield and Kelly Barden for their help in preparing this manuscript.

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GENERAL THESIS INTRODUCTION

A major objective of present day insect pest control is to insure, via environmentally compatible and economically sound methods, that damage stays below an acceptable level. The use of parasitic insects in biological control has proven to be an environmentally compatible and economically sound form of pest control. Attempts at biological control have resulted in a number of successes but have also resulted in numerous failures. Since projects to initiate biological control are initially expensive, failures to achieve effective control are highly undesirable. Thus, basic research on the theory and practice of biological control is necessary in order to increase the probabilities of success in attempts to establish this form of pest control.

Methods of achieving or improving biological control using parasitic insects fall into three general categories: importation of exotic parasites, augmentation of established exotic or endemic parasites, and management of existing parasites (Debach 1973). Management entails any action taken to improve the effectiveness of a parasite in reducing the population levels of its host. When management can be successfully implemented, it will likely be more cost effective than importation or augmentation.

Before we can successfully implement management strategies for parasites a set of "first principles" (or relations) must be developed which relate factors operating on the parasites life system to sets of management options. Once this is accomplished, we have a basis for evaluating specific parasites-host systems in terms of alternative management strategies. While each system will clearly be unique, this set of relations will narrow the scope of potentially important

interactions, thereby reducing the expenditure of time and resources necessary to permit the identification of available management options. Because of their stability and the diversity of ecological interactions, many forest ecosystems provide excellent experimental environments for conducting investigations aimed at determining important factors impacting on host-parasite systems.

The factors which determine the suitability of particular parasite species in biological control have not been well studied. These factors can however be thought of as belonging to one of the following general categories:

1. Intrinsic factors, i.e., factors operating from within the biological system of the parasite. Examples of intrinsic factors are sex ratio, fecundity, host searching capacity, longevity, host range, temporal synchrony with host, etc.
2. Extrinsic factors, or factors extraneous to the biological system of the parasite. Examples of extrinsic factors are environmental variability, mortality factors operating on the parasite population, abundance of food sources for free living stages of the parasite, abundance of alternate hosts of the parasite, etc.

Hyperparasitism, spatial incoincidence, and temporal asynchrony between the host and parasite populations are thought to be important factors influencing the dynamics of host-parasite systems (Huffacker and Messenger 1976, Hassel 1978). However, few investigations have been undertaken to elucidate the importance of these factors in actual ecological systems.

Two factors may account for the rarity of such investigations. First, parasites have highly specialized habits and sampling their populations requires basic knowledge of their biology; as a result, sampling techniques often need to

be developed for each situation (Roach et al. 1979). In many instances, techniques appropriate for such studies are not available. Most studies of host-parasite systems involve the collection of hosts from which parasites are reared. The parasites are then identified and an expression of relative abundance and percentage parasitism is computed to measure their impact on the hosts population (Huffacker 1971). Estimates derived by this method are frequently subject to considerable bias (Simmonds 1948, Van Driesch 1983) and furthermore, they yield no information about the dynamics of the adult stage of the parasite, a life stage for which the potential for increased efficacy via management practices may be high (Van Den Bosch and Telford 1964, Weseloh 1976).

Second, a theoretical basis for interpreting the results of such studies is not well developed. The research reported in this thesis was conducted in the jack pine (Pinus banksiana Lamb.) ecosystem because of the diversity and relative stability of ecological interactions in such a forested system. Specifically, a system consisting of the jack pine budworm (Choristoneura pinus Freeman), and certain parasites and hyperparasites which operate within this system was studied. Relative techniques were used for monitoring the adult population densities of the parasites and hyperparasites and these techniques were used to relate adult density to spatial and temporal patterns of environmental variability and to parasitism rates. Field and laboratory studies of the ecology and behavior of the adults of certain parasitic species were done in order to determine the importance of various factors on the dynamics of their populations. Lastly, the influence of environmental variability on the activity of adult populations of the parasite Glypta fumiferanae Viereck was studied by the construction of a mathematical model. The utility of the model for predicting

variation in activity levels as a function of previous levels of activity and environmental factors that influence activity was discussed.

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LITERATURE REVIEW

In this section the relevant literature on the ecology of the jack pine budworm, its parasites, and hyperparasites is reviewed.

Life history and impact of the jack pine budworm

Depending on the locality and weather conditions, adult jack pine budworm emerge from late June to early August, with mid-July being about average for Michigan (Graham 1935). Males emerge slightly earlier than females and are active fliers. Gravid females are relatively sedentary, but spent females fly actively and can sometimes disperse great distances. Flight activity is greatest at night. The females lay egg masses consisting of approximately 50 eggs on old growth needles throughout the crowns of jack pine trees. Eggs are laid from late June to early August depending on weather and locality; they hatch seven to ten days after they are deposited. The first instar larvae wander and disperse on the wind for a few days and then spin silken hibernaculae in sheltered locations on the trees. First instar larvae do not feed. The small overwintered larvae break diapause in May at about the same time that male staminate flowers are opening. They undergo another period of dispersal before settling in to begin feeding. Development of the new shoots is well advanced before the larvae leave the male flowers and begin to feed on new foliage (Dixon 1961). Feeding on foliage is wasteful and many partially eaten needles are incorporated into the feeding shelters constructed along the axis of the shoots. The larvae are fully developed by mid-June to mid-July and pupate within their feeding shelters. In about a week adults emerge to form the next generation (Kulman and Hodson 1961b).

Jack pine budworm defoliation may cause mortality, top-killing, reduced growth, and reduced pollen production. Up to 33 percent mortality of merchantable trees and 90 percent mortality of intermediate and suppressed trees has been reported as a result of severe outbreaks of the jack pine budworm (Batzer and Millers 1970, Benjamin 1965). Understocked, overmature, or stands growing on poor sites tend to suffer more damage than well stocked stands growing on good sites (Batzer and Miller 1970, Benjamin 1965). Tree mortality is more likely to occur when budworm outbreaks coincide with or are preceded by drought or outbreaks of other jack pine defoliators (MacAloney 1944, Batzer and Millers 1970).

Population dynamics of the jack pine budworm

Numerous studies have been undertaken to investigate the biology of the jack pine budworm, its natural enemies, the influence of pollen abundance and stand characteristics, and the influence of environmental factors on the population dynamics of the jack pine budworm (Allen et al. 1969, Allen et al. 1970, Batzer and Jennings 1980, Benjamin 1965, Benjamin and Drooz 1954, Dixon 1961, Dixon and Benjamin 1963, Drooz and Benjamin 1956, Foltz et al. 1972, Jennings 1971, Kulman and Hodson 1961a, Lejeune 1950, Mattson et al. 1968, Simmons and Sloan 1974, and others). However only Foltz et al. (1972) and Batzer and Jennings (1980) utilized quantitative methods for studying the population dynamics of the budworm. These studies utilized life tables similar to those developed for the spruce budworm (Morris and Miller 1954). They employed age interval models for the description of within generation survival, and a components of variance technique described by Mott (1966) was used to elucidate the influence of survival of various age classes on generation survival.

Foltz et al. (1972) analyzed 29 life tables based on sampling ten areas in Michigan from 1965-1968. Survival over the interval from egg to third instar had the greatest impact on population trends. Survival of late instars (fifth and sixth instars) and realized fecundity were also found to influence population trends. Of factors influencing survival from egg to third instar, fall and spring dispersal were thought to be the most important, with egg parasitism by Trichogramma minutum (Riley) exerting only a minor effect. Predation by birds was thought to be an important component of large larval survival, however a major portion of large larval survival could not be accounted for by any known factor. Parasitism generally accounted for 10 percent or less of total large larval mortality. Five species of Diptera were responsible for most of the parasitism of this stage.

The major mortality factors affecting small larval survival (third and fourth instars) was parasitism by Hymenopterous species; a complex of species of the genus Apanteles and Glypta fumiferanae (Viereck) were the primary parasites involved. In a supplementary study of three cohorts of jack pine budworm it was found that apparent combined parasitism by these parasites was 51.3, 26.5, and 36.2 percent of small larvae. Small larval survival was not considered to be a significant factor in determining population levels in the succeeding generation.

Parasitism was considered to be the most important factor influencing pupal survival. Apparent parasitism ranged from 7 to 25 percent in their study. Itoplectis conquisitor (Say) was the major pupal parasite recovered from reared pupae. I. conquisitor is a highly ubiquitous pupal parasite (Weseloh, 1976); it is highly polyphagous and multivoltine and as such cannot be expected to exhibit a significant numerical response to increases in jack pine budworm density.

A major proportion of pupal mortality was attributed to unknown causes. Pupal survival contributed only a minor amount to population fluctuations.

Realized fecundity accounted for the second largest portion of the variance in influencing population numbers in the next generation. This term was made up of a number of component sources which were not individually measured, such as the proportion of adults that were female, mating success, survival and dispersal of adults, and potential fecundity; as such the major factors influencing realized fecundity were not determined.

Batzer and Jennings (1980) based their study on 48 life tables from sampling 20 plots in Minnesota from 1965-1968. They found that large larval survival was most closely associated with population trends at high budworm densities. However, at low budworm densities, small larval survival was more important. There was no age interval that was consistently correlated with the size of the next generation for all data groups when the data were grouped according to year or jack pine budworm population density.

Mortality during the egg stage was consistently low, though there was a reduction in average egg mass size as the outbreak aged. Mortality of first instar larvae was low and attributed primarily to fall dispersal losses. Spring dispersal losses averaged 32-40 percent of third instars. However, undetermined causes, perhaps overwintering mortality, were as important as dispersal in determining total mortality of this stage. Large larval (third through sixth instars) mortality was decomposed into that due to parasitism by Apanteles spp. and G. fumiferanae, and that due to unknown causes. Combined apparent mortality due to parasites averaged 12-33 percent, with mortality due to unknown causes accounting for most of the variation in large larval mortality.

Pupal mortality was decomposed into that due to parasites and that due to unknown causes. Pupal parasites accounted for an average of 34 percent apparent mortality but this factor was highly variable.

Survival of adults was highly correlated with population size in the next generation, however little was known of the factors affecting adult survival. Numerous factors could have been acting, including mortality due to predators, moth dispersal, mating failure, and factors determining characteristics such as body size and egg mass size.

Natural enemies, weather, food, habitat, and genetic attributes of populations have been implicated as factors influencing population fluctuations of the jack pine budworm. It appears that no single factor can be identified that can account for a high proportion of observed fluctuations in budworm numbers under all conditions. Natural enemies are thought to be important at low budworm densities. Parasitism by Apanteles spp. was found to be more important in dense stands than in poorly stocked stands (Batzer and Jennings 1980). Parasitism by G. fumiferanae was found to be greater in the interior of stands than at the periphery (Kulman and Hodson 1961a). It is thought that parasites and predators exert some control over populations that are at endemic levels, but that once an outbreak is triggered by favorable environmental conditions natural enemies have little or no effect on damping the release phase of the outbreak; they may, however speed the rate of population collapse once the outbreak has begun to decline. It appears that parasites and predators show little numerical response or functional response to budworm population fluctuations. In the case of parasites responses may be limited because most budworm parasites have alternate hosts. However, other than rearing hosts to

obtain estimates of parasitism rates, little biological or ecological work has been done on budworm parasites.

The possible effect of weather on the release and decline of outbreaks has been described. Batzer and Jennings (1980) believed that the collapse of an outbreak in Minnesota may have been associated with increased humidity and rainfall during the late larval stage as the infestation aged. They observed that large larval survival was greater in low density stands, and that the drier warmer conditions in the low density stands might favor survival because disease levels might be lower than in cool moist environments.

Temperature and humidity were thought to be important factors influencing pupal survival, with warm dry conditions favoring pupal survival (Foltz et al. 1972, Graham 1935). Foltz et al. (1972) hypothesized that variation in dispersal losses to early instar larvae and fecund adults were the principal factors responsible for population fluctuations. They theorized that reduced mortality due to sunny, nonwindy weather could cause populations to increase above endemic levels. The subsequent defoliation caused by the high populations caused changes in the quality of the vegetation and perhaps also in the quality of the jack pine budworm population, which increased dispersal losses. This led to the collapse of the outbreak.

It is believed that pollen, the preferred food source of larval budworm may provide a nutritional advantage over foliage, and feeding in the male cones may also provide a microhabitat that is favorable to larval survival (Lejeune and Black 1950, Lejeune 1950). Fluctuations in male cone production from year to year may affect population trends because of fluctuations in the quality of the food source, and because of changes in dispersal behavior associated with male

cone abundance. When male cones are abundant, larvae settle in and feed with little wandering and thus, less dispersal loss (Batzner and Millers 1970, Heron 1956, Kulman et al. 1963, Foltz et al. 1972).

Tree and stand characteristics play an important role in determining the abundance of jack pine budworm (Graham 1935, Hodson and Zehngraff 1946, Benjamin 1954, Heron and Prentice 1957, Rudolf 1958, Dixon 1961, Rose 1973, Batzner and Jennings 1980). Stands which tend to be most susceptible to heavy defoliation by the budworm are typically understocked, overmature, growing on poor sites, and composed mostly of orchard type trees, or trees of poor vigor. Young, well stocked stands in good growing condition are generally resistant to heavy budworm attack. Trees in such stands generally produce few male flowers. In contrast, trees in poorly managed stands, such as those described above, produce large numbers of male flowers. Thus, the differing susceptibility of jack pine stands to jack pine budworm feeding damage may be related to differences in the resistance of trees to attack (Batzner and Jennings 1980).

Parasites of the jack pine budworm

Sixty-three species of primary parasites and hyperparasites have been reared from the jack pine budworm (Walley 1953, Benjamin and Drooz 1954, Drooz and Benjamin 1956, Kulman and Hodson 1961a, Dixon and Benjamin 1963, Allen et al. 1969). The vast majority of species are of sporadic and infrequent occurrence. Only ten or so parasite species appear to be consistently associated with jack pine budworm populations, and of these, parasites which attack the early larval and pupal stages predominate. Apanteles fumiferanae Viereck and Glypta fumiferanae are the only parasite species essentially limited to the

budworm. All other species are polyphagous, and some, such as Itopectis conquisitor have very broad host spectra. A complex of three or more species of Apanteles attack early instars of the budworm; but whether these species attack first and second instars in the summer or attack overwintered larvae the following spring is unknown. Previous reports suggest that first and second instars are attacked in the summer (Dixon and Benjamin 1963, Allen et al. 1969). However, Miller and Renault (1976) noted that Apanteles species, other than A. fumiferanae associated with spruce budworm populations, probably attack the budworm the following spring. The Apanteles parasites emerge primarily from fourth instars. If the parasites must pass through an alternate host, their abundance would be primarily determined by the abundance of their alternate hosts.

All existing studies of jack pine budworm parasites were done in outbreak and declining populations. Thus, the relationships among parasite species observed in those studies may not have been indicative of those in endemic populations. Miller and Renault (1976) observed major differences in the abundance and diversity of species in the parasite complex attacking endemic and outbreak phase budworm populations. No information exists concerning the functional or numerical responses of jack pine budworm parasites to increases in budworm density. In the spruce budworm system A. fumiferanae and G. fumiferanae both show a limited numerical response to increases in host density. However, the magnitude of the numerical response is insufficient to dampen the release phase of spruce budworm population outbreaks (Miller 1959, Miller and Renault 1976). In the spruce budworm system, A. fumiferanae shows a decrease in host searching efficiency with increasing host density (Miller 1959). Miller

felt that changes in fecundity, adult food supply, parasite mortality of parasite larvae, mortality of parasite adults, mortality of parasite cocoons due to hyperparasitism, or sex ratio could have accounted for this phenomenon.

A general conclusion from studies of the population dynamics of the jack pine budworm is that parasites and other natural enemies have limited effectiveness in maintaining budworm populations at endemic levels. Natural enemies are thought to be able to maintain budworm populations at low levels for a period of time, but when environmental conditions favor population increases, natural enemies cannot dampen the population explosion. Once the outbreak has run its course, parasites and other natural enemies may speed the rate of collapse. Studies directed at determining factors other than host density which limit parasite populations have not been undertaken.

Hyperparasites of jack pine budworm parasites

The role of hyperparasites in the dynamics of jack pine budworm populations has not been studied. Studies of other host-parasite-hyperparasite systems are relatively uncommon in the literature, and studies directed at determining the effects of hyperparasitism on host-parasite system dynamics are even less common. Notable exceptions include the work of Gutierrez (1970a, 1970b, 1970c, 1970d), Gutierrez and Van Den Bosch (1970), Vansickle and Weseloh (1974), Weseloh (1978, 1979), Beddington and Hammond (1977), Ehler (1979), Stamp (1981), Morris (1976). The following important results have emerged from these studies:

1. Hyperparasites are important extrinsic factors limiting the effectiveness of parasites in biological control.

2. Parasites are frequently attacked by complexes containing numerous species of polyphagous hyperparasites.
3. Hyperparasite species within this complex exhibit variation in both their temporal and spatial patterns of attack.
4. Host switching may be a common phenomenon for many polyphagous hyperparasite species (Hassel 1978). Host switching implies that the proportion of a host type attacked by a polyphagous hyperparasite changes from less than expected to more than expected as the proportion of the host type available increases relative to other host types. Host switching can be viewed as an aggregative response whereby the hyperparasites allocate a greater fraction of their searching time to whichever microhabitats are most profitable (in terms of hosts attacked per unit time). Regardless of the behavioral mechanism which causes this phenomenon, the essential result is that host switching can be considered as merely an extension of the aggregative response where the hyperparasite spends more time searching in patches of high host density than in low density patches.
5. The importance of hyperparasites varies greatly among different parasite complexes.
6. The importance of hyperparasites varies among species of primary parasites within a given parasite complex.
7. The effect of hyperparasites on the efficiency with which the parasite complex exploits the host population may depend on the precise nature of the interaction. For example, the presence of a facultative hyperparasite which exploits both the host and the primary parasite may increase the effectiveness of the parasite complex (Ehler 1979).

Hyperparasites can potentially be considered objects of control when developing strategies for parasite management. In order to evaluate this management option, principles must be developed which allow us to relate management actions to their probable effects on the dynamics of the host-parasite system under consideration.

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**STUDIES OF THE NATURAL HISTORY OF
GLYPTA FUMIFERANAE AND APANTELES SPP.**

INTRODUCTION

Numerous studies have been done to determine the factors responsible for fluctuations of populations of the jack pine budworm (Choristoneura pinus Freeman) (hereafter referred to as JPB). Foltz (1972) and Batzer and Jennings (1980) constructed life tables and used components of variance analysis (Mott 1966) to elucidate the importance of survival of various age classes to total generation survival. In addition they determined the contribution of some specific mortality factors to stage specific mortality. Their studies could isolate no factor consistently accounting for a high proportion of the observed fluctuations in JPB populations. Predators and parasites were thought to be important at low JPB population densities and in populations declining at the end of an outbreak. However, natural enemies were thought to be of limited importance in damping the release of populations to outbreak. The importance of parasites and predators has been established under certain ecological conditions. Thus, studies of the life systems of these organisms are warranted. Such studies could yield insight into those factors limiting natural enemy populations.

Field studies on parasites and predators which include detailed analyses are rare (Hughes et al. 1984). This reflects the difficulties involved in carrying out such studies rather than their lack of importance. The first step in studying the life system of an organism is determining its life history characteristics and phenology. Then, the trophic relationships between it and other organisms in the community need to be determined as do the relationships to environmental factors (Hughes et al. 1984).

This represents the initiation of life system studies of parasites of JPB. Parasites that attack early instar larvae of JPB were chosen because theoretical work in biological control suggests that certain of these parasites possess biological characteristics often found in species that make successful biological control organisms (Beddington et al. 1978, Hassell 1977) and because of their apparent importance in the life system of JPB. The parasite species of primary interest in this study were Apanteles fumiferanae Viereck and Glypta fumiferanae (Viereck). Both species are univoltine, monophagous, and are apparently well adapted to their host. The parasites emerge from 4-6th instars and pupate on jack pine foliage. Adults emerge and attack 1st and 2nd instars (Brown 1946a, 1946b, Miller 1959,1960). In this chapter the results of studies of host-parasite synchrony, adult food relationships, spatial and temporal activity patterns, impact on the hosts populations, and relationships with other parasite species are presented.

MATERIALS AND METHODS

Description of Study Areas

The field studies were done at a number of locations in Michigan's Lower Peninsula during the summers of 1982, 1983, and 1984. In 1982 all studies were done at a single site (sec. 25, T26N, R10W, Grand Traverse Co. (GR)). In 1983 studies were done at the GR site and an additional site (sec. 15, T24N, R9W, Wexford Co. (WE)). In 1984 the following four sites were used: sec. 32, T24N, R4W, Crawford Co. (CR); sec. 21, T32N, R2E, Montmorency Co. (MO); sec. 11, T32N, R1W, Otsego Co. (OT1); sec. 20, T29N, R1W, Otsego Co. (OT2) (Figure 1). Study plots were constructed in the following manner: at each location a random point was selected along a stretch of road passing through a mature jack pine (Pinus banksiana Lamb.) stand; from the random point an azimuth was chosen randomly and followed a random distance (between 60 and 160 m); the point reached by this method was established as the plot center; a plot of radius ca. 25 m was established around the center point.

The composition of the plant communities at each of the sites was similar but varied somewhat in the composition of minor species. All sites were predominantly jack pine with other tree species comprising less than 5 percent of dominant, codominant, and intermediate trees. Jack pine trees averaged between 9-12 m in all of the stands, and the trees were of mixed age classes. The composition of the understory vegetation varied from mostly conifers such as white pine (Pinus strobus L.) and red pine (Pinus resinosa Ait.) to predominantly oaks (Quercus sp.) and cherry (Prunus spp.). Ground vegetation at most sites was predominantly sweetfern (Comptonia peregrina (L.)), blueberry

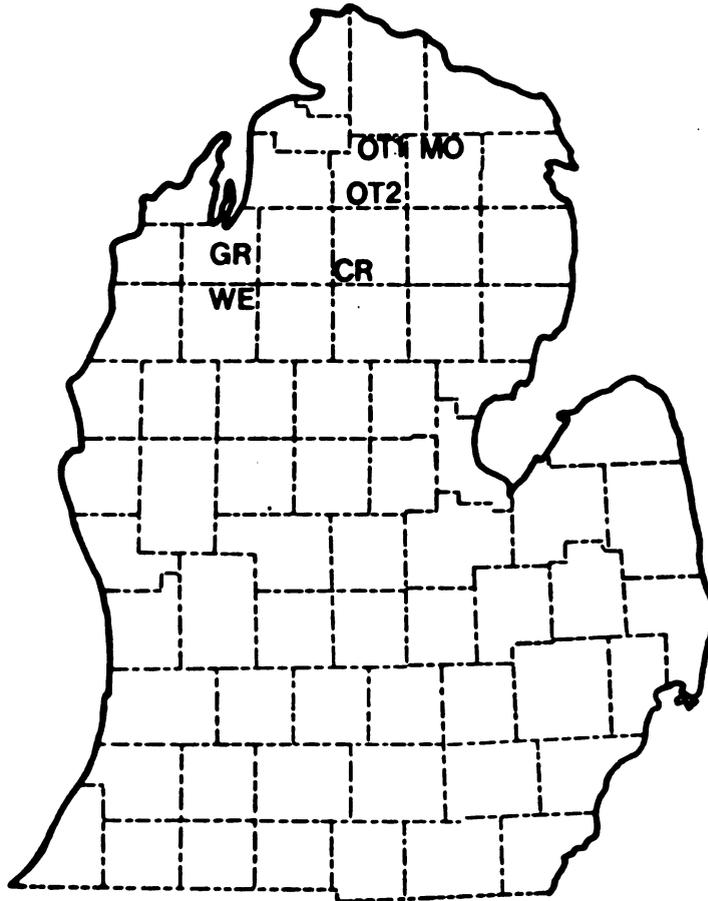


Figure 1. Map of the locations of the study plots in Michigan's Lower Peninsula.

(Vaccinium sp.), and reindeer lichen (Cladonia spp.) and various grasses; wild flowers such as sweet goldenrod (Solidago odora L.), indian blanket (Gaillardia pulchella L.), harebell (Campanula rotundifolia L.), and rattlesnake weed (Hieracium venosum L.) occurred sporadically in open areas within the stands.

Meteorological Information

Meteorological data used in the studies done in 1981 and 1982 were obtained from two sources. Daily rainfall, relative humidity, and average daily temperature was calculated from records compiled at the Cherry Capital Airport, Traverse City, MI. The airport was located ca. 15 km northwest of the GR site. Degree day accumulations were obtained from records maintained by the Cooperative Crop Monitoring System (CCMS) for the Lake City, MI weather station. Degree day accumulations for emergence of reared specimens were determined from minimum and maximum daily temperatures measured at a weather instrument shelter located adjacent to the open air insectary.

Determining the Relative Abundance of Parasites of Early Instar JPB Larvae

Two methods were used to assess the relative abundance of parasites of early instar larvae of JPB: first, foliage sampling was done to obtain host material from which parasites were reared; second, parasite pupae were collected directly from foliage. In both methods samples were obtained by removing the terminal portion of branches at various heights in randomly selected trees within the study plots. Parasites that emerged were identified to species by comparison with known specimens.

During 1982 parasite pupae were sampled at intervals of 2-3 days from the date the first pupae were observed on foliage until all parasites had emerged as adults. Samples consisted of the terminal 46 cm of a single branch cut from the lower crown and mid crown of each of 15 randomly selected trees within the GR site. All parasite pupae were removed and held individually in 1 dram glass vials for emergence of adults.

During 1983 host material was obtained from branches pruned from trees within the study plots. Host collections were made at time intervals which corresponded as nearly as possible with the peak occurrence of the 3rd, 4th, and 6th instars of JPB. At each sampling interval, larvae were obtained by removing the terminal 46 cm of a single branch taken from the lower crown and mid crown of each of 15 trees. All larvae on each branch were removed and placed in plastic cottage cheese containers (10-15 larvae per container) with 0.5 cm holes cut in the top; the holes were covered with fine cloth which permitted enough air flow to prevent excessive moisture from building-up within the containers. Freshly cut foliage was placed in each container daily; parasites that had emerged from hosts were removed, placed in 1 dram glass vials, and reared for emergence of adults. Parasite pupae were sampled as described above for the GR site in 1982.

In 1984 a host collection was made at the peak of the 4th instar in the CR site by the same method used in 1983, and at the peak of the 5th instar at an additional site in Oscoda Co. (Parasite pupal collections were made in the CR, OT1, OT2, and MO sites by the following method: the terminal 60 cm of 3 branches were taken from both mid crown and lower crown from each of 10 dominant or codominant jack pine, from 10 suppressed jack pine, and from 10

suppressed white pine. Thus, each sample consisted of 120 branches with the exception of the OT2 in which jack pine and white pine were not present in the understory and the MO site in which white pine was not present in the understory. Parasites were reared as described above.

Pupation and Emergence rates of parasite species

Pupation and emergence rates of A. fumiferanae, A. morrisoni, and G. fumiferanae were determined for parasites reared from a large sample of predominantly 4th instars during 1983 at the GR site. Accumulated degree days (base 8.9°C) were calculated from minimum and maximum temperatures recorded at a weather instrument station located adjacent to the insectary. Degree day accumulations (Baskerville and Emin 1969) for on-site data were begun on June 24 and added to the accumulated Degree days through June 23 recorded at the Lake City CCMS weather station.

Temporal and Spatial Activity Patterns of Adult Parasites

The seasonal, diurnal, and spatial activity patterns were studied during 1982 using Malaise traps (Nyrop 1982) to measure the relative densities of adult parasites over time and in various strata within jack pine stands. In 1982, 48 Malaise traps were positioned in trees in two plots within the GR stand; 24 traps were stationed in each of the two plots. One of the plots (plot A) was the same plot in which larval sampling was done. The second plot (plot B) was located ca. 300 m from plot A in a portion of the stand with a more diverse composition of tree species. In this area trees such as red oak (Quercus macrocarpa Michx.), white pine, red pine, cherry, and aspen (Populus tremuloides Michx.) made up

more than 10 percent of the total dominant, codominant, and intermediate trees. In each plot, a single trap was positioned in each of 24 randomly selected dominant or codominant jack pine trees; 12 of the traps were placed in the lower half of the crowns and 12 traps were placed in the upper half of the crowns. Traps were monitored daily at 0800 hours from June 23 through August 13. All parasites of early instar JPB larvae were removed and stored in 5 oz plastic vials; they were then returned to the laboratory and identified to species. Because it was not possible to make unambiguous determinations of male Apanteles, only female populations of the two species of this genus were studied.

To determine the diurnal activity patterns of the adult parasites traps were checked bihourly (from 0800 through 2000 hours) for a period of 7 days during the period of peak seasonal activity of the parasites.

In 1983 traps were placed in both the GR (32 traps in plot A) and WE (15 traps) sites. In the GR site, a single trap was placed in the upper half of the crown of each of 25 randomly selected trees. Seven traps were placed on the forest floor at distances of 10 m apart. In the WE site a single trap was placed in the upper half of the crown of each of 10 trees and 5 traps were placed on the forest floor. Traps were checked at 0800 hour from June 11 through August 22.

Food Sources of Adult Parasites

To obtain information on the food sources of G. fumiferanae and A. fumiferanae two tests were performed. In the first, parasites were exposed in a cylindrical 14.5 x 12 cm clear plastic container to 3 potential food sources. The food sources were the following: jack pine sprigs soaked with diluted honey, aphid honeydew on jack pine sprigs collected in the field, and bouquets composed

of three flower species (H. venosum, S. odora, and C. rotundifolia) which were collected in the field. These three flower species were the most common species occurring in the jack pine stand from which they and the parasites were obtained (site CR). The food sources were held at 40-50^oC until the tests were done. All tests were conducted between 1000 and 1400 hours using naive parasites. The food material was used in tests within 48 hours from when it was collected in the field. In each repetition of the test, 6-10 parasites of a single sex and species were introduced into the container and observed at 15 minute intervals. At each interval the number of parasites observed on each food source and the number of parasites apparently feeding on a food source were recorded. Chi-square tests were used to determine whether the number of parasites visiting and feeding on particular food sources differed from what would be expected if there were no preferences for any of the foods.

A second test was performed to determine the quality of honey and aphid honeydew as food sources for G. fumiferanae and A. fumiferanae. From 6-8 parasites of a particular sex and species were maintained in glass canning jars covered with fine mesh saran screen. Water was provided on moist cotton and jack pine needles coated with either aphid honeydew, honey, or distilled water were introduced to the containers daily. The number of parasites that died was recorded each day until all parasites had succumbed. Analysis of variance was used to determine if differences existed in average number of days parasites survived on the different treatments.

RESULTS

Relative Abundance of Parasites of Early Instar Jack Pine Budworm Larvae

In Table 1 percent parasitism of 3-4 instar JPB in 4 cohorts is presented. Van Driesche (1983) cautioned against the use of estimates of parasitism based on a single sample as estimates of parasite impact per host generation. However, results to be presented later indicate that the estimates for the GR, WE, and CR cohorts are probably reasonably good estimates of impact of the respective parasite species since parasite oviposition was complete and neither hosts nor parasites had begun to exit the life stages sampled. For these three cohorts parasitism averaged 14.5, 8.9, and 3.6 percent for A. fumiferanae, A. morrиси, and G. fumiferanae respectively. The estimates of impact for the other cohort was not reliable. Apanteles morrиси was not reared from samples of 2-3 instar JPB collected when the larvae were in the flower mining stage. However, the species was present in later samples from the same cohort (Table 1). This suggests that the species parasitizes predominantly 3-4 instar JPB in the spring of the year unlike A. fumiferanae and G. fumiferanae which parasitize 1-2 instar larvae in the summer of the preceding year. Reexamination of Apanteles reared from C. pinus by Allen et al. (1969) indicated that A. morrиси was absent from samples taken when JBP were in the flower mining stage (2-3 instars), but the species was present in collections of large larvae.

Analysis of variance was used to determine if there were differences in the numbers of cocoons per dm^2 of foliage surface area among the upper crown, lower crown, and suppressed trees for data collected at the CR, OT1, and MO sites in 1984. There was no evidence that differences existed in the numbers of

Table 1. Parasitism of third and fourth instar C. Pinus in samples from four cohorts.

Sample Date (Julian)	3154	3174	3173	4166	4176
Location	GR	GR	WE	CR	Oscoda Co.
Degree Days 8.9°C (From April 1)	194	475	455	525	659
Total Number Hosts	176	244	141	110	55
<u>Apanteles</u> <u>fumiferanae</u>	20.5 : 3.0	13.9 : 2.2	10.6 : 2.6	19.1 : 3.7	30.9 : 6.2
<u>Apanteles</u> <u>morrisi</u>	0	6.1 : 1.5	4.3 : 1.7	16.4 : 3.5	14.5 : 4.7
<u>Glypta</u> <u>fumiferanae</u>	2.8 : 1.2	3.3 : 1.1	2.1 : 1.2	5.5 : 2.2	9.1 : 3.1

parasites per dm² surface area of foliage among the three strata for A. fumiferanae, A. morrissi, or G. fumiferanae (Table 2). This does not mean that there were no differences in percent parasitism among strata since the host density in each stratum was unknown.

The Phenologies of Parasites of Early Instar Jack Pine Budworm

The base temperatures required for development of the parasite species are not known; however since degree day accumulations for similar base temperatures are highly correlated (Hughes et al. 1984), a base temperature of 8.9°C was used in determining developmental rates for the species, since 8.9°C is probably close to the actual base temperatures of the parasite species. The rate of pupation was estimated for A. fumiferanae and A. morrissi from reared specimens collected at the GR study plot (Figure 2). Insufficient numbers of G. fumiferanae were present in the sample to provide a meaningful estimate. The average number of degree days necessary for pupation (and hence emergence from JPB larvae) for A. morrissi was 568 (se=10.0) and 593 (se=12.1) for males and females, respectively; with an average of 582 (se=8.6) for males and females combined. For A. fumiferanae the corresponding values were 575 (se=13.2) for males and 642 (se=14.2) for females, with an average of 614 (se=11.2) for both sexes combined. Adult emergence was estimated from the same sample (Figure 3). The mean adult emergence for A. morrissi was 718 (se=7.4) for males and 715 (se=12.8) for females and averaged 716 (se=7.7) for the combined sexes. For A. fumiferanae adult emergence averaged 725 (se=9.8) for males and 806 (se=15.3) for females; for the combined sexes average adult emergence was 773 (se=12.0). Thus, the peak emergence of adults of A. morrissi occurred before that for A.

Table 2. Results of three stage nested analyses of variance among sites, trees, strata (upper crown, lower crown, and suppressed trees), and branches. The dependent variables for each analysis were the number of parasites per dm². foliage surface area. F-tests were used to determine treatment differences.

<u>Species</u>	<u>Source</u>	<u>Df.</u>	<u>SS</u>	<u>F</u>
<u>A. fumiferancee</u>	Site	2	0.977	0.12
	Tree (Site)	27	0.622	0.78
	Stratum (Site,Tree)	60	2.776	0.34
	Branch (Site,Tree,Stratum)	180	7.967	-
<u>G. fumiferancee</u>	Site	2	0.238	0.06
	Tree (Site)	27	0.900	0.23
	Stratum (Site,Tree)	60	2.331	0.60
	Branch (Site,Tree,Stratum)	180	3.911	-
<u>A. morrisi</u>	Site	2	0.028	0.01
	Tree (Site)	27	0.333	0.11
	Stratum (Site,Tree)	60	1.128	0.38
	Branch (Site,Tree,Stratum)	180	2.960	-

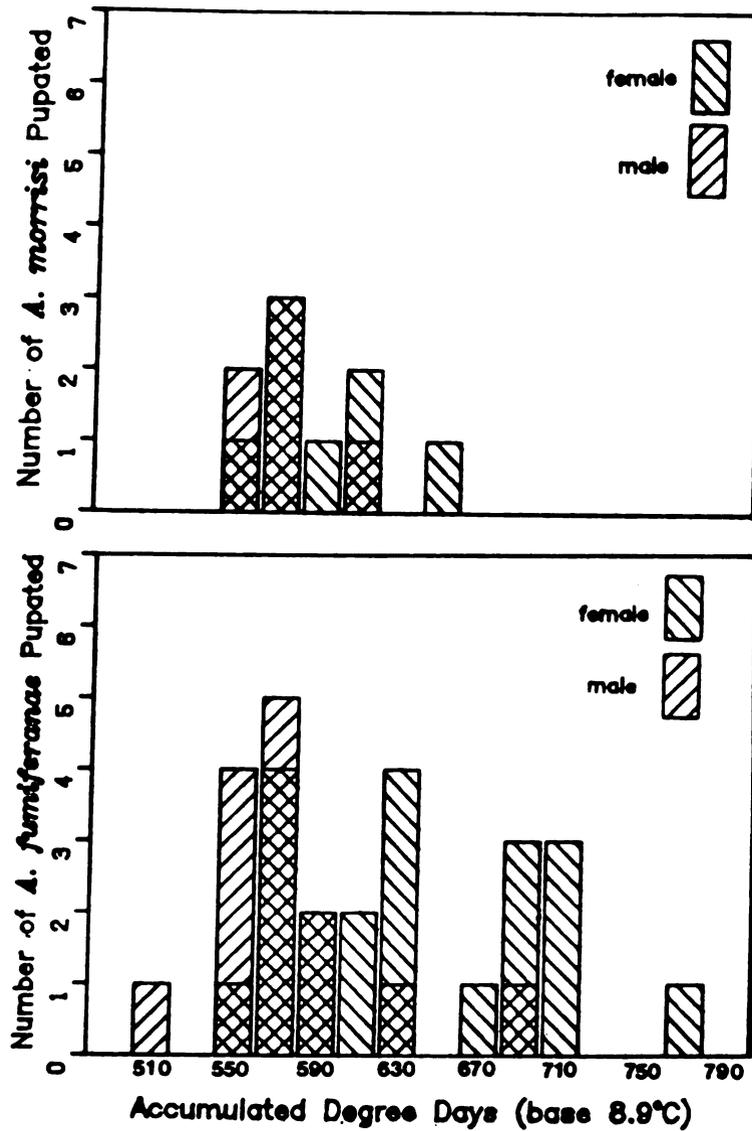


Figure 2. Frequency distribution of pupation of *A. morrissi* and *A. fumiferanae* reared in an outdoor insectary in relation to accumulated degree days base 8.9° C.

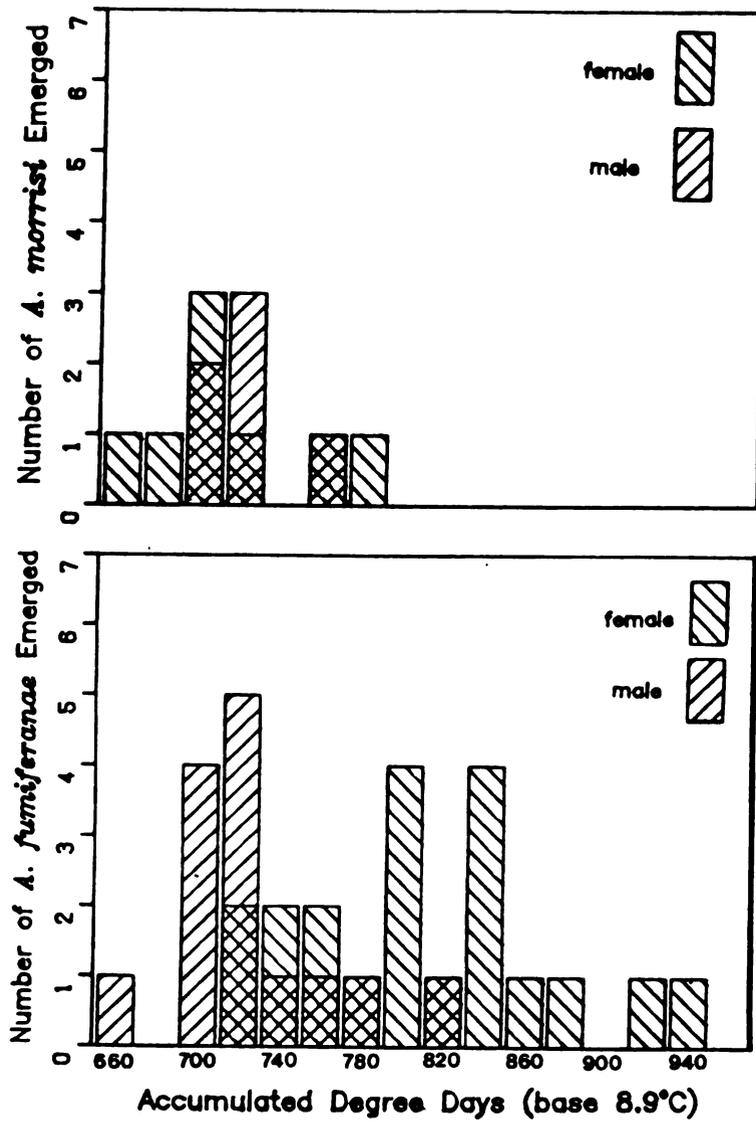


Figure 3. Frequency distribution of emergence of *A. morrissi* and *A. fumiferanae* reared in an outdoor insectary, in relation to accumulated degree days base 8.9° C.

fumiferanae. Estimated emergence dates for Apanteles spp. based on percent of eclosed cocoons agreed well with the data for reared specimens (Figure 4); however, it was not possible to determine emergence for each species individually from the field data because cocoons of the two species could not be differentiated. Emergence of G. fumiferanae was later than for Apanteles spp. in field samples (Figure 4).

Spatial and Temporal Activity Patterns of Adult Parasites

Seasonal Activity Patterns of Adult Parasites of JPB

Both A. fumiferanae and G. fumiferanae exhibited seasonal activity patterns that corresponded well with the eclosion of JPB eggs. During 1982 the females of G. fumiferanae were active in the GR study plot for about 600 DD (950-1550 DD) and exhibited a peak in activity at about 1200 DD (Figure 5); the female parasites were active for a total of 36 calendar days. During 1983 the females of this species were active for about 675 DD (900-1675 DD) and exhibited a peak in activity at about 1220 DD (Figure 5); during this year the parasites were active for 34 calendar days. Peak activity of male G. fumiferanae preceded that of females. The peak in seasonal activity for females corresponded closely to the peak in the rate of eclosion of JPB eggs in both years suggesting that the parasite females are synchronized with the peak activity of 1st instar JPB. It has been suggested that G. fumiferanae is adapted for parasitizing 2nd instars in hibernaculae (Miller 1959, Lewis 1960). Thus, the species may not be well synchronized with the life stage which it is best adapted for parasitizing. It should be mentioned here that the estimates of activity were based on daily Malaise trap catch totals and numerous factors may influence

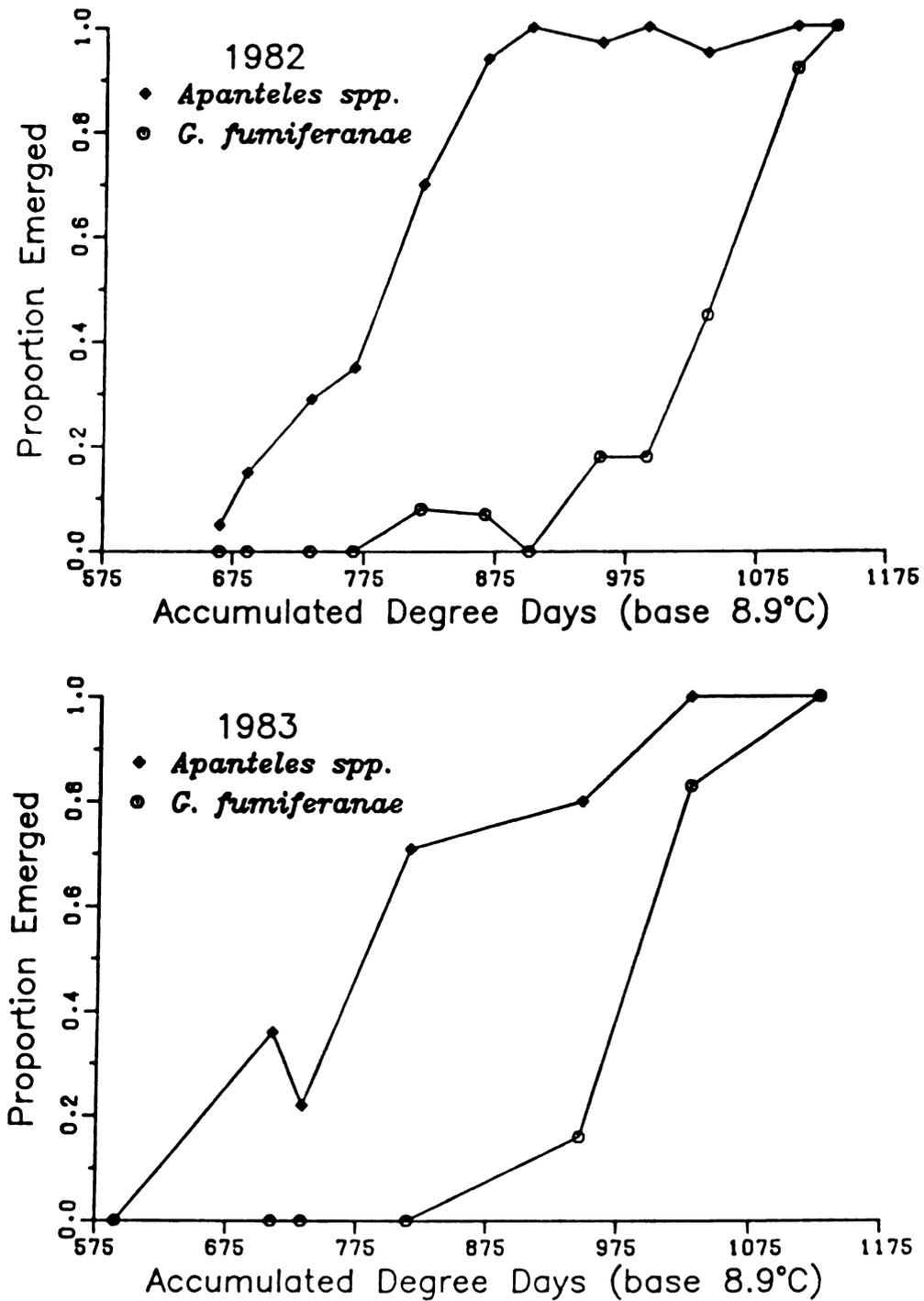


Figure 4. Cumulative emergence of *Apanteles* spp. and *G. fumiferanae* in the GR site in 1982 and 1983.

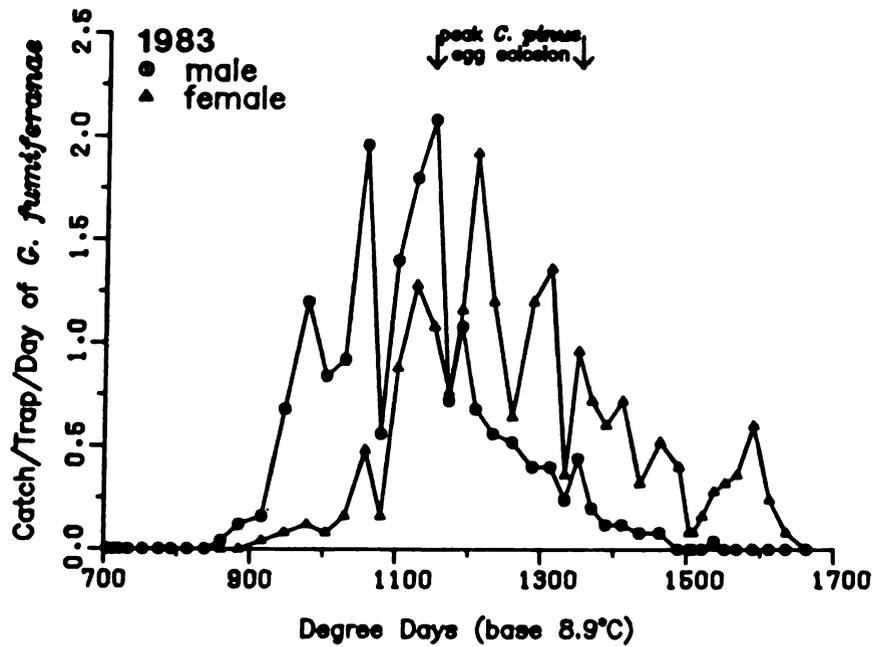
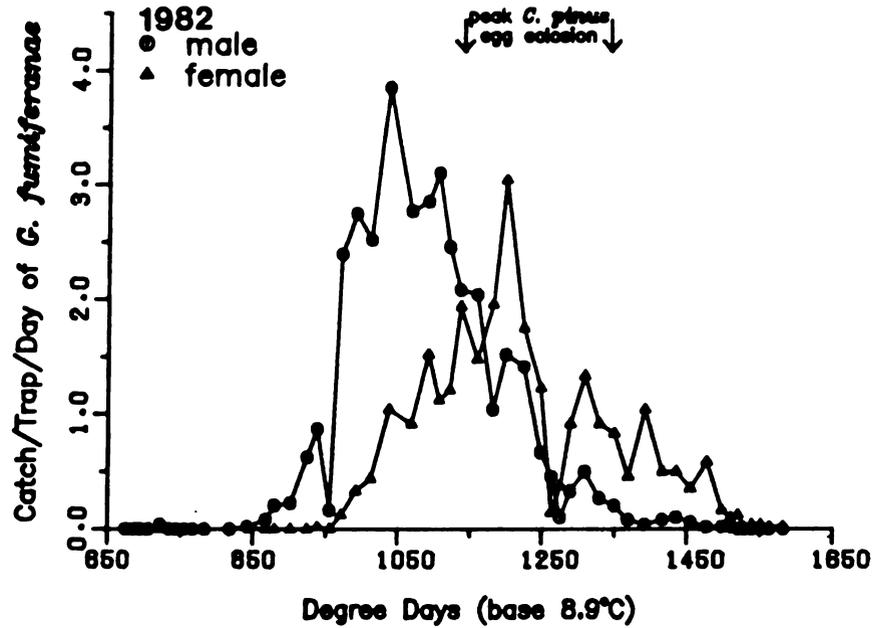


Figure 5. Malaise trap catch of adult *G. fumiferanae* at the GR site in 1982 and 1983 in relation to accumulated degree days base 8.9° C.

catch; thus it cannot be definitely concluded that the patterns observed in the daily trap catch totals were associated primarily with host searching and may in fact have been related to other activities such as mating and feeding. However, it is assumed in what follows that host searching parasites made up a major portion of those captured, but further studies would be needed to support this assumption.

Seasonal activity patterns of A. fumiferanae were similar to those for G. fumiferanae but are slightly longer and begins somewhat earlier. In 1982 A. fumiferanae was active for about 700 DD (850-1550 DD) and exhibited a peak in activity at about 1240 DD (Figure 6). In 1983 the parasite was active for 750 DD (850-1600 DD) and exhibited a peak in activity at about 1175 DD. In both years the peak in activity coincided with the peak in the rate of eclosion of JPB eggs. This species is thought to be most efficient at parasitizing 1st instars (Lewis 1960, Simmons personal communication) and the data reported here suggest that adult activity is well synchronized with the presence of 1st instar JPB.

Apanteles morrisoni was infrequently caught in Malaise traps in 1982 in spite of the fact that more than half of the Apanteles emerging from field collected cocoons that year were A. morrisoni. The few that were caught appeared in the traps between 750-1100 DD (Figure 7). In 1983 traps were monitored from an earlier date than in 1982, and two peaks in activity were exhibited by females of A. morrisoni, one at about 350 DD and another at about 800 DD (Figure 7). Previous workers have suggested that A. morrisoni attacks the spruce budworm (Choristoneura fumiferanae) in the spring and probably overwinters in an alternate host (Mason 1975, Miller and Renault (1976). In conjunction with the estimates of percent parasitism presented above, the observed bimodal seasonal

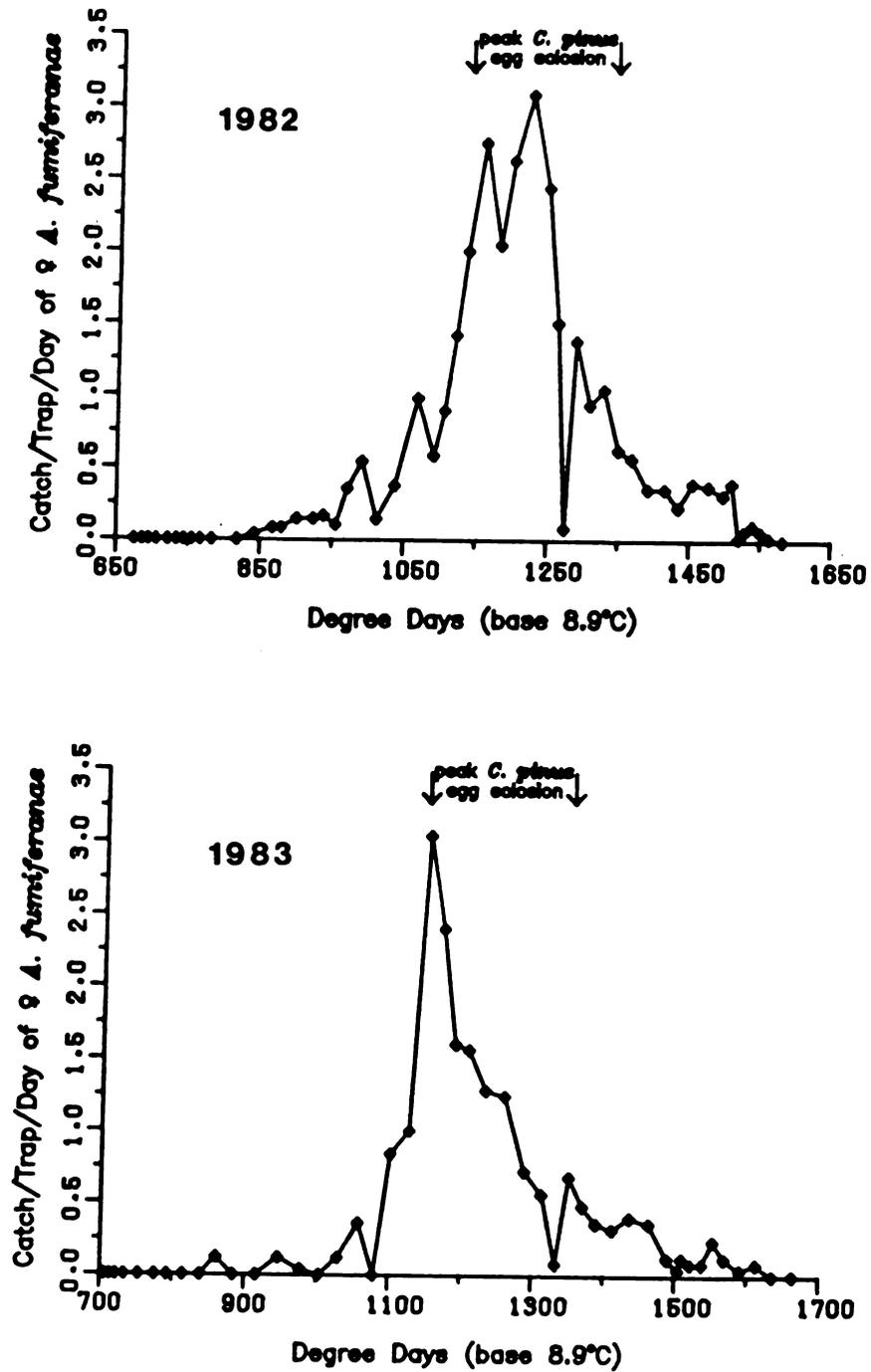


Figure 6. Malaise trap catch of adult female *A. fumiferanae* in relation to accumulated degree days base 8.9°C at the GR site in 1982 and 1983.

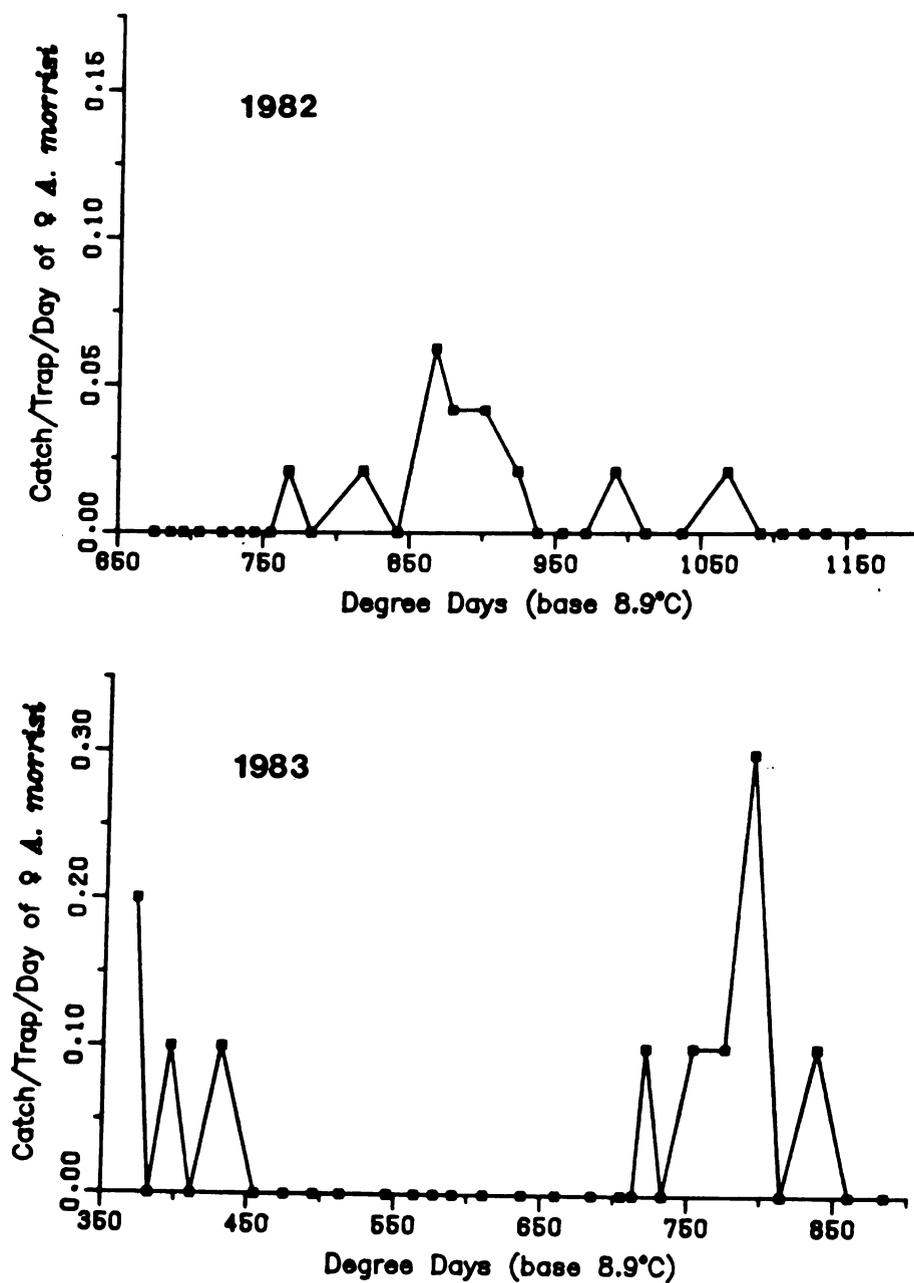


Figure 7. Malaise trap catch of adult female *A. morrisi* in relation to accumulated degree days base 8.9°C at the GR site in 1982 and 1983.

activity pattern exhibited by the species supports their suggestion; thus it appears that A. morrisi has multiple generations and apparently one, or more, alternate hosts in which it overwinters, but JPB is apparently not, or only an infrequent host, for the overwintering stage of the parasite.

The alternate host(s) of A. morrisi are not known though the species has been reared from at least four different Lepidopteran species (Mason 1975). Mason lists Zelleria haimbachi Busck, which feeds primarily on jack and Ponderosa pines (Wilson 1977) as a possible host of A. morrisi; during June and July of 1983 a total 92 larvae of Z. haimbachi were collected from the GR and WE sites and reared for parasites. No A. morrisi were among the parasites reared from the collected specimens.

Daily Activity Patterns of Adult Parasites

Females of A. fumiferanae were active throughout the daylight hours and were most active from 1200-1800 hours (Figure 8); however 11 percent of the total daily activity occurred between 2000 and 0800 hours indicating that the parasites were active after sunset and probably in the early morning, before 0800 h. Traps were emptied at dusk (2130 hours) and again at dawn (0600 hours) on two consecutive days and female A. fumiferanae were captured between 2130 and 0600 hours and a few were caught between 0600 and 0800 hours confirming that the parasites were active at night and at a low level in the early-morning hours. A similar pattern of diurnal activity was observed for G. fumiferanae, however even a greater proportion (28 percent) of the total daily activity occurred between 2000 and 0800 hours (Figure 8). Females of this species were also found to be active after dusk and again between 0600 and 0800 hours on the

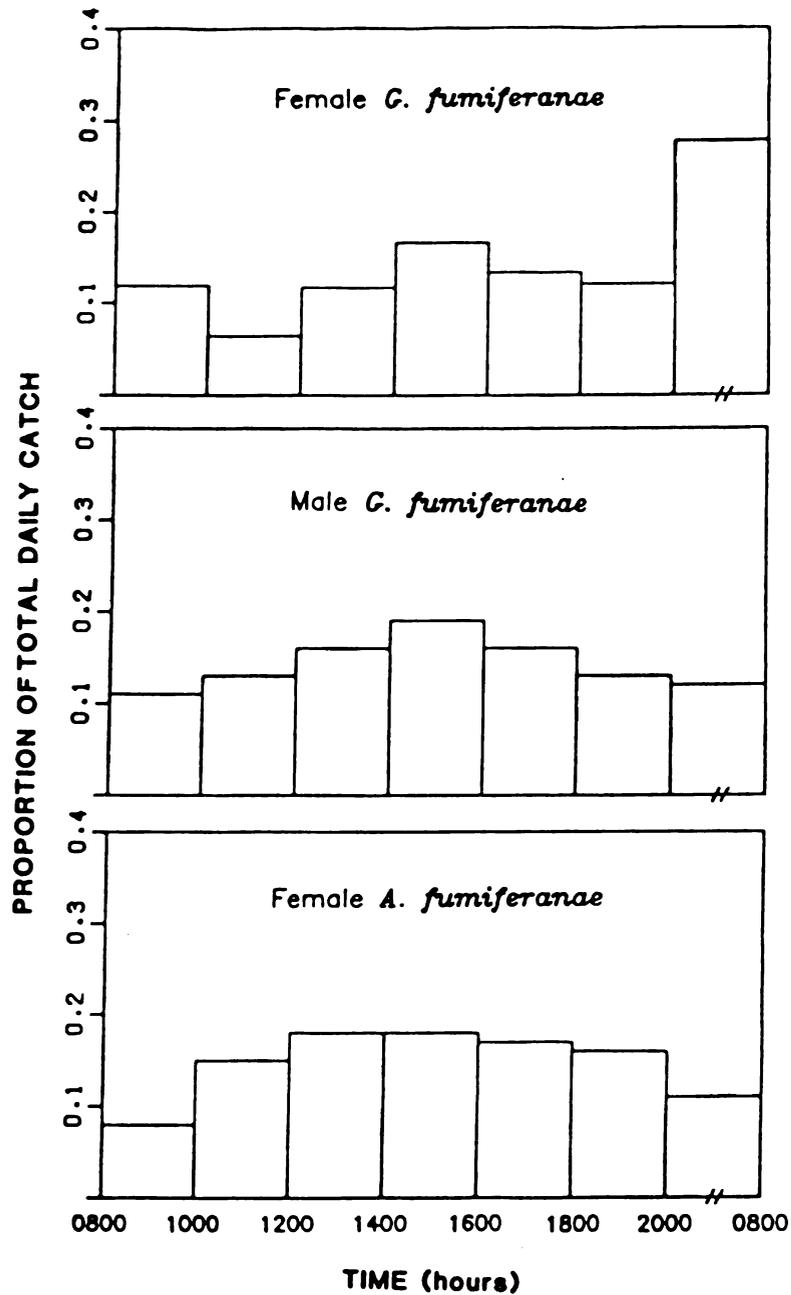


Figure 8. Average proportion of total daily Malaise trap catch of adult *A. fumiferanae* and *G. fumiferanae* for seven time intervals within a day. The sample period was six days. The data was collected at the GR site in 1982.

two days traps were checked at those times. The daily activity pattern of male G. fumiferanae was similar to that for females but did not exhibit a high level of activity between 2000 and 0800 hours (Figure 8).

Relationship of Temperature to Adult Parasite Activity

Two factors likely account for the observed diurnal patterns of adult parasite activity: temperature and climatological variables closely correlated to temperature and behavioral mechanisms that produce cyclical diurnal patterns of activity that are relatively independent of temperature over a fairly broad range. Linear statistical models were fitted to the bihourly trap catch data and corresponding bihourly average temperature data to determine if temperature (and related variables) played a significant role in determining diurnal activity patterns over the limited range of temperatures (19-30°C) encountered in the field study. Models were fitted to the activity data for females of A. fumiferanae and G. fumiferanae assuming linear relationships between trap catch and temperature and assuming different slopes and intercepts for each of the lines relating trap catch to temperature for each two hour period from 0800 to 2000 (6 time periods). The models thus accounted for fixed differences in the overall level of activity (different intercepts), which would result from cyclical variation in behavior and average temperature effects, and for the response of the parasites to variation in temperature within each two hour time interval (different slopes). The regressions for the model described above were significant and accounted for 62 percent and 60 percent of the variation in trap catch for G. fumiferanae and A. fumiferanae, respectively. By comparing the residual sum of squares of reduced models with the residual sum of squares of

the full models, as described by Neter and Wasserman (1974), it was possible to obtain further insight of the influence of temperature on daily activity patterns of the parasites. For G. fumiferanae a model with unique slopes and intercepts for the time intervals 0800-1000 hours and 1000-1200 hours, and a common slope and intercept for observations taken at time intervals between 1200-2000 hours was found to provide as good a fit to the data as the full model (Figure 9). The slopes for the 0800-1000 and 1000-1200 time intervals were greater than for the data from the afternoon for which the line is almost horizontal. This suggests that variation in temperature has a greater affect on the activity levels of the parasites in the early morning hours when the parasites need to increase body temperatures to levels necessary for flight.

Similar results were evident for A. fumiferanae for which a unique slope and intercept was fitted for the 0800-1000 h time interval and data from all other time intervals were adequately described by a common slope and intercept (Figure 10).

Relationship of Trap Height to Parasite Activity

Apanteles fumiferanae and G. fumiferanae were trapped more frequently in traps placed in the upper crowns of trees than in traps placed in the lower crown and no individuals of either species was ever caught in traps stationed on the ground within the study plots. Regression was used to explore the relationship of trap catch of female A. fumiferanae and female G. fumiferanae to temperature and trap height. Both of the variables were related to trap catch, but there was no evidence of interaction among the variables in their effects on trap catch (Table 3). This suggests that the parasites stratified within

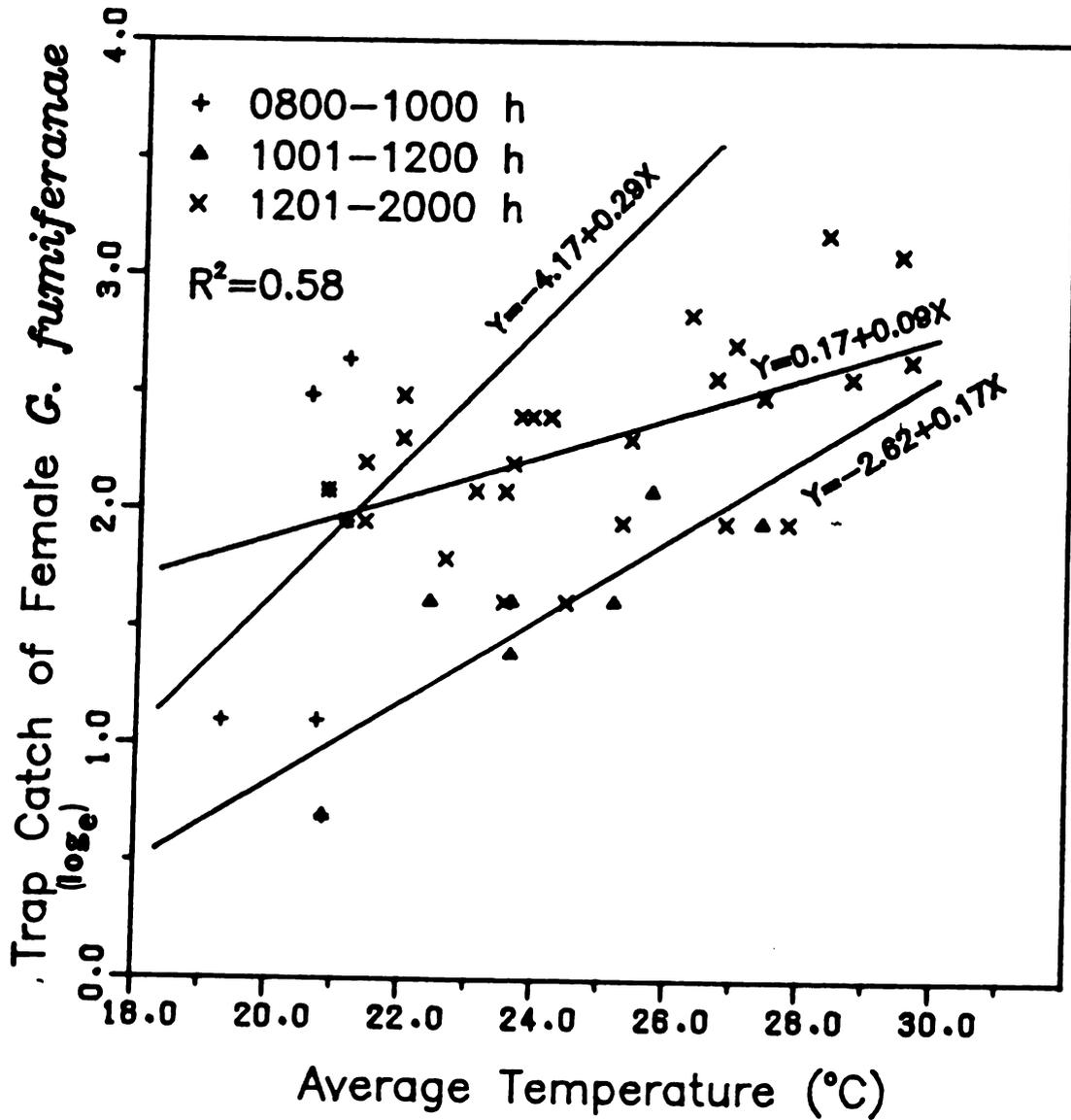


Figure 9. The relationship between Malaise trap catch of adult female *G. fumiferanae* and temperature for various time intervals within the day. Data collected at the GR site in 1982.

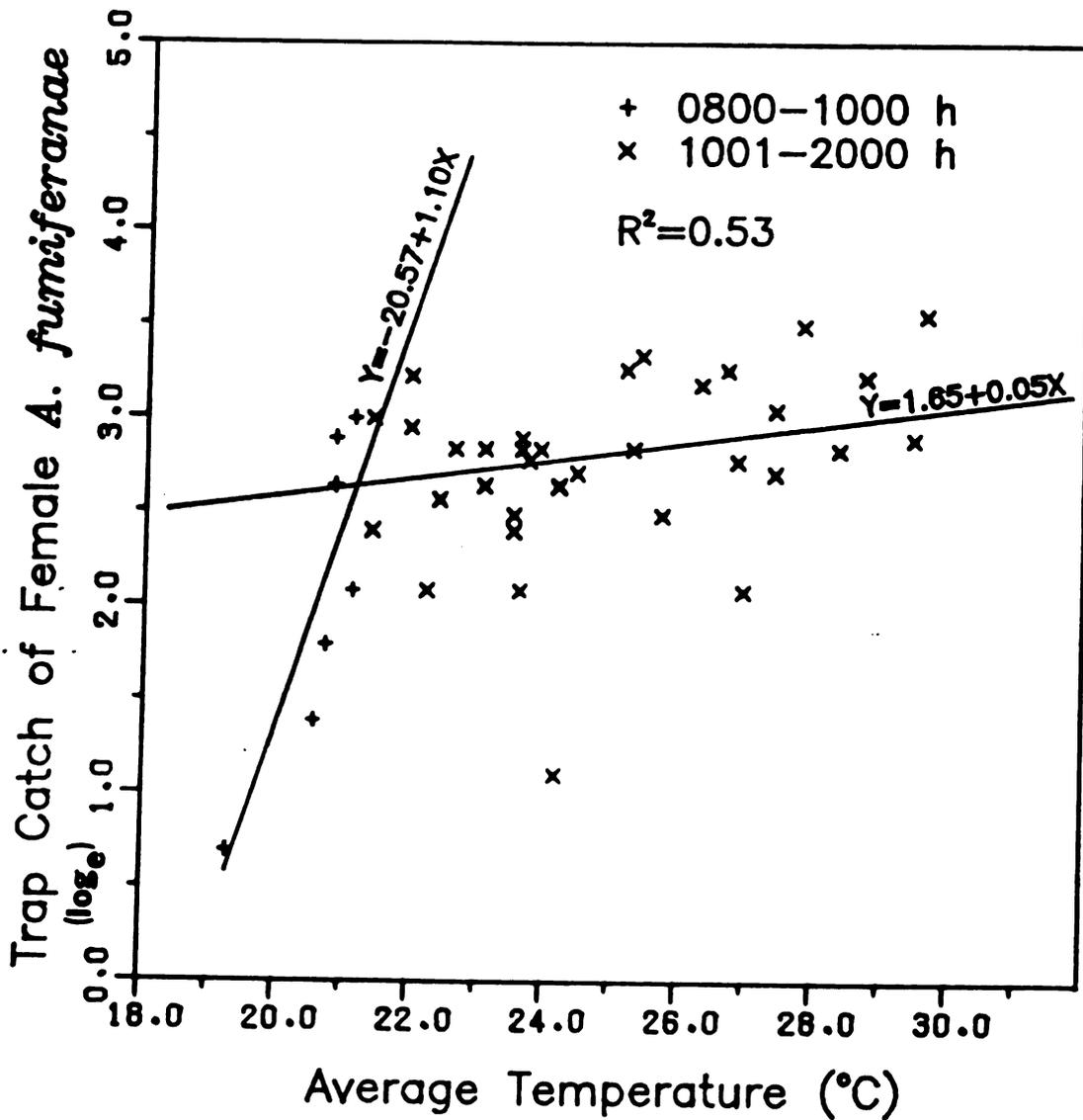


Figure 10. The relationship between Malaise trap catch of adult female *A. fumiferanae* and temperature for various time intervals within the day. Data collected at the GR site in 1982.

Table 3. ADV Tables for regression of Malaise trap catch of female parasites (separate regressions done for A. fumiferonae and G. fumiferonae) using the independent variables trap height (TH) and average temperature (AT) over the two hour interval between observations. F-tests were used to assess the significance of the regressions. F* indicates a test of the full versus reduced model.

<u>Species</u>	<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>F*</u>
<u>G. fumiferonae</u>	Regression	4	5.85	17.42*	
	TH	1			
	TH X TH	1			
	AT	1			
	TH X AT	1			
	Residual	2011	168.83		0.024
	Regression	3	5.83	23.17*	
	TH	1			
	TH X TH	1			
	AT	1			
	Residual	2012	168.85		
Total	2015	174.69			
<u>A. fumiferonae</u>	Regression	4	4.93	15.70*	
	TH	1			
	TH X TH	1			
	AT	1			
	TH X AT	1			
	Residual	2011	157.91		0.76
	Regression	3	4.87	20.67*	
	TH	1			
	TH X TH	1			
	AT	1			
	Residual	2012	157.97		
Total	2015	162.84			

the tree crown and that the parasites did not migrate vertically within the crown in response to variation in temperature, but rather tended to be consistently more active within particular strata.

To explore the relationship between trap catch and trap height in more detail, regression was used to relate the total catch per trap over a 29 day period from 15 July to 13 August, 1982 for the 48 Malaise traps located in the two study plots in the GR site. The overall level of activity did not differ among plots for females of A. fumiferanae or G. fumiferanae but did differ for male G. fumiferanae. Thus, a single regression was used to relate trap catch to temperature for females, but the two sites were considered independently when fitting regression models for male G. fumiferanae activity.

For females of A. fumiferanae and G. fumiferanae total trap catch was found to increase with increasing trap height up to a height of about 8.5 m and then decrease with increasing trap height above this level. The trap catch versus trap height relationships were adequately described by quadratic equations for females of both species (Figures 11,12). For male G. fumiferanae trap catch was approximated well by a linear relationship with trap catch increasing with increasing trap height; there was no decline in trap catch for traps placed high in tree crowns (Figure 13). The average height of jack pine in the two plots was 9.53 m (se=0.26), thus the activity of females of both species was greatest in the upper crowns of trees.

Food Sources of Adult Parasites

In preference tests females of G. fumiferanae preferred to visit and feed on jack pine shoots coated with honey over branches coated with the honeydew

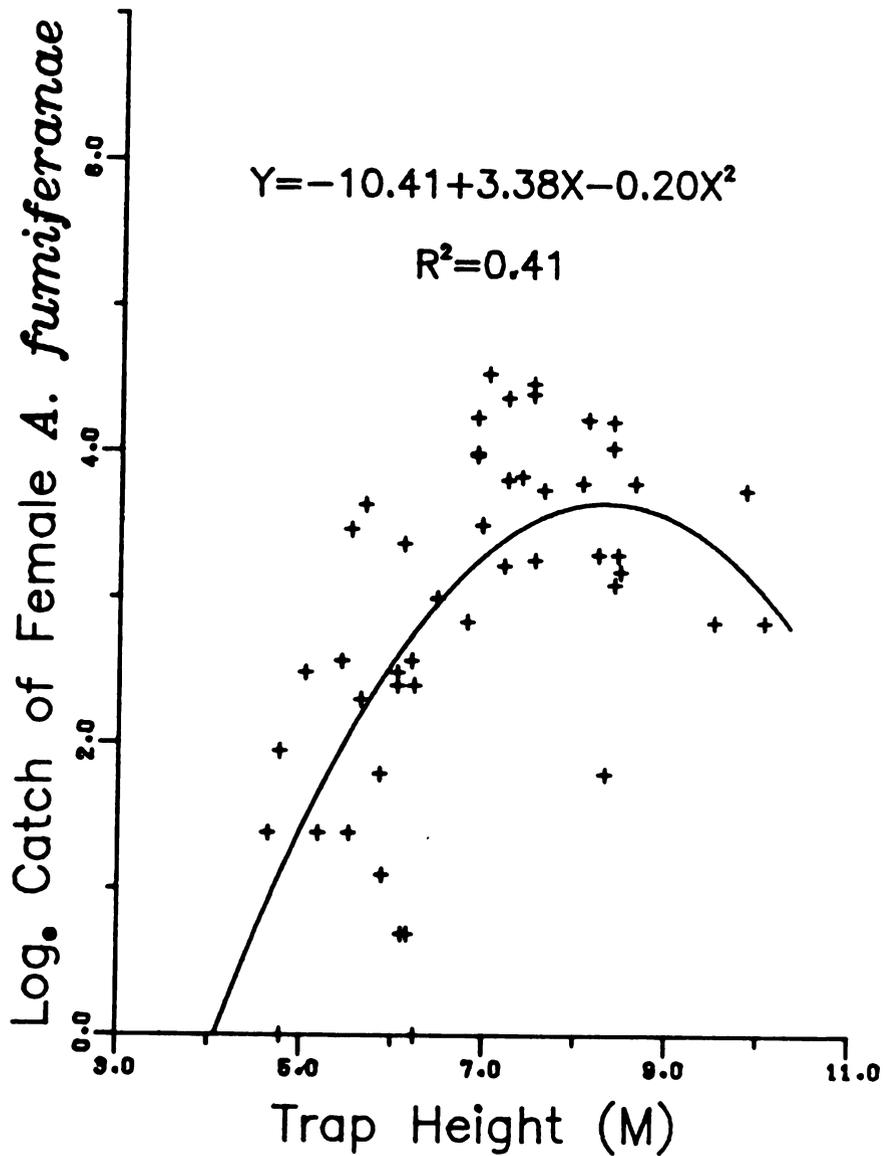


Figure 11. The relationship between Malaise trap catch of female *A. fumiferanae* and trap height in the crowns of jack pine trees. Data transformed to natural logarithms before analysis. Data collected at the GR site in 1982.

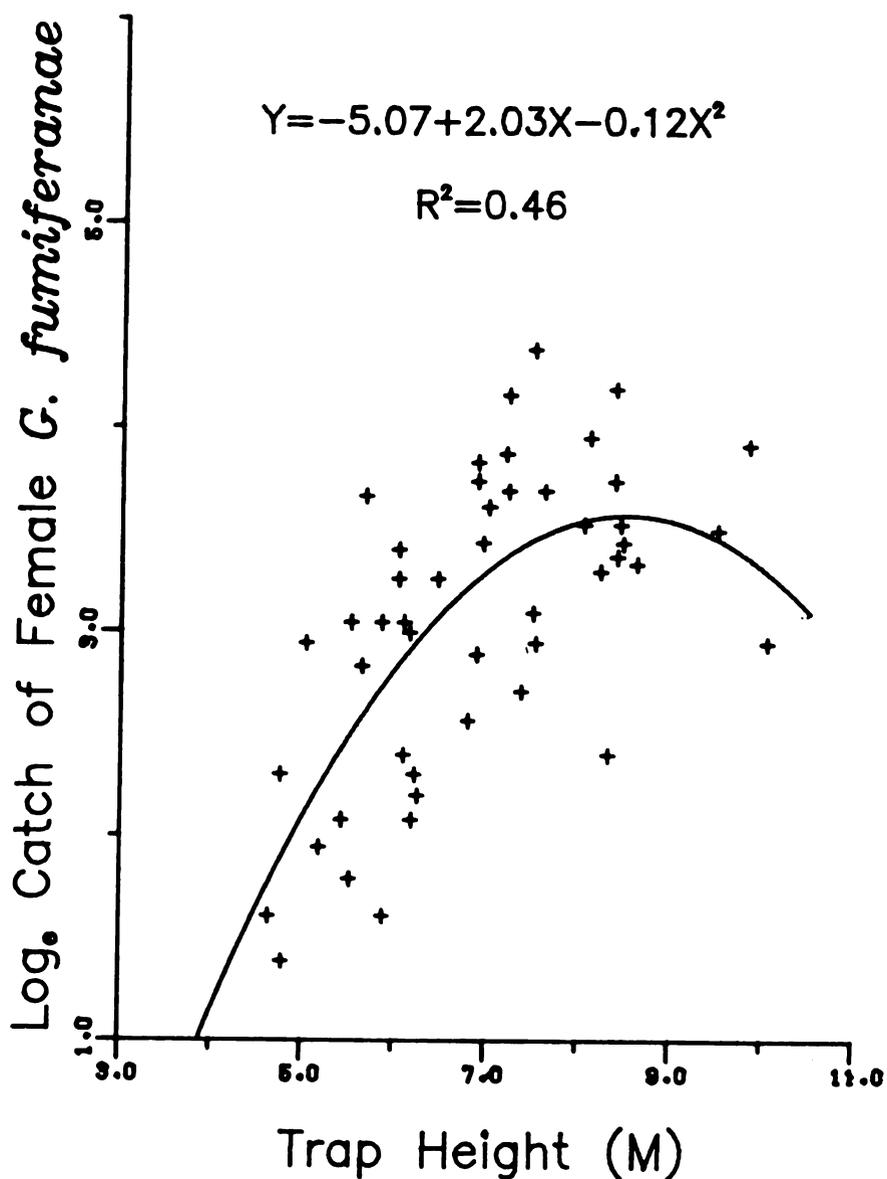


Figure 12. The relationship between Malaise trap catch and the height of traps in the crowns of jack pine trees. Data transformed to natural logarithms before analysis. Data collected at the GR site in 1982.

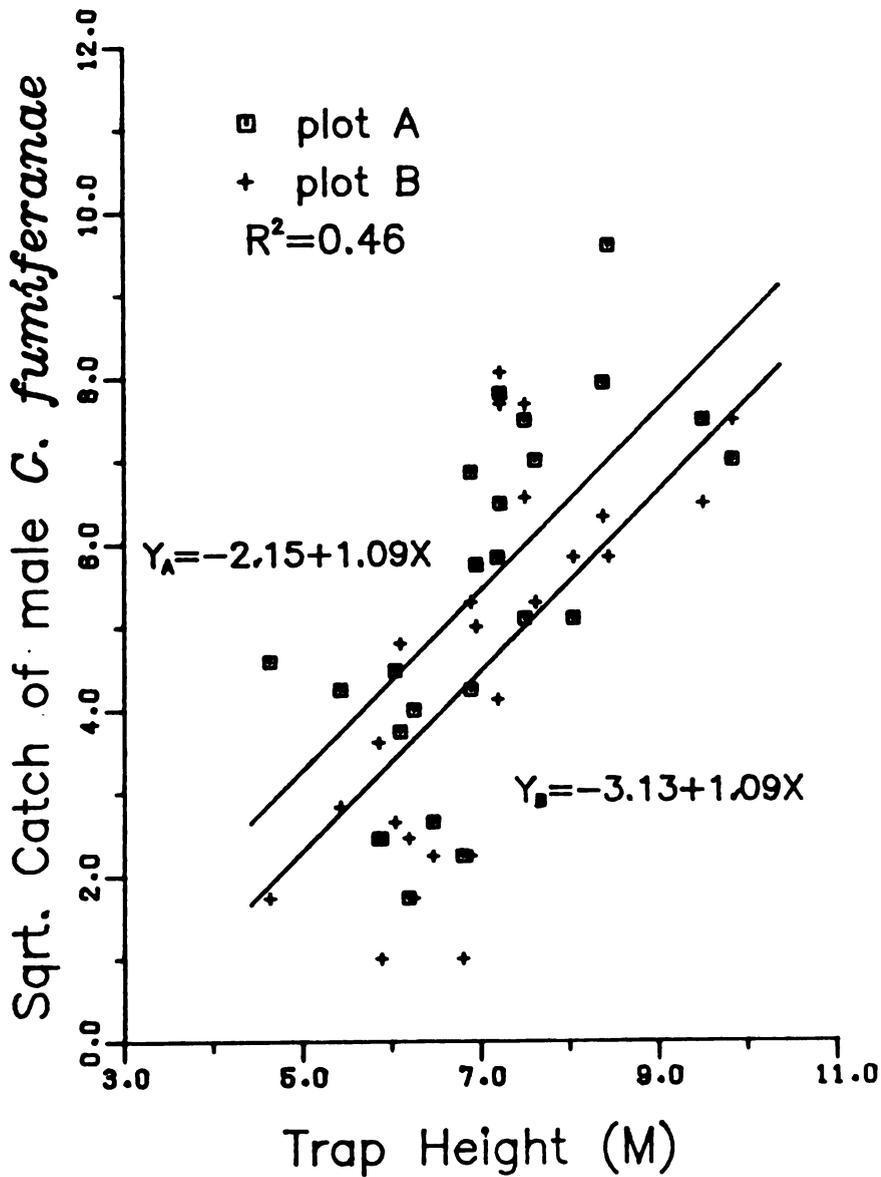


Figure 13. The relationship between Malaise trap catch of adult male *G. fumiferanae* and the height of traps in the crowns of jack pine trees. Data transformed to square roots before analysis. Data collected at the GR site in 1982.

of aphids which feed on jack pine, and only infrequently were observed visiting bouquets of wild flowers; they were never observed feeding on flowers (Table 4). The results of similar tests on A. fumiferanae were inconclusive because the parasites were lethargic and did not move about the arena. Only six of the parasites were observed feeding during the tests, but none of these was observed feeding on flowers though some sat motionless on the bouquets for long periods of time. The individuals of this species used in the tests had eclosed 6-10 days before the tests were conducted and may have been senescent, possibly accounting for their lack of response. Since G. fumiferanae apparently does not utilize the forest floor it has probably not adapted to to use flowers as a food source; this would explain the lack of response observed in the tests. Females of G. fumiferanae that were fed honey throughout their adult lifetime lived 8-18 days while males lived 7-14 days. Females of A. fumiferanae lived from 7-19 days. Parasites of both species and sexes that were maintained on honey lived longer than those fed honeydew, but those maintained on honeydew lived no longer than those which were not fed (Table 5). The honeydew used in the tests was produced by an unidentified species of aphid that occurred commonly on jack pine in the plot where the tested parasites were obtained. Honeydew from this aphid species is apparently of little or no nutritional value to the parasites.

Table 4. Comparison of numbers of *G. fumiferanae* visiting and feeding on three food sources. A Chi-square test was used to determine if the frequency of observed visitations and feedings differed from expectations if the parasites showed no preference for any of the three foods.

Sex	repetition	Number of visits			Chi-square
		flowers	honeydew	honey	
Female	1	5	33	43	28.7*
	2	2	9	49	64.3*
Male	1	3	8	25	22.2*
	2	6	30	42	25.8*

Sex	repetition	Number of feeding visits			Chi-square
		flowers	honeydew	honey	
Female	1	0	11	16	14.9*
	2	0	2	22	33.7*
Male	1	0	1	9	14.5*
	2	0	5	20	26.0*

Table 5. Mean longevity (\pm SE) of Glypta fumiferanae and Apanteles fumiferanae fed various foods. Analysis of variance was used to determine treatment differences. Multiple comparisons were made using Scheffe's Method. Means with different superscripts differ at the 95% level.

Species	Sex	Food Source	n	Mean Longevity (\pm SE)
<u>Glypta fumiferanae</u>	Male	None	6	^a 3.2 \pm 0.75
		Honeydew	6	^a 2.8 \pm 0.41
		Honey	6	^b 10.3 \pm 2.3
	Female	None	7	^a 4.0 \pm 0.82
		Honeydew	7	^a 4.4 \pm 0.53
		Honey	7	^b 12.7 \pm 2.87
<u>Apanteles fumiferanae</u>	Female	None	8	^a 3.0 \pm 0.53
		Honeydew	8	^a 3.1 \pm 0.64
		Honey	8	^b 13.6 \pm 4.31

DISCUSSION

The role of parasites and predators in the life system of JPB has only been studied at a superficial level and firm conclusions regarding the influence of natural enemies on JPB population dynamics are difficult to make with the information presently available. The general consensus is that parasites and other natural enemies are important at low population densities and exert some control over endemic populations and perhaps speed the rate of decline of outbreak populations already in the process of declining as the result of other factors such as insufficient food supply. Once an outbreak is triggered by an appropriate combination of environmental and biological factors, natural enemies exert little effect on damping or halting the release of populations to outbreak (Foltz et al. 1972, Batzer and Jennings 1980, and others). However, there are many exceptions to this generality; populations in some geographic areas are remarkably resistant to JPB outbreaks. The factor or factors accounting for such phenomena are not known, though natural enemies may play a significant role in this resistance. Thus, more must be known about the biology and ecology of parasites and predators of JPB before firm conclusions can be formulated concerning the conditions under which natural enemies will be effective in controlling JPB populations, if in fact such conditions exist.

Mortality of 3-6 instar JPB larvae is believed to be an important factor accounting for a large portion of total generation survival of JPB populations (Batzer and Jennings 1980). The most important source of this mortality is apparently associated with the 5-6 instars, with parasitism of 1-3 instars being of lesser importance (Foltz et al. 1972); but the factors accounting for mortality of

these life stages are poorly known. However, even the influence of parasitism of early instars, has not been established with certainty. Theoretical studies suggest that the parasite A. fumiferanae possesses many of the biological attributes associated with parasite species that are successful in biological control (Beddington et al. 1978, Hassell 1977), including monophagy and a high intrinsic rate of increase. In addition, the interactions of natural enemies with JPB, each other, and other components in their life systems are generally unknown.

The results of this study indicate that the complex of parasites that parasitize instars 1-4 of JPB in outbreak and declining populations in Michigan was consistent, and composed of three species that were primarily responsible for the observed levels of parasitism of these stages. Other parasites known to utilize 3-4 instar JPB were uncommon and of sporadic occurrence. Apanteles morrиси was not reared from 2-3 instar JPB sampled early in late May or early June when the larvae are mining flowers and new growth. However, the species was consistently reared from 4-5 instar JPB sampled later in the season. The bimodal pattern of adult female A. morrиси activity suggests that the species parasitizes JPB in the spring and that parasite oviposition is complete by about 450-500 DD (base 8.9°C). At the GR site in 1983 the JPB population was near the peak of the fourth instar at about 450-500 DD. To assess the role of a parasite as a mortality factor the percentage of susceptible hosts parasitized must be determined (Simmonds 1948, Van Driesche 1983). The life stages of JPB parasitized by A. morrиси are not known, though it is clear that the parasite must utilize 3rd instars, 4th instars, or both. If there is no differential mortality between JPB larvae parasitized by A. morrиси and those not parasitized by this

parasite, sampling to determine impact should be done at about 500 DD to obtain reliable estimates. If sampling is done earlier some parasites will still be ovipositing and if sampling is done later some parasites will have emerged from hosts; in both instances biased estimates of parasitism will result. The results of some studies suggest that spruce budworm larvae parasitized by A. fumiferanae and G. fumiferanae suffer proportionally fewer losses to dispersal than unparasitized larvae because of a reduced propensity to disperse caused by the presence of the parasite or chemical substances injected into the host by the adult parasite during oviposition (Lewis 1960). However, other studies indicate that there are no differential losses of unparasitized and larvae parasitized by the two species (Miller 1960, Mcleod 1977). In any event it appears that A. morrisi parasitizes JPB after the major periods of larval dispersal, fall and spring, and differential mortality due to dispersal is not major a factor. Additional work needs to be done to determine if JPB parasitized by A. morrisi are subject to differential mortality due to other causes. The results of this and other work indicate that reliable estimates of parasitism by A. fumiferanae and G. fumiferanae can probably be obtained at any point up to about 550 DD if parasitized and unparasitized larvae have equal probabilities of mortality to causes such as dispersal and predation. However, until more is known about the existence of differential mortality of unparasitized and parasitized larvae the dissection of overwintering larvae might be the most reliable method for estimating the impact of A. fumiferanae and G. fumiferanae (Kemp and Simmons 1976).

The significance of parasitism by A. morrisi as a mortality factor operating on JPB populations in Michigan is not known. Life table studies suggest that

unidentified sources of mortality operating on 3-6 instars are significantly correlated with total generation survival (Foltz et al. 1972, Batzer and Jennings 1980). Parasitism by A. morrisoni made up at least a portion of this unidentified mortality since in both studies the sampling intervals were constructed in such a way that impact due to this parasite would go largely undetected. Miller and Renault (1976) studied parasitism in endemic populations of the spruce budworm and found that parasitism by Apanteles species other than A. fumiferanae was generally low and sporadic, probably because most species have alternate and/or alternative hosts the abundance of which, in part, determines the abundance of these parasite species. The ubiquity of A. morrisoni in the populations surveyed in this study suggests that parasitism by this species may be an important source of mortality in outbreak and declining populations of JPB. Further studies would be necessary to determine its influence in low density populations.

The vertical patterns of adult female parasite activity observed in this study suggest that parasitism rates should be higher in the mid- and upper crowns of trees than in the lower crown or on suppressed trees provided that parasite activity levels measured by Malaise trap catch are related to host searching and other activities in equal proportions at all heights (e.g., the parasites do not use some strata for purposes of feeding, mating, etc. and others for host searching). Kaya and Anderson (1974) found that the catch of the parasite Ooencyrtus ennomophagus (Yoshimoto) on sticky panels in various microhabitats was consistent with observed patterns of parasitism by the species. Weseloh (1972) found that the distribution of the catch of Apanteles melanoscelus (Ratzeburg) on sticky panels agreed with the distribution of parasitism, but that parasitism and trap catch of O. kuwanai (Howard) gave contradictory results. Results of

previous studies have found parasitism by A. fumiferanae and G. fumiferanae to be higher in the mid-and upper crowns of trees (Jaynes 1954, Miller 1959, Kulman and Hodson 1961, Allen et al. 1969). These observations support the contention that much of the activity measured by Malaise trap catch was related to host searching.

The observation that cocoons of A. fumiferanae and G. fumiferanae were equally distributed among the upper crown, lower crown, and suppressed trees suggests that considerable redistribution of parasitized larvae occurs during larval dispersal periods in the fall and spring since little adult parasite activity occurred in the lower crown and virtually none occurred within 1 m of ground level. Apanteles morrisoni cocoons were also equally distributed among strata. This suggests that this species parasitizes JPB larvae in all strata since adults of this species apparently oviposit after the majority of larval dispersal has occurred.

The peak in activity of female populations of A. fumiferanae and G. fumiferanae is well synchronized with the peak eclosion rate of JPB eggs. Whether or not the observed peak in trap catch coincided with the peak in oviposition activity of the parasite populations is not known, but if so it suggests peak oviposition by A. fumiferanae is well synchronized with the peak in abundance of 1st instar JPB, the life stage it is apparently best adapted to exploit (Lewis 1960). Mason (1975) suggested the possibility that A. fumiferanae may oviposit in eggs of JPB. While this phenomenon has not been documented, the activity patterns of females of this species suggest that considerable activity occurs at a time when few 1st instars are available for oviposition. Utilization of eggs for oviposition could increase the reproductive efficiency of the parasite.

Glypta fumiferanae is most efficient at parasitizing 2nd instars in hibernaculae (Miller 1960, Lewis 1960). In laboratory studies this parasite begins to oviposit immediately upon emergence (Stairs 1983). If the observed peak in trap catch of females of this species corresponds to the peak oviposition, primarily 1st instar JPB would be present in the population. In this case the parasite would be poorly synchronized with the life stage it is most efficient at parasitizing. Oviposition experiments with G. fumiferanae and A. fumiferanae indicate reproductive potentials of 100-150 eggs per female for both species (Miller 1959, 1960, Stairs 1983). The consistently low parasitism rates by G. fumiferanae, as compared with A. fumiferanae, observed in field studies may be attributed in part to poor temporal synchrony with 2nd instar of JPB. However, other factors could be responsible for the low parasitism rates such as lower searching efficiency and longer handling time (Hassel 1977). There are many opposing pressures operating on populations. The apparent lack of synchrony between G. fumiferanae and its host could result from the costs associated with increased mortality. Predation and hyperparasitism would play a role if more time were spent in the pupal stage. Increased losses could occur due to intrinsic competition with A. fumiferanae. In cases of multiparasitism, the ability of A. fumiferanae to inhibit embryonation of G. fumiferanae eggs increases sharply with the number of days that G. fumiferanae precedes that by A. fumiferanae (Lewis 1960). At low host densities competition for hosts may be intense. The lack of synchrony of G. fumiferanae with the presence of 2nd instar JPB probably results from the necessity of optimizing a number of variables within its life system.

Apanteles morrisi pupates and emerges slightly earlier than A. fumiferanae; both parasites spin silken cocoons and pupate on foliage within the feeding shelter of the host, or nearby. The species are morphologically similar and apparently closely related (Mason 1975). Because of their phylogenetic and ecological similarity they are probably subject to many of the same mortality factors such as disease, predation, and hyperparasitism. The presence of A. morrisi could influence the probabilities of survival of A. fumiferanae. The earlier pupation and emergence of A. morrisi could negatively influence the survival of A. fumiferanae from polyphagous hyperparasites which attack the parasites in the pupal stage; these hyperparasites might increase their host searching activities in the microhabitat where the parasites pupate in response to the increase in pupal density of A. morrisi, particularly when population densities of the parasite are high. The mechanism proposed to account for this behavior by the hyperparasites is host-switching Murdoch (1969). Hassel (1977) has discussed this phenomenon in reference to parasitic insects and suggests that it might be a common phenomenon. The increase in hyperparasite activity might be somewhat delayed as has been observed in for hyperparasites of the gypsy moth (Lymantria dispar L.) parasite Apanteles melanoscelus (Weseloh 1979). In this instance the host searching population might increase in response to A. morrisi and host searching might be at a high level when A. fumiferanae begin to enter the pupal stage, resulting in increased losses to hyperparasitism.

The adults of A. fumiferanae and G. fumiferanae are active primarily during the daylight hours. Most parasites of forest insects are diurnal (Weseloh 1976). There is some indication that female G. fumiferanae have two periods of increased activity, in the early morning and again at dusk. Juillet (1960) found

that ichneumonids were generally most active in the early morning and evening hours. A portion of the total daily activity of both species occurs during the night, but whether this activity is related to host searching or some other function is unknown. Much of the variation in daily activity is related to temperature, the effects of which vary and are superimposed on an apparent inherent rhythmicity. During the early morning hours parasite activity levels are very sensitive to temperature with slight increases in temperature resulting in marked increases in activity. Later in the day, activity levels are relatively insensitive to temperature over the range of temperatures observed in this study (19-30°C). These results suggest that the relationship of parasite activity to temperature is nonlinear, as might be expected. Temperature exerts only a minor influence on parasite activity over a fairly wide range of temperatures, but at lower or higher temperatures activity may be rapidly reduced. When temperatures are high early in the morning total daily activity levels may be high because peak activity levels are reached earlier in the day. The insensitivity to variation in ambient temperature during mid-day may be due to the effects of radiant heat. The days during which this study was performed were all cloudless and calm. On sunny days the parasites may be capable of regulating their internal temperature via behavioral mechanisms (Matthews and Matthews 1978). Thus, the relationship of flight activity to temperature is not independent of other variation in the environment.

The activity of G. fumiferanae and A. fumiferanae was greater in the mid- and upper crowns of jack pine trees than in the lower crown, but was reduced in traps placed in the upper crowns of trees that were above the average height of the canopy. Responses to physical factors (light intensity, temperature,

humidity, etc.), tree form, or host abundance may be responsible for the vertical distribution of parasite activity. The distribution of 1st instar JPB would be difficult to determine, but the population intensity of JPB egg masses is generally greater in the lower half of the crowns of trees in mature jack pine stands (Drapek personal communication). However, since the larvae are positively phototropic (Miller 1959,1960, Lewis 1960) the density of small larvae may, in fact, be greater in the upper half of crowns.

It is clear that the spatial and temporal relationships of these parasite species are complex. In order to measure the activity of adult parasite populations and relate this activity to parasitism in a meaningful way, additional information is needed on the relationship of reproductive condition of the parasite population, perhaps measured as ovariol content, to temporal patterns of activity of the populations. The feeding ecology of the parasite species should be studied in detail to determine if the availability of food is a limiting factor in determining rates of parasitism and under what ecological circumstances food is limiting. Results of this study indicate that the longevity of A. fumiferanae and G. fumiferanae is increased by provision of adequate food sources. However, even though the parasites were observed to feed on aphid honeydew, this food had no apparent nutritive value to the parasites. Leius (1961a) found that the honeydew of two aphid species was detrimental to Scambus buolianae (Htg.), reducing both the longevity and fecundity of the parasite. Neither of the parasite species appear to be attracted to flowers and did not feed on them in tests. Furthermore, neither species utilizes the forest floor since no individuals of either species was ever caught in this stratum. However, it is possible that the parasites might make use of food sources occurring at ground level in

situations such as plantations where trees are small and the both the hosts and parasites occur in close proximity to the ground. Nyrop (1982) estimated that G. fumiferanae lived an average of 10 days in the spruce-fir stands in which he studied the parasite. G. fumiferanae appeared to live as long or longer in the populations studied here, and A. fumiferanae lived slightly longer than G. fumiferanae. Thus, the parasites apparently do derive food from their environment. Flowers occurred only sporadically on the forest floor in jack pine stands studied, and to utilize nectar or pollen from them, the parasites would need to spend a large portion of their time foraging in a microhabitat spatially quite removed from that where their host occurs. The subsequent expenditure of energy, and other associated costs, such as predation risk and the risk of being lost to the system because of failure to successfully orient back to the tree crown, suggests that flower feeding might be an inefficient method for these parasites to obtain energy. It is probably not correct to assume that the parasites feed on all available food sources or that adequate nutrition can be obtained from any available food source. Many adult parasites have rather specific nutrient requirements and food preferences (Leius 1960, 1961a, 1961b, 1967, Syme 1974, Shahjahan 1974). The food sources utilized by A. fumiferanae and G. fumiferanae were not determined during this study, however it was evident that they probably obtain food in the same microhabitat in which they search for hosts and that their food requirements may be rather specific.

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**THE APPLICATION OF TIME SERIES ANALYSIS FOR PREDICTING
ACTIVITY PATTERNS OF ADULT FEMALE Glypta fumiferanae POPULATIONS**

INTRODUCTION

Box-Jenkins modeling and forecasting techniques (Box and Jenkins 1976) have been in existence for many years, however only in recent years have the techniques been employed for modeling and predicting ecological processes. The number of published examples of the use of the methodology in the ecological and entomological literature are few (Poole 1972, Hacker et al. 1973a, 1973b, 1975, Poole 1972, Garsd and Howard 1982, Roubik 1983).

Statistical forecasting techniques have been used extensively in economics, a field that is burdened with many problems similar to those in ecology. In economics, it has been found that so-called "naive" models of the Box-Jenkins type usually outperform the usual econometrics models in terms of accurately forecasting future trends (Cooper 1972, Makridakis 1976, Granger and Newbold 1975). It has been suggested that this class of models might also be more efficient than simulation models for predicting trends in ecological systems (Getz and Gutierrez 1982).

The potential for the application of discrete time stochastic difference equation models of the Box-Jenkins type for investigating population processes has been discussed by several authors (Royama 1977, 1981, Pielou 1981, Tong 1983). Stochastic difference equation modeling techniques can be used to determine aspects of population dynamics in instances where the biological information available about a species is insufficient to warrant the development of more complex models. The resulting models, while simple in structure, can clarify the important features of population processes that are present in an observed time series. For example, they can provide insight into the existence

of density dependence or the strength of interactions among species in a community (Royama 1981, Poole 1976).

All that is required in order to develop a Box-Jenkins model is a time sequence of measurements of a population process taken at regular intervals of time. For example, estimates of the annual density of a population of a univoltine insect taken over many years would provide the necessary data from which to build a time series model; if two or more processes were measured simultaneously, then the resulting time series would provide the data base for constructing a bivariate time series model. Furthermore, the models are relatively efficient in terms of computer and development time.

While Box-Jenkins models have many desirable features they also have limitations. Perhaps the most important limitation is the requirement that the stochastic process being modeled be wide sense stationary. Wide sense stationarity means that all the first and second order moments of the process are independent of time. If a stationary stochastic process is the input to a linear time invariant system then the resulting output will be a stationary stochastic process. Most ecological processes are not linear and hence Box-Jenkins models can only serve as approximations of system dynamics. Thus, the models may not be well suited for data exhibiting sudden bursts of large amplitude such as the double equilibria processes studied by May (1977). However, linear models often provide robust approximations of nonlinear phenomena (Roughgarden 1975, Nisbet et al. 1977, Poole 1977, Patten 1975). Furthermore, many types of nonstationarity can be removed from the time series data to produce a process satisfying the stationarity criteria (Box and Jenkins 1976). Once a model is estimated for the stationary series the nonstationarity is reintroduced. For

example, nonstationarity in the mean and variance can sometimes be removed by the application of appropriate transformations. Thus, models for nonstationary processes can often be developed using the Box-Jenkins methodology.

The purpose of this study was to determine the usefulness of Box-Jenkins modeling techniques for a particular ecological time series; the series consisted of a sequence of data collected over a three year period on the daily Malaise trap catch totals of the Ichneumonid parasite, Glypta fumiferanae (Viereck), which parasitizes the jack pine budworm (Choristoneura pinus Freeman) and the spruce budworm (C. fumiferana (Clemens)). This series may be typical of many series obtained in studies of ecological systems in that it has a large variance and is nonstationary. Univariate models, and multivariate models incorporating meteorological variables known to affect parasite activity levels were developed. In the paper a detailed account of the analyses is given and the practical problems associated with the application of the modeling techniques is provided. The major features of the fitted models are described and the utility of the models for predicting future population trends is assessed.

CONSTRUCTION OF THE TIME SERIES MODELS

Field techniques

The data from which the parasite activity models were constructed and validated was generated at three study sites in Northern Michigan. The primary study site was located in the Fife Lake State Forest, Grand Traverse Co., Michigan. This site consisted of two study plots each ca. 2000 m² in a mature, naturally seeded jack pine stand. The plots were separated by a distance of ca. 200 m. A more detailed description of the site is given in Elliott (1985). A single Malaise trap (Nyrop 1982) was secured in the mid- or upper-crown of each of 24 randomly selected dominant or codominant trees within the site (12 trees in each plot). The traps were monitored each day at 0800 hours throughout the adult life span of the parasite species, and the number of Glypta fumiferanae females caught per trap per day was recorded. The resulting data provided a time series of the relative activity of adult G. fumiferanae over the two year period.

In order to obtain a larger series of data for analysis, data from another population of G. fumiferanae was obtained from Nyrop (1982). Nyrop used Malaise traps of the same design as those used in 1982 and 1983, and operated them under similar conditions in two spruce-fir stands in Delta Co., MI. Because of the striking similarity in the seasonal activity patterns of G. fumiferanae in the two different locations and because the objective of this study was to explore the properties of stochastic difference equation models fitted to ecological data of this type (rather than constructing forecasting models for a particular population), it was felt that pooling data from the two sites for the

purpose of modeling was justified. The time series was constructed from 34 days of trap catch data for each year starting from the date of the first occurrence of non-zero trap catch for each year and continuing for 34 successive days. Thus a total of 102 observations on the relative daily activity of female G. fumiferanae were available for analysis (Figure 14).

A third study site was established in a mature jack pine stand in Wexford Co., MI during the summer of 1983. Ten malaise traps were secured in the mid-crown of 10 randomly selected jack pine trees within this stand. The trap catch data obtained from this study site were used to validate the fitted time series models.

Environmental Data

Meteorological data was obtained from the National Climatic Center, Asheville, North Carolina; hourly temperature measurements and rainfall measurements taken at six hour intervals were extracted from the daily records submitted by the Cherry Capital Airport, Traverse City, Michigan, located ca. 15 km Northwest of the Grand Traverse Co. study site; and by Sawyer Airforce Base, located ca. 30 km from the Delta Co. study sites. Hourly temperatures from 0700 to 2200 hours were averaged for each day for which parasite trap catch data were available. This was done because most of the daily activity of adult G. fumiferanae occurred during this time interval (Elliott 1985). The temperatures recorded at Sawyer Airforce Base were generally lower than those from Cherry Capital Airport. The parasite populations in each of the two locations are probably adapted to the range of temperatures encountered at their particular geographic location. In order to avoid misrepresentation of the

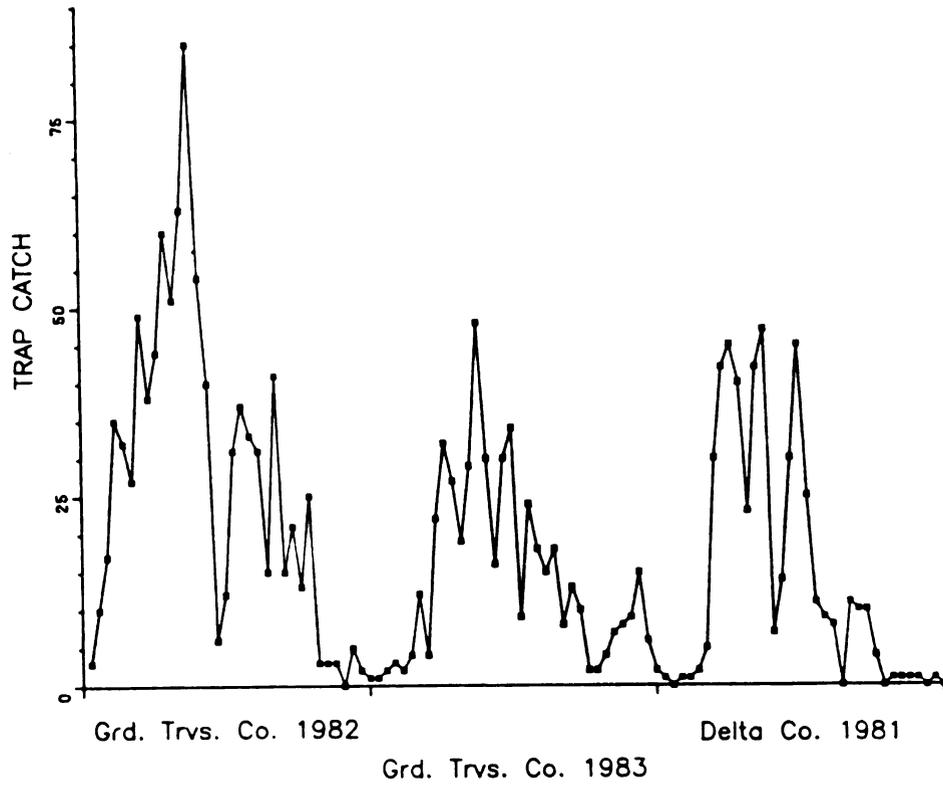


Figure 14. Daily Malaise trap catch of adult female *Glypta fumiferanae* over a three year period.

effects of temperature on parasite activity in the transfer function models, temperatures needed to be standardized in some manner. Thus, the temperature data for each year were transformed by subtracting the mean of each year's data from each observation from that year and dividing by the standard deviation; the result was a time series of "standardized" daily temperatures (Figure 15). The number of cm of rainfall from 0700 to 2200 hours was also determined from the meteorological records (Figure 16).

Statistical Methodology

Box-Jenkins time series models (ARIMA models) were fitted to the daily parasite activity (trap catch) series. For the purposes of model identification the properties of the mean, variance, and covariance of the series were used to indicate stationarity (i.e., wide sense stationarity) rather than the strict definition (Granger and Newbold 1977), since the strict stationarity is not a useful definition in practice, when attempting to determine an appropriate model for an observed series.

A two parameter power transformation was employed to instantaneously transform the observed series (Box and Cox 1964). A modification of a method described by Granger and Newbold (1977) was used to determine the power transformation parameters such that the likelihood function of the transformed process was maximized, assuming the process to be stationary and Gaussian. An algorithm was developed for this purpose and is described in Appendix I. A test described by Granger and Newbold (1977) was used to test for normality of the marginal distribution of the instantaneously transformed time series.

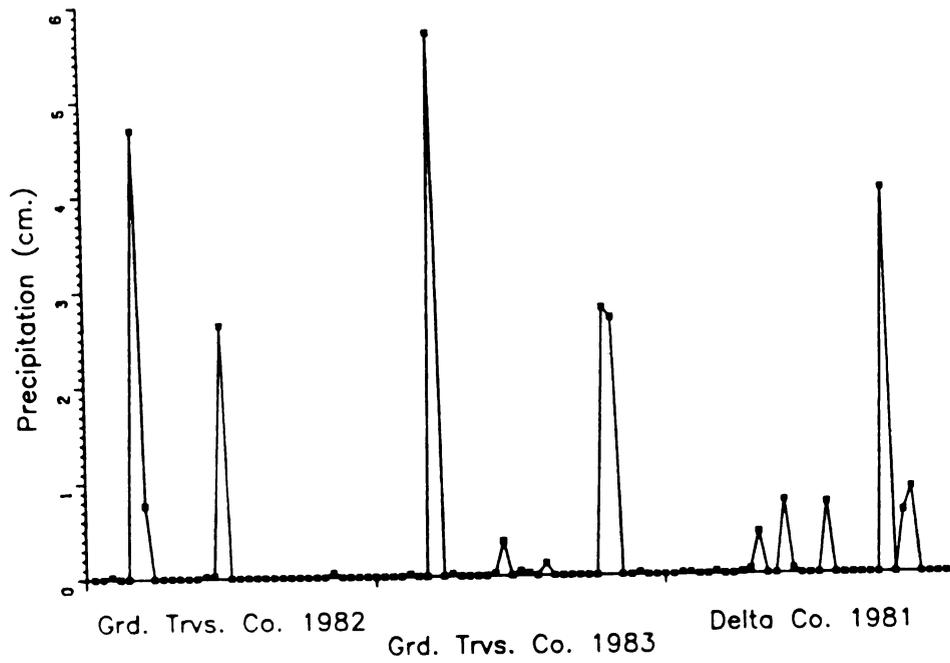


Figure 16. Daily cm of precipitation over a three year period corresponding to the period of adult female Glypta fumiferanae activity.

Model identification, estimation, and checking were done as described by Box and Jenkins (1976) and Abraham and Ledolter (1983) using computer programs written by Dr. D. J. Pack of Ohio State University. The sample autocorrelations and partial autocorrelations were estimated from the transformed data for lags ranging from 1 to 36. Differencing operators were used to produce stationarity in the mean (Box and Jenkins 1976). The sample autocorrelations and partial autocorrelations were used to determine the orders of the autoregressive and moving average polynomials for the appropriately transformed and differenced time series. The sample autocorrelation function of the model residuals and statistical tests (Q-tests) based on the sample autocorrelation function of the residual series were used to check the adequacy of the fitted model (Ljung and Box 1978). Once an adequate model was identified and estimated more complex models were estimated to determine if they provided significant improvements.

Once an appropriate ARIMA model was identified, estimated forecasts were produced. Both median point and mean point forecasts were produced. Median point forecasts were derived by backtransforming the forecast to the original scale, mean point forecasts were derived by a method described by Granger and Newbold (1976). The derivation of mean point forecasts for the univariate ARIMA model is outlined in Appendix II. The properties of the fitted model and the median and mean point forecasts were investigated by computing forecasts for various lead times for the data used in model estimation and for the independent data set (Wexford Co., 1983).

Transfer function models (Box and Jenkins 1976) were fitted to the G. fumiferanae activity series using the standardized temperature series and the

total precipitation series as input processes. Model identification, estimation, and checking were done by the methods described by Granger and Newbold (1977). The statistical properties of the fitted transfer function models were compared with those of the univariate ARIMA model.

Model Development

The time series consisted of 102 data points taken over a three year period (Figure 14). Inspection of the series suggested that it was nonstationary in both the mean and variance. The variance of the series was dependent on the mean as indicated by the significant correlation between the observations $x(t)$ and the absolute value of $x(t+1)-x(t)$ $r^2=0.381$ ($p<.05$). The presence of a non-stationary mean was evident from the cyclical nature of the observed series. Nonstationarity in the mean of a discrete stochastic process can be removed by the application of an appropriate differencing transformation (Box and Jenkins 1976), however nonstationarity in variance cannot be corrected by differencing (Granger and Newbold 1977) and an instantaneous two parameter power transformation (Box and Cox 1964) was employed to remove that source of nonstationarity (Granger and Newbold 1977). The transformation parameters were chosen to maximize the likelihood function of the conditional distribution of the differenced process, $X'(t)$, where $X'(t)=(1-B)(1-B^{34})X(t)$ was assumed to have constant mean (see Appendix I). The resulting transformed series was given by,

$$Y(t) = X'(t)^{0.3333} / 0.3333$$

(Figure 17). The correlation of $y(t)$ and the absolute value of $y(t+1)-y(t)$ was $r^2 = -0.155$ ($.10 < p < .05$) suggesting that the mean and variance of the transformed time series were independent. There was no evidence to suggest that the transformed series $Y(t)$ differed from Gaussian $g_1/s_{g_1} = 0.139$ ($.5 < p < .25$) $g_2/s_{g_2} = 1.702$ ($.25 < p < .10$).

The sample autocorrelation function (ACF) and partial autocorrelation function (PACF) of $Y(t)$ gave no indication that the series was non-stationary, and indicated that an ARIMA $(p,d,q) \times (P,D,Q)_s$ model might provide an satisfactory univariate time series model (Figure 18). Numerous models were fitted to the data. An ARIMA $(1,1,1) \times (0,1,1)_{34}$ was found to provide the most satisfactory fit to the observed series. The ACF of the model residuals contained no coefficients that differed significantly from zero (Figure 19); and the Q-statistic was not significant compared with the upper 5 percentage point of the Chi-square distribution with 21 degrees of freedom. Thus, there was no evidence of autocorrelation among the model residuals (Table 6). The difference equation of the final fitted model was,

$$y_t = 1.42y_{t-1} - 0.42y_{t-2} + y_{t-34} - 1.42y_{t-35} + 0.42y_{t-36} + e_t \\ - 0.99e_{t-2} - 0.85e_{t-34} + 0.85e_{t-35}$$

the estimated residual variance was $s_e^2 = 3.93$. The unconditional variance of the original transformed data was $s_y^2 = 10.30$. The estimated residual variance is the one step ahead ($L=1$) prediction variance on the transformed scale. Thus, the model accounted for 61.8 percent of the variance in the fluctuations in the transformed time series for forecasts of lead time one day. The conditional

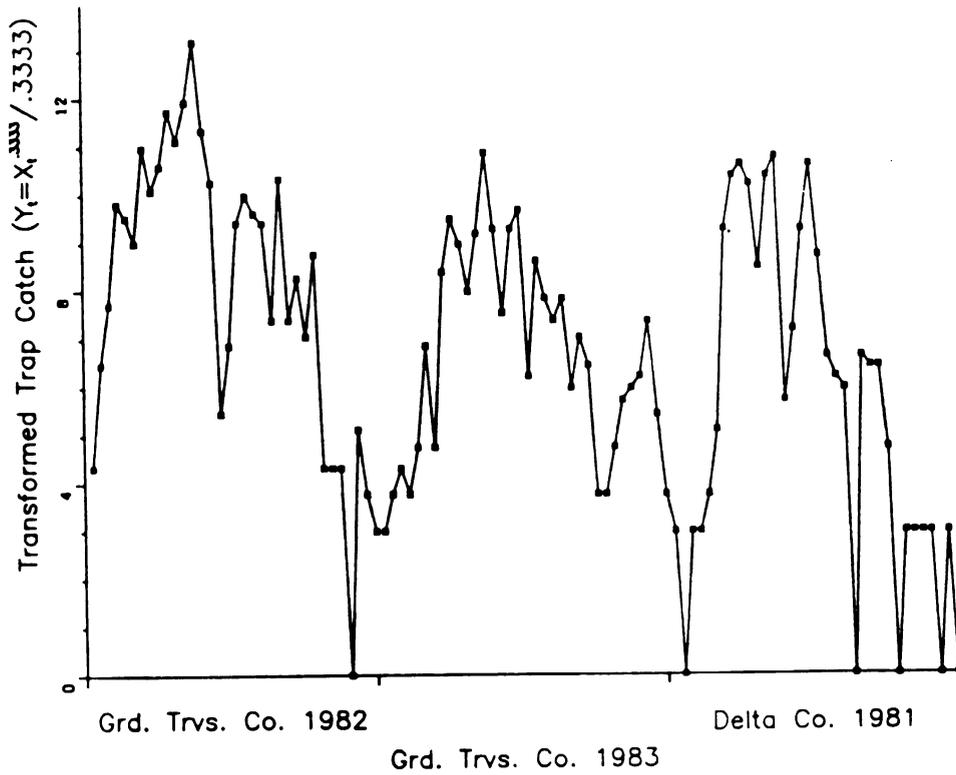


Figure 17. Transformed daily Malaise trap of adult female Glypta fumiferanae over a three year period. The data were transformed using the Box-Cox transformation (Box and Cox 1964).

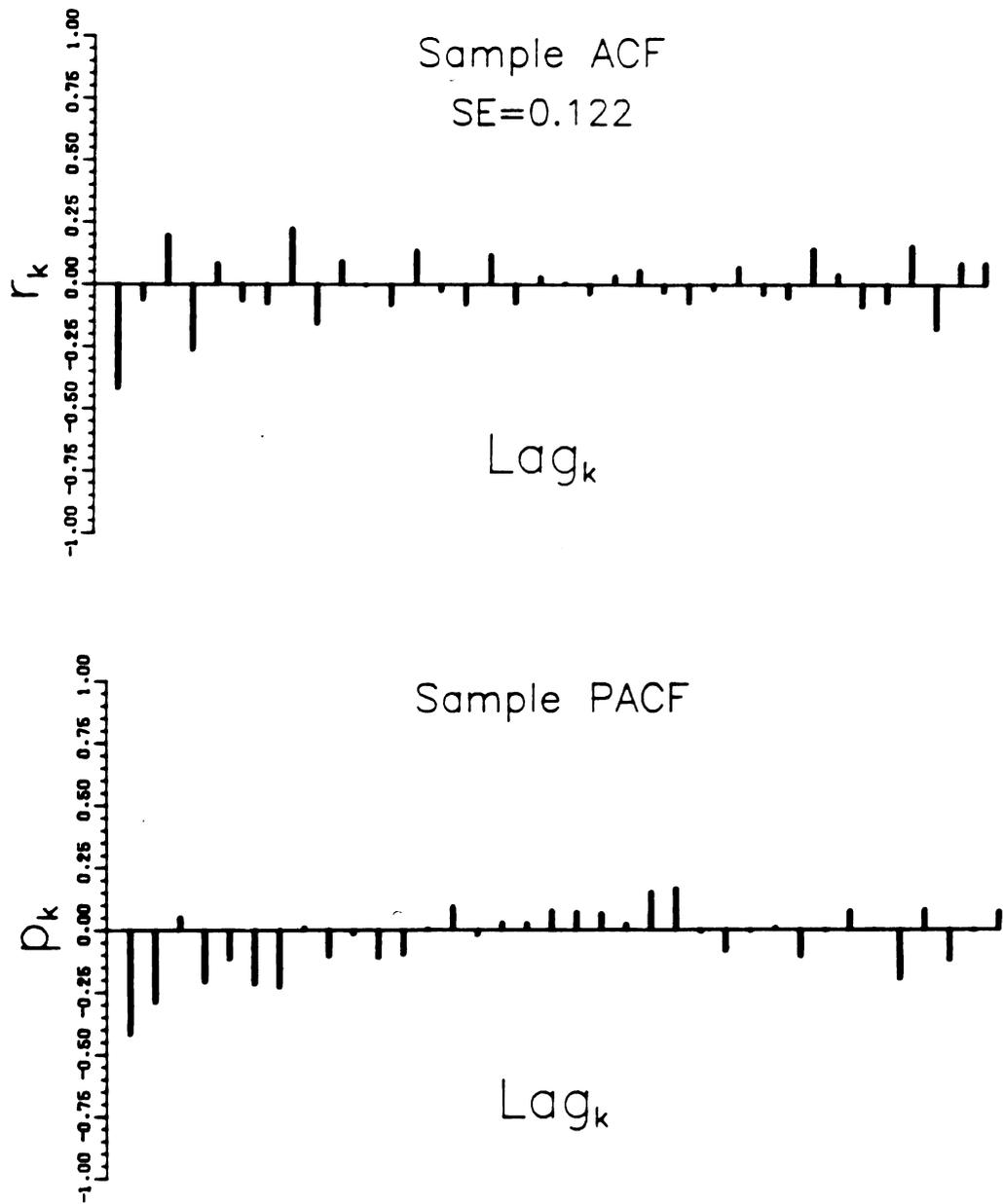


Figure 18. The sample autocorrelation and partial autocorrelation functions of the transformed and differenced adult female Glypta fumiferanae daily Malaise trap catch series.

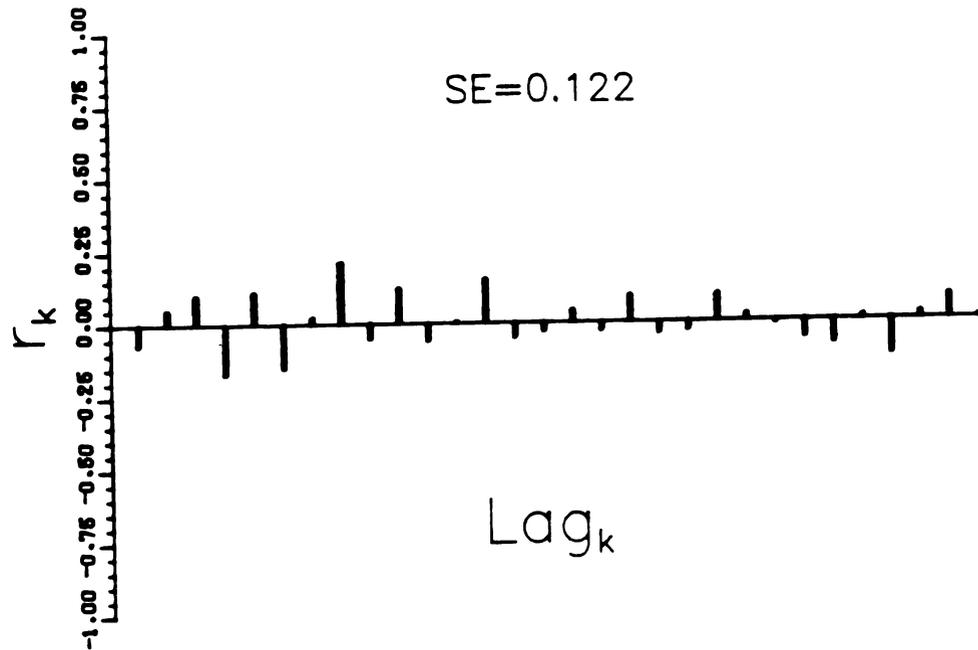


Figure 19. The autocorrelation function of the residual series generated from the fitted ARIMA (1 1 1)x(0 1 1)₃₄ model.

Table 6. Four models for forecasting transformed trap catch of female Glypta fumiferanae: Model I is a univariate model; Model II incorporates average temperature; Model III incorporates rainfall; Model IV incorporates average temperature and rainfall.

Model	SSE	ERV	χ^2 ACF	χ^2 CCF Temp.	χ^2 CCF Rainfall
I. $(1 - .42B)^{\circ\circ 34} y_t = (1 - .99B)(1 - .85B^{34})e_t$	263.4	3.93	22.6	-	-
II. $y_t = .60T_t + N_t$ $(1 - .19B)^{\circ\circ 34} N_t = (1 - .82B)(1 - .84B^{34})e_t$	253.4	3.78	18.8	18.3	-
III. $y_t = -.76R_t + N_t$ $(1 - .32B)^{\circ\circ 34} N_t = (1 - .92B)(1 - .85B^{34})e_t$	260.1	3.88	22.7	-	17.6
IV. $y_t = .53T_t - .50R_t + N_t$ $(1 - .19)^{\circ\circ 34} N_t = (1 - .83B)(1 - .84B^{34})e_t$	250.3	3.73	19.4	18.4	20.9

SSE: error sum of squares of the relevant model.

ERV: estimated residual variance of the relevant model.

χ^2_{ACF} : chi-square statistic on the residual series
auto correlation function.

χ^2_{CCF} : chi-square statistic for the residual series of the relevant
model with the prewhitened input series.

variance on the original scale was dependent on the conditional mean and therefore was not time invariant (see Appendix II). In computing forecasts e_t was suppressed.

To demonstrate the precision of the model, one-step forecasts were computed from the fitted model and compared with the original data for each year from which the model was constructed. In generating the predicted curves the last year's data was used to start the recursion for predicting the observed values of the first year's data. Then successive values were entered into the equation until the entire curve was calculated. One-step ahead median point forecasts generally underestimated the observed data (Figures 20,21). One-step ahead mean point forecasts more closely approximated the observed data. The ratio of the sum of squared errors of mean and median forecasts over all three years was 0.36 indicating that the mean point forecasts were about three times as accurate as median point forecasts in predicting the true values of the observations. Both forecasts consistently reproduced the general shape of the annual fluctuations in adult female G. fumiferanae trap catch (and hence presumably annual fluctuations in density), but much of the detail of the daily fluctuations in trap catch was poorly reproduced. Predictions of the dips and peaks in abundance that characterize the daily trap catch data generally lagged 1 or 2 days behind the observed values and often did not reproduce the properties of the fluctuations well.

One-step ahead and four-step ahead mean and median point forecasts, and median point forecasts without updating were computed for the independent data set (Wexford Co. 1983). One-step ahead mean point forecasts consistently overestimated the curve, while median point forecasts underestimated the

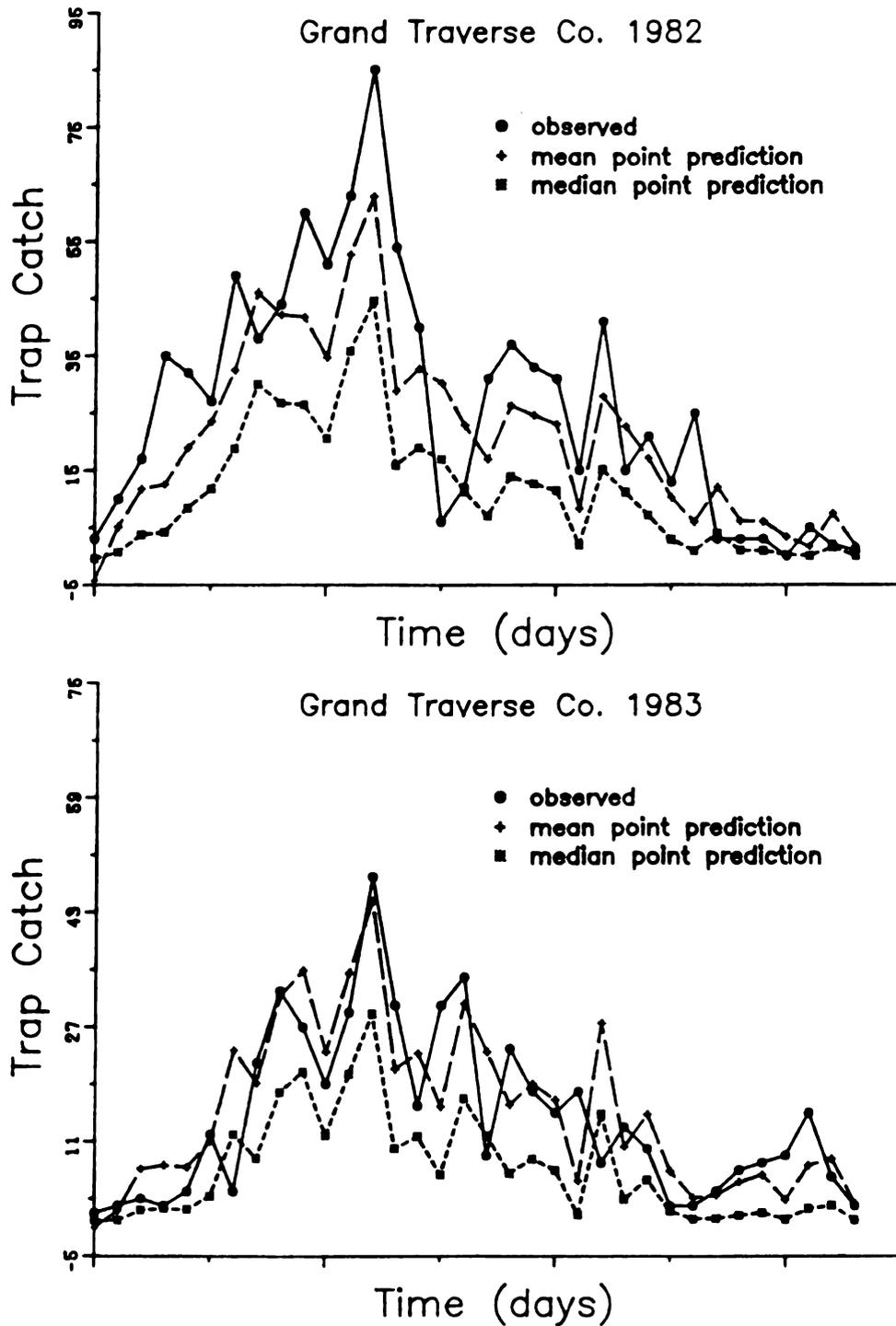


Figure 20. One-step ahead predictions for the Grand Traverse Co. 1982 and Grand Traverse Co. 1983 trap catch data based on an ARIMA $(1\ 1\ 1) \times (0\ 1\ 1)_{34}$ model.

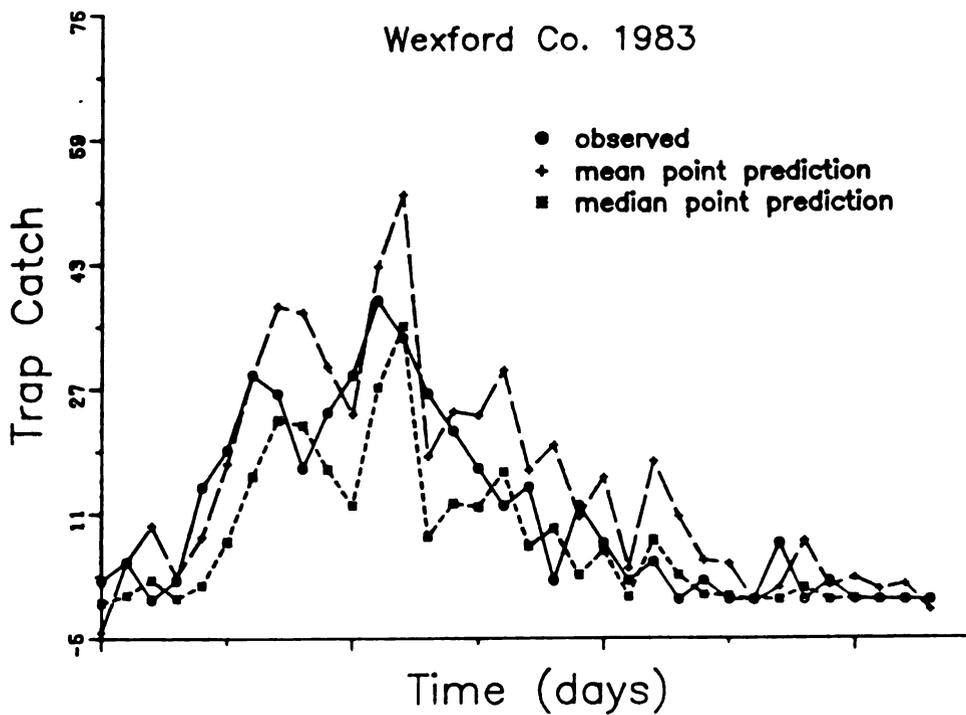
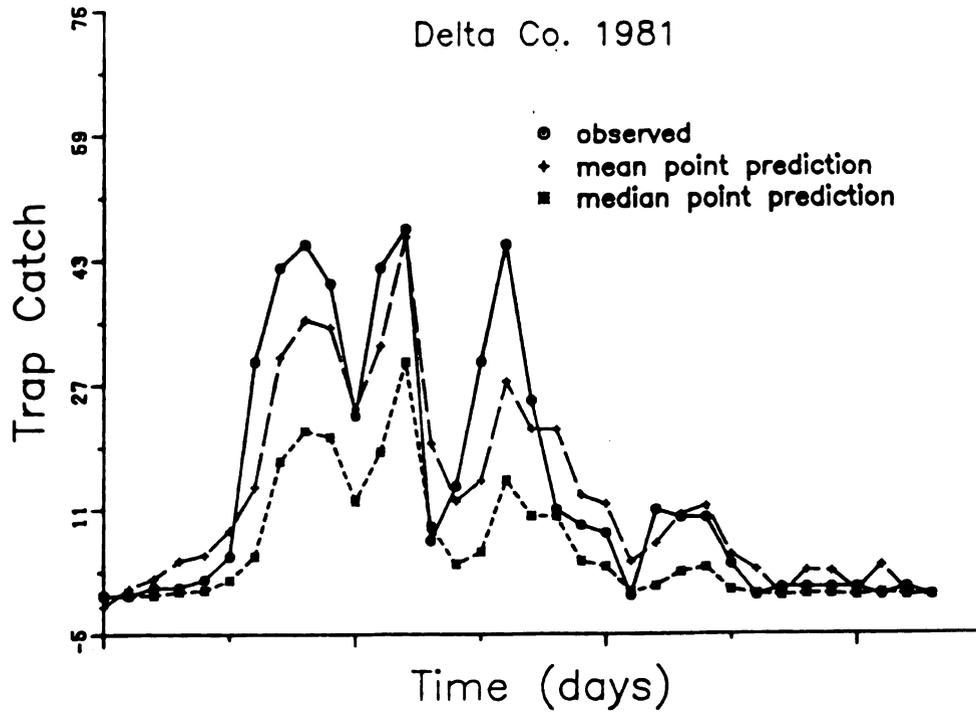


Figure 21. One-step ahead predictions for the Delta Co. 1981 and Wexford Co. 1983 trap catch data based on an $ARIMA(1\ 1\ 1) \times (0\ 1\ 1)_{34}$ model.

observed data (Figure 21). Because this data was not a continuation of the actual observed process the forecasts might be expected to provide poor predictions of the data. Thus the lack of accuracy cannot necessarily be attributed to model inadequacy. In fact, that the model provided a fairly accurate fit to the annual pattern in the fluctuation in parasite activity for this data may indicate that the model is reasonably robust. As the lead-time of the forecasts increased, the accuracy in detail of the forecasts was gradually lost as a consequence of the increase in the error variance associated with longer lead-time forecasts. Thus, the forecasts essentially reproduced the periodic component induced by the previous year's data values with large deviations between the observed and predicted values occurring at points where fluctuations in environmental conditions caused major changes in daily trap catch in either the current or the previous year (Figures 22, 23).

In an attempt to improve the predictability of the time series model, two environmental processes were incorporated into multivariate time series models. Average daily temperature and total rainfall between 0700 to 2200 hours were incorporated into transfer function-noise models (Box and Jenkins 1976) to determine if environmental variables known to affect parasite flight activity (Julliet 1960, Nyrop 1982) could be incorporated linearly to improve the predictability of the time series models. Appropriate models were estimated for temperature, rainfall, and the two processes in conjunction (Table 6). The incorporation of these variables resulted in little improvement in model fit or predictability. The residual sums of squares were only slightly reduced by the incorporation of either variable alone or both variables simultaneously (Table 6). The variance of one-step predictions was slightly increased in some cases as a

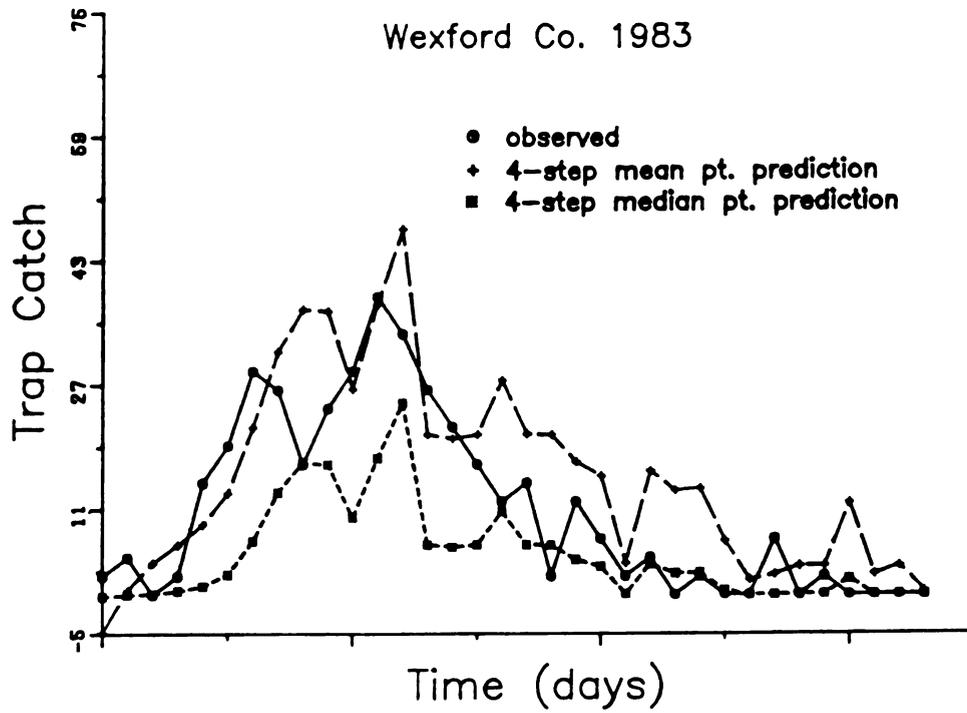


Figure 22. Four-step ahead predictions for the Wexford Co. 1983 trap catch data based on an $ARIMA(1\ 1\ 1) \times (0\ 1\ 1)_{34}$ model.

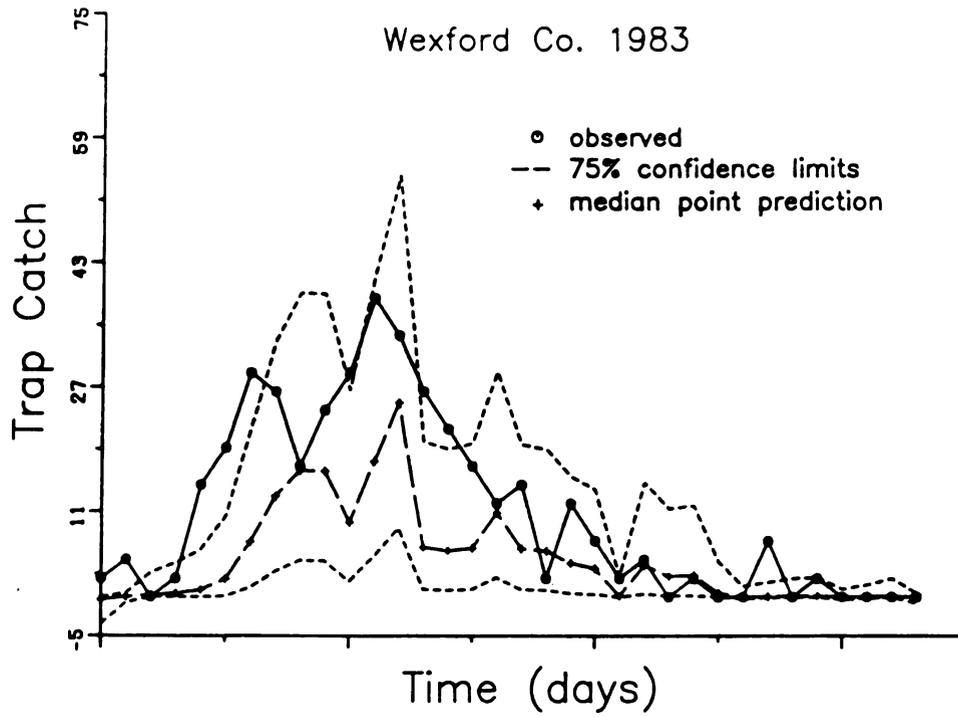


Figure 23. Predictions for the Wexford Co. 1983 Malaise trap catch data based on an $ARIMA(1\ 1\ 1) \times (0\ 1\ 1)_{34}$ model without the use of an updating recursion.

result of the necessity of forecasting temperature and/or rainfall in addition to trap catch (Table 7).

Table 7. Estimated variance of forecasting error for transformed trap catch.

Model	Lead Time		
	1	2	4
I	3.93	4.63	4.80
II	4.00	4.57	5.02
III	3.94	4.55	4.77
IV	3.93	4.54	4.95

DISCUSSION

The processes determining population dynamics are generally assumed to operate nonlinearly and the adequacy of linear models as approximations of population processes is a question of considerable interest for several reasons: the extensive theoretical framework developed for the analysis of linear systems; the relative ease of computation and short development time necessary; and the success of linear models as approximations of processes in other scientific fields such as economics and engineering (Tong 1983). Some theoretical studies suggest that linear models provide fairly robust approximations of nonlinear population phenomena (Nisbet et al. 1977, Roughgarden 1975); though other work has shown linear models to be unsatisfactory (Dwyer and Perez 1983).

Few published examples exist on the application of linear stochastic difference equation models for the purposes of analysis or prediction of population processes; this is surprising because the concepts involved in the statistical analysis of time series data on population processes has been extensively discussed and the potential for the application of this class of models appears to be relatively promising (Royama 1977, 1981, Poole 1977).

The results obtained in this study demonstrated that a univariate linear time invariant model provided a reasonable representation of the fluctuations of adult female Glypta fumiferanae populations over the range of densities studied. Optimal quadratic loss forecasts (mean point forecasts) were more accurate than median point forecasts for these data. Optimal quadratic loss forecasts are unbiased estimates of the conditional mean of the untransformed process (See

Appendix II for a discussion of the properties and derivation of mean point forecasts). Minimization of a quadratic loss function, e.g. minimum mean square error, is a commonly used and desirable criterion in statistical estimation. However, the median can sometimes be a useful statistic for describing the distribution of probability for data from particular distributions, and may, in some cases yield more useful forecasts than the conditional mean. This suggests that a variety of forecasting procedures should be employed when attempting to forecast population processes. When this is done, the most reliable procedure, or combination of procedures, can be identified and used for forecasting.

The univariate model was deficient in some respects. The lack of accuracy of one-step ahead forecasts was difficult to ascertain with complete assurance because the series from which the model was estimated was not obtained from a single population. However, it seemed reasonable to assume that the intra-generation pattern of parasite activity was reasonably well depicted by the model since the processes of development, host searching, death, etc., would be expected to act similarly in different populations of the insect. Likewise, variability in the environment should affect different populations similarly, though they would be expected to adapt responses to the average environmental conditions encountered in their geographic area; thus, they would respond similarly to average values of environmental variables encountered in their environment. One-step ahead predictions frequently deviated markedly from observed values. The model accounted for 61.8 percent of the variation in trap catch for predictions of lead time one day and the observed deviations were principally a reflection of this uncertainty. As the lead time of the forecasts increased the deviations from the observed values

increased, reflecting the corresponding increase in forecast variance. The high level of variability in the observed data was probably typical of levels that would normally occur in field measurements of densities of insect populations, and may indicate that it will often prove difficult to produce univariate forecasting models with the required degree of precision necessary for forecasting daily fluctuations in population levels.

Daily variation in population levels or activity may be of limited significance in many population studies compared to longer term trends. The model appeared to mimic the seasonal trends in the activity of the parasite populations well but the overall level of activity was not always well predicted (Figures 20,21). There was no reason to expect the overall level of activity to be well predicted in all cases since the series forecasted were not future values of a single observed process. Rather, the series from which the model was built was composed of data from two sites. Under these circumstances the good correspondence between predictions and the observed data suggests that the model may be quite robust for predicting the seasonal fluctuations in activity of populations adults of G. fumiferanae. Thus, biased estimates of the level of activity probably resulted because the model was estimated from data derived from two distinct populations and because the data used to validate the model was not a continuation of the process from which the model was developed.

Only three years data were used in estimating the model. The short time series, representing only three full oscillations in the cyclical component of the model, was probably insufficient for depicting the true dynamics of population change for the species; thus imprecise estimates of the parameters of the cyclical component of the model would be expected. Hence, even if the model

were produced from data from a single population it is likely that the estimation error would be high. All of the above mentioned factors probably contributed to the observed error in the predictions of population levels.

Another point deserving consideration in evaluating the evident bias in forecasts from the fitted model was the application of a nonlinear transformation to the original data. The main objective of the transformation was to produce residuals with a constant variance (strictly speaking to produce identically distributed model residuals). Improper choice of the transformation parameters would result in biased forecasts if the data were overtransformed or undertransformed because the model, which attaches weight to previous observations in producing forecasts for future times, would yield forecasts that misrepresented the true magnitude of the seasonal variation (Wilson 1973). The following discussion clarifies this point. For a purely deterministic process consisting of a linear trend and a fixed cyclical component, differencing of the type employed in this analysis would completely eliminate any trend in the data. It is known that a stochastic process can be decomposed into deterministic and random components (Hannan 1960), with the deterministic pattern being only one component of a process modeled by a Box-Jenkins model; the other component is random and nonstationary allowing for variation in both the trend and cyclical pattern (Wilson 1973). In a fitted Box-Jenkins model, the operators are applied so that the stochastic component of the model is well represented, and the forecasts that result will be minimum mean square error forecasts (Box and Jenkins 1976). If a series has been incorrectly transformed, e.g. the deterministic component exactly follows a linear trend plus a seasonal component, then this component will be incorrectly extrapolated in forecasting,

resulting in biased forecasts. It is frequently difficult to identify the appropriate transformation to be applied to the data, if in fact such a transformation exists. The problems encountered by Chatfield and Prothero (1973) in the analysis of a particular economic time series emphasized this point. Some data may be relatively insensitive to the choice of the transformation applied (Jenkins 1979), and thus misspecification of the transformation parameters (as for example in the Box-Cox transformation employed in this study) would have only a small effect on the accuracy of forecasts. However, other data may be very sensitive to transformation and the application of an inappropriate transformation might induce considerable bias in forecasts (Jenkins 1979). Maximum likelihood estimation of the transformation parameters, as outlined in Appendix I, should find the scale for the data that most nearly produces the Gaussian model form (Box and Jenkins 1973). The method of estimation of the residual variance employed in this analysis was suggested by Granger and Newbold (1977) as an appropriate method. However, the properties of the estimator have not been studied and its robustness to deviations from the principle underlying assumptions associated with the technique, in particular stationarity, the absence of which renders the estimate of the error variance inappropriate (the spectrum is not defined for nonstationary processes). Methods used in determining whether or not a series is stationary are only approximate; thus the possibility exists that an observed time series is nonstationary and this nonstationarity is simply not detected by the analyst. The adequacy of the transformation technique was not determined in this study; but a plot of the likelihood function versus the transformation parameters was reasonably flat in the neighborhood of the estimated maximum (Figure 24). If the slope of the

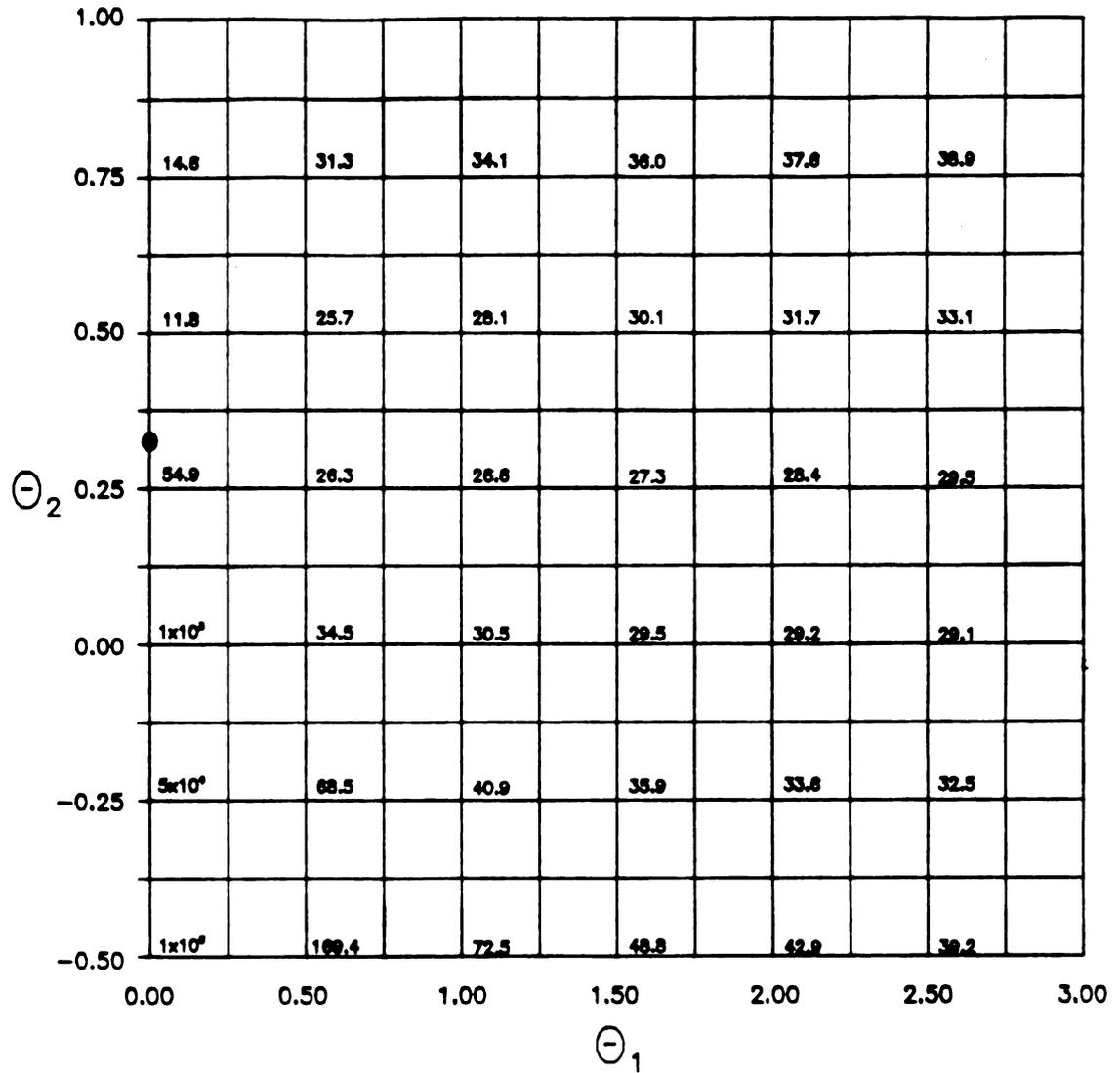


Figure 24. The likelihood surface as a function of the parameters of the Box-Cox transformation. Note that the values actually plotted are those of the estimated prediction error variance which differ by a constant from the values of the likelihood function. The estimated optimum is marked by the black dot.

likelihood surface was not markedly affected by any undetected deviations from the assumptions implicit in the use of the estimator the gradual slope of the likelihood surface suggests that the data were relatively insensitive to the choice of the transformation parameters over a relatively wide range. In this case bias in forecasts associated with misspecification of the transformation parameters would have been minimal.

Lack of uniqueness of models is an undesirable characteristic associated with the use of the Box-Jenkins methodology (Granger and Newbold 1977). It is frequently possible to obtain several models which appear to provide adequate representations of a particular observed time series. This is a common problem for short time series where it is sometimes not possible to satisfactorily identify the true structure of the generating process (Jenkins 1979). Such was the case for the analysis reported here. Models indicative of quite different structure of the underlying process were found to fit the data equally well in many respects. Examination of the sample autocorrelation and partial autocorrelation functions did not suggest a unique model structure but did prove useful for limiting the choice of potential models to a small number. The model finally determined to be most appropriate was arrived at primarily by examination of the estimated error variance and characteristics of the model residuals. However, some models were rejected because model structure was inconsistent with the presumed structure of the population processes producing the series. For example, an ARIMA $(1\ 0\ 0) \times (0\ 1\ 1)_{34}$ with a non-zero trend parameter provided a slightly better fit than the model finally determined to be most adequate. However, the presence of the purely deterministic cyclical component was not considered biologically realistic because it implied a constant amplitude for the

cyclical component of the model; the model was rejected for that reason. To justify the lack of uniqueness sometimes observed when modeling time series, Box and Jenkins (1976) argue that given the level of error present in some observed series, several models may provide equally good forecasts because the estimation error will be large. The performance of alternative univariate models was not considered in this study.

Multivariate models (transfer function models) incorporating weather variables were no improvement over the univariate model. Models that were adequate in a statistical sense were fitted but were of no help in reducing forecast error. Numerous factors could have contributed to this observation. The use of environmental data from a remote source, rather than on-site data obviously contributed to the poor performance of the models. However, it is likely that other factors were also important. The effects of rainfall and temperature on parasite activity are undoubtedly nonlinear, even though they may appear linear over a limited range. Field studies demonstrated that the effects of variation in temperature on parasite activity were complex even over a limited range of temperatures (Elliott 1985). The response of parasite activity to temperature over a wider range might be nonlinear with a step-like response, due to the threshold effect of very low and very high temperatures on flight. Furthermore, factors other than ambient temperature and rainfall are known to influence parasite activity (Weseloh 1976). For example, the interaction between the effects of ambient and radiant heat on activity was not considered in this study. These two components may differ in their effects on insect activity. Thus a given temperature could have different effects on insect activity depending on levels of solar radiation. Detailed studies of the response

of these parasites to temperature and other factors determining activity levels would be necessary in order to develop an appropriate measure for describing the effect of heat on parasite activity levels. As a consequence of the nonlinear response of parasite activity to environmental variability, models incorporating these effects in a linear, additive fashion, such as the transfer function models employed in this study may have limited applicability for modeling the effects of temperature, rainfall, and related variables on parasite activity. This would depend on the nature of the nonlinearity, as many nonlinear processes are well approximated by linear functions whereas others are not. Techniques of nonlinear multivariate time series analysis are not well developed (Tong 1983), and thus the statistical approach to time series modeling may be of limited value for analysis of multivariate data of the type used in this study until nonlinear models of general applicability are developed.

Physiological processes in insects are integrally linked with temperature and this effect is incorporated in the history of the parasite activity time series. Thus, much of the effect of temperature may be accounted for in univariate time series models. The univariate model developed in this study was driven by calendar time as opposed to physiological time (degree days). Units of degree days generally are considered to be a more accurate measure of time for modeling processes in insect populations. Because temperature effects are implicitly incorporated in the univariate model it is possible that univariate time series models driven by calendar time share many of the properties of models driven by physiological time. Research would be necessary to substantiate this suggestion.

In summary, there were a number of limitations to the data analyzed in this study. In spite of this fact it was clearly demonstrated that univariate stationary stochastic difference equations are potentially useful for modeling and predicting the fluctuations of insect populations. Published studies support this conclusion (Poole 1977). Some of the potential problems associated with the analysis of ecological data were illustrated in this study. The necessity of a preliminary transformation of the data was evident, and the ubiquities of mean-variance relationships in measurements of biological populations suggests that preliminary transformations will frequently need to be applied to such data. Care must be taken in the choice of the transformation employed to avoid introducing bias into the resulting forecasting function. It may not always be possible to find a transformation that results in a transformed series that is approximately Gaussian. However, this is not a major problem since a best linear predictor can be found for every wide sense stationary stochastic process, though this predictor will not necessarily be optimal in a quadratic loss sense (Granger and Newbold 1977). Furthermore, every wide sense stationary stochastic process can be written in linear form as an infinite weighted sum of orthogonal, identically distributed random variables, a finite sum of sine and cosine terms, and a mean (Hannan 1970). Thus, regardless of the distribution it is always possible to find a best linear predictor for a process provided it is wide sense stationary.

The use of independent variables to improve the performance of the forecasting model was of limited value in this study, possibly because the variables did not affect the system in linear fashion. Other attempts to use transfer function models to predict ecological processes have shown similar

results, perhaps for similar reasons (Murphy and Dunn 1977) though there exist examples where the models have been quite effective (Hacker et al. 1975, Poole 1977). It may have been possible to utilize other variables effectively in transfer function models. For example, an estimate of pupal density entered as an indicator process may have been helpful in producing better forecasts of the overall level of parasite activity.

A major limitation of time series analysis techniques is the necessity of taking observations at equally spaced intervals of time. In this study it was possible to avoid the problems associated with the dependence of insect development on heat accumulation as opposed to chronological time by arbitrarily choosing the first day of nonzero trap catch as the origin for the collection of annual data. However, for general forecasting purposes this point in time will not be known, and in fact it may be a major goal of the forecasts to predict this date. In addition, the first day of nonzero trap catch will generally be related to population density and sampling effort. It may be possible to circumvent these problems by establishing a "biofix" for starting the predictions much as is frequently done with phenological models of insect development. For the situation studied here an easily measurable event in the life history of the insect, such as the point when a certain proportion of the pupal population has emerged could serve to mark the beginning forecasts.

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**MORTALITY OF Apanteles spp. PUPAE
DUE TO HYPERPARASITISM, PREDATION, AND
UNKNOWN CAUSES**

INTRODUCTION

Two species of Apanteles (Apanteles fumiferanae Viereck and Apanteles morrisoni (Mason)) commonly attack the jack pine budworm (Choristoneura pinus Freeman) in Michigan's lower peninsula (Elliott 1985). Apanteles fumiferanae is a specific, solitary, internal parasite which attacks first and second instars of the budworm shortly after they eclose in the summer (Allen et al. 1969). A. morrisoni apparently attacks third, and possibly second and fourth instars, in the spring of the following year, after the budworm larvae emerge from hibernaculae after overwintering in diapause (Elliott 1985). Both parasite species emerge from predominantly fourth instar budworm and spin silken cocoons on jack pine (Pinus banksiana Lamb.) foliage where they pupate. The pupal stage averages about 10 days during which time both species are vulnerable to hyperparasites, predators, and other mortality factors. Because of the potentially important role of A. fumiferanae and A. morrisoni in the dynamics of budworm populations, the present study was initiated to obtain information about the temporal and spatial distribution of mortality factors operating on the free-living pupal stages of the parasites.

MATERIALS AND METHODS

These studies were done in jack pine stands located in Michigan's lower peninsula. Jack pine budworm populations were in the declining phase of an outbreak during the years the studies were done.

Temporal distribution of hyperparasitism

These studies were done in a site located at T26N R0W sec. 25 Grand Traverse Co., MI (site GR) during the summers of 1982 and 1983. The study site consisted of a plot ca. 2000 m² in a mixed aged naturally seeded jack pine stand. Jack pine trees averaged 9.53 m (n=100, se=0.26) with an average DBH of 13.89 cm (se=1.99). The basal areas of jack pine, red pine (Pinus resinosa Ait.) cherry (Prunus spp.), red maple (Acer rubrum L.), and red oak (Quercus rubra L.) were estimated to be 7.76, 0.31, 0.08, 0.23, and 0.09 m²/hectare, respectively. Jack pine, white pine (Pinus strobus L.), and various oaks (Quercus spp.) made up the majority of the understory vegetation. Ground vegetation consisted primarily of sweet fern (Comptonia peregrina (L.)), blueberry (Vaccinium spp.), and various grasses, with wild flowers occurring sporadically in open areas within the plot.

To determine the temporal distribution of mortality due to various factors Apanteles spp. cocoons were sampled every two to four days from the date that the first Apanteles spp. cocoon was observed on foliage until all Apanteles spp. adults had emerged.

Samples were taken by examining the terminal 46 cm of a single branch from each of the mid- and lower crown of fifteen dominant and codominant jack pine trees selected randomly from within the study plot. All Apanteles spp.

cocoons found on each branch were removed, placed in separate vials, and reared in an outdoor insectary. Parasites and hyperparasites that emerged were removed daily, pinned, or preserved in 70% alcohol, and labeled with the date of collection and date of emergence. The percentage of mortality was calculated for each observed mortality factor for each sampling date.

Spatial distribution of mortality

These studies were done in jack pine stands at the following locations:

- (1) sec. 32, T24N, R4W, Crawford Co. (site CR)
- (2) sec. 21, T32N, R2E, Montmorency Co. (site MO)
- (3) sec. 11, T32N, R1W, Otsego Co. (site OT1)
- (4) sec. 20, T29N, R1W, Otsego Co. (site OT2)

All four stands consisted predominantly of mature, mixed age, naturally seeded jack pine trees. The average height of trees was approximately the same in all four stands; ranging from 9-11 m. Jack pine accounted for approximately 95 percent of dominant, codominant, and intermediate trees in all of the plots, but the composition of minor tree species varied among plots, as did the composition of the understory and ground vegetation.

To determine if differences existed in the spatial distribution of mortality of Apanteles spp. pupae samples of cocoons were made in four different microhabitats in the stands: (1) upper crown of dominant and codominant, jack pine trees, (2) lower crown of dominant and codominant jack pine trees, (3) midcrown of suppressed jack pine trees less than 2 m in height, and (4) midcrown of suppressed white pine trees less than 2 m in height. White pine was present only in the understory of the stands. All four microhabitats were sampled in

stands 1 and 3, but no white pine occurred in stands 2 and 4 so only microhabitats 1, 2, and 3, were sampled in these stands.

Plots were established at a random point selected within each stand. The terminal 60 cm of three branches were sampled from the upper and lower crowns of each of the 10 dominant or codominant, jack pines closest to the random point. Similarly, the terminal 60 cm of three branches were sampled from the suppressed jack pine nearest to each sampled dominant or codominant tree, and the nearest suppressed white pine. Each branch sample was searched for Apanteles spp. cocoons and all cocoons found were placed in separate petri dishes and reared at 23.9^o C and 16L:8D photoperiod. Parasites and hyperparasites that emerged were identified to species by comparison with known specimens. The four stands were sampled over a three day period (1 July - 3 July, 1984) in an attempt to minimize variation in temporal patterns of mortality.

RESULTS AND DISCUSSION

Total average percent mortality of Apanteles spp. due to different sources for the two years at the GR site are given in Table 8. At least 8 different species of hyperparasites were reared from Apanteles cocoons. During 1982 jack pine budworm larvae were reared as part of another study (Elliott 1985); none of the species listed in Table 8 were reared from budworm larvae in that study. Thus, these species parasitize Apanteles spp. primarily while they are in the free-living pupal stage. Work on other parasitic species in the genus Apanteles has shown that hyperparasitism of pupae is common (Weseloh 1978, 1983, Morris 1976, Stamp 1981). Tetrasticus coerulescens Ashmead and Hypopteromalus percussor Girault were the most abundant hyperparasites encountered in this study, followed by Mesopelobus verditer (Norton) and Elasmus atratus Howard. Predation accounted for approximately 10% of the observed mortality of Apanteles spp. pupae in both years. Estimates of mortality due to predation were probably biased for two reasons. First, mortality by predators was assumed if cocoons were found to be torn open and the parasite either gone or mutilated with no evidence that it had emerged. Some of the former inhabitants of cocoons found in this condition probably died from causes other than predation. Second, mortality due to some predators would leave no visible evidence; for example, bird predation might often go undetected because the entire cocoon would be removed from the foliage.

Mortality due to unknown causes was high in both years. No factor was identified to account for this source of mortality. Dissection of unemerged cocoons showed that the parasites died in a variety of different developmental

Table 6. Percent mortality of Apanteles spp. pupae due to hyperparasitism, predation, and unknown causes at the GR site during 1982 and 1983.

(Total Cocoons)	<u>1982</u> (606)	<u>1983</u> (189)
<u>Source</u>		
Hyperparasites		
<u>T. coerulescens</u> Ashmead	6.7	10.6
<u>H. percussor</u> Girault	6.5	6.3
<u>M. verditer</u> (Norton)	2.2	2.6
<u>E. atratus</u> Howard	0.8	2.6
<u>Testrocticus</u> sp.	0.3	0.5
<u>Gelis</u> spp.	0.5	0.0
<u>P. phycidis</u> Ashmead	0.3	0.0
<u>Spilochalcis</u> sp.	0.1	0.0
unknown species	<u>7.4</u>	<u>2.1</u>
Total Hyperparasitism	24.8	27.0
Predation	9.7	13.7
Unknown Causes	<u>35.3</u>	<u>21.5</u>
Total Mortality	69.8	62.2

stages, from pharate pupae to adults nearly ready to emerge. A few dissected cocoons were found to have been hyperparasitized, but this was an uncommon occurrence.

Percent parasitism by the different species of hyperparasites varied throughout the season for the two years and is summarized in Figure 25. Hypopteromalus percussor and M. verditer were active early, while the majority of Apanteles spp. were pupating. Tetrastichus coeruleus and E. atratus were not recovered in samples until after emergence of Apanteles spp. adults commenced. In spite of this, T. coeruleus accounted for a high level of parasitism of Apanteles spp. cocoons.

Differences in percent parasitism of cocoons collected in various microhabitats in trees during 1984, are given in Table 9. Hypopteromalus percussor was more abundant in the lower crown of dominant and codominant trees and in suppressed trees. Pteromalus phycidis Ashmead was abundant in all microhabitats. The wingless Gelis spp. were found only in samples taken from suppressed trees. These results suggest that different hyperparasites are primarily responsible for mortality in different microhabitats within the forest. Weseloh (1978) found that A. melanoscelus (Ratzeburg) cocoons were differentially parasitized by hyperparasitic species in different microhabitats in oak forests.

To determine if mortality by P. phycidis and H. percussor was related to the density of Apanteles spp. cocoons, regression analyses were done between arcsine-transformed percent parasitism and the density of Apanteles spp. cocoons per dm^2 foliage surface area. Because the spatial scale at which the measurements are made can influence the ability to detect spatial density

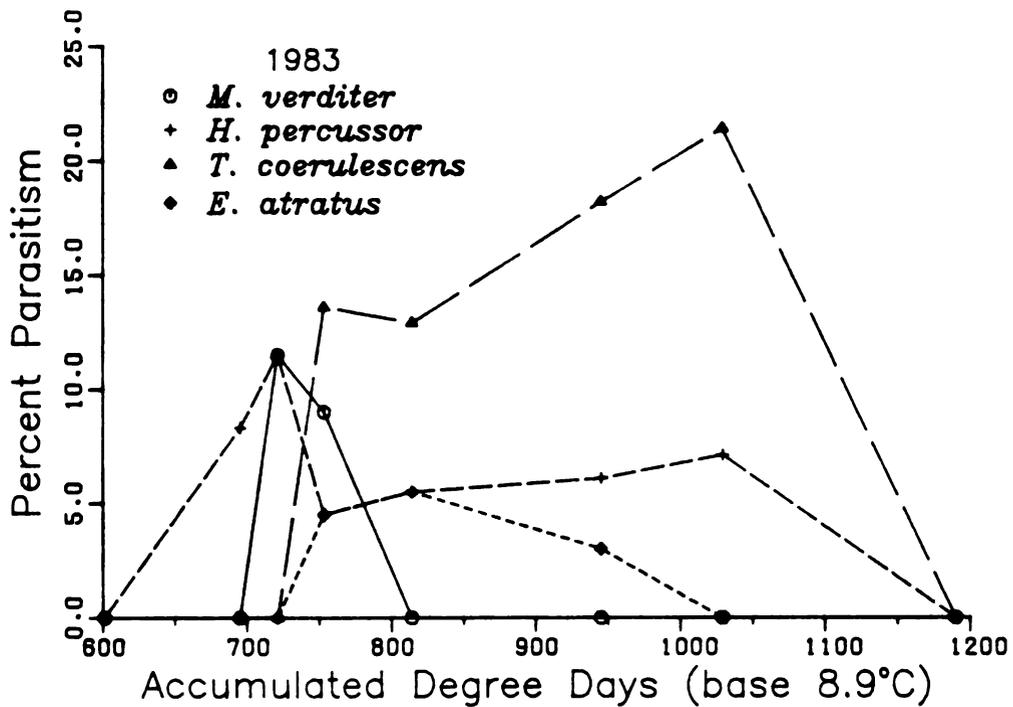
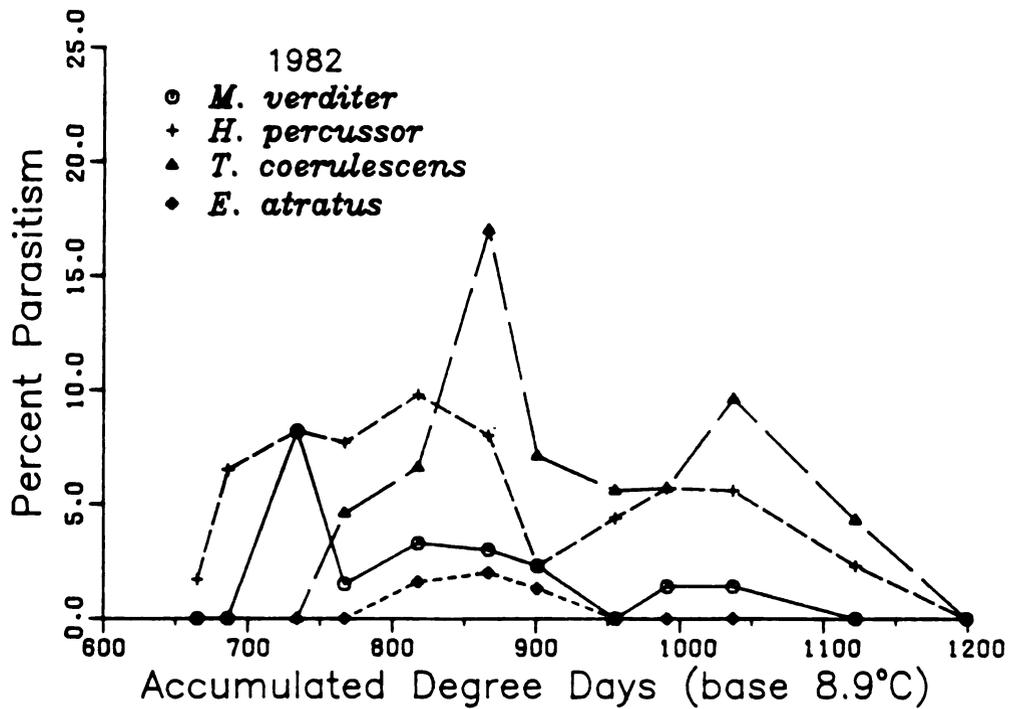


Figure 25. Percent parasitism of *Apanteles* spp. pupae by four species of hyperparasites in successive samples of pupae collected from a study site in Grand Traverse Co. Michigan during 1982 and 1983.

Table 9. Percent parasitism of Apanteles spp. pupae in different microhabitats in four study sites in 1984.

Site: CR	upper crown	lower crown	suppressed jack pine	suppressed white pine
n	(15)	(35)	(27)	(40)
Hyperparasite				
<u>H.percussor</u>	0.0	8.5 ± 4.7	0.0	7.5 ± 4.2
<u>P. phycidis</u>	6.6 ± 6.4	2.9 ± 2.8	14.8 ± 6.8	7.5 ± 4.2
<u>Gelis</u> spp.	0.0	0.0	7.4 ± 5.0	5.0 ± 3.4
Site: QT2	upper crown	lower crown	suppressed jack pine	suppressed white pine
n	(10)	(12)	(27)	(-)
Hyperparasite				
<u>H.percussor</u>	0.0	0.0	3.7 ± 3.6	-
<u>P. phycidis</u>	0.0	8.3 ± 8.0	0.0	-
<u>Gelis</u> spp.	0.0	0.0	3.7 ± 3.6	-
Site: QT1	upper crown	lower crown	suppressed jack pine	suppressed white pine
n	(42)	(87)	(34)	(32)
Hyperparasite				
<u>H.percussor</u>	0.0	8.0 ± 2.9	14.7 ± 6.1	6.3 ± 4.3
<u>P. phycidis</u>	9.5 ± 4.5	14.9 ± 3.8	2.9 ± 2.9	3.1 ± 3.1
<u>Gelis</u> spp.	0.0	0.0	0.0	3.1 ± 3.1
Site: MQ	upper crown	lower crown	suppressed jack pine	suppressed white pine
n	(85)	(135)	(76)	(-)
Hyperparasite				
<u>H.percussor</u>	1.2 ± 1.0	2.2 ± 1.3	13.1 ± 3.9	-
<u>P. phycidis</u>	3.5 ± 2.0	9.6 ± 2.5	3.9 ± 2.2	-
<u>Gelis</u> spp.	0.0	0.0	2.6 ± 1.8	-

dependence in parasitism rates (Morrison and Strong 1980), the analyses were performed on the data grouped at various spatial scales, 60 cm branch, upper or lower crown, and entire trees. Only the data for dominant and codominant trees in the sites were used in the analyses because the manner in which suppressed trees were sampled differed from that of dominant and codominant trees (only 3 branches were sampled from the crowns of suppressed trees whereas 6 branches were taken from dominant and codominant trees). Preliminary analyses showed no evidence of differences in the slopes or intercepts of the regressions of arcsine percent parasitism versus Apanteles spp. density among sites or crown classes. Thus, simple linear regression was used to examine the arcsine percent parasitism versus host density relationships. There was no evidence of non-random (ie. density dependent) patterns of mortality imposed by H. percussor measured at any spatial scale (Table 10). None of the slopes for any of the regressions differed significantly from zero. In contrast, a significant density dependent mortality rate was imposed on Apanteles spp. pupae by the hyperparasite P. phycidis. The slopes of all of the regression lines differed significantly from zero; however, the r^2 values for the regressions were low indicating that the models did not account for much of the variation in parasitism rates. Some of the variation was undoubtedly caused by measurement error associated with estimates of branch surface area and sampling error associated with the measurement of host density per crown and per tree. However, some of the variability in the data probably resulted because the parasites respond to factors other than host density. Still, the results indicate that P. phycidis is capable of concentrating attacks in patches of habitat where the density of hosts is high.

Table 10. Results of linear regression analysis of mortality versus host density for the hyperparasites P. phycidis and H. percussor. The dependant variables were transformed by $y' = 2 \cdot \sin^{-1}(y^{1/2})$ before analysis. Significant regressions are indicated by "".**

Species	Sampling Area	Slope	r²	Pr(X₂x)
<u>P. phycidis</u>	60 cm branch	0.043	0.049	0.0219*
	crown	0.395	0.266	0.0001*
	tree	0.429	0.225	0.0080*
<u>H. percussor</u>	60 cm branch	0.037	0.008	0.9200
	crown	0.104	0.029	0.2283
	tree	-0.029	0.016	0.5044

The slope of the regression lines of arcsine percent parasitism versus host density for P. phycidis increase with increasing patch size from 60 cm branches to entire trees. Heads and Lawton (1983) found the parasitism of the holly leafminer (Phytomyza ilicis Curtis) by the parasite Chrysocharis gemma (Walker) was aggregated at some spatial scales but not at others. The intensity of the aggregative response, as indicated by the magnitude of the slope of the regression line, should be greatest on a scale that corresponds to the size of the habitat unit recognized as a "patch" by the parasite (Heads and Lawton 1983). It is not possible to elucidate the behavioral mechanism responsible for the observed patterns of hyperparasitism by P. phycidis from observed patterns of mortality. However, we can speculate that P. phycidis may not be efficient at finding small patches where the density of hosts is high, but may be capable of orienting to variation in host density on a larger scale. The species is highly polyphagous and because it has a variety of hosts, many of which may be distributed quite differently in space, it might be expected that highly specialized host location mechanisms would not be well developed. Thus, for such species an efficient foraging strategy might be to treat small units of habitat as fine-grained, searching more or less randomly over such units. On a larger spatial scale the hyperparasite may be adapted at finding profitable areas of high host density and remaining in such areas as long as they remain profitable in terms of hosts parasitized per unit time. Thus, it would treat larger units of habitat as course-grained. As pointed out by Morrison and Strong (1980), the spatial scale at which observations are made is important when attempting to determine whether or not parasite attacks occur at random or are aggregated.

This study suggests that mortality during the pupal stage may be a major factor limiting the numerical response of A. fumiferanae and perhaps also A. morrissi to increasing populations of the jack pine budworm. A complex of hyperparasites was identified that appear to consistently inflict high levels of mortality on Apanteles spp. populations, at least at high densities. At least one of the hyperparasites appears to respond to local differences in host density in the sense that mortality inflicted by the hyperparasite is positively density dependent. Weseloh (1983) showed that certain hyperparasites of A. melanoscelus inflict positive density dependent mortality. This may be an important finding in light of the controversy over the role of hyperparasites in biological control (Luck et al. 1981). These results are preliminary, but indicate that more work is needed on the role of hyperparasites in the life systems of parasites of the jack pine budworm. Further work should be done to determine the extent of density dependent mortality inflicted by hyperparasites on parasites of the budworm; and to determine the importance of hyperparasites in endemic and increasing populations of the budworm.

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APPENDIX I

To apply the Box-Jenkins methodology to the analysis of time series, a preliminary transformation of the data is often desirable. There are two main reasons for transforming the observed data. The first is to produce a transformed series, $Y(t) = T(X(t))$, where $Y(t)$ is Gaussian. The major advantage of a Gaussian series is that conditional expectation of a Gaussian series is a linear function of Gaussian random variables and therefore is itself Gaussian. The conditional distribution of a stationary time series with arbitrary, but generally unknown distribution will often be a nonlinear function of random variables (Granger and Newbold 1977). Box-Jenkins forecasting models are linear and hence optimal forecasting models, in the sense that they provide minimum mean square error forecasts; when non-Gaussian series are modeled the error properties of linear forecasting models will generally not be known, but the forecasts can frequently be far from optimal (Granger and Newbold 1976). The second reason is that the variance of the transformed series, whether Gaussian or not, may have a constant variance, whereas the variance of the original series varied with time. Constancy of the mean and variance of time series (weak stationarity) is a necessary requirement in order for linear, time invariant difference equation models, such as Box-Jenkins models, to be adequate representations of a linear system. Evidence suggests that the correct choice of a preliminary transformation is critical. Chatfield and Prothero (1973) have discussed this issue in relation to modeling and forecasting economic time series; they showed that the improper choice of transformation can result in highly biased forecasts. The power transformations proposed by Box and Cox (1964)

have been proposed as a flexible family of transformations that could be used to improve forecasting performance (Box and Jenkins 1976, Granger and Newbold 1977). The two parameter power transformation is given by,

$$Y(t) = T(X(t)) = (X + \theta_1)^{\theta_2} / \theta_2, \neq 0 \quad (1)$$

$$= \ln(X + \theta_1), = 0$$

where $X(t)$ is an original observed value of the time series, $Y(t)$ is the transformed observation, and θ_1 and θ_2 are transformation parameters. Throughout the remainder of this discussion it is assumed that there exists some subset of the parameter space of θ_1 and θ_2 such that, equation (1) can be applied to the original series, $X(t)$, to produce a Gaussian series, $Y(t)$. The objective then is to choose from among the set of admissible values for θ_1 and θ_2 such that an optimal Gaussian series is obtained. There are numerous criteria available for defining optimal transformation. In the context of this discussion we define an optimal choice of θ_1 and θ_2 as those values that maximize the conditional likelihood function for a stationary Gaussian series. This definition has considerable appeal in terms of statistical theory.

Ansley et al. (1977) developed an algorithm for obtaining maximum likelihood estimates of θ for the one dimensional power transformation. However, their method assumes that a single ARIMA model provides an adequate fit to the series, as θ varies over all permissible values. Granger and Newbold (1976) showed that the autocorrelation function of a transformed process depends on θ in general, and hence a separate ARIMA model might have to be fitted for every value of θ .

The algorithm developed here utilizes a nonparametric estimate of the error variance of a stationary, discrete time, stochastic process in computations

of the likelihood function. Thus, a maximum likelihood estimate is obtained without actually going through the modeling process.

Derivation of the Likelihood Function

The notation used in this section is standard notation as employed by Box and Jenkins (1976) and others. The theoretical development is similar to that found in Ansley et al. (1977).

Assume that for some value of the transformation parameter

$$\lambda = (\theta_1, \theta_2)$$

of the power transformation, the series

$$Y(\lambda, t) = T(\lambda, X(t))$$

follows an ARIMA (p,d,q) x (P,D,Q) process. Also assume that the error terms $e(t)$ are uncorrelated white noise eg. follow a $n(0, \sigma^2)$ distribution. Since $Y(\lambda, t)$ follows a seasonal ARIMA process,

$$W(\lambda, t) = \nabla^d \nabla_S^D Y(\lambda, t), \quad \nabla Y(\lambda, t) = (1-B) Y(\lambda, t)$$

where $B(Y(t)) = Y(t-1)$ is the backward difference operator, is an ARIMA(p,q) x (P,Q) process. The joint density function of $W(\lambda, t)$, $t = 1, 2, \dots, n$, is

$$f_n(W_\lambda | \phi, \theta, \Phi, \Theta, \sigma^2) = (2\pi\sigma^2)^{-\frac{1}{2}n} |M_n|^{-\frac{1}{2}} \exp\{-S/2\sigma^2\}$$

where, $\phi, \theta, \Phi, \Theta$, are polynomials in B of orders p, q, P , and Q respectively,

$$S = \sum_{t=1}^n [E(e(t) | W(\lambda, t); \phi, \theta, \Phi, \Theta)]^2 \quad (2)$$

and,

$$\sigma^2 M_n^{-1} = \sigma^2 M_n^{-1}(\phi, \theta, \Phi, \Theta)$$

is the variance-covariance matrix of $W(\lambda, t)$.

Assume that the first $d+sD$ observations in the time series are fixed. Our

objective is to determine the joint probability density function of the n most recent observations, $x(n), x(n-1), \dots, x(1)$, of the process conditional on $x(0), x(-1), \dots, x(-c-sD+1)$. Given these assumptions the jacobian of the transformation

$$W(\ell, t) = \nabla^d \nabla_s^D Y(\ell, t) = \nabla^d \nabla_s^D T(\ell, X(t))$$

is,

$$J = \prod_{t=1}^n \left| \frac{\partial y(\ell, t)}{\partial x(t)} \right| = \prod_{t=1}^n (x(t) + \theta_1)^{(\theta_2 - 1)}$$

Thus, the conditional joint probability density function of the series $X(t), t=1, \dots, n$ is

$$h\{x \mid y(0), \dots, y(-d-sD+1); \phi, \theta, \Phi, \Theta, \sigma^2, \ell\} \\ = (2\pi\sigma^2)^{-\frac{1}{2}n} |M_n|^{-\frac{1}{2}} \exp\{-S/2\sigma^2\} J$$

Thus the likelihood function of $X(t)$ is

$$L = \text{constant} - \frac{1}{2}n \ln \sigma^2 + \frac{1}{2} \ln |M_n| - S/2\sigma^2 + \ln J \quad (3)$$

Assuming n to be moderately large, the term $\frac{1}{2} \ln |M_n|$ in equation (3) is small compared to $S/2\sigma^2$ (Box and Jenkins 1976); ignoring this term yields

$$L' = \text{constant} - \frac{1}{2}n \ln \sigma^2 - S/2\sigma^2 + \ln J \quad (4)$$

which is the approximation of the likelihood function, given by equation (3), we will seek to maximize. Note that

$$\hat{\sigma}^2 = S/n$$

is the solution of the normal equation thus obtained.

In order to simplify equation (4) an additional transformation suggested by Box and Cox (1964) was applied to $W(\ell, t)$ to produce a "standardized" series

$$Z(\ell, t) = W(\ell, t)/J^{1/n}$$

Assuming $x(1), x(2), \dots, x(n)$ to be a realization of the process $X(t)$ we can write

$$\phi(B)\phi(B^S)E\{W(\ell, t) \mid W; \phi, \theta, \Phi, \Theta, \ell\} = \theta(B)\theta(B^S)E\{e(t) \mid W; \phi, \theta, \Phi, \Theta, \ell\}$$

and dividing by $J^{1/n}$ yields

$$\phi(B)\phi(B^S)E\{Z(\ell,t) | Z; \phi, \theta, \Phi, \Theta, \ell\} = \theta(B)\theta(B^S)E\{e(t) | Z; \phi, \theta, \Phi, \Theta, \ell\}$$

where

$$E\{Z(\ell,t) | Z; \phi, \theta, \Phi, \Theta, \ell\} = E\{W(\ell,t) | Z, \phi, \theta, \Phi, \Theta, \ell\} J^{-1/n}$$

$$E\{e(t) | Z; \phi, \theta, \Phi, \Theta, \ell\} = E\{e(t) | W, \phi, \theta, \Phi, \Theta, \ell\} J^{-1/n}$$

Thus, it is clear that the coefficients of the ARMA model for $W(\ell,t)$ are identical to those obtained for $Z(\ell,t)$. The sum of squares, S , of equation (2) is

$$S = J^{-2/n} S_Z$$

where

$$S_Z = \sum_{t=1}^n [E\{e(t) | W, \phi, \theta, \Phi, \Theta, \ell\}]^2$$

Thus, equation (3) becomes

$$L^n = \text{constant} - \frac{1}{2}n \ln(J^{2/n} S_Z) + \ln J = \text{constant} - \frac{1}{2}n \ln S_Z \quad (5)$$

from which it is clear that the problem of maximizing the likelihood function, (3), is reduced to minimizing the sum of squares, S_Z of the transformed time series $Z(\ell,t)$.

Estimation of the Error Variance

Assume that $X(t)$ is a stationary, discrete, time series. Then the error variance of the best linear predictor, in the sense of minimum squared error, is given by

$$\sigma^2 = \exp\left\{-\frac{1}{2\pi} \int_{-\pi}^{\pi} \ln(2\pi f(\omega)) d\omega\right\}$$

where $f(\omega)$ is the spectral density function of $X(t)$ (Kolmogorov 1941). Hannan and Nichols (1977) derived a family of estimates of σ^2 :

$$\hat{\sigma}_m^2 = \text{mexp}\left\{\frac{1}{M} \sum_{j=0}^{M-1} \ln(|W(\omega_{jm+k})|^2) - \psi(m)\right\} \quad (6)$$

where

$$M = [(n-1)/2m], \quad \psi(m) = d \ln \Gamma(m) / dm$$

is the digamma function, and

$$W(\omega_j) = n^{-\frac{1}{2}} \sum_{t=1}^n x(t) e^{i t \omega_j}, \omega_j = 2\pi j/n, 0 < j < n/2$$

with j an integer is the periodogram of $X(t)$. Taking $m=1$ in equation (6) yields

$$\hat{\sigma}_1^2 = \exp\left\{ \frac{1}{M} \sum_{j=0}^{M-1} \ln\left(\sum_{k=1}^m |W(\omega_{jm+k})|^2\right) - \psi(1) \right\} \quad (7)$$

as an estimate of σ^2 . Substituting equation (7) into equation (5) yields

$$L^n = \text{constant} - \frac{1}{2} \ln \hat{S}_Z \quad (8)$$

where

$$\hat{S}_Z = n \hat{\sigma}_1^2(\ell)$$

Thus, the maximization of the likelihood function, equation (3), is achieved by minimization of equation (8), which is quadratic in $W(\omega)$. An algorithm was developed for this purpose (Figure 26). The algorithm utilizes a non-linear minimization routine to minimize the objective function (equation (8)). The program implementing this algorithm was written in Fortran V; the program listing is in Appendix III.

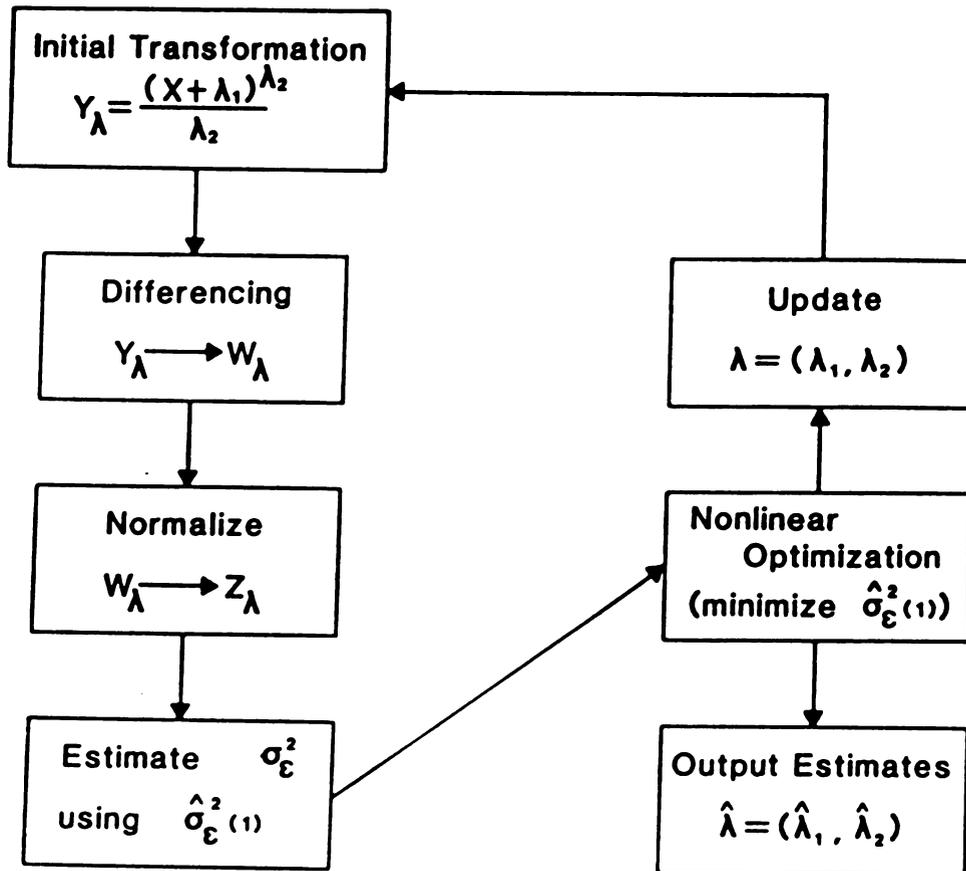


Figure 26. A flow chart of the procedure for estimating the prediction error variance that minimizes the likelihood function for a Gaussian process.

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APPENDIX II

The use of Hermite polynomials for determining optimal, in the sense of quadratic loss, forecasts of a transformed time series has been discussed by Granger and Newbold (1976). They showed that optimal quadratic loss forecasts could be derived for the original time series, $X(t)$, provided a transformation could be found, which when applied to $X(t)$ resulted in a stationary Gaussian series $Y(t)$. The basic mathematics involved in their method will be reviewed in this appendix and the techniques will be applied to the Box-Cox transformation (Box and Cox 1964) to derive optimal quadratic loss forecasts for the parasite activity time series analyzed in chapter I of this thesis.

The system of Hermite polynomials for the standard normal distribution is given by

$$\begin{aligned} H_n(x) &= \exp(x^2/2) (-d/dx)^n \exp(-x^2/2) \\ &= (-1)^n \phi^{(n)}(x)/\phi(x) \end{aligned}$$

where $\phi(\cdot)$ is the standard normal p.d.f. Thus,

$$H_n(x) = n! \sum_{m=0}^{(n/2)} (-1)^m \{2^m m! (n-2m)!\}^{-1} x^{n-2m} \quad (1)$$

where $(n/2)$ is the largest integer less than or equal to $n/2$. Evaluating equation (1) for different values of n yields,

$$H_0(x) = 1, H_1(x) = x, H_2(x) = x^2 - 1, H_3(x) = x^3 - 3x$$

and so on.

The Hermite polynomials have the following orthogonality properties with respect to the standard normal distribution:

$$E[H_n(x)H_k(x)] = 0 \quad n \neq k \quad (2)$$

$$= n! \quad n = k$$

$$E[H_m(x)H_k(y)] = 0 \quad n \neq k \quad (3)$$

$$= \rho^n n! \quad n = k$$

In equation (3) ρ represents the correlation coefficient between the standard normal random variables X and Y .

Consider the transformation $Y(t) = T(Z(t))$, where $Z(t) = (X(t) - M)/\sigma$ and $X(t)$ is a stationary Gaussian time series with mean μ and variance σ^2 . Thus, $T(Z)$ can be expanded in terms of Hermite polynomials in the form

$$Y = T(Z) = \sum_{j=0}^m \alpha_j H_j(Z) \quad (4)$$

Using equations (2) - (4) it follows that

$$E(Y(t)) = \alpha_0 \quad (5)$$

and

$$\text{cov}(Y(t), Y(t-\tau)) = \sum_{j=1}^m \alpha_j^2 \rho_\tau^j$$

If $X(t)$ is Gaussian and an ARIMA model has been fitted to it an optimal quadratic loss forecast of $X(t+L)$, given $X(1), \dots, X(t)$, can be formed and it will be linear in the $X(t-j)$.

Write,

$$X(t+L) = f_{t,L} + e_{t,L}$$

where $f_{t,L}$ is the optimal quadratic loss forecast of $X(t+L)$ and $e_{t,L}$ is the error of this L step ahead forecast. Since $X(t)$ is Gaussian the conditional distribution of $X(t+L)$ is normal with mean $f_{t,L}$ and variance $S^2(L) = \text{va}(e_{t,L})$. Using equation (4),

$$Y(t+L) = \sum_{j=0}^m \alpha_j H_j(W(t+L)) \quad (7)$$

where,

$$W(t+L) = (X(t+L) - f_{t,L})/S(L)$$

is distributed $n(0,1)$. Using equation (5) the optimal quadratic loss forecast of $Y(t+L)$, eg. the conditional expectation of $Y(t+L)$ is

$$E[Y(t+L) | Y(t-j), j \geq 0] = \sum_{j=1}^m \alpha_j^2 \rho_j \quad (9)$$

Applying these results to the Box-Cox transformation

$$Y(t, \ell) = T(X(t)) = (X(t) + \theta_1)^{\theta_2 / \theta_2}$$

where $\ell = (\theta_1, \theta_2)$ was estimated by the maximum likelihood method, assuming normality of $X(t)$ (see Appendix I). Thus, $\hat{\ell} = (\hat{\theta}_1, \hat{\theta}_2) = (0, 1/3)$. Using equation (7)

$$\begin{aligned} Y(\hat{\ell}, t+L) &= \sum_{j=0}^{\infty} \alpha_j H_j(W(t+L)) \\ &= \alpha_0 + \alpha_1 H_1(W(t+L)) + \alpha_2 H_2(W(t+L)) + \alpha_3 H_3(W(t+L)) \end{aligned}$$

where,

$$\begin{aligned} \alpha_0 &= \hat{\theta}_1 + f_{t,L}^3 / 27 + S^2(L) f_{t,L} / 9 \\ \alpha_1 &= (S(L) f_{t,L}^2 + s^2(L)) / 9 \\ \alpha_2 &= S^2(L) f_{t,L} / 9 \\ \alpha_3 &= S^2(L) / 27 \end{aligned}$$

Since the parasite activity time series is nonstationary the mean depends on time. In the development given above the Gaussian time series was assumed to be stationary. The results still hold except we replace μ by μ_t to emphasize the time varying nature of the parameter. Thus the coefficients (α_j) in the expansion of $T(x)$ are no longer time invariant.

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APPENDIX III

Computer Program Listing

```

PROGRAM MAXLIK (INPUT,OUTPUT,TAPE60=INPUT,TAPE62,TAPE61=OUTPUT)
REAL X1,X2,E1,E2,Y1,Y2,Y1PLSD,Y2PLSD,FY,FX,ALPHA
REAL X(1000),D1,D2,FYPLSD,XMIN,SUMK,INCRMT
INTEGER K,N,DIFF,SDIFF

```

PURPOSE:

TO COMPUTE MAXIMUM LIKELIHOOD ESTIMATES, ASSUMING NORMALITY, OF THE BOX-COX POWER TRANSFORMATION PARAMETERS P1 AND P2 FOR AN INSTANTANEOUSLY TRANSFORMED STATIONARY TIME SERIES.

DESCRIPTION OF PROGRAM:

THE PROGRAM USES A METHOD SUGGESTED BY GRANGER AND NEWBOLD (1977) (CHAPTER 9) TO MAXIMIZE THE LIKELIHOOD FUNCION OF THE CONDITIONAL DISTRIBUTION (CONDITIONED ON THE OBSERVED VALUES OF THE PROCESS) OVER ALL PARAMETERS INCLUDING P1 AND P2 FOR A NORMALLY DISTRIBUTED STATIONARY DISCRETE STOCHASTIC PROCESS. THE ALGORITHM PROCEEDS BY THE FOLLOWING STEPS.

1. CALCULATE $Y = ((X+P1)^{P2})/P2$

2. DIFFERENCE THE TIME SERIES TO OBTAIN A STATIONARY SERIES. NOTE THE DEGREE OF DIFFERENCING NECESSARY TO INDUCE STATIONARITY MUST BE KNOWN PRIOR TO USING THE PROGRAM SINCE NO PROVISIONS FOR TESTING FOR STATIONARITY ARE INCLUDED IN THE PROGRAM, AND THE ESTIMATION TECHNIQUE EMPLOYED REQUIRES THAT THIS CONDITION BE SATISFIED.

3. ESTIMATE THE PREDICTION ERROR VARIANCE FOR Y. A METHOD DESCRIBED BY HANNAN AND NICHOLS (1977) IS USED IN THE ESTIMATION.

4. CALCULATE THE LOG LIKELIHOOD FUNCTION. THE PROGRAM OPERATES ON A STANDARDIZED SERIES SO THAT MAXIMIZATION OF THE LIKELIHOOD FUNCTION IS ACCOMPLISHED BY MINIMIZATION OF THE ESTIMATED PREDICTION ERROR VARIANCE, WHICH IS ESSENTIALLY A SUM OF SQUARED PRODUCTS OF TIME SERIES VALUES AND SINE AND COSINE TERMS.

5. REPEAT STEPS ONE TO FOUR UNTIL A MAXIMUM IS REACHED. AN ALGORITHM DEVELOPED BY HOOK AND JEEVES (1961) IS USED IN THE MAXIMIZATION OF THE LOG LIKELIHOOD FUNCTION.

DESCRIPTION OF PRIMARY VARIABLES USED IN THE MAIN PROGRAM AND SUBROUTINES:

X - A VECTOR OF N OBSERVATIONS OF THE TIME SERIES

Y - A VECTOR OF N OBSERVATIONS OF THE TRANSFORMED TIME SERIES

Z - A VECTOR OF N-DIFF-SDIFF DIFFERENCED OBSERVATIONS OF THE SERIES Y


```

SUMK=1.0
K=1
Y1=X1
Y2=X2
CALL EVALFC (X1,X2,X,N,DIFF,SDIFF,FX)
FX=FX+BARRFC(X1,SUMK,XMIN)
FY=FX
10 Y1PLSD=Y1+D1
SUMK=SUMK+INCRMT
IF (K.GE.50) GOTO 55
CALL EVALFC (Y1PLSD,Y2,X,N,DIFF,SDIFF,FYPLSD)
FYPLSD=FYPLSD+BARRFC(Y1PLSD,SUMK,XMIN)
IF (FYPLSD.LT.FY) GOTO 20
Y1PLSD=Y1-D1
CALL EVALFC (Y1PLSD,Y2,X,N,DIFF,SDIFF,FYPLSD)
FYPLSD=FYPLSD+BARRFC(Y1PLSD,SUMK,XMIN)
IF (FYPLSD.LT.FY) GOTO 20
Y1PLSD=Y1
FYPLSD=FY
20 FY=FYPLSD
Y2PLSD=Y2+D2
CALL EVALFC (Y1PLSD,Y2PLSD,X,N,DIFF,SDIFF,FYPLSD)
FYPLSD=FYPLSD+BARRFC(Y1PLSD,SUMK,XMIN)
IF (FYPLSD.LT.FY) GOTO 30
Y2PLSD=Y2-D2
CALL EVALFC (Y1PLSD,Y2PLSD,X,N,DIFF,SDIFF,FYPLSD)
FYPLSD=FYPLSD+BARRFC(Y1PLSD,SUMK,XMIN)
IF (FYPLSD.LT.FY) GOTO 30
Y2PLSD=Y2
FYPLSD=FY
30 IF (FYPLSD.GE.FX) GOTO 50
X1TEMP=Y1PLSD
X2TEMP=Y2PLSD
FX=FYPLSD
WRITE (61,120) K,X1TEMP,X2TEMP,FX,BARRFC(X1TEMP,SUMK,XMIN)
Y1=X1TEMP+ALPHA*(X1TEMP-X1)
Y2=X2TEMP+ALPHA*(X2TEMP-X2)
CALL EVALFC (Y1,Y2,X,N,DIFF,SDIFF,FY)
FY=FY+BARRFC(Y1,SUMK,XMIN)
X1=X1TEMP
X2=X2TEMP
K=K+1
GOTO 10
50 IF ((D1.LE.E1).AND.(D2.LE.E2)) GOTO 60
D1=D1/2.0
D2=D2/2.0
Y1=X1
Y2=X2
FY=FX
WRITE (61,120) K,Y1,Y2,FY,BARRFC(Y1,SUMK,XMIN)
PRINT =,' DELTA1 DELTA2'
WRITE (61,130) D1,D2
K=K+1
GOTO 10
55 PRINT =
PRINT =,'-----AFTER 50 ITERATIONS NO SOLUTION FOUND-----'
PRINT =
GOTO 65
60 PRINT =
PRINT =,'-----SOLUTION FOLLOWS-----'
PRINT =
65 PRINT =,'ITERATIONS - LAMDA1 - LAMDA2 - ERROR VAR. - BARRIER FC.'
PRINT =
WRITE (61,120) K,X1,X2,FX,BARRFC(X1,SUMK,XMIN)
C *****LIST OF FORMAT STATEMENTS FOR PROGRAM MAXLIK*****
100 FORMAT (I4)
110 FORMAT (E16.6)
120 FORMAT (4X,I2,6X,F7.3,2X,F7.3,3X,F9.3,5X,F9.3)
130 FORMAT (6X,F6.4,5X,F6.4)
STOP
END

```

```

SUBROUTINE EVALFC (LAMDA1,LAMDA2,X,N,DIFF,SDIFF,VAREST)
REAL X(1000),Y(1000),Z(1000),LAMDA1,VAREST
REAL LAMDA2
INTEGER N,N1,I,J,M,DIFF,SDIFF
  CALL TRNSFM (X,Y,LAMDA1,LAMDA2,N,DIFF,SDIFF)
  CALL DIFRNC (Y,Z,N,M,DIFF,SDIFF)
  CALL MMSOE (Z,M,VAREST)
RETURN
END
C

SUBROUTINE TRNSFM (X,Y,LAMDA1,LAMDA2,N,DIFF,SDIFF)
REAL X(1000),Y(1000),LAMDA1,LAMDA2,LOGJ,J
INTEGER N,DIFF,SDIFF,M
M=DIFF+SDIFF+1
LOGJ=0.0
  DO 10 I=M,N
    LOGJ=LOGJ+ALOG(X(I)+LAMDA1)
10  CONTINUE
LOGJ=(LAMDA2-1.0)/LOGJ
LOGJ=LOGJ/FLOAT(N-DIFF-SDIFF)
J=EXP(LOGJ)
IF (LAMDA2.EQ.0.0) GOTO 30
IF ((LAMDA2).LT.0.0) GOTO 50
  DO 20 I=1,N
    Y(I)=((X(I)+LAMDA1)**LAMDA2)/LAMDA2
20  CONTINUE
  GOTO 70
  DO 40 I=1,N
    Y(I)=ALOG(X(I)+LAMDA1)
40  CONTINUE
  GOTO 70
  DO 60 I=1,N
    Y(I)=((1.0/((X(I)+LAMDA1)**ABS(LAMDA2)))/LAMDA2)
60  CONTINUE
  C
70  DO 80 I=1,N
    Y(I)=Y(I)/J
80  CONTINUE
RETURN
END
C

SUBROUTINE DIFRNC (Y,Z,N,M,DIFF,SDIFF)
REAL Y(1000),Z(1000)
INTEGER N,M,DIFF,SDIFF
M=N
IF (DIFF.EQ.0) GOTO 50
M=N-DIFF
  DO 40 I=1,M
    Z(I)=Y(I+DIFF)-Y(I)

```

```

40     CONTINUE
      GOTO 70
50     DO 60 I=1,N
      Z(I)=Y(I)
60     CONTINUE
70     IF(SDIFF.EQ.O) GOTO 100
      M=M-SDIFF
      DO 80 I=1,M
      Z(I)=Z(I+SDIFF)-Z(I)
80     CONTINUE
100    RETURN
      END

C
      SUBROUTINE MMSQE(Z,N,VAREST)
      REAL Z(1000),VAREST,W,A1,A2,NREAL,N1REAL,WI,SSOPRD
      INTEGER N,N1,NONE
      NREAL=FLOAT(N)
      N1=INT((N/2)-1)
      IF (IFIX(NREAL/2.O+.501).NE.IFIX(NREAL/2.O+.001)) N1=INT((N-1)/2)
      N1REAL=FLOAT(N1)
      A1=O.O
      A2=O.O
      SSOPRD=O.O
      DO 10 I=1,N1
      W=2.O*3.141593=FLOAT(I)/NREAL
      DO 20 J=1,N
      C1=COS(W=FLOAT(J))
      C2=SIN(W=FLOAT(J))
      A1=A1+Z(J)=C1
      A2=A2+Z(J)=C2
20     CONTINUE
      WI=(A1==2+A2==2)/(NREAL-3.141593)
      SSOPRD=SSOPRD+ALOG(WI)
      A1=O.O
      A2=O.O
10     CONTINUE
      SSOPRD=SSOPRD/N1REAL+O.57721
      VAREST=EXP(SSOPRD)
      RETURN
      END

C
      FUNCTION BARRFC(X,SUMK,XMIN)
      BARRFC=(1.O/SUMK)*(1.O/ABS(ABS(XMIN)-ABS(X)))
      RETURN
      END

```

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